Biodiversity outcomes of novel land management within semi-natural grassland: A landscape-scale experiment

Robert William Hawkes

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Supervisors:

Professor Paul M. Dolman (University of East Anglia), Dr Jennifer Smart (RSPB), and Dr Andy Brown (Natural England)

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Abstract

Knowledge of land-use history and the autecological requirements of priority species encourages novel conservation management interventions that incorporate physical-disturbance and spatio-temporal variability. This thesis evaluates the biodiversity outcomes of such interventions through a landscape-scale management experiment conducted across an extensive (c.3,850 ha) semi-natural grassland dominated by closed-swards. Treatments (deep- and shallow-cultivation) were built-up over three years (2015-2017) creating 40 x 4-ha plots, each comprising four 1-ha sub-plots: repeat cultivation, first-time cultivation, one-year-fallow and two-year-fallow. The study focussed on the responses of two 'flagships' for which the area is designated (Eurasian Stone-curlew *Burhinus oedicnemus* and Woodlark *Lullula arborea*), vascular plants and invertebrates from eight taxonomic groups. Unlike unmodified grassland controls, recently-cultivated treatments created suitable Stone-curlew nesting habitat. Five GPS-tracked adult Stone-curlews also selected treated plots over unmodified grassland as foraging areas both during and after breeding attempts. Woodlark numbers were higher on plots closer to woodland and on treated plots, regardless of cultivation depth. Sampling of 132,251 invertebrates from 878 species and 28,846 observations of 167 plant species showed both treatments doubled the overall richness of priority species (rare, scarce or threatened). Crucially, those invertebrates associated with dry-open habitats and *a priori* predicted to require physical disturbance responded most strongly to treatment, confirming the success of bio-regional analyses in targeting appropriate interventions within this system. Within plots, most sub-plots supported distinct assemblages, suggesting heterogeneity in treatment (shallow- and deep-cultivation) with frequent reapplication (providing continuity of fallowed and recently disturbed areas) maximises biodiversity outcomes. To optimise the cumulative richness of non-priority and priority invertebrates, these treatments need to take place across 40 – 60% of the landscape. Based on these findings, this thesis encourages the widespread adoption of complex physical-disturbance treatments across semi-natural dry grassland and lowland heathland. Incorporating such interventions into future agri-environment schemes would help to facilitate this recommendation.

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Contents

List of figures

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

Note, supplementary figures are not reported in this list

List of tables

Chapter 4

Note, supplementary tables are not reported in this list

Table of contributions

	Chapter 2	Chapter 3	Chapter 4	Chapter 5	Chapter 6	Appendix A	Appendix B
Initial concept and study design	**RWH**, AB, JS, PMD	**RWH**, AB, JS, PMD	**RWH**, AB, JS, PMD, RG	**RWH**, AB, JS, PMD	**RWH**, AB, JS, PMD	**RWH,** CL, SAL	NZ, PMD, **RWH**
Data collection	**RWH**, DW, HJ, SAL	**RWH**, HJ	**RWH**, HJ, JS, RG	**RWH**, ARB, CL, DW, HJ, JM, JRW, NO, SAL, SG	**RWH**, ARB, CL, DW, HJ, JM, NO, SAL, SG	**RWH,** CL, HJ, SAL	NZ, HJ, **RWH**
Data analysis	**RWH**	**RWH**	**RWH**	**RWH**	**RWH**	NA	NZ, JRB
Led the writing	**RWH**	**RWH**	**RWH**	**RWH**	**RWH**	**RWH**	NZ
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Robert W. Hawkes (RWH), Amanda Ratier Backes (ARB), Andy Brown (AB), Colin Lucas (CL), Doreen Wells (DW), Helen Jones (HJ), James McGill (JM), Jon R. Webb (JRW), Jennifer Smart (JS), Natalia B. Zielonka (NBZ), Nick Owens (NO), Paul M. Dolman (PMD), Rhys Green (RG), Robert J. Burnside (RJB), Steve A. Lane (SAL), Steve Gilham (SG).

Note, Chapters 1 & 7 (the general introduction and discussion, respectively) were led by **RWH,** with support and input from his supervisory team (AB, PMD, JS)

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Chapter 1

General Introduction

1.1 The role of evidence-based conservation management

During the latter half of the 20th century conservation practice was often based upon personal anecdote and perception rather than rigorous appraisal of the available evidence (Sutherland, Pullin, Dolman & Knight 2004). Worryingly, it remains the case that too little evidence is collected on the consequence of current practices, limiting our capacity to base future decisions on what does and does not work. Despite this, where conservation evidence is available and accessible, conservation practitioners are often willing to change their approach to management (Walsh, Dicks & Sutherland 2015). Given increasing calls for governments and wider society to invest substantial financial resource to address global conservation problems, there is an urgent need to demonstrate outcome (Pullin & Knight 2009). This will also help to ensure that what limited investment is made is being used well.

Numerous examples highlight the value of using evidence to underpin conservation practice. For example, European agri-environment schemes (AES) designed to support the maintenance and restoration of biodiversity using widely applied but generalised prescriptions are often ineffectual (Kleijn *et al.* 2006; Still & Byfield 2010; Fuentes-Montemayor, Goulson & Park 2011; Wood, Holland & Goulson 2015; MacDonald *et al.* 2019). By contrast, where the design and implementation of AES are informed by rigorous conservation research, and implemented over a sufficiently large scale (Bellebaum & Koffijberg 2018), prescriptions can enhance populations of target species (e.g. O'Brien, Green & Wilson 2006; Brereton, Warren, Roy & Stewart 2008; Perkins, Maggs, Watson & Wilson 2011) and species groups (e.g. pollinators, Dicks *et al.* 2015).

AES clearly demonstrate the purpose and value of evidence-based conservation, yet the repercussions of poorly informed management extend beyond habitat interventions alone. Predator control, for example, can enhance ground nesting bird populations by improving breeding productivity (e.g. Fletcher, Aebischer, Baines, Foster & Hoodless 2010), but its efficacy can vary according to initial predator densities (Bolton, Tyler, Smith & Bamford 2007) and meso-predator interactions (Bodney, Mcdonald, Sheldon & Bearhop 2011). Only through conservation evidence can practitioners ensure the right level of predator control is implemented under the right circumstances – failure to do so raises serious ethical concerns.

The take-home message is conservation practice needs to be underpinned by robust evidence if we are to have confidence in outcome. In many cases this important detail is often perceived as difficult to incorporate because of pragmatic, logistic, financial or political concerns (AES are a good example of this). Nonetheless, if investment in conservation is to achieve its primary purpose, these obstacles cannot prevent sound science from influencing practice.

1.2 Taxonomic biases in conservation research and practice

It is well-established that taxonomic biases exist in both conservation research and practice (Fazey, Fischer & Lindenmayer 2005). Thus, whilst some groups such as vertebrates have received considerable attention (Clark & May 2002), for many others accurate information about their distributions, conservation requirements, and potentially threat status is limited. Given such biases exist, it is unsurprising that land management interventions are also restricted in their taxonomic focus. Yet again, AES are good example of this; they include generalised prescriptions for 'biodiversity' (informed by broad measures such as species richness, MacDonald *et al.* 2019), and bespoke targeted options for a suite of declining bird species (Bright *et al.* 2015) and pollinators (Ouvrard, Transon & Jacquemart 2018), but lack tried and tested cross-taxa prescriptions which support rare, scarce and threatened species (hereafter, 'priority species'). To address this problem, conservationists often advocate single species surrogates (e.g. 'umbrella species') - the idea that managing for one species will benefit many others - as a way of justifying biodiversity conservation through single species actions. However, whilst many studies have examined whether the overall richness or abundance of other species are higher where the umbrella species is present (Suter, Graf & Hess 2002), or whether they occupy similar habitats (Maslo *et al.* 2016; Sibarani, Di Marco, Rondinini & Kark 2019), congruence - cross-taxa correlations in species richness – is typically weaker at smaller spatial scales (e.g. individual sites) (Westgate, Barton, Lane & Lindenmayer 2014) and for rarer species (Grenyer *et al.* 2006). Thus these 'traditional' approaches to surrogate testing cannot reliably establish whether localised habitat interventions, designed for the focal species, actually benefit wider biodiversity.

Even where the consequences of management interventions are considered among traditionally less well-studied taxa, studies typically focus on groups with a larger body of taxonomic expertise, such as plants (Mossman, Davy & Grant 2012), Lepidoptera (Goodenough & Sharp 2016), Odonata (Harabiš, Tichanek & Tropek 2013), and Carabidae (MacDonald, Maniakowski, Cobbold, Grice & Anderson 2012). In contrast, groups such as Diptera, Staphylinidae, and Cicadellidae, are almost never considered. Thus, in many instances, the wider biodiversity value of conservation interventions remain unknown, even though these rarely assessed groups may contain large numbers of threatened species (Hayhow *et al.* 2019). To address ongoing and widespread biodiversity declines (Pereira *et al.* 2010), management needs to be optimised for cross-taxa groups, not just small taxonomic subsets.

In regions where biodiversity is well characterized and autecological knowledge is strong (such as in much of Western Europe), the Biodiversity Audit approach provides a tool to quantify and characterise the shared habitat, resource and ecological requirements of a diverse range of priority species (Dolman, Panter & Mossman 2012). By identifying conservation priorities (e.g. species of conservation concern) and synthesising their management requirements (across all identified priority species), this approach integrates multiple species into cross-taxa management guilds with shared requirements. Although this approach presents an objective model to help facilitate cross-taxa conservation within any given region, crucially, recommended management actions are based on inferred ecological requirements, which is particularly problematic for understudied taxa (where autecological knowledge is weaker, and such species tend to form the overwhelming majority of species in any assemblage). Multi-taxa experiments are needed to confirm the consequence of recommended management actions.

1.3 Acquiring evidence to inform conservation practice

1.3.1 The role of experiments

Many studies inform management based on the observed relations between focal species (or a species subset) and habitat composition (van den Berg, Bullock, Clarke, Langston & Rose 2001; Boughey, Lake, Haysom & Dolman 2011; Border, Henderson, Redhead & Hartley 2017). Whilst this type of study can imply suitable practice (treatments), alternative treatments or interventions (e.g. novel mechanical interventions versus more 'traditional' methods such as grazing) may produce far more successful results. Experiments which test multiple treatments, ideally across a range of habitats, are needed to test intervention efficacy and inform best practice (Buckingham, Atkinson & Rook 2004).

Most land management experiments focus on single species (Bro, Mayot, Corda & Reitz 2004), limited species subsets (Williams *et al.* 2001), a single taxonomic group (Gibson, Hambler & Brown 1992; Cameron & Leather 2011), or vegetation proxies (Dunn, Morris & Grice 2015). Notwithstanding the previously discussed issues around taxonomic bias, there are some advantages to this type of study. For example, because resources are not expended on challenging identifications, researchers can sample more treatment replicates, enabling more robust analysis. Also, where focal species conservation is the goal, treatment prescriptions can be tailored to the specific resource needs of the target species (e.g. O'Brien *et al.* 2006). Last, by distributing treatments across a range of landscape features that are of ecological significance to the target species (e.g. across patches that differ in their distance to nearest woodland), focal species experiments are able to test whether habitat interventions are more effective within certain landscape contexts.

Multi-taxa experiments are considerably rarer, yet they present the only reliable way to determine consequence of habitat interventions for a wider complement of biodiversity. Where they occur, they often utilise a range of sampling methods to adequately incorporate taxonomic groups with contrasting traits, behaviours and habitats associations (e.g. Barlow *et al.* 2007; Schall *et al.* 2018). For invertebrates, pitfall traps provide an ideal sampling method for ground-active species (e.g. Carabidae, Araneae, Staphylinidae), 'suction sampling' or 'sweeping-netting' are more suited to species associated with taller vegetation (e.g. Cicadellidae), 'beating' can be used to sample arboreal species, and pan or malaise traps are usually used to sample aerial species (e.g. Aculeata, Diptera) (Drake, Lott, Alexander & Webb 2007). Vascular plants, lichens and bryophytes, are typically sampled using quadrats (frequency counts or percentage cover estimates, pooled or averaged across quadrats) (e.g. Pywell *et al.* 2007; Pedley, Franco, Pankhurst & Dolman 2013). Crucially, the choice of sampling technique(s) will not only depend on the available resource, but also habitat context (e.g. 'beating' would be redundant in a treeless landscape). Last, multi-taxa experiments, particularly those in higher latitudes, often sample repeatedly throughout the year to capture markedly different assemblages available in different seasons, due to species' phenology (e.g. Gibson *et al.* 1992; Pedley *et al.* 2013; Schall *et al.* 2018).

A rapidly emerging technology, metabarcoding, has the potential to revolutionise the way multi-taxa experiments carried out by rapidly characterising the species compositions of mass samples (Ji *et al.* 2013), removing the reliance on taxonomic expertise. However, this approach is currently highly costly, and reliant upon a complete catalogue of reference barcode sequences to enable accurate identification across the entire species-pool. Simply understanding species richness (a relatively simple metric to attain from metabarcoding) does not equate to species identity, which is needed to quantify treatment response among species of conservation concern.

1.3.2 Establishing success in conservation

For focal species studies, intervention success can be measured in different ways. For example, most studies typically compare the abundance of the target species (e.g. for birds, inferred number of territorial males; for lepidoptera, inferred from timed counts) between treated areas to untreated controls (Bright *et al.* 2015; Daskalova, Phillimore, Bell, Maggs & Perkins 2019), or more rarely examine consequences of interventions for demographic rates, such as nest success (Sheldon, Chaney & Tyler 2007) and fledging success (Calladine, Baines & Warren 2002; Fletcher *et al.* 2010; McHugh, Prior, Grice, Leather & Holland 2017). For cryptic and or nocturnal species GPS tracking can be used to determine whether intervention areas are used for inconspicuous behaviours (e.g. foraging Schlaich, Klaassen, Bouten, Both & Koks 2015), but this is rarely done in the context of experiments.

For multi-species studies, measures such as abundance and species richness (overall, and per taxonomic groups) are often used to assess intervention efficacy (Barlow *et al.* 2007; MacDonald *et al.* 2012; Pedley *et al.* 2013; Schall *et al.* 2018). Whilst this provides a useful measure of the overall consequence of treatment, it does not determine whether responses differ between widespread generalists and the intended recipients (e.g. priority species). Where the objective of the study is an assessment of biodiversity gain, splitting the sampled taxa into 'non-priorities' and 'priorities' can allow researchers to determine whether responses vary according priority status – providing a more refined measure of intervention consequence.

Whilst measures such as richness and abundance can determine whether management enhances certain taxonomic groups, this does not establish the extent and combination of treatments required to enhance cumulative species richness at the landscape-scale (gamma diversity). Establishing this sort of detail is a key challenge for conservation researchers (Wilson, Evans & Grice 2010) as they strongly suspect management is likely often applied at an insufficient scale (Bellebaum & Koffijberg 2018). However, as far as I am aware, no previous study has attempted to explore how much management is needed to enhance cross-taxa assemblages within a semi-natural system. Instead, where researchers have attempted to establish this detail, they have focused on focal species or species groups (e.g. pollinators) in arable farmland (e.g. Perkins *et al.* 2011; Dicks *et al.* 2015).

1.3.3 Analysing assemblage data

There are two main ways of analysing richness and abundance data. First, regression models can be used to test whether richness / abundance (the response variable) differs between treated areas and controls (as a fixed effect) (e.g. MacDonald *et al.* 2012; Pedley *et al.* 2013). These models can also test whether the response is also influenced by additional parameters, such as landscape or habitat; they can also test whether treatment efficacy varies according to these landscape or habitat contexts through an interaction term. Where experiments are carried out over large geographic areas, site identity can be included as a random effect to control for geographic variation in richness / abundance (e.g. Dunn, Hartwell, Grice & Morris 2013). Second, for multi-species studies, sample-based rarefaction is often used to examine cumulative richness differences between treatment(s) and controls (e.g. Barlow *et al.* 2007; Schall *et al.* 2018), while accounting for relative sampling effort. This technique controls for unequal sampling effort (e.g. sampling may be more or less intensive in treated areas, Chao *et al.* 2014), or even where effort is similar, sampling may be less effective – for example if species density differs, or trapping efficiency differs, in treated relative to untreated areas (Chao 1987).

Irrespective of relative richness, treatments and controls may support radically different species compositions. To determine whether compositions differ, ordination method are frequently used to order species and/or samples along real or perceived ecological gradients. There are several ordination methods available, each suited to a particular research question (Kenkel & Orloci 1986); but for experiments, unconstrainted methods (e.g. Non-metric Multidimensional Scaling), which are based solely on composition data (i.e. the abundance or presence/abundance of each species in each sampling unit), are often used to visualise how assemblage composition varies between treatments and controls (e.g. Matthews & Spyreas 2010). By way of contrast, constrained methods (e.g. Canonical correspondence analysis) directly relate compositions to a linear combination of environmental variables, which allows researchers to test the effects of environmental data (e.g. altitude, soil pH) on assemblage composition (ter Braak & Šmilauer 2015). Note, with some unconstrainted methods, researchers can test similar predictions by regressing axis scores (generated from the ordination) against environmental predictors.

1.4 Semi-natural habitats and their conservation

Over half of the habitats in Europe which warrant special protection, according to the EU Habitats and Species directive, are low-intensity (in terms of chemical inputs and productivity) anthropogenic ‘semi-natural’ habitats (Bignal & McCracken 1996); but how did these areas come about and why are they important for biodiversity? In Western Europe, preindustrial land-use (c. 1200-1750) was characterised by intense resource exploitation and significant levels of biomass harvest, complex nested structural heterogeneity, overlaying of multiple land uses, and spatial and temporal variability in management (Fuller, Williamson, Barnes & Dolman 2017). Some of these severe anthropogenic land-use pressures substituted more natural processes, which would have persisted prior to the Neolithic period (e.g. through natural disturbance dynamics such as river meanders, the grazing pressure imposed by large herbivores, or actions of other ecosystem engineers such as beavers). In this way, human activities provided many complex ecological niches required by natural species. Nevertheless, the intensity and complexity of preindustrial land-use filtered the species-pool, favoring open-habitat and thermophilous species (Buckland & Dinnin 1993). Intensification of agricultural practice throughout the 20th century drastically altered the farmland landscape across Europe, and these semi-natural areas become increasingly scarce and fragmented as a result (Bullock *et al.* 2011; Hooftman & Bullock 2012). The surviving species-pool that now persists within semi-natural remnants is often scarce or absent across the wider landscape, where intensive farming creates and sustains unsuitable homogenous, eutrophic, high-intensity habitats.

Despite special conservation measures, semi-natural habitats continue to decline in extent (albeit at a slower rate, Ridding, Watson, Newton, Rowland & Bullock 2020b) and many are Threatened (Janssen *et al.* 2016). Furthermore, whilst it is well established that such losses pose a serious threat to many plant and animal species (Fuller 1987; Krebs, Wilson, Bradbury & Siriwardena 1999; Wright, Lake & Dolman 2012), species declines continue to occur within surviving remnants (Hülber *et al.* 2017; Seibold *et al.* 2019). To prevent further species declines and facilitate recovery, there is a pressing need to optimise conservation efforts across the remaining semi-natural resource.

The drivers of ongoing biodiversity loss and decline within surviving semi-natural remnants vary between habitats, regions, and sites; but some are of almost universal significance. For example, increased rates of atmospheric nutrient disposition (Tipping *et al.* 2019), reduced biomass removal (Power, Ashmore & Cousins 1998) and the cessation of historical management practices (Wells 1969; Webb 1998; Uchida, Takahashi, Shinohara & Ushimaru 2016) have accelerated succession (i.e. vegetation growth) in such a way that characteristic semi-natural assemblages, typical of a low nutrient status, have declined (e.g. Ridding *et al.* 2020a). In addition, recent evidence suggests that landscape composition is also important, with invertebrate declines occurring more rapidly where sites are surrounded by high-intensity farmland (Söderström, Svensson, Vessby & Glimskär 2001; Seibold *et al.* 2019). Whilst landscape-scale strategies are needed to address some of these issues (e.g. nutrient deposition and agricultural impacts), site-based interventions are also urgently needed to alleviate these pressures (e.g. nutrient deposition, Härdtle, Niemeyer, Niemeyer, Assmann & Fottner 2006) and maximise biodiversity gains (Fuller *et al.* 2017).

AES often provide the main policy initiatives for delivering biodiversity objectives in semi-natural systems, but these typically focus on broad site scale maintenance, recreation and restoration options (Bullock *et al.* 2011). Whilst these are effective at maintaining the status quo (Critchley, Burke & Stevens 2004) or facilitating semi-natural restoration within formerly high-intensity farmed areas (Marrs, Snow, Owen & Evans 1998), bespoke semi-natural habitat land management prescriptions which target cross-taxa groups of priority species are lacking. If such prescriptions could be identified, AES would provide the ideal mechanism to facilitate their wide-spread adoption.

Another important pressure is climate change. Given colonisations, changes in species range and phenology, and potential alterations to habitat structure and composition all set to alter assemblage composition within semi-natural habitats (Mossman, Franco & Dolman 2013), should we still manage for existing sets of priority species? Climate envelope models suggest that mobile groups (e.g. lepidoptera, Pateman, Hill, Roy, Fox & Thomas 2012; and birds, Pearce-Higgins & Green 2014) will undergo considerable turnover in the coming decades (i.e. some species will leave and others will colonise), but less mobile groups are often omitted from these assessments. For colonising species, semi-natural habitats will facilitate range expansion disproportionately more than the surrounding unprotected landscape (Thomas *et al.* 2012); whilst for less-mobile species such as molluscs, brachypterous insects or plants lacking structures for long-distance dispersal, conservation interventions are needed within existing strongholds to buffer these species against the effects of climate change (Mossman *et al.* 2013). Either way, management interventions are needed to ensure that semi-natural habitats are optimized for existing assemblages and new colonisers in a changing environment.

Whilst there is widespread consensus that human intervention is needed to support priority assemblages within semi-natural systems (Bignal & McCracken 1996), the intensity and design of land management strategy are hotly debated topics. As summarised by Fuller *et al.* (2017), semi-natural habitat conservation is at a crossroads, with the paradigm of ‘traditional management’ – ‘mimicking’ perceived ideas of land-use history on the assumption that such practice will support assemblages that persisted through human activity (Wright *et al.* 2012) – being increasingly challenged by the idea of restoring more natural processes through a spectrum of ‘re-wilding’ approaches

(Linnell, Kaczensky, Wotschikowsky, Lescureux & Boitani 2015). Crucially, perceived notions of 'traditional-management' are often limited and simplistic, which has resulted in overly homogenised prescriptions (Fuller *et al.* 2017); whilst aspects of re-wilding which lack dynamic and destructive processes will undoubtably negatively impact those open-habitat and thermophilous assemblages for which semi-natural habitats are valued. Instead, synthesising cross-taxa autecological knowledge (derived from biodiversity auditing, Dolman *et al.* 2012) with an understanding of the intensity and complexity of historic land-use (Linnell *et al.* 2015; Fuller *et al.* 2017) inspires novel interventions (hereafter, 'enhanced management'), often with an emphasis on physical-disturbance, grazing, nutrient removal, spatio-temporal variability, early-successional habitats and structural complexity (Fuller *et al.* 2017). In some cases, enhanced management may involve the use of large herbivores, consistent with some of the principles of rewilding (Van Klink & WallisDeVries 2018); but in others it may be appropriate to adopt radically new approaches (e.g. using crushed concrete to create new brownfield sites, or excavating vast areas of stabilised costal dune) to create the resources for the widest range of species.

1.5 Thesis aims

Whilst what we know of the ecological requirements of priority species supports the idea that the historical management within semi-natural systems is important (Dolman *et al.* 2012), there is a pressing need for experimental confirmation. In this thesis, I explore the focal species and multi-taxa consequences of implementing enhanced management interventions across a mosaic of semi-natural lowland dry-grassland and heathland (hereafter 'grassland'). I selected grassland because conservation practices have long emphasised the role of grazing (Wells 1969; Bakker, De Bie, Dallinga, Tjaden & De Vries 1983) but it is becoming increasingly apparent that the needs of many priority species may better be met by temporally- and spatially-dynamic physical-disturbance than by promoting temporal stability and uniformity of management prescriptions (e.g. Pywell *et al.* 2007; Cameron & Leather 2011; Pedley *et al.* 2013). Within this system land-use history (Fuller *et al.* 2017) and autecological knowledge of priority non-vertebrate grassland species (Dolman *et al.* 2012) suggest that creating overlapping mosaics of cultivations that vary in disturbance age and frequency is likely to benefit currently scarce biodiversity. This form of overlapping complex design (hereafter, 'treatment complexes') is also justified by the ecological requirements of two focal bird species of conservation concern – Eurasian Stone-curlew *Burhinus oedicnemus* (hereafter 'Stone-curlew') and Woodlark *Lullula arborea.* Stone-curlew require sparsely-vegetated ground for nesting (Stone-culrew, Green, Tyler & Bowden 2000), whilst Woodlark and potentially Stone-curlew require these conditions for foraging (Bowden 1990; Mallord, Dolman, Brown & Sutherland 2007).

To test whether the enhanced treatment complex interventions benefits grassland biodiversity, I established the largest land management experiment ever attempted in a European grassland. The selected interventions focussed on two methods of promoting structural complexity through ground-disturbance (shallow- or deep-cultivation) using widely available machinery. The aim of this thesis is to establish the consequence of this treatment for Stone-curlew, Woodlark, and a diverse range of non-vertebrate taxa.

1.6 Thesis structure

Chapter 2 explores whether the ground disturbance interventions during the first year of the experiment, when treatments were optimised for a high-profile species (Stone-curlew) protected under European legislation (EC 2009) and widely accorded 'flagship', enhanced other biota; providing a rare test of the biodiversity consequence (with a particular focus on priority species) of managing for a conservation surrogate. **Chapter 3** examines whether the abundance of a species of conservation concern (Woodlark) increased in response to the complexes over the three-year experiment, and tests whether treatment detail (establishment method and treatment complexity) alters outcomes for this species. For Stone-curlew, given it is well-established that mechanical ground disturbance of semi-natural grassland provides suitable nesting habitat (Johnston 2009), **Chapter 4** uses GPS tracking to explore whether this cryptic nocturnal species also utilised the complexes for foraging even when breeding elsewhere in the landscape.

Chapters 5 and 6 explore the multi-taxa consequences of the interventions once they had fully developed into enhanced treatment 'complexes' (comprising a mosaic of subplots that vary in cultivation age and frequency) utilizing an exceptional data set of

132,251 sampled invertebrates from 878 species and 28,846 plant observations from 167 species. **Chapter 5** explores whether the treatment complexes enhanced biodiversity, and whether the intended recipients responded as anticipated (i.e. the priority species for which the intervention was designed). **Chapter 6** builds on the previous chapter by assessesing whether certain subplots within the complexes were more effective than others, and whether their efficacy varied according to details of the habitat in which replicates were established, in terms of calcareous grassland or acidic ‘heathland’. To help facilitate the widespread adoption of this management, this chapter also explores how much management in terms of proportionate extent is needed to optimise species richness at the landscape scale.

I have written and presented each chapter in the style of a stand-alone scientific paper, with figures, bibliographies and supporting information (appendices) presented at the end of each chapter. I have indicated which chapters are published or under review.

References

Bakker, J.P., De Bie, S., Dallinga, J.H., Tjaden, P. & De Vries, Y. (1983). Sheep-grazing as a management tool for heathland conservation and regeneration in the Netherlands. *Journal of Applied Ecology,* 20(2), 541-560.

Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C. & Peres, C.A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences,* 104(47), 18555-18560.

Bellebaum, J. & Koffijberg, K. (2018). Present agri-environment measures in Europe are not sufficient for the conservation of a highly sensitive bird species, the Corncrake *Crex crex*. *Agriculture, Ecosystems & Environment,* 257, 30-37.

Bignal, E.M. & McCracken, D.I. (1996). Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology,* 33(3), 413-424.

Bodney, T.W., Mcdonald, R.A., Sheldon, R.D. & Bearhop, S. (2011). Absence of effects of predator control on nesting success of Northern Lapwings *Vanellus vanellus*: implications for conservation. *Ibis,* 153(3), 543-555.

Bolton, M., Tyler, G., Smith, K.E.N. & Bamford, R.O.Y. (2007). The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *Journal of Applied Ecology,* 44(3), 534-544.

Border, J.A., Henderson, I.G., Redhead, J.W. & Hartley, I.R. (2017). Habitat selection by breeding Whinchats *Saxicola rubetra* at territory and landscape scales. *Ibis,* 159(1), 139-151.

Boughey, K.L., Lake, I.R., Haysom, K.A. & Dolman, P.M. (2011). Improving the biodiversity benefits of hedgerows: How physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. *Biological Conservation,* 144(6), 1790-1798.

Bowden, C. (1990). Selection of foraging habitats by Woodlarks (*Lullula arborea*) nesting in pine plantations. *Journal of Applied Ecology,* 27, 410.

Brereton, T.M., Warren, M.S., Roy, D.B. & Stewart, K. (2008). The changing status of the Chalkhill Blue butterfly *Polyommatus coridon* in the UK: the impacts of conservation policies and environmental factors. *Journal of Insect Conservation,* 12(6), 629-638.

Bright, J.A., Morris, A.J., Field, R.H., Cooke, A.I., Grice, P.V., Walker, L.K., Fern, J. & Peach, W.J. (2015). Higher-tier agri-environment scheme enhances breeding densities of some priority farmland birds in England. *Agriculture, Ecosystems & Environment,* 203(Supplement C), 69-79.

Bro, E., Mayot, P., Corda, E. & Reitz, F. (2004). Impact of habitat management on grey partridge populations: assessing wildlife cover using a multisite BACI experiment. *Journal of Applied Ecology,* 41(5), 846-857.

Buckingham, D.L., Atkinson, P. & Rook, A.J. (2004). Testing solutions in grass-dominated landscapes: A review of current research. *Ibis,* 146, 163-170.

Buckland, P.C. & Dinnin, M.H. (1993). *Holocene woodlands, the fossil evidence. Dead wood matters: The ecology and conservation of Saproxylic invertebrates in Britain (eds K.J. Kirby & C.M. Drake)*. English Nature, Peterborough.

Bullock, J.M., Jefferson, R.G., Blackstock, T.H., Pakeman, R.J., Emmett, B.A., Pywell, R.J., Grime, J.P. & Silvertown, J. (2011). *Semi-natural grasslands*. Cambridge, UK, UNEP-WCMC. (In: Technical Report: The UK National Ecosystem Assessment, pp 162-195).

Calladine, J., Baines, D. & Warren, P. (2002). Effects of reduced grazing on population density and breeding success of black grouse in northern England. *Journal of Applied Ecology,* 39(5), 772-780.

Cameron, K.H. & Leather, S.R. (2011). Heathland management effects on carabid beetle communities: the relationship between bare ground patch size and carabid biodiversity. *Journal of Insect Conservation,* 16(4), 523-535.

Chao, A. (1987). Estimating the population size for capture-recapture data with unequal catchability. *Biometrics,* 43(4), 783-791.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. & Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs,* 84(1), 45-67.

Clark, J.A. & May, R.M. (2002). Taxonomic bias in conservation research. *Science,* 297(5579), 191-192.

Critchley, C.N.R., Burke, M.J.W. & Stevens, D.P. (2004). Conservation of lowland semi-natural grasslands in the UK: a review of botanical monitoring results from agri-environment schemes. *Biological Conservation,* 115(2), 263-278.

Daskalova, G.N., Phillimore, A.B., Bell, M., Maggs, H.E. & Perkins, A.J. (2019). Population responses of farmland bird species to agri-environment schemes and land management options in Northeastern Scotland. *Journal of Applied Ecology,* 56(3), 640-650.

Dicks, L.V., Baude, M., Roberts, S.P.M., Philips, J., Green, M. & Carvell, C. (2015). How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge. *Ecological Entomology,* 40(S1), 22-35.

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology,* 49, 986-997.

Drake, C.M., Lott, D.A., Alexander, K.N.A. & Webb, J. (2007). Surveying terrestrial and freshwater invertebrates for conservation evaluation. Natural England Research Report NERR005.

Dunn, J.C., Hartwell, V., Grice, P. & Morris, A.J. (2013). Multi-taxa benefits of a targeted single-species agri-environment option. *Aspects of Applied Biology,* 118, 137-143.

Dunn, J.C., Morris, A.J. & Grice, P.V. (2015). Testing bespoke management of foraging habitat for European turtle doves *Streptopelia turtur*. *Journal for Nature Conservation,* 25, 23-34.

EC (2009). *Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds*. European Commission, Brussels.

Fazey, I., Fischer, J. & Lindenmayer, D.B. (2005). What do conservation biologists publish? *Biological Conservation,* 124(1), 63-73.

Fletcher, K., Aebischer, N.J., Baines, D., Foster, R. & Hoodless, A.N. (2010). Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology,* 47(2), 263-272.

Fuentes-Montemayor, E., Goulson, D. & Park, K.J. (2011). Pipistrelle bats and their prey do not benefit from four widely applied agri-environment management prescriptions. *Biological Conservation,* 144(9), 2233-2246.

Fuller, R.J., Williamson, T., Barnes, G. & Dolman, P.M. (2017). Human activities and biodiversity opportunities in pre-industrial cultural landscapes: relevance to conservation. *Journal of Applied Ecology,* 54(2), 459-469.

Fuller, R.M. (1987). The changing extent and conservation interest of lowland grasslands in England and Wales: A review of grassland surveys 1930–1984. *Biological Conservation,* 40(4), 281-300.

Gibson, C.W.D., Hambler, C. & Brown, V.K. (1992). Changes in spider (Araneae) assemblages in relation to succession and grazing management. *Journal of Applied Ecology,* 29(1), 132-142.

Goodenough, A.E. & Sharp, M.H. (2016). Managing calcareous grassland for the declining Duke of Burgundy *Hamearis lucina* butterfly: effects of grazing management on Primula host plants. *Journal of Insect Conservation,* 20(6), 1087-1098.

Green, R.E., Tyler, G.A. & Bowden, C.G.R. (2000). Habitat selection, ranging behaviour and diet of the stone curlew (*Burhinus oedicnemus*) in southern England. *Journal of Zoology,* 250(2), 161-183.

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.-S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006). Global distribution and conservation of rare and threatened vertebrates. *Nature,* 444(7115), 93-96.

Harabiš, F., Tichanek, F. & Tropek, R. (2013). Dragonflies of freshwater pools in lignite spoil heaps: Restoration management, habitat structure and conservation value. *Ecological Engineering,* 55, 51-61.

Härdtle, W., Niemeyer, M., Niemeyer, T., Assmann, T. & Fottner, S. (2006). Can management compensate for atmospheric nutrient deposition in heathland ecosystems? *Journal of Applied Ecology,* 43(4), 759-769.

Hayhow, D.B., Eaton, M.A., Stanbury, A.J., Burns, F., Kirby, W.B., Bailey, N., Beckmann, B., Bedford, J., Boersch-Supan, P.H., Coomber, F., Dennis, E.B., Dolman, S.J., Dunn, E., Hall, J., Harrower, C., Hatfield, J.H., Hawley, J., Haysom, K., Hughes, J., Johns, D.G., Mathews, F., McQuatters-Gollop, A., Noble, D.G., Outhwaite, C.L., Pearce-Higgins, J.W., Pescott, O.L., Powney, G.D. & Symes, N. (2019). The State of Nature 2019. The State of Nature partnership.

Hooftman, D.A.P. & Bullock, J.M. (2012). Mapping to inform conservation: A case study of changes in semi-natural habitats and their connectivity over 70years. *Biological Conservation,* 145(1), 30-38.

Hülber, K., Moser, D., Sauberer, N., Maas, B., Staudinger, M., Grass, V., Wrbka, T. & Willner, W. (2017). Plant species richness decreased in semi-natural grasslands in the Biosphere Reserve Wienerwald, Austria, over the past two decades, despite agri-environmental measures. *Agriculture, Ecosystems & Environment,* 243, 10-18.

Janssen, J.A.M., Rodwell, J.S., García Criado, M., Gubbay, S., Haynes, T., Nieto, A., Sanders, N., Landucci, F., Loidi, J., Ssymank, A., Tahvanainen, T., Valderrabano, M., Acosta, A., Aronsson, M., Arts, G., Attorre, F., Bergmeier, E., Bijlsma, R.-J., Bioret, F., Biţă-Nicolae, C., Biurrun, I., Calix, M., Capelo, J., Čarni, A., Chytrý, M., Dengler, J., Dimopoulos, P., Essl, F., Gardfjell, H., Gigante, D., Giusso del Galdo, G., Hájek, M., Jansen, F., Jansen, J., Kapfer, J., Mickolajczak, A., Molina, J.A., Molnár, Z., Paternoster, D., Piernik, A., Poulin, B., Renaux, B., Schaminée, J.H.J., Šumberová, K., Toivonen, H., Tonteri, T., Tsiripidis, I., Tzonev, R. & Valachovič, M. (2016). *European red list of habitats. Part 2. Terrestrial and freshwater habitats*. Publications Office of the European Union, Luxembourg.

Ji, Y., Ashton, L., Pedley, S.M., Edwards, D.P., Tang, Y., Nakamura, A., Kitching, R., Dolman, P.M., Woodcock, P., Edwards, F.A., Larsen, T.H., Hsu, W.W., Benedick, S., Hamer, K.C., Wilcove, D.S., Bruce, C., Wang, X., Levi, T., Lott, M., Emerson, B.C. & Yu, D.W. (2013). Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding. *Ecology Letters,* 16(10), 1245-1257.

Johnston, A. (2009). Demographic analsis of the impact of conservation action on Stone-curlew populations. PhD Thesis, University of Cambridge

Kenkel, N.C. & Orloci, L. (1986). Applying metric and nonmetric multidimensional scaling to ecological studies: Some new results. *Ecology,* 67(4), 919-928.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters,* 9(3), 243-254.

Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. (1999). The second Silent Spring? *Nature,* 400(6745), 611-612.

Linnell, J.D.C., Kaczensky, P., Wotschikowsky, U., Lescureux, N. & Boitani, L. (2015). Framing the relationship between people and nature in the context of European conservation. *Conservation Biology,* 29(4), 978-985.

MacDonald, M.A., Angell, R., Dines, T.D., Dodd, S., Haysom, K.A., Hobson, R., Johnstone, I.G., Matthews, V., Morris, A.J., Parry, R., Shellswell, C.H., Skates, J., Tordoff, G.M. & Wilberforce, E.M. (2019). Have Welsh agri-environment schemes delivered for focal species? Results from a comprehensive monitoring programme. *Journal of Applied Ecology,* 56(4), 812-823.

MacDonald, M.A., Maniakowski, M., Cobbold, G., Grice, P.V. & Anderson, G.Q.A. (2012). Effects of agri-environment management for stone curlews on other biodiversity. *Biological Conservation,* 148(1), 134-145.

Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. (2007). Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology,* 44(1), 185-195.

Marrs, R.H., Snow, C.S.R., Owen, K.M. & Evans, C.E. (1998). Heathland and acid grassland creation on arable soils at Minsmere: identification of potential problems and a test of cropping to impoverish soils. *Biological Conservation,* 85(1), 69-82.

Maslo, B., Leu, K., Faillace, C., Weston, M.A., Pover, T. & Schlacher, T.A. (2016). Selecting umbrella species for conservation: a test of habitat models and niche overlap for beach-nesting birds. *Biological Conservation,* 203, 233-242.

Matthews, J.W. & Spyreas, G. (2010). Convergence and divergence in plant community trajectories as a framework for monitoring wetland restoration progress. *Journal of Applied Ecology,* 47(5), 1128-1136.

McHugh, N.M., Prior, M., Grice, P.V., Leather, S.R. & Holland, J.M. (2017). Agri-environmental measures and the breeding ecology of a declining farmland bird. *Biological Conservation,* 212, 230-239.

Mossman, H.L., Davy, A.J. & Grant, A. (2012). Does managed coastal realignment create saltmarshes with ‘equivalent biological characteristics’ to natural reference sites? *Journal of Applied Ecology,* 49(6), 1446-1456.

Mossman, H.L., Franco, A.M.A. & Dolman, P.M. (2013). Terrestrial biodiversity climate change impacts report card technical paper. Biodiversity report card 3, invertebrates. University of East Anglia.

O'Brien, M., Green, R.E. & Wilson, J. (2006). Partial recovery of the population of Corncrakes *Crex crex* in Britain, 1993–2004. *Bird Study,* 53(3), 213-224.

Ouvrard, P., Transon, J. & Jacquemart, A.-L. (2018). Flower-strip agri-environment schemes provide diverse and valuable summer flower resources for pollinating insects. *Biodiversity and Conservation,* 27(9), 2193-2216.

Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R. & Thomas, C.D. (2012). Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. *Science,* 336(6084), 1028.

Pearce-Higgins, J.W. & Green, R.E. (2014). *Birds and Climate Change: Impacts and Conservation Responses*. Cambridge University Press, Cambridge.

Pedley, S.M., Franco, A.M.A., Pankhurst, T. & Dolman, P.M. (2013). Physical disturbance enhances ecological networks for heathland biota: A multiple taxa experiment. *Biological Conservation,* 160, 173-182.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R. & Walpole, M. (2010). Scenarios for global biodiversity in the 21st Century. *Science,* 330(6010), 1496-1501.

Perkins, A.J., Maggs, H.E., Watson, A. & Wilson, J.D. (2011). Adaptive management and targeting of agri-environment schemes does benefit biodiversity: a case study of the corn bunting *Emberiza calandra*. *Journal of Applied Ecology,* 48(3), 514-522.

Power, S.A., Ashmore, M.R. & Cousins, D.A. (1998). Impacts and fate of experimentally enhanced nitrogen deposition on a British lowland heath. *Environmental Pollution,* 102(1, Supplement 1), 27-34.

Pullin, A.S. & Knight, T.M. (2009). Doing more good than harm – Building an evidence-base for conservation and environmental management. *Biological Conservation,* 142(5), 931-934.

Pywell, R.F., Bullock, J.M., Tallowin, J.B., Walker, K.J., Warman, E.A. & Masters, G. (2007). Enhancing diversity of species-poor grasslands: An experimental assessment of multiple constraints. *Journal of Applied Ecology,* 44(1), 81-94.

Ridding, L.E., Bullock, J.M., Pescott, O.L., Hawes, P., Walls, R., Pereira, M.G., Thacker, S.A., Keenan, P.O., Dragosits, U. & Pywell, R.F. (2020a). Long-term change in calcareous grassland vegetation and drivers over three time periods between 1970 and 2016. *Plant Ecology*.

Ridding, L.E., Watson, S.C.L., Newton, A.C., Rowland, C.S. & Bullock, J.M. (2020b). Ongoing, but slowing, habitat loss in a rural landscape over 85 years. *Landscape Ecology,* 35, 257–273.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Schulze, E.-D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T. & Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology,* 55(1), 267-278.

Schlaich, A.E., Klaassen, R.H.G., Bouten, W., Both, C. & Koks, B.J. (2015). Testing a novel agri-environment scheme based on the ecology of the target species, Montagu's Harrier *Circus pygargus*. *Ibis,* 157(4), 713-721.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S. & Weisser, W.W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature,* 574, 671-674.

Sheldon, R.D., Chaney, K. & Tyler, G.A. (2007). Factors affecting nest survival of Northern Lapwings *Vanellus vanellus* in arable farmland: an agri-environment scheme prescription can enhance nest survival. *Bird Study,* 54(2), 168-175.

Sibarani, M.C., Di Marco, M., Rondinini, C. & Kark, S. (2019). Measuring the surrogacy potential of charismatic megafauna species across taxonomic, phylogenetic and functional diversity on a megadiverse island. *Journal of Applied Ecology,* 56(5), 1220-1231.

Söderström, B., Svensson, B., Vessby, K. & Glimskär, A. (2001). Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity & Conservation,* 10(11), 1839-1863.

Still, K.S. & Byfield, A.J. (2010). Is Environmental Stewardship working for rare and threatened plants? *Aspects of Applied Biology,* (100), 279-286.

Suter, W., Graf, R.F. & Hess, R. (2002). Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conservation Biology,* 16, 778–788.

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004). The need for evidence-based conservation. *Trends in Ecology & Evolution,* 19(6), 305-308.

ter Braak, C.J.F. & Šmilauer, P. (2015). Topics in constrained and unconstrained ordination. *Plant Ecology,* 216(5), 683-696.

Thomas, C.D., Gillingham, P.K., Bradbury, R.B., Roy, D.B., Anderson, B.J., Baxter, J.M., Bourn, N.A.D., Crick, H.Q.P., Findon, R.A., Fox, R., Hodgson, J.A., Holt, A.R., Morecroft, M.D., O'Hanlon, N.J., Oliver, T.H., Pearce-Higgins, J.W., Procter, D.A., Thomas, J.A., Walker, K.J., Walmsley, C.A., Wilson, R.J. & Hill, J.K. (2012). Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences,* 109(35), 14063-14068.

Tipping, E., Davies, J.A.C., Henrys, P.A., Jarvis, S.G., Rowe, E.C., Smart, S.M., Le Duc, M.G., Marrs, R.H. & Pakeman, R.J. (2019). Measured estimates of semi-natural terrestrial NPP in Great Britain: comparison with modelled values, and dependence on atmospheric nitrogen deposition. *Biogeochemistry,* 144(2), 215-227.

Uchida, K., Takahashi, S., Shinohara, T. & Ushimaru, A. (2016). Threatened herbivorous insects maintained by long-term traditional management practices in semi-natural grasslands. *Agriculture, Ecosystems & Environment,* 221, 156-162.

van den Berg, L.J.L., Bullock, J.M., Clarke, R.T., Langston, R.H.W. & Rose, R.J. (2001). Territory selection by the Dartford warbler (*Sylvia undata*) in Dorset, England: the role of vegetation type, habitat fragmentation and population size. *Biological Conservation,* 101(2), 217-228.

Van Klink, R. & WallisDeVries, M.F. (2018). Risks and opportunities of trophic rewilding for arthropod communities. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 373(1761).

Walsh, J.C., Dicks, L.V. & Sutherland, W.J. (2015). The effect of scientific evidence on conservation practitioners' management decisions. *Conservation Biology,* 29(1), 88-98.

Webb, N.R. (1998). The traditional management of European heathlands. *Journal of Applied Ecology,* 35(6), 987-990.

Wells, T.C.E. (1969). Botanical aspects of conservation management of chalk grasslands. *Biological Conservation,* 2(1), 36-44.

Westgate, M.J., Barton, P.S., Lane, P.W. & Lindenmayer, D.B. (2014). Global meta-analysis reveals low consistency of biodiversity congruence relationships. *Nature Communications,* 5(1), 3899.

Williams, M.R., Abbott, I., Liddelow, G.L., Vellios, C., Wheeler, I.B. & Mellican, A.E. (2001). Recovery of bird populations after clearfelling of tall open eucalypt forest in Western Australia. *Journal of Applied Ecology,* 38(5), 910-920.

Wilson, J.D., Evans, A.D. & Grice, P.V. (2010). Bird conservation and agriculture: a pivotal moment? *Ibis,* 152(1), 176-179.

Wood, T.J., Holland, J.M. & Goulson, D. (2015). Pollinator-friendly management does not increase the diversity of farmland bees and wasps. *Biological Conservation,* 187, 120-126.

Wright, H.L., Lake, I.R. & Dolman, P.M. (2012). Agriculture—a key element for conservation in the developing world. *Conservation Letters,* 5(1), 11-19.

Chapter 2

Multi-taxa consequences of management for an avian umbrella species

Robert W. Hawkes[a], Jennifer Smart[b,c], Andy Brown[d], Helen Jones[b], Steve Lane[e], Doreen Wells[f], and Paul M. Dolman[a]

[a] *School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK*

[b] *RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK*

[c] *School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK*

[d] *Natural England, Suite D, Unex House, Bourges Boulevard, Peterborough, PE1 1NG, UK*

[e] *5 Lancaster Way, East Winch, King's Lynn, PE32 1NY, UK*

[f] *1 Cobden Terrace, Great Yarmouth, NR30 1BT, UK*

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Abstract

Whether management for so-called umbrella species actually benefits co-occurring biota has rarely been tested. Here, we studied consequences for multiple invertebrate taxa of two ground-disturbance treatments designed to support an avian umbrella species (Eurasian stone-curlew, *Burhinus oedicnemus*), and whether analysing ecological requirements across the regional species pool predicted beneficiaries. Responses were assessed for the abundance of five bird species of conservation concern, and the abundance, species richness and composition of carabids, staphylinids, other beetles (non-carabid, non-staphylinid), true bugs and ants, sampling 31258 individuals of 402 species in an extensively-replicated experiment across the UK's largest grass-heath. Both treatments provided suitable habitat for the umbrella species, in contrast to controls. Treatment influenced the abundance of only one bird species; but carabid, other beetle and ant richness increased with one or both treatments, while staphylinid richness and abundance increased and true bug richness and abundance decreased with both treatments. Richness of 'priority' (rare, scarce or threatened) invertebrates *a priori* considered to share ecological requirements with the umbrella species (predicted beneficiaries) increased with both treatments. Resampling and rarefaction showed landscapes diversified by treatment supported a greater cumulative species richness of other beetles, ants and true bugs, and importantly priority invertebrates, than a landscape comprising only untreated controls. Such experiments provide strong evidence to assess co-benefits of umbrella species management, but are costly and time consuming. The systematic examination of the autoecological requirements of co-occurring taxa (the 'Biodiversity Audit Approach') successfully predicted likely beneficiaries. Demonstrating wider biodiversity benefits strengthens the case for avian conservation management.

Keywords: Surrogate species, conservation management, Eurasian stone-curlew, *Burhinus oedicnemus*, invertebrate conservation, grassland

2.1 Introduction

Major taxonomic biases exist in conservation (Fazey, Fischer & Lindenmayer 2005; Troudet, Grandcolas, Blin, Vignes-Lebbe & Legendre 2017). Thus, whilst some groups have received considerable attention (e.g. vertebrates, Clark & May 2002), others have not, with conservation practitioners often lacking information on which species are present within a region, which ought to be prioritized, and the management interventions each requires (Dolman, Panter & Mossman 2012). Single-species surrogates (e.g. 'umbrella' species), especially those that garner public support and funds for conservation ('flagship' species) are often used to drive ecosystem management (Hunter *et al.* 2016). However, tests of the wider biodiversity consequences of their subsequent conservation have rarely been conducted (Roberge & Angelstam 2004; Branton & Richardson 2011).

Traditional tests of the umbrella species concept examine whether the overall richness or abundance of other species (generally a single taxon or a limited species subset) is higher where the umbrella species is present (e.g. Suter, Graf & Hess 2002), or whether they occupy similar habitats (e.g. Maslo *et al.* 2016; Sibarani, Di Marco, Rondinini & Kark 2019). Whilst such tests may be appropriate for determining where in the landscape protection should occur (Caro & O'Doherty 1999; Fontaine, Gargominy & Neubert 2007), they do not establish whether interventions designed for the umbrella species benefit either wider biodiversity, or co-occurring species of conservation concern. Within 'semi-natural' habitats, where conservation requires management interventions that modify vegetation composition and/or structure (Webb 1998; Wright, Lake & Dolman 2012), experiments that evaluate responses to trial prescriptions, across multiple taxa, provide the necessary evidence-base to allow the beneficiaries of umbrella species management to be appraised.

Here, we test the consequences of habitat management for Eurasian stone-curlew (*Burhinus oedicnemus*, hereafter 'stone-curlew'), a UK threatened (Stanbury *et al.* 2017), high-profile species protected under European legislation (EC 1979) and widely accorded 'flagship' status, not only for a set of other bird species of conservation concern, but also for multiple invertebrate groups. We selected stone-curlew because they breed in managed semi-natural landscapes, where their requirement for bare-open grassland is well-known (Green, Tyler & Bowden 2000). Additionally, a systematic bioregional process that classified species with shared autecological requirements into multi-taxa ‘management guilds’ (the 'Biodiversity Audit Approach'; Dolman *et al.* 2012), suggests many nationally rare, scarce or threatened species (hereafter ‘priority’ species) should benefit from similar conditions (see details in Appendix S.2.1). However, without validating this experimentally, it is unclear whether management designed for the umbrella species does indeed improve the status of the intended beneficiaries, or whether such gains are offset by reductions in other priority species.

We thus devised an extensively replicated landscape-scale experiment across the UK’s largest (3850 ha) lowland grass-heath (66 treatment plus 36 control plots, total 204 ha) to examine outcomes of ground-disturbance interventions designed to benefit stone-curlew. Responses were examined for priority bird species and five invertebrate groups, each speciose and taxonomically well-resolved. Although extensive, the assessment of biodiversity is incomplete, as we lacked expertise (fungi, bryophytes, soil macro-fauna), or personnel (vascular plants) to sample other important elements. First, we *a priori* predicted that our treatments would create suitable stone-curlew nesting habitat. Next, we predicted that treatment would increase the abundance of birds and the abundance and species richness (hereafter ‘richness’) of some invertebrates groups, while diversifying invertebrate composition. We specifically hypothesized treatment would increase the richness of priority invertebrates associated with physically-disturbed and/or heavily-grazed grassland, but decrease the richness of those associated with lightly-grazed undisturbed grassland. We further predicted that the entire landscape with treatments and controls would support greater cumulative richness of each invertebrate group, and of overall priority species, relative to a control-only landscape.

2.2 Methods

2.2.1 Study area

The study was carried out in Breckland, a bio-geographic region (1000 km^2) of Eastern England characterised by a semi-continental climate and sandy soils that supports over 2000 priority plant and invertebrate species (26% of all UK priority species, Dolman *et al.* 2012). Multi-taxa responses to ground-disturbance treatments were examined across grass-heath (lightly-grazed undisturbed grassland) on the Stanford Military Training Area

(STANTA) (0°76'E, 52°51'N, 3500 ha), Bridgham Heath (0°83'E, 52°44'N, 150 ha) and Brettenham Heath (0°83'E, 52°43'N, 200 ha) (see Appendix S.2.2 for study area details, and Fig. S.2.2 for map).

2.2.2 Experimental treatments

Between January and early May 2015, 66 treated plots (33 deep- and 33 shallow-cultivated) and 36 uncultivated controls, each 2 ha (a size advocated for stone-curlew, Appendix S.2.1), were located at least 100 m apart in open grass-heath mostly excluding, but sometimes near, scattered trees or scrub. Shallow-cultivations were created with a rotovator, which broke up and turned the surface (10 - 13 cm), and deep-cultivations with an agricultural plough, which inverted soil and vegetation (25 - 28 cm) bringing up mineral sub-soil. Following usual conservation practice, shallow-cultivated plots were immediately retreated if the first attempt failed to create sufficient exposed bare substrate (>50%). Four plots (two shallow-cultivated, two deep-cultivated), located within dense heather (*Calluna vulgaris*), were topped with a tractor-mounted flail prior to disturbance. Plots with regenerating thistle (*Cirsium arvense*, *Cirsium vulgare*) or common nettle (*Urtica dioica*) were topped, also with a flail, in late June and July.

The risk posed by unexploded ordnance precluded cultivation treatments in the central STANTA 'impact area', restricting treatments to outer areas of STANTA, plus Bridgham and Brettenham Heaths. Thus constrained, treatments and controls were randomly allocated to plots within four strata, based on soil (NSRI 2014), age since cultivation (Sheail 1979) and plant composition; these were calcareous grass-heath of any age (hereafter 'calcareous grass-heath'), young grass-heath (≤110 years old), intermediate grass-heath (111-167 years old), and ancient-acid grass-heath (≥168 years old) (see Table S.2.1 for details). Both treatments and controls were distributed similarly with respect to Latitude and Longitude (Kruskal-Wallis, $H = 0.79$, $p = 0.67$; $H = 0.46$, $p = 0.79$, respectively; $n = 102$), but vegetation strata (four groups) were not (Latitude, $H = 19.26$, $p < 0.001$; Longitude, $H = 47.19$, $p < 0.001$; $n = 102$) (Fig. S.2.2).

2.2.3 Responses to treatment

In June 2015, we assessed habitat suitability for stone-curlew within a randomly selected half (1 ha subplot) of each 2 ha plot. We recorded vegetation height using a sward stick (diameter 90 mm, weight 250 g; following Green & Griffiths 1994) at 42 points distributed evenly along two parallel 100 m transects (placed 30 - 33 m apart), and also whether bare substrate covered over 50% at each point (25 mm diameter), giving incidence from 0 to 42. Where an individual height measurement (on treatment plots) exceeded 2.5 cm due to uneven topography caused by soil disturbance, a new measurement was taken in a different cardinal direction. Vegetation structure of deep-cultivated, shallow-cultivated and control plots was related to thresholds of stone-curlew nesting habitat suitability informed by *a priori* knowledge (see Appendix S.2.1) of the species preferences for grass-heath vegetation height and bare ground cover (here quantified as the proportion of 42 sampled points in each plot); examining whether modelled 95% CI limits were <2 cm and >40%, respectively.

Birds and ground active invertebrates were also sampled in 2015. Bird sampling was conducted at the scale of the whole 2 ha plot whilst invertebrate sampling was conducted in the same 1 ha subplot as the vegetation structure sampling. Bird responses were examined across all plots, whereas invertebrate responses were examined across 20 deep-cultivated, 20 shallow-cultivated and 16 control plots located outside the impact area, to limit risks from unexploded ordnance.

Bird abundance was sampled for five species of UK conservation concern, defined as 'Red' or 'Amber' listed (Eaton *et al.* 2015); woodlark (*Lullula arborea*), yellowhammer (*Emberiza citronella*), common linnet (*Linaria cannabina*), Northern lapwing (*Vanellus vanellus*), and Eurasian curlew (*Numenius arquata*). Abundant, ubiquitous breeding species (e.g. skylark, *Alauda arvensis*), were not considered. Analyses considered the maximum number of individuals detected on any one of three, 40-minute visits, made to each plot between 1 April and 31 May (mean visit interval: 13.8 days ± 6.5 SD) between dawn and 11:00 during dry, still mornings (Beaufort wind force <4), with at least one week between plot establishment and the first survey to allow territory settlement. During visits, we recorded individuals on, or singing directly above, the plot; initially from a vehicle, followed by walking through the plot edge and center. Observations were restricted to vehicles for three of 306 plot-visits (affecting three deep-cultivated treatments) to minimize disturbance to breeding stone-curlew; for these vehicles were repositioned to maximize coverage.

Invertebrates on each plot were sampled using six pitfall traps (11 cm depth, 8 cm diameter, covered with 12 mm wire mesh, with 50 ml of a saturated salt solution, NaCL), set 15 m apart in a 15 m x 30 m grid, opened for seven consecutive days, separately in each of June, August and October. Samples were pooled across pitfalls and months giving one composite sample per plot. Subsequent analyses controlled for cumulative ‘trap-days’ arising from partially-successful (considered inactive for half the exposure period) or failed traps (considered inactive for the whole exposure period), and unavoidable, though slight, variation in exposure (traps on two deep-cultivated, one shallow-cultivated, and one control plot were deployed two days longer in August due to military restrictions, affecting 2.4% of all seven-day plot deployments).

Invertebrates within five groups were identified to species: carabid, staphylinid, all other beetles, true bugs (but excluding aphids), and ants. Following Dolman *et al.* (2012), priority species were identified as those designated as: (i) threatened (critically endangered, endangered and vulnerable) or near-threatened based upon red list guidelines developed by the International Union for Conservation of Nature; or (ii) Nationally Rare (NR) and Nationally Scarce (NS), or the older designations of Red Data Book (RDB) and Nationally Notable (Na, Nb). A few beetles (1.2%) and true bugs (1.9%) were only identifiable to genus, or a group of species (Table S.2.2).

Following Dolman *et al*. (2012), priority invertebrate species with similar autecological requirements were grouped into ‘management guilds’, which allowed us to classify those species associated with dry-open terrestrial habitats (excluding other habitats) as either requiring physical disturbance or heavy grazing to create bare ground or short-open turf (hereafter ‘disturbed-grassland’ species), or associated with lightly-grazed and physically undisturbed to only lightly-disturbed conditions (hereafter ‘undisturbed-grassland’ species) (Table S.2.2).

2.2.4 Data analysis

Separate analyses considered: vegetation structure (height and bare ground cover, to examine suitability for the umbrella species); bird abundance (five analyses, one per species); richness and abundance of each invertebrate group and of priority invertebrates; and richness of disturbed-grassland and undisturbed-grassland priority invertebrates. Using Generalised Linear Models (GLMs), we examined fixed effects of treatment (three levels), vegetation strata (initially four levels, see below), and for invertebrates the cumulative number of trap-days per sample. Ants were omitted from abundance analyses as coloniality can locally inflate abundance. All models were run in R (R Core Team 2015).

For each analysis the appropriate error term (normal, binomial, Poisson, or negative binomial) was selected by examining the ratio of deviance / residual degrees of freedom of full (global) models; with normal error, response variables were log or square-root transformed where appropriate. For parsimony, vegetation strata were combined if parameter estimates were similar and their merger did not reduce model performance (change in Akalike's Information Criterion corrected for small sample size, ΔAICc, on combination ≤2; Burnham & Anderson 2002); where all vegetation strata were similar then levels were not combined and subsequent model selection removed this variable. Next, candidate models comprising all possible variable combinations were examined using the package ‘lme4’ (Bates, Maechler, Bolker & Walker 2017); the top ranked model was considered ‘best’ if ΔAICc >2 relative to the next-ranked model; where competing models were within 2 ΔAICc the most parsimonious was selected, as additional variables lacked strong support (Burnham and Anderson, 2002). Where treatment was retained, category means were compared by Tukey’s pairwise comparison. For analyses of vegetation structure and bird abundance, separate models were examined that considered either all control plots, including those within the central impact area (where there are no ground-disturbance plots); or that excluded ten ‘impact area controls’ located >200 m inside the impact area boundary. Spatial autocorrelation of model residuals was examined by Moran’s I in the package ‘Ape’ (Paradis, Claude & Strimmer 2004).

For each invertebrate group, sampling efficiency of treatments and controls was assessed by comparing sample-based rarefaction (re-scaled to the number of individuals, using the Mao Tau function) extrapolated to the predicted asymptote, using the package iNEXT (Hsieh, Ma & Chao 2018).

Assemblage composition of treatments and controls was examined separately for each invertebrate group by Non-Metric Multidimensional Scaling (NMDS) performed using a Bray–Curtis dissimilarity-matrix of abundance data (square root transformed with Wisconsin double standardization, following Clarke & Warwick 2001) using the 'Vegan' package (Oksanen *et al.* 2018). Invertebrate records not resolved to species, and plots with fewer than three observations for that group, were omitted. Model performance was assessed by examining stress (<0.05 excellent; <0.1 good; <0.2 potentially usefull; >0.3 close to arbitrary, Clarke & Warwick 2001) and NMDS axis one and two scores were compared between treatment and control (three levels) using Kruskal Wallis tests with Dunn-Bonferroni pairwise comparisons (p <0.05).

To determine whether diversifying the landscape through umbrella species management, would support a higher cumulative richness of each invertebrate group and of (multi-taxa) priority species, we used rarefaction (resampling among plots). Five scenarios were examined: resampling control plots only ('control-only' landscape); the existing landscape diversified by management for the umbrella species ('treatment-control' landscapes, resampling either from: control and shallow-cultivated plots; control and deep-cultivated plots; or control, deep-cultivated, and shallow-cultivated plots); and a 'treatment-only' landscape (resampling both deep- and shallow-cultivated plots, but without control plots). For each scenario, sample-based rarefaction was extrapolated to the sampling intensity (number of individuals) of the full set, examining the overlap in 95% CIs.

2.3 Results

2.3.1 Stone-curlew habitat suitability

Vegetation height decreased progressively from control to shallow- then deep-cultivation (Fig. 2.1) and was lower on pooled young and calcareous than on pooled intermediate and ancient-acid grass-heath. Conversely, bare ground cover increased from control to shallow then deep cultivation and was not influenced by vegetation strata (Table S.2.5). Both treatments, but not controls, provided habitat suitable for nesting stone-curlew (Fig. 2.1).

Residuals from the bare ground cover model (but not the vegetation height model) were weakly spatially autocorrelated (Moran's I = 0.05), suggesting some variation attributable to a spatially correlated factor(s) not considered in the modeling.

Nevertheless, we consider inference for treatment effects to be robust, as treatments and controls were distributed randomly and were balanced across vegetation strata (Table S.2.1). Impact-area controls were retained in both analyses, as their inclusion did not affect model inference.

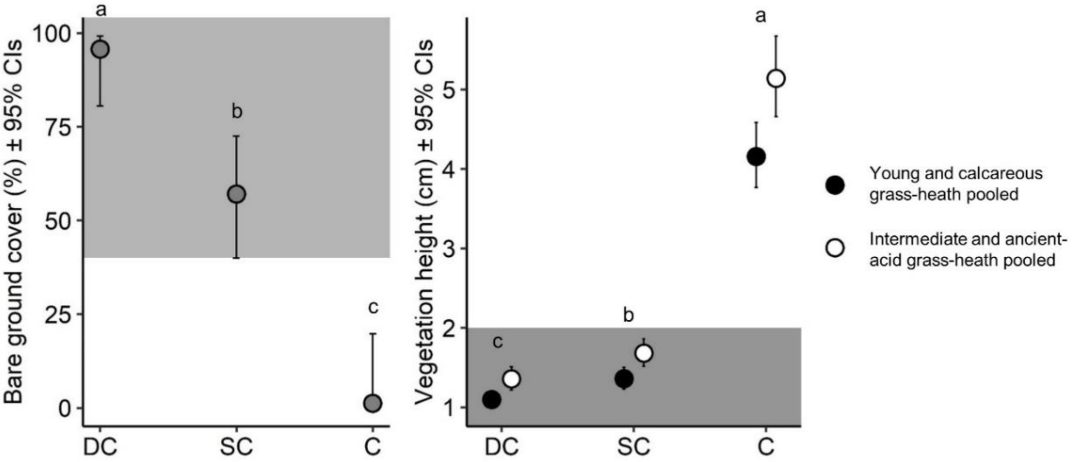

Figure 2.1. Bare ground cover and vegetation height across deep-cultivated (DC), shallow-cultivated (SC) and control (C) grass-heath plots ($n = 102$). Showing means and 95% CI (bars) from Generalized Linear Models that included the fixed effect of treatment (three levels, both models), and vegetation strata in the bare ground cover model (two categories, see legend); means that share a superscript (homogenous sub-sets, a – c) do not differ significantly (Tukey pairwise comparisons $p > 0.05$). Shading denotes limits of suitable Eurasian stone-curlew *Burhinus oedicnemus* nesting habitat. See Table S.2.5 for selected models.

2.3.2 Management consequences for wider biodiversity

Sampling gave 187 bird registrations, comprising 52 woodlark, 41 Northern lapwing, 49 Eurasian curlew, 12 yellowhammer, and 33 common linnet; and 31258 invertebrates from 402 species (Table S.2.2), including: 4740 carabids from 57 species; 5580 staphylinids from 116 species; 1617 other beetles from 139 species (largely from 4 families; 498 Curculionidae, 31%; 243 Elateridae, 15%; 216 Chrysomelidae, 13%; 192 Scarabaeidae, 12%); 1874 true bugs from 72 species; and 17447 ants from 18 species. Of the 402 invertebrates, 52 were priority species, including eleven carabids, ten staphylinids, twenty other beetles, nine true bugs, and two ants. For carabids, staphylinids, other beetles, and ants, sample-based rarefaction approached the asymptote in treatments and controls (Fig. S.2.1) indicating sampling had effectively captured the composition of these assemblages. However, true bugs were uncommon on, and therefore insufficiently sampled from, deep-cultivated treatments (but approached the asymptote on controls and shallow-cultivated treatments).

Although residuals of the carabid, staphylinid, other beetle, true bug and ant richness and abundance models (both all species and priority species models) were not spatially autocorrelated, residuals from two of the five models considering bird abundance (Northern lapwing and Eurasian curlew) and the priority disturbed-grassland species model (but not the priority undisturbed-grassland species model) were significantly, though again weakly, autocorrelated (Moran's I = 0.05, 0.04, and 0.09, respectively). However, for each affected model, we consider inference of treatment effects to be robust for the reasons explained above. For the priority disturbed-grassland species model, where Moran's I was greatest, removing one particularly abundant species (*Philonthus lepidus*, that comprised 48% of the 471 individuals in this group), removed autocorrelation and gave similar interpretation.

2.3.3 Birds

Of the five species considered, treatment only influenced Northern lapwing abundance (Table S.2.4), with more recorded on shallow-cultivated treatments than controls (with abundance intermediate on deep-cultivated treatments, Fig. 2.2). Vegetation strata influenced woodlark and yellowhammer abundance (but was not important in other models), with fewer woodlarks on young than pooled intermediate, calcareous and ancient-acid grass-heath, and more yellowhammers on ancient-acid than on pooled young, intermediate and calcareous grass-heath (Table S.2.3 and Table S.2.5). Impact-area controls were retained in all analyses, as their inclusion did not affect model inference.

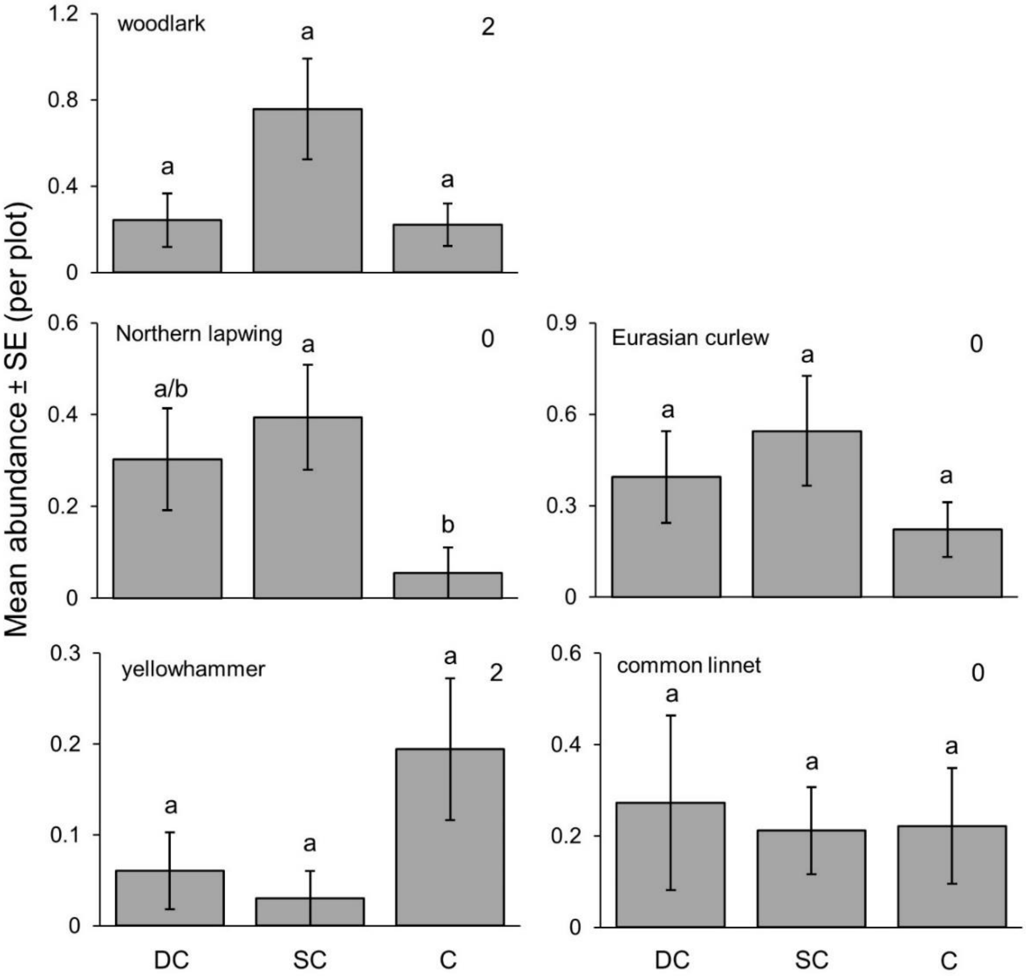

Figure 2.2. Observed mean (± S.E.) abundance of five bird species of conservation concern across deep-cultivated (DC), shallow-cultivated (SC), and control (C) grass-heath plots (*n* = 102). Treatments and controls were compared by Generalized Linear Models, controlling for vegetation strata (panels show the number of categories in each analysis, see Table S.2.3 for identities; '0' indicates vegetation strata is excluded from the model); means that share a superscript (homogenous sub-sets, a – b) did not differ significantly (Tukey pairwise comparisons *p* >0.05). See Table S.2.5 for selected models.

2.3.4 Carabids

For all carabids, richness was greater on shallow-cultivated treatments than deep-cultivated treatments or controls (Fig. 2.3) and was not influenced by vegetation strata (Table S.2.4), while abundance was lower on ancient-acid than pooled young, intermediate and calcareous grass-heath, but was not influenced by treatment (Table S.2.3 and Table S.2.5). For priority carabids, richness and abundance were greater on the controls than deep-cultivated treatments (while shallow-cultivated treatments did not differ from controls, they held a greater abundance than deep-cultivated treatments), and on pooled young, intermediate and calcareous than ancient-acid grass-heath. Assemblage composition of treatments and controls differed along NMDS axis one (but not axis two, Fig. 2.4), with composition contrast relative to controls increasing from shallow to deep-cultivation.

2.3.5 Staphylinids

For all staphylinids, richness and abundance were greater on both treatments than controls (Fig. 2.3), and for abundance only, on young than pooled intermediate, calcareous and ancient-acid grass-heath (Table S.2.5) (though retaining both young and calcareous grass-heath as distinct gave similar models, Table S.2.3). For priority staphylinids, neither treatment nor vegetation strata influenced richness (Table S.2.4), but abundance was again greater on young grass-heath (again retaining young and calcareous grass-heath as distinct gave similar models). Composition of treatments and controls differed along NMDS axis one (but not axis two, Fig. 2.4), with contrast relative to controls again increasing from shallow- to deep-cultivation.

2.3.6 Other beetles

For all other beetles, richness was greater on shallow-cultivated than deep-cultivated treatments or controls (Fig. 2.3), and on pooled young and intermediate than pooled ancient-acid or calcareous grass-heath (Table S.2.3 and Table S.2.5). Abundance was greater on shallow-cultivated than deep-cultivated treatments, but with controls similar to both and no effect of vegetation strata (Table S.2.4). For priority other beetles, richness and abundance were greater on both treatments than controls (vegetation strata were not important). Composition of shallow- and deep-cultivated treatments were similar, but differed from controls along both axes (Fig. 2.4).

2.3.7 True bugs

Richness and abundance of true bugs declined from control to shallow- then deep-cultivation (Fig. 2.3) and was greater on intermediate than pooled young, calcareous, and ancient-acid grass-heath (Table S.2.3 and Table S.2.5). Neither treatment nor vegetation strata influenced the richness or abundance of priority true bugs (Table S.2.4). Composition of treatments differed from controls along NMDS axis one (Fig. 2.4), while on axis two controls and shallow-cultivation differed from deep-cultivation.

2.3.8 Ants

For all ants, richness was greater on both treatments than on controls (Fig. 2.3, Table S.2.5) (vegetation strata were not important, Table S.2.4). Neither treatment nor vegetation strata influenced the richness of priority ants. Composition of shallow- and deep-cultivated treatments were similar, but differed from controls along NMDS axis two (but not axis one, Fig. 2.4).

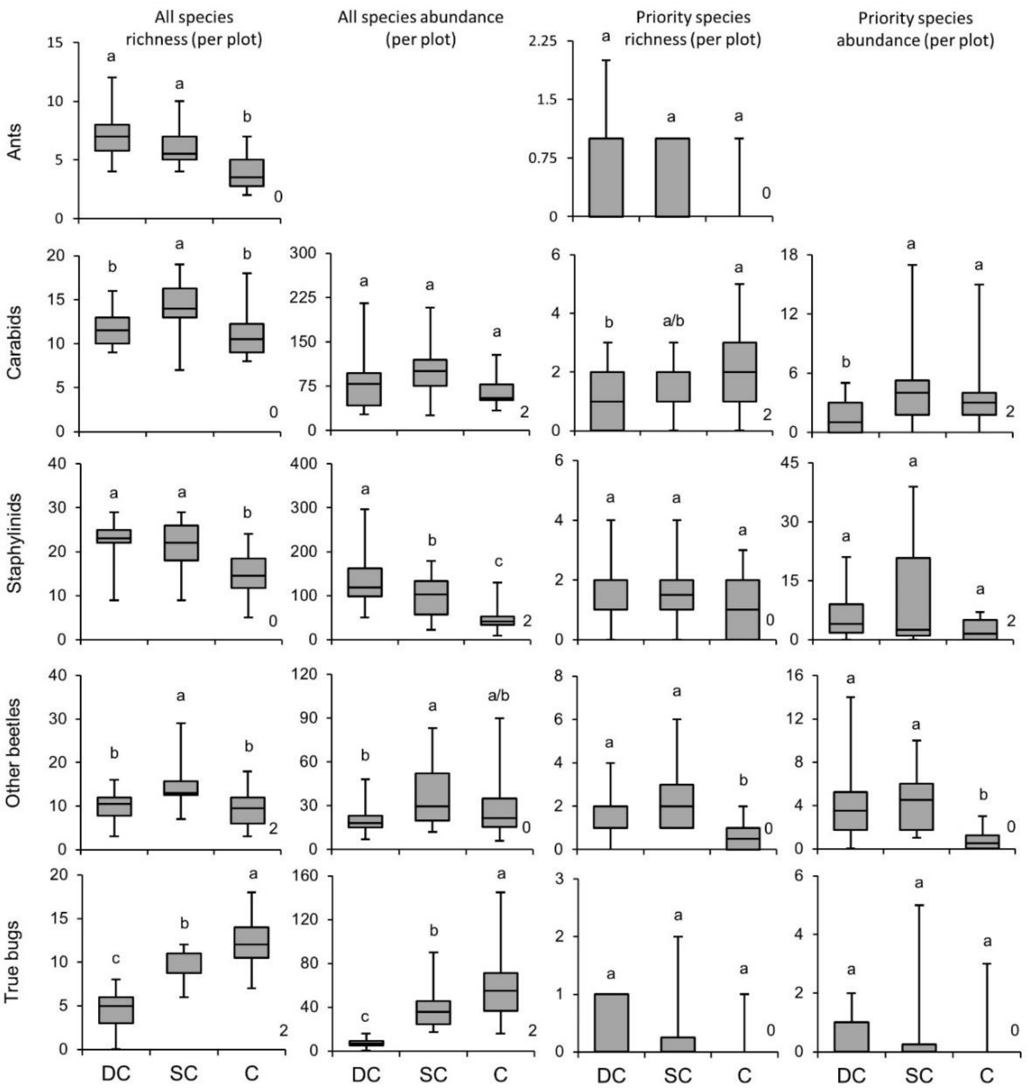

Figure 2.3. Observed richness and abundance of all species or just priority (rare, scarce or threatened) species, separately for each of five invertebrate groups, across deep-cultivated (DC), shallow-cultivated (SC) and control (C) grass-heath plots (*n* = 56). Treatments and controls were compared by Generalized Linear Models controlling for vegetation strata (panels show the number of categories in each analysis, see Table S.2.3 for identities; '0' indicates vegetation strata is excluded from the model); means that share a superscript (homogenous sub-sets, a – c) did not differ significantly (Tukey pairwise comparisons *p* >0.05). Box plots show the median (central line), 25th and 75th percentiles (box) and range (whiskers).

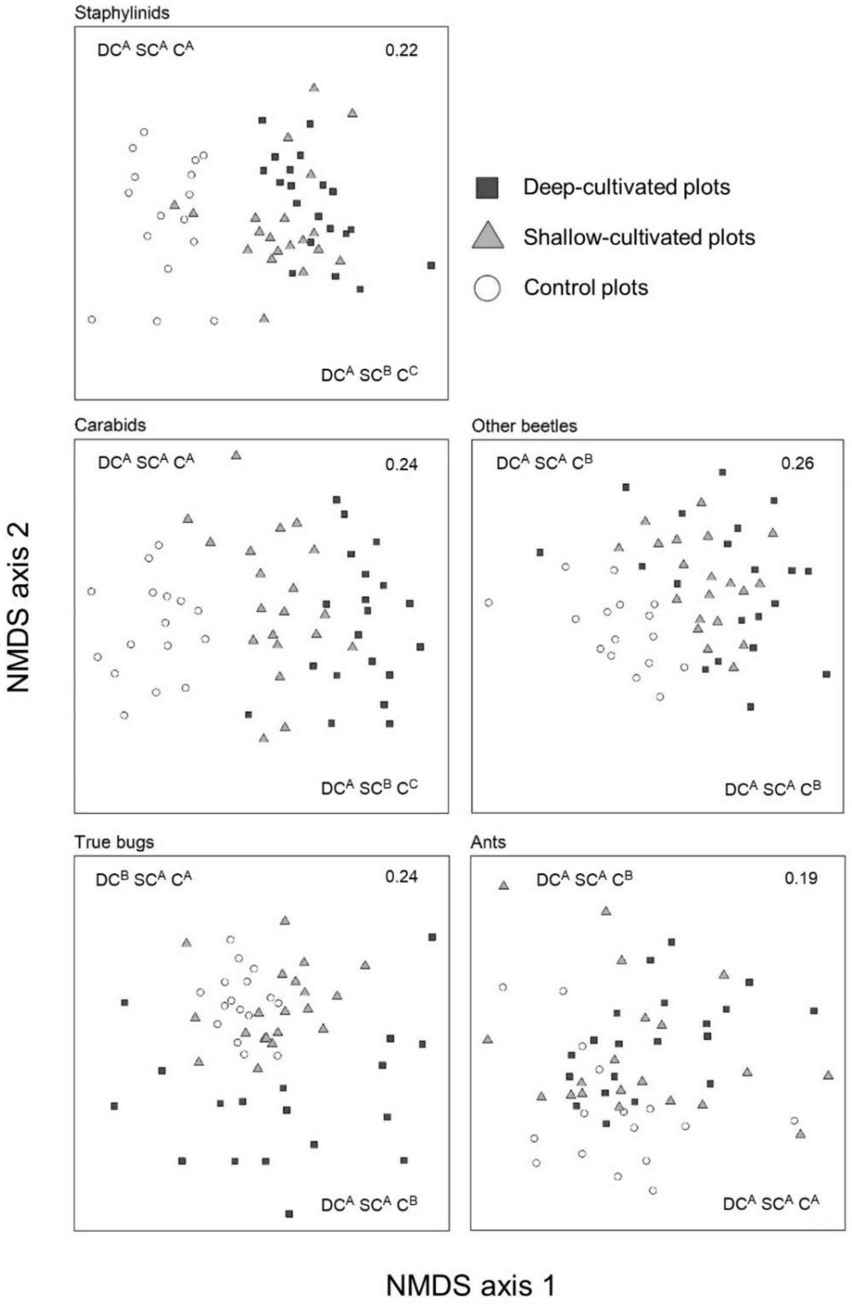

Figure 2.4. Non-metric Multidimensional Scaling (NMDS) ordination for each of five invertebrate groups across deep-cultivated (DC), shallow-cultivated (SC), and control (C) plots (*n* = 56; except for true bugs *n* = 54 as two deep-cultivated plots with fewer than three observations were omitted). Differences between axis scores of treatment and control plots were compared through Kruskal Wallis tests; categories that share a superscript (homogeneous subset, a-c ranked highest to lowest) do not differ significantly (Dunn-Bonferroni pairwise comparisons $p < 0.05$), reported separately for axis 1 (bottom right) and axis 2 (top left) on each. Stress values are shown on each (top right).

2.3.9 Disturbed-grassland and undisturbed-grassland priority invertebrates

Of the 52 priority invertebrate species, 22 (471 individuals) and 19 (287 individuals) were classified as disturbed-grassland and undisturbed-grassland species, respectively (ten were not principally associated with dry-open terrestrial habitats, and for one, insufficient autecological information prohibited classification, see Table S.2.2). Richness of disturbed-grassland species was greater on both treatments than controls, whilst the richness of undisturbed-grassland species was not influenced by treatment (Fig. 2.5). Pooled young, intermediate and calcareous grass-heath held a greater richness of disturbed-grassland and undisturbed-grassland species than ancient-acid grass-heath (Table S.2.5); though disturbed-grassland models which retained intermediate and ancient-acid grass-heath as distinct, or all vegetation strata categories as distinct, were similar (Table S.2.3).

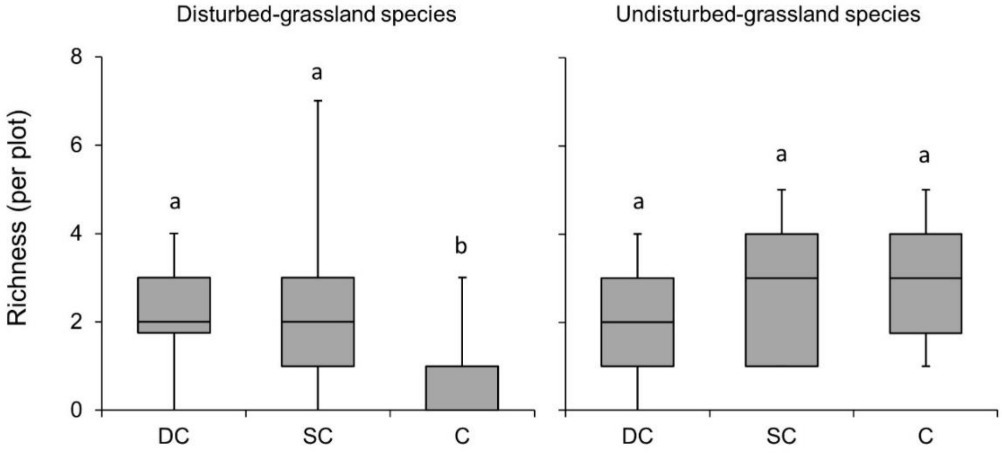

Figure 2.5. Observed cross-taxa richness of priority (rare, scarce or threatened) invertebrate species, shown separately for those associated with disturbed (i.e. physically-disturbed and/or heavily-grazed) grassland or with undisturbed grassland, across deep-cultivated (DC), shallow-cultivated (SC) and control (C) grass-heath plots (*n* = 56). Treatments and controls were compared by Generalized Linear Models controlling for vegetation strata (ancient-acid grass-heath vs pooled young, intermediate and calcareous grassland); means that share a superscript (homogenous sub-sets, a – b) do not differ significantly (Tukey pairwise comparisons *p* >0.05). Box plots show the median (central line), 25th and 75th percentiles (box) and range (whiskers).

2.3.10 Landscape-scale management consequences

Extrapolated rarefaction curves showed that the cumulative richness of other beetles, true bugs, ants, and priority invertebrates (but not of carabids or staphylinids) increased when both treatments were combined with controls (treatment-control landscape), relative to the control-only landscape (Fig. 2.6). Scenarios that re-sampled controls plus only one treatment, or both treatments but not controls (the treatment-only landscape), gave greater cumulative richness of other beetles, ants and priority invertebrates, compared to the control-only landscape, but did not differ from resampling controls plus both treatments. For true bugs, resampling either deep-cultivated and control plots, or a treatment-only landscape, increased cumulative richness relative to the control-only landscape; however resampling shallow-cultivated plus control plots did not. For staphylinids, a treatment-only landscape gave lower cumulative richness than any treatment-control landscape, but not than the control-only landscape.

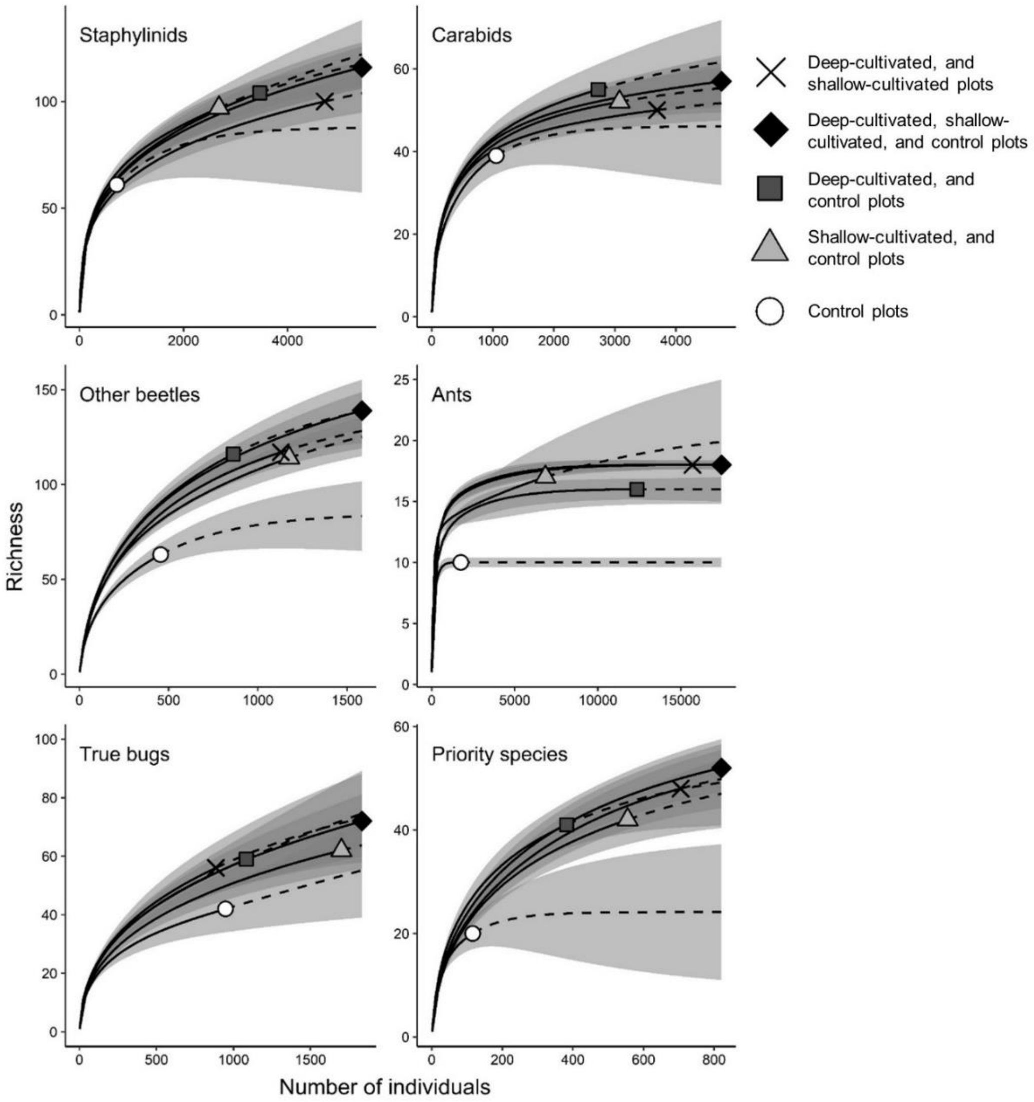

Figure 2.6. Extrapolated rarefaction curves and 95% CI limits for each of five invertebrate groups, and for all priority (rare, scarce or threatened) invertebrate species, for five hypothetical landscapes comprising different combinations of control and treatment plots (see key). Symbols denote observed richness; solid and dashed lines interpolated and extrapolated richness respectively; shading represents 95% CI bounds. Sample-based rarefactions are rescaled to numbers of sampled individuals.

2.4 Discussion

We quantified the multi-taxa consequences of stone-curlew management through a well-replicated landscape-scale experiment making over 200 bird observations and obtaining 30000 invertebrate records. Both treatments, unlike controls, supported suitable stone-curlew nesting habitat, and five treatment plots (four deep-cultivated, one shallow-cultivated, but not controls) were colonized by breeding pairs during this study (2015) (confirmed during avian surveys or additional follow up visits). Whilst staphylinid richness / abundance and ant richness increased with both treatments, and carabid richness, other beetle richness, and Northern lapwing abundance increased with shallow-cultivated treatments (but not deep-cultivated), the richness / abundance of one group (true bugs) declined with both treatments. However, the richness of disturbed-grassland priority invertebrate species (predicted beneficiaries) increased with both treatments, invertebrate assemblage composition differed between treatments and controls for every group, and diversified landscapes with treatments and control plots supported a higher cumulative richness of ants, other beetles, true bugs, and priority invertebrates, than a control-only landscape.

2.4.1 Contrasting taxonomic responses

Treatment only influenced Northern lapwing abundance from the five bird species studied (increased with shallow-cultivation); though woodlark subsequently increased when management was re-applied annually, and was then greater on both treatments than controls (Hawkes, Smart, Brown, Jones & Dolman 2018). Either shallow-cultivation, or both shallow- and deep-cultivation, were associated with increased staphylinid, carabid, other beetle and ant richness, as well as staphylinid abundance, but lower true bug richness and abundance. Consistent with evidence from Swedish semi-natural grasslands, where different taxa have contrasting habitat-process requirements (Vessby, Söderström, Glimskär & Svensson 2002), our results demonstrated that whilst stone-curlew management benefitted some groups, others were disadvantaged. When only priority species were considered, only the richness and abundance of priority carabids (that declined with deep- but not shallow-cultivation) and other beetles (that increased with both treatments) were influenced by treatment. Importantly, just four of the 52 priority species were found exclusively on controls, of which two, *Harpalus pumilus* and

Leiodes longipes, are regarded as NR / RDB. Thus, although the richness / abundance of priority species was similar among treatment and control plots for most groups, few species were lost entirely though treatment.

Invertebrate assemblage composition differed between treatments and controls for all five groups, probably because the open sparsely-vegetated structure created by treatments promoted the warmer micro-climate (Krämer, Kämpf, Enderle, Poniatowski & Fartmann 2012) required by thermophilous species (Cameron & Leather 2011; Pedley, Franco, Pankhurst & Dolman 2013), whilst controls retained the taller vegetation and plant assemblage required by many herbivores (Woodcock & Pywell 2010). Interestingly, this difference increased progressively from control to shallow- then deep-cultivation for carabids, staphylinids and true bugs, consistent with the observed increase in extent of bare ground from controls (largely closed swards), through shallow-cultivation then greatest in deep-cultivation (almost entirely bare) (Fig. 2.1).

Our knowledge that stone-curlew and large numbers of priority species share similar management requirements (informed by Biodiversity Auditing, Dolman *et al.* 2012) provides us with an important justification for regarding the bird as an umbrella species, but establishing whether these species respond as expected is important. In agreement with our *a priori* prediction, the richness of disturbed-grassland priority invertebrates, the predicted beneficiaries, increased with both treatments. It is noteworthy that sampling revealed 22 priority disturbed-grassland species within eight months of treatment establishment, as many of the most range-restricted species within this region are often absent from isolated suitable habitat (Lin, James & Dolman 2006; Bertoncelj & Dolman 2013). We anticipate more disturbed-grassland associated priority species will gradually accrue, as reported for specialist carabids and plants in response to similar ground-disturbance management (Pedley *et al.* 2013).

2.4.2 Consequences of landscape diversification and transformation

Thus far we have examined how birds and invertebrates differed in richness (alpha diversity), abundance and composition between treatments and controls. Whilst this demonstrates the consequences of management, focal-species conservation is rarely implemented across entire landscapes. We were therefore particularly interested in the effects management might have on total species-richness (beta diversity) by diversifying the landscape.

Resampling a hypothetical landscape comprising treatments plus controls, gave greater cumulative richness of ants, other beetles, true bugs and priority invertebrates compared to a control-only landscape. However, the decision to implement either one, or both, treatments did little to influence this outcome in all but one instance (true bug richness did not increase with the addition of shallow-cultivations). This reflects that, although invertebrate assemblage composition tended to be distinctly different between treatments and controls (Fig. 2.4), the two treatments tended to show at least some (carabids) or considerable (other beetles, ants) overlap in composition. Differences between our hypothetical intervention (treatment-only or treatment-control) and non-intervention (control-only) landscapes are consistent with other studies, which show a positive relationship between richness or abundance and landscape heterogeneity (Weibull, Bengtsson & Nohlgren 2000; Smith, Dänhardt, Lindström & Rundlöf 2010). Considering a hypothetical treatment-only landscape lacking any undisturbed grassland gave a greater cumulative richness of ants, other beetles, true bugs and priority invertebrates, than a control-only landscape, but fewer staphylinids than any control-treatment landscape. This suggests that conservation scenarios that diversify but do not entirely replace grasslands through stone-curlew management, would support the most species.

2.4.3 Consequences for Biodiversity conservation of grassland and heath

Lowland heath and dry (chalk, acid or dune) grasslands have distinct assemblages but similar ecological processes (Rodwell 1991; Rodwell 1992); and biodiversity response to management (Dolman *et al.* 2012). In this mosaic of soils (podsol to rendzina) and grass-heath age, vegetation strata influenced woodlark and yellowhammer abundance; carabids, staphylinids, other beetles, and true bugs richness / abundance; and cross-taxa richness of both disturbed and undisturbed-grassland priority species. Crucially, no stratum was consistently better than others, which is unsurprising given grassland invertebrates differ in their habitat preference (Woodcock & Pywell 2010).

Invertebrate assemblage composition consistently differed between treatments and controls, though richness / abundance (alpha diversity, per plot) did not increase for all groups. Focusing on priority invertebrates, just two groups (carabids and other beetles) were influenced by treatment, while for those priority species associated with disturbed-grassland (i.e. predicted beneficiaries) cross-taxa richness increased with both treatments, consistent with our *a priori* prediction. Combining ground-disturbance management with controls increased the cumulative landscape-wide richness (beta-diversity) of most invertebrate groups, and importantly of priority invertebrates across groups. It is on this basis that we conclude that stone-curlew represent a suitable management surrogate within this landscape, and recommend strategies that promote heterogeneity by implementing stone-curlew management, across vegetation strata, whilst also maintaining undisturbed grassland. Further work will investigate whether the immediate benefits observed by this study are retained with follow-up management (e.g. repeat disturbance to maintain open habitats), or whether retaining some plots fallow beyond their suitability for stone-curlew offers different outcomes to broader biodiversity.

2.5 Conclusion

Because the requirements of single species rarely embrace the requirements of all co-occurring biota, the appropriateness of the umbrella species concept has been questioned (e.g. Roberge & Angelstam 2004). However, most tests of efficacy fail to consider the consequences of umbrella species management on other biota; the appropriate appraisal within semi-natural landscapes, where adoption of umbrella species drives interventions beyond site protection (e.g. Thornton *et al.* 2016). Our study demonstrated that appropriate experiments can provide strong evidence to assess both co-beneficiaries and the disadvantaged from umbrella species management. Importantly, responses differed strongly between taxa suggesting that experimental tests of surrogacy must be broad in taxonomic scope. A precautionary approach, to retain areas untreated, is also advised given uncertain responses of unsampled taxonomic groups.

Whilst experiments such as ours provide the best means of assessing umbrella species management efficacy, they are costly and time consuming. Systematically examining autoecological requirements across multiple co-occurring taxa (the ‘Biodiversity Audit Approach’) successfully predicted the beneficiaries of umbrella management in our study and may offer a feasible alternative. Here, we were able to test these *a priori* expectations with an experiment, with both our results and existing autoecological knowledge providing important justification for the widespread adoption of avian conservation management. Similar approaches would be valuable in regions with high concentrations of priority species, especially where management interventions currently focus on a limited, unrepresentative and biased subset of species.

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References

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2017). Linear mixed-effects models using 'Eigen' and S4. *R package Version 1.1-1.5*. Available at: https://cran.r-project.org/web/packages/lme4/ (accessed May 2018).

Bertoncelj, I. & Dolman, P.M. (2013). Conservation potential for heathland carabid beetle fauna of linear trackways within a plantation forest. *Insect Conservation and Diversity,* 6(3), 300-308.

Branton, M. & Richardson, J.S. (2011). Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. *Conservation Biology,* 25(1), 9-20.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York.

Cameron, K.H. & Leather, S.R. (2011). Heathland management effects on carabid beetle communities: the relationship between bare ground patch size and carabid biodiversity. *Journal of Insect Conservation,* 16(4), 523-535.

Caro, T.M. & O'Doherty, G. (1999). On the use of surrogate species in conservation biology. *Conservation Biology,* 13(4), 805-814.

Clark, J.A. & May, R.M. (2002). Taxonomic bias in conservation research. *Science,* 297(5579), 191-192.

Clarke, K.R. & Warwick, R.M. (2001). *Change in marine communities: an approach to statistical analysis and interpretation,* 2nd edn edn. Plymouth Marine Laboratory, Plymouth.

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology,* 49, 986-997.

Eaton, M., Aebischer, N., Brown, A., Hearn, R., Lock, L., Musgrove, A., Noble, D., Stroud, D. & Gregory, R. (2015). Birds of conservation concern 4: the population status of birds in the UK, Channel Islands and Isle of Man. *British Birds,* 108, 708-746.

Fazey, I., Fischer, J. & Lindenmayer, D.B. (2005). What do conservation biologists publish? *Biological Conservation,* 124(1), 63-73.

Fontaine, B., Gargominy, O. & Neubert, E. (2007). Priority sites for conservation of land snails in Gabon: testing the umbrella species concept. *Diversity and Distributions,* 13(6), 725-734.

Green, R.E. & Griffiths, G.H. (1994). Use of preferred nesting habitat by stone curlews Burhinus oedicnemus in relation to vegetation structure. *Journal of Zoology,* 233(3), 457-471.

Green, R.E., Tyler, G.A. & Bowden, C.G.R. (2000). Habitat selection, ranging behaviour and diet of the stone curlew (*Burhinus oedicnemus*) in southern England. *Journal of Zoology,* 250(2), 161-183.

Hawkes, R.W., Smart, J., Brown, A., Jones, H. & Dolman, P.M. (2018). Experimental evidence that ground-disturbance benefits Woodlark *Lullula arborea*. *Ibis,* 161, 447-452.

Hsieh, T., C, Ma, K., H & Chao, A. (2018). Interpolation and extrapolation for species diversity. http://chao.stat.nthu.edu.tw/blog/software-download (accessed July 2018).

Hunter, M., Westgate, M., Barton, P., Calhoun, A., Pierson, J., Tulloch, A., Beger, M., Branquinho, C., Caro, T., Gross, J., Heino, J., Lane, P., Longo, C., Martin, K., McDowell, W.H., Mellin, C., Salo, H. & Lindenmayer, D. (2016). Two roles for ecological surrogacy: indicator surrogates and management surrogates. *Ecological Indicators,* 63, 121-125.

Krämer, B., Kämpf, I., Enderle, J., Poniatowski, D. & Fartmann, T. (2012). Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability. *Journal of Insect Conservation,* 16(6), 857-865.

Lin, Y.-C., James, R. & Dolman, P.M. (2006). Conservation of heathland ground beetles (Coleoptera, Carabidae): the value of lowland coniferous plantations. *Biodiversity and Conservation,* 16(5), 1337.

Maslo, B., Leu, K., Faillace, C., Weston, M.A., Pover, T. & Schlacher, T.A. (2016). Selecting umbrella species for conservation: a test of habitat models and niche overlap for beach-nesting birds. *Biological Conservation,* 203, 233-242.

NSRI (2014). National soil map of England and Wales - NATMAP, 1:250,000 Scale, Cranfield University, Bedfordshire. http://www.landis.org.uk (accessed July 2014).

Oksanen, J., Blanchet, F., G, Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., R, O'Hara, R., B, Simpson, G., L, Solymos, P., Henry, M., Stevens, H., Szoecs, E. & Wagner, H. (2018). Community ecology package version 2.5-2. https://cran.r-project.org/web/packages/vegan/vegan.pdf (accessed July 2018).

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics,* 20(2), 289-290.

Pedley, S.M., Franco, A.M.A., Pankhurst, T. & Dolman, P.M. (2013). Physical disturbance enhances ecological networks for heathland biota: A multiple taxa experiment. *Biological Conservation,* 160, 173-182.

R Core Team (2015). *R: a language and environment for statistical computing. Version 3.2.2*. R Foundation for Statistical Computing, Vienna.

Roberge, J.-M. & Angelstam, P.E.R. (2004). Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology,* 18(1), 76-85.

Rodwell (1991). *British Plant Communities. Volume 2: Mires and Heaths*. Cambridge University Press, Cambridge.

Rodwell (1992). *British Plant Communities. Volume 3: Grasslands and Montane Vegetation*. Cambridge University Press, Cambridge.

Sheail, J. (1979). Documentary evidence of the changes in the use, management and appreciation of the grass-heaths of Breckland. *Journal of Biogeography,* 6(3), 277-292.

Sibarani, M.C., Di Marco, M., Rondinini, C. & Kark, S. (2019). Measuring the surrogacy potential of charismatic megafauna species across taxonomic, phylogenetic and functional diversity on a megadiverse island. *Journal of Applied Ecology,* 56(5), 1220-1231.

Smith, H.G., Dänhardt, J., Lindström, Å. & Rundlöf, M. (2010). Consequences of organic farming and landscape heterogeneity for species richness and abundance of farmland birds. *Oecologia,* 162(4), 1071-1079.

Stanbury, A., Brown, A., Eaton, M., Aebischer, N., Gillings, S., Hearn, R., Noble, D., Stroud, D. & Gregory, R. (2017). The risk of extinction for birds in Great Britain. *British Birds,* 110, 502-517.

Suter, W., Graf, R.F. & Hess, R. (2002). Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conservation Biology,* 16, 778–788.

Thornton, D., Zeller, K., Rondinini, C., Boitani, L., Crooks, K., Burdett, C., Rabinowitz, A. & Quigley, H. (2016). Assessing the umbrella value of a range-wide conservation network for jaguars (*Panthera onca*). *Ecological Applications,* 26(4), 1112-1124.

Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R. & Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports,* 7(7), 9132.

Vessby, K., Söderström, B., Glimskär, A. & Svensson, B. (2002). Species-richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology,* 16(2), 430-439.

Webb, N.R. (1998). The traditional management of European heathlands. *Journal of Applied Ecology,* 35(6), 987-990.

Weibull, A.-C., Bengtsson, J. & Nohlgren, E. (2000). Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography,* 23(6), 743-750.

Woodcock, B.A. & Pywell, R.F. (2010). Effects of vegetation structure and floristic diversity on detritivore, herbivore and predatory invertebrates within calcareous grasslands. *Biodiversity and Conservation,* 19(1), 81-95.

Wright, H.L., Lake, I.R. & Dolman, P.M. (2012). Agriculture—a key element for conservation in the developing world. *Conservation Letters,* 5(1), 11-19.

Chapter 2

Supplementary material

Appendix S.2.1. Stone-curlew management requirements and its predicted impact on priority biota.

Appendix S.2.2. Study area details.

Figure S.2.1. Sample-based rarefaction curves of invertebrate groups for treatment and control plots.

Figure S.2.2. Study area map.

Table S.2.1. Vegetation strata details.

Table S.2.2. (a) sampled invertebrates, and (b) their habitat classification details.

Table S.2.3. Combining vegetation strata categories.

Table S.2.4. Candidate GLM model sets.

Table S.2.5. Coefficients from selected GLM model.

Appendix S.2.1

Eurasian Stone-curlew habitat requirements and conservation

Eurasian stone-curlew (*Burhinus oedicnemus*) (hereafter 'stone-curlew') is a ground-nesting bird species that utilize areas of short vegetation, ruderal or bare stony, chalky or sandy soil (Green, Tyler & Bowden 2000). In the UK, the majority of pairs breed in the Breckland region of Eastern England, where they breed in semi-natural grassland and spring-sown arable farmland, with smaller populations breeding elsewhere in Southern and Eastern England. Although UK populations declined during the 20th century, detailed study of their natural history informed an intensive program of conservation measures (Green *et al.* 2000) that led to a partial population recovery (Johnston 2009). Conservation efforts over this period have focused on interventions to minimize nest and brood loss from arable operations, and the deployment of 1 – 2 ha disturbed 'plots' to create suitable breeding habitat within arable and grassland habitats (Johnston 2009).

On grassland, stone-curlew breed on short vegetation (<2 cm), conditions created and maintained by heavy livestock grazing and/or ground disturbance (Green & Griffiths 1994). On experimental arable split-plots in Southern England, that comprise half managed (1 ha, recently cultivated) and half unmanaged (1 ha, fallow from management undertaken in the previous year) plots, birds almost exclusively nest on half-plots where bare ground cover exceeded 40 % (Green 2013). Given this detailed ecological information, we consider grassland management interventions that reduce vegetation height to <2 cm and create >40 % bare substrate cover to provide suitable nesting habitat for stone-curlew (though other considerations such as the placement of management in the landscape are also important, Clarke, Liley, Sharp & Green 2013).

Predicted impact of stone-curlew management on regional priority biodiversity

Bio-regional Biodiversity Audit of the Breckland region (the location of this study) identified a few focal management guilds (multi-taxa sets of species known or predicted to have shared ecological, process and management requirements) of rare, scarce or threatened species ('priority' species) (Dolman, Panter & Mossman 2012). Here, within 598 priority species found in various dry-terrestrial habitats, lightly or ungrazed habitats, with little/no physical disturbance, support 218 priority species (Panter, Mossman &

Dolman 2013). Supplementing these habitats with disturbance to create suitable stone-curlew habitat, through; heavy grazing, heavy grazing plus ground disturbance, or ground disturbance with little/no grazing, is predicted to provide conditions suitable for an additional 84, 97 and 199 priority species, respectively (collectively 380 additional species; 64% of the 598 species associated with dry-terrestrial habitats). Since much of the remaining grass-heath resource in Breckland is characterized by lightly-grazed grassland without disturbance (Holt, Fuller & Dolman 2010), including our study sites (Appendix S.2.2), we predicted that introducing ground disturbance to provide nesting habitat for stone-curlew will also enhance the richness of these priority disturbance-dependent species (Panter *et al.* 2013)

Appendix S.2.2

Plant assemblages determined by soil and land-use history

The study was carried out across the Stanford Military Training Area (STANTA), Bridgham Heath, and Brettenham Heath National Nature Reserve, in Breckland, Eastern England (Fig. S.2.2). The study sites are designated under the EC Birds Directive (EC 1979) and EC Habitats Directive (EC 1992) as part of the Breckland Special Protection Area (SPA) and Special Area of Conservation (SAC), respectively, to protect internationally important populations of flora and fauna. They are also protected under domestic UK legislation as Sites of Special Scientific Interest (SSSI).

The Breckland biogeographic region has a semi-continental climate, sandy, nutrient-poor soils and a land use history characterised by intensive grazing of grass-heath and warrens (particularly on plateau and interfluves) and arable cultivation with extended fallow periods (Dolman & Sutherland 1992; Dolman *et al.* 2012). Historically, although episodes of arable intakes from grass-heath or reversion of exhausted fields to grazing land occurred through the Medieval period, in response to fluctuation in population density and economies, many grass-heaths were relatively long-lived within the landscape and persisted uncultivated until the 1800s (Holt *et al.* 2010). Thus, some remaining grass-heaths may not have been cultivated for many centuries. Following widespread conversion of grass-heath to arable from the parliamentary enclosures during the 18th and 19th century, subsequent large-scale abandonment of arable (in two main phases, the latter 19th century and then after creation of the military training area in 1942) allowed spontaneous regeneration of fallows that developed into grass-heath of varying age (Farrell 1989). Historic land use records from the Tithe Survey of 1846, the Ordnance Surveys of 1883 and 1904 and the Land Utilization Survey of 1932, document grass-heath age (i.e. time since last cultivation). For the Stanford Training Area (STANTA) these land use records were summarised by Sheail (1979), and for Bridgham and Brettenham Heath these records were held by the Norfolk county Historic Environment team. Both sets of records were subsequently digitized into a Geographic Information System (ESRI 2011) which documented grass-heath age across the three study sites.

Across the study sites the synergistic influences of soil (acidic brown sand, calcareous sand, or rendzina), historic land use and contrasting grass-heath age (young, ≤110 years; intermediate, 111 – 167 years, and ancient ≥168 years), have shaped plant assemblages that span ecological gradients. Composition varies from calcareous grass-heath on shallower rendzina (e.g. *Festuca ovina, Hieracium pillosela, Thymus praecox/pulegioides* calcareous grassland), through assemblages characterized by sporadic presence of calcareous species and more nutrient-demanding species such as *Holcus* spp., creeping thistle (*Cirsium arvense*), and nettle (*Urtica dioica*) predominant on grasslands developed following arable use (including deep ploughing) during 1900-1940; areas of intermediate age cultivated earlier during the 19th century (that were often 'marled' through surface application of chalk rubble to ameliorate soil acidity); through to grass-heath on acidic podzols that were last cultivated before 1845 and typically dominated by wavy hair-grass (*Deschampsia flexuosa*) and heather (*Calluna vulgaris*). Older grass-heath is characterised by an accumulation of organic litter, areas of common gorse (*Ulex europaeus*), or bracken (*Pteridium aquilinum*), and swards dominated by large, mature tussocks of wavy hair-grass (considered indicative of higher nutrient states and a phase shift from oligotrophic dwarf-shrub to nutrient-impacted grass-dominated states; Heil & Diemont 1983; Heil & Bruggink 1987; Rodwell 1992; Diemont 1994). We stratified experimental treatments and controls across, based on these differences in soil type, grass-heath age-class and vegetation composition (Fig. S.2.2), that was confirmed by surveys of indicator plants prior to treatment, considering four vegetation strata: (1) calcareous grass-heath of any age; (2) young grass-heath; (3) intermediate grass-heath; and (4) ancient acid grass-heath (see Table S.2.1 for detailed classification criteria).

Recent land use history across the study area

Generally in western Europe, as well as across Breckland, declines in the habitat quality, biodiversity value, and abundance of species of conservation concern of grass-heath, chalk-heath and dwarf-shrub heath are attributable to synergistic effects of reduced grazing, lack of physical disturbance, biomass accumulation (Webb 1986; Webb 1998) and anthropogenic nutrient deposition. Here, across all three study sites, major land use changes have occurred during the 20th century, which have caused changes in grass-heath composition and structure, with consequences for associated biodiversity. On STANTA (the largest of the three sites), the most significant changes have been: (1) the shift from heavy European rabbit (*Oryctolagus cuniculus*) grazing, following myxomatosis in the mid-20th century and a program of intensive rabbit culling from the 1980s, to a relatively low-density hefted sheep grazing system (approximately one ewe per ha, supported by supplementary feeding), which does not exert the grazing pressure of previous centuries, and (2) the loss of episodic periods of cultivation (the youngest grasslands were 73 years old at the time of this study, Sheail 1979). Formerly STANTA supported populations of bird species that require gravel and or short-sward, including common ringed plover (*Charadrius hiaticula*) and Northern wheatear (*Oenanthe oenanthe*) into the mid-20th century and 1980’s respectively (Dolman & Sutherland 1992). In contrast the grass-heath now supports long-established, relatively high-biomass (roots, litter and above ground vegetation) closed grassland, attributable to these two major landuse changes (Panter *et al.* 2013). Bracken on STANTA is managed annually by mechanical cutting and aerial herbicide application.

Land use changes on Bridgham and Brettenham Heath are similar, though episodic cultivation has been absent on these areas since at least 1846. A period of reduced management, including the near complete loss of sheep grazing during the 1970’s and 1980’s (though pre 1970’s stocking densities was substantially less than previous centuries), allowed scrub to establish across both sites (predominately silver birch, *Betula pendula*, and common hawthorn, *Crataegus monogyna*) with bracken predominant over most of Bridgham (Levett pers. comm. & Sibbett 2007). Since the 1990’s targeted scrub removal has occurred, bracken has been managed annually on Brettenham by mechanical cutting and periodically on Bridgham by herbicide treatment (though on Bridgham Heath herbicide treatment has been replaced by an annual cut since 2010), and sheep grazing has been re-established since 1990 (Bridgham) and 1982

(Brettenham). Like STANTA, Bridgham and Brettenham now support long-established, relatively high-biomass closed grassland. Rabbits are almost absent across both sites apart for a few localized warrens present during this study (2015), but away (at least 200 m) from treatment and control plots.

Relevance of ground disturbance prescriptions to addressing ecological stressors and processes

In terms of micro-habitat and vegetation proxies for conservation value, experimental physical ground-disturbance treatments have been shown to have long-term residual effects reducing biomass (Dolman & Sutherland 1992) and increasing the cover of stress tolerant plant species indicative of low swards and disturbed micro-sites (e.g. winter-annuals, terricolous lichens and acrocarpous mosses) (Dolman & Sutherland 1992; Dolman & Sutherland 1994) suitable for a range of priority (rare, scarce or threatened) species (Dolman *et al.* 2012).

Distribution of priority species in relation to the study area

Although Breckland supports a considerable number of priority species (over 2,000) (Dolman *et al.* 2012), the study area (towards the North-east of Breckland), which is characterized by a more mesic suite of grass heaths, represents a geographically marginal area for priority species (Holt *et al.* 2010). The highest densities of priority species occur within the Southwestern and Western Breckland, where they coincide with high-value calcareous (e.g. Weeting Heath, Dead Mans Graves) or acidic (e.g. Foxhole, Icklingham Plains) grass-heaths; which per equivalent area, contain a greater representation of priority dry-open habitat species than STANTA (Panter *et al.* 2013). Although the reason for such gradients in priority species distribution are probably attributable to a range of ecological, abiotic (particularly climatic) and anthropogenic processes spanning many centuries, it is likely that the shift from open intensively-grazed swards to lightly-grazed closed swards during the latter half of the 20th century across the entire study area also contributed (given our knowledge of species requirements, Appendix S.2.1).

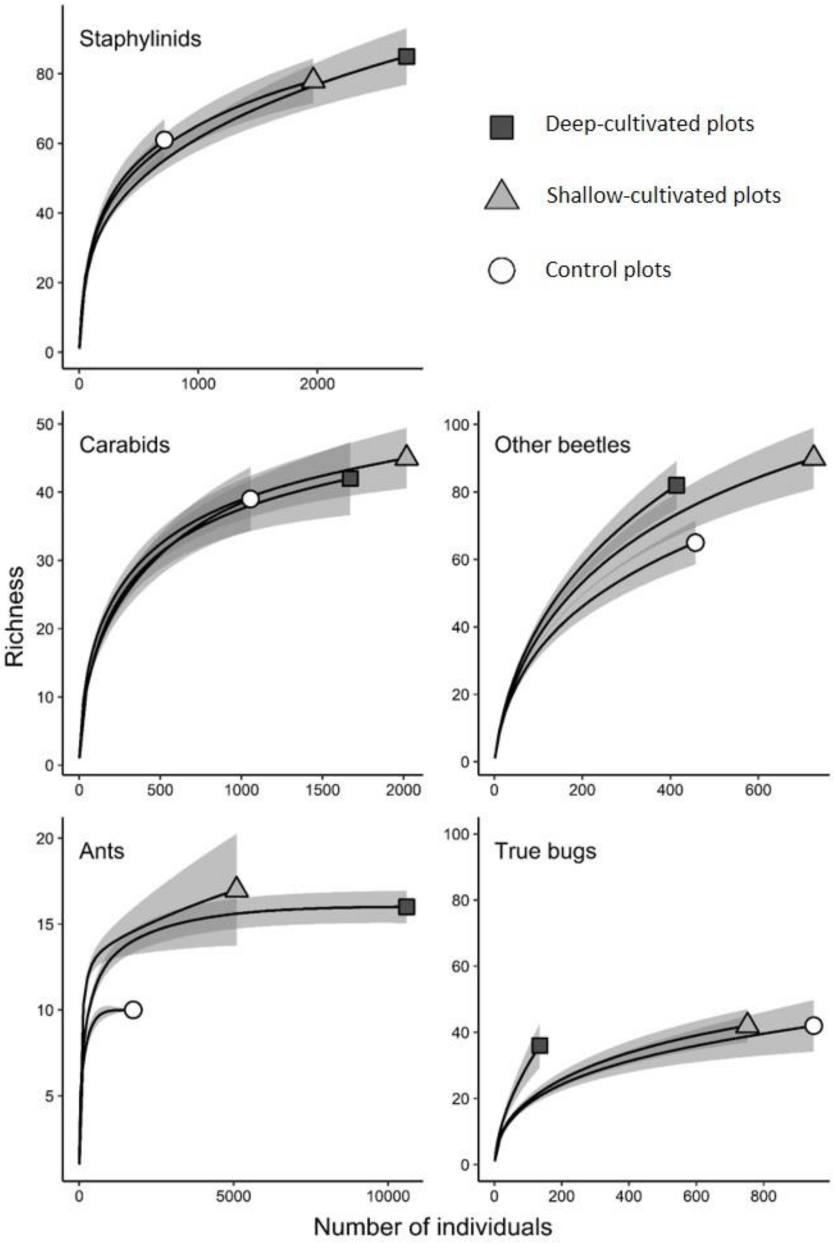

Figure S.2.1. Sample-based rarefaction curves (number of species encountered related to the numbers of individual captured) and 95% CI limits of five invertebrate groups, shown separately for deep-cultivated, shallow-cultivated, and control plots.

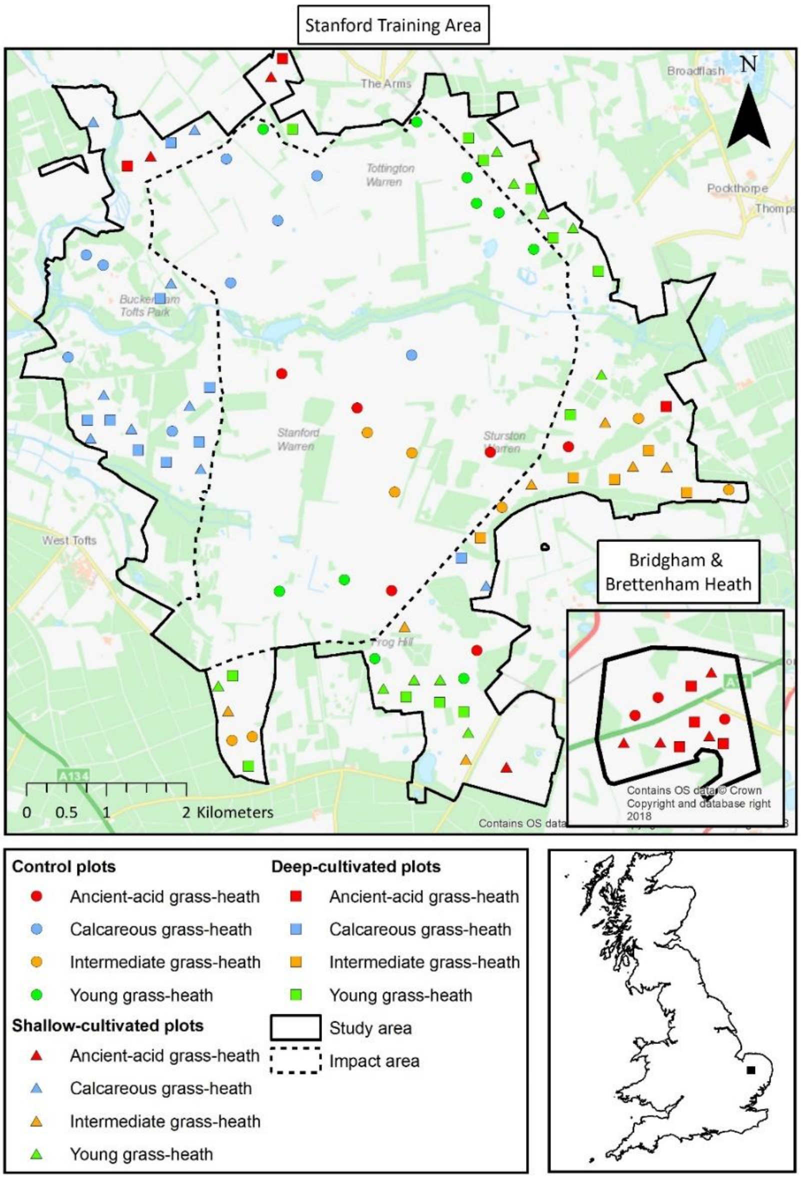

Figure S.2.2. Plot treatment and vegetation strata identity across the study sites (the Stanford Training Area, Bridgham heath and Brettenham Heath) showing the impact area boundary (where physical ground disturbance plots were precluded due to unexploded ordinance). Vegetation strata identity was informed based on soil (NSRI 2014), age since cultivation (for Bridgham Heath and Brettenham Heath, from historic landuse records held by the Norfolk County Council environment team; for the Standford Training Area, from Sheail 1979) and plant composition (see Table S.2.1 for vegetation strata details). Insert shows location of study area.

Table S.2.1. Vegetation strata categories, their definition, and number of replicate ground-disturbance and control plots per strata.

Strata group	Definition[a,b]	Control	Deep-cultivated	Shallow-cultivated
Calcareous grass-heath of any age	Grass-heath of any age (Sheail 1979) located on well-drained brown calcareous sands or rendzinas (soil association codes: 0521 and 0343f, respectively, NSRI 2014)	9	9	9
Young grass-heath	Young grass-heath (arable between 1904-1932, ≤110 years old) located on acidic brown sands (soil association code: 0554b), with evidence of historic soil amelioration through 'marling' (with presence of both acidiphilous, *Calluna vulgaris* (2), *Rumex acetosella* (4), *Galium saxatile* (3), *Teucrium scorodonia* (4); and calcareous, *Thymus* spp. (6 - 8), *Pilosella officinarum* (7), *Galium verum* (6) indicator plants)	10	12	10
Intermediate grass-heath	Mostly intermediate aged grass-heath (arable at 1846 but not by 1904, 111-167 years old, 16 plots), but some ancient grass-heath (no cultivation after 1845, ≥168 years old, 4 plots), located on acidic brown sands, with evidence of historic soil amelioration through 'marling'	8	5	7
Ancient-acid grass-heath	Mostly ancient grass-heath (20 plots), but some intermediate aged grass-heath (3 plots), located on acidic brown sands, with no evidence of historic soil amelioration through marling (infrequent calcareous indicator plants). Two plots were mapped as rendzinas and one plot as deep permeable peaty sands affected by groundwater (soil association code: 0861b); however, their plant community and soil pH were characteristic of this strata (confirmed through indicator plant and soil surveys; Marsden 2017)	9	7	7

[a] Grass-heath ages were based on the Tithe Survey of 1846, the Ordnance Surveys of 1883 and 1904 and the Land Utilization Survey of 1932; for STANTA these were previously overlain and collated by Sheail (1979), a similar approach was taken to classifying age on Brettenham and Bridgham Heaths (see Apendix S.2.2).

[b] Paranethsis, after each indicator plant, give the Ellenberg indicator scores for soil PH (1 = extremely acidic, 5 = mildly acidic, 9 = alkaline, Hill, Preston & Roy 2004)

Table S.2.2(a). Invertebrate species identified in the sampling programme across control (C, *n* = 16), shallow-cultivated (SC, *n* = 20) and deep-cultivated (DC, *n* = 20) plots, showing their status in the UK, habitat classification (for rare, scarce or threatened species, only), frequency (‘occur’, number of plots where the species was recorded), and abundance (‘abun’, summed across all plots).

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Ant	Formicidae	*Formica cunicularia*			0	0	1	29	0	0
Ant	Formicidae	*Formica fusca*			1	6	4	67	5	57
Ant	Formicidae	*Formica lemani*			1	8	2	23	2	33
Ant	Formicidae	*Lasius flavus*			16	589	19	962	20	3000
Ant	Formicidae	*Lasius fuliginosus*			0	0	0	0	4	4
Ant	Formicidae	*Lasius meridionalis*			0	0	1	1	2	2
Ant	Formicidae	*Lasius mixtus*			0	0	2	55	0	0
Ant	Formicidae	*Lasius niger s.s.*			13	453	19	1810	19	2326
Ant	Formicidae	*Lasius psammophilus*			4	122	5	246	10	180
Ant	Formicidae	*Lasius sabularum*			0	0	1	1	1	7
Ant	Formicidae	*Lasius umbratus*			0	0	5	10	9	15
Ant	Formicidae	*Myrmica karavajevi*	RDB3	Undisturbed-grassland	0	0	1	1	3	5
Ant	Formicidae	*Myrmica lobicornis*			4	4	5	39	7	32
Ant	Formicidae	*Myrmica ruginodis*			1	6	13	261	14	184
Ant	Formicidae	*Myrmica sabuleti*			5	25	12	109	15	348
Ant	Formicidae	*Myrmica scabrinodis*			13	528	20	1431	20	4356
Ant	Formicidae	*Myrmica schencki*	Nb	Disturbed-grassland	2	10	5	48	5	21
Ant	Formicidae	*Tetramorium caespitum*			0	0	1	2	3	31
Carabid	Carabidae	*Amara aenea*			4	4	1	1	0	0
Carabid	Carabidae	*Amara communis*			3	3	0	0	0	0
Carabid	Carabidae	*Amara consularis*	NS	Disturbed-grassland	1	1	1	1	1	1

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Carabid	Carabidae	*Amara convexior*			16	216	13	21	4	4
Carabid	Carabidae	*Amara equestris*	NS	Undisturbed-grassland	12	21	6	12	3	3
Carabid	Carabidae	*Amara familiaris*			1	1	0	0	0	0
Carabid	Carabidae	*Amara fulva*	NS	Undisturbed-grassland	0	0	0	0	6	7
Carabid	Carabidae	*Amara lunicollis*			16	405	17	141	14	39
Carabid	Carabidae	*Amara montivaga*	NS	Disturbed-grassland	3	3	0	0	0	0
Carabid	Carabidae	*Amara tibialis*			1	1	3	5	0	0
Carabid	Carabidae	*Badister bullatus*			2	2	1	1	3	4
Carabid	Carabidae	*Bembidion femoratum*			0	0	0	0	7	9
Carabid	Carabidae	*Bembidion lampros*			0	0	7	16	7	14
Carabid	Carabidae	*Bembidion lunulatum*			1	1	0	0	0	0
Carabid	Carabidae	*Bembidion obtusum*			0	0	1	1	0	0
Carabid	Carabidae	*Bembidion properans*			0	0	5	15	5	7
Carabid	Carabidae	*Bembidion quadrimaculatum*			0	0	3	3	6	12
Carabid	Carabidae	*Bradycellus ruficollis*			0	0	1	4	1	1
Carabid	Carabidae	*Calathus ambiguus*	NS	Disturbed-grassland	0	0	2	2	1	4
Carabid	Carabidae	*Calathus cinctus*			0	0	2	2	2	3
Carabid	Carabidae	*Calathus fuscipes*			12	100	20	984	17	647
Carabid	Carabidae	*Calathus melanocephalus*			2	3	12	37	11	41
Carabid	Carabidae	*Carabus nemoralis*			3	3	2	4	1	2
Carabid	Carabidae	*Carabus problematicus*			2	4	7	14	0	0
Carabid	Carabidae	*Carabus violaceus*			3	4	3	4	2	12
Carabid	Carabidae	*Cicindela campestris*			0	0	1	1	1	2
Carabid	Carabidae	*Cychrus caraboides*			1	1	0	0	0	0
Carabid	Carabidae	*Dyschirius politus*	NS	Disturbed-grassland	0	0	0	0	1	1
Carabid	Carabidae	*Harpalus affinis*			0	0	8	8	11	18

Group	Family	Species$^{a\ b}$	Status^{c}	Habitat classification^{d}	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Carabid	Carabidae	*Harpalus latus*			6	15	5	5	3	3
Carabid	Carabidae	*Harpalus pumilus*	NR	Disturbed-grassland	1	1	0	0	0	0
Carabid	Carabidae	*Harpalus rubripes*			1	1	4	6	4	5
Carabid	Carabidae	*Harpalus rufipalpis*			4	7	3	23	3	22
Carabid	Carabidae	*Harpalus rufipes*			9	13	16	31	12	20
Carabid	Carabidae	*Harpalus tardus*			10	15	9	19	7	11
Carabid	Carabidae	*Laemostenus terricola*			1	2	1	1	1	1
Carabid	Carabidae	*Leistus terminatus*			0	0	1	1	0	0
Carabid	Carabidae	*Licinus depressus*	NS	Undisturbed-grassland	7	10	3	3	1	1
Carabid	Carabidae	*Loricera pilicornis*			1	1	1	2	0	0
Carabid	Carabidae	*Microlestes minutulus*			0	0	6	15	1	1
Carabid	Carabidae	*Nebria brevicollis*			4	8	18	99	16	165
Carabid	Carabidae	*Nebria salina*			1	2	17	118	20	380
Carabid	Carabidae	*Notiophilus aquaticus*			2	2	5	6	0	0
Carabid	Carabidae	*Notiophilus biguttatus*			0	0	4	4	4	4
Carabid	Carabidae	*Notiophilus substriatus*			1	1	0	0	0	0
Carabid	Carabidae	*Ophonus laticollis*	NS	Disturbed-grassland	0	0	0	0	1	1
Carabid	Carabidae	*Ophonus rufibarbis*			0	0	0	0	1	1
Carabid	Carabidae	*Panagaeus bipustulatus*	NS	Undisturbed-grassland	2	2	1	1	0	0
Carabid	Carabidae	*Poecilus versicolor*			12	71	9	63	3	3
Carabid	Carabidae	*Pterostichus madidus*			13	77	14	97	14	129
Carabid	Carabidae	*Pterostichus melanarius*			3	4	3	4	2	7
Carabid	Carabidae	*Pterostichus niger*			1	1	1	1	1	1
Carabid	Carabidae	*Stomis pumicatus*			2	2	3	7	2	3
Carabid	Carabidae	*Syntomus foveatus*			8	31	13	141	5	9
Carabid	Carabidae	*Syntomus truncatellus*	NS	Undisturbed-grassland	7	15	13	71	7	12

Group	Family	Species$^{a\ b}$	Status^{c}	Habitat classification^{d}	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Carabid	Carabidae	*Synuchus vivalis*			2	2	3	3	3	3
Carabid	Carabidae	*Trechus quadristriatus*			0	0	7	10	18	58
Other beetle	Apionidae	*Apion cruentatum*			0	0	1	1	0	0
Other beetle	Apionidae	*Apion haematodes*			0	0	1	1	2	4
Other beetle	Apionidae	*Catapion pubescens*	Nb	Disturbed-grassland	0	0	0	0	1	1
Other beetle	Apionidae	*Exapion ulicis*			0	0	0	0	1	1
Other beetle	Apionidae	*Holotrichapion pisi*			0	0	1	1	0	0
Other beetle	Apionidae	*Perapion marchicum*			0	0	1	1	0	0
Other beetle	Buprestidae	*Aphanisticus pusillus*	NS	Undisturbed-grassland	2	2	3	3	0	0
Other beetle	Byrrhidae	*Byrrhus arietinus*	Nb	Other habitat	0	0	1	1	0	0
Other beetle	Byrrhidae	*Byrrhus fasciatus*			0	0	2	2	0	0
Other beetle	Byrrhidae	*Byrrhus pilula*			2	5	4	6	1	1
Other beetle	Byrrhidae	*Byrrhus pustulatus*			0	0	1	1	0	0
Other beetle	Byrrhidae	*Curimopsis maritima*			0	0	3	3	2	2
Other beetle	Byrrhidae	*Simplocaria semistriata*			0	0	1	1	0	0
Other beetle	Cantharidae	*Cantharis rustica*			9	20	3	3	1	1
Other beetle	Chrysomelidae	*Apteropeda orbiculata*			0	0	0	0	2	2
Other beetle	Chrysomelidae	*Chaetocnema concinna*			0	0	0	0	1	2
Other beetle	Chrysomelidae	*Chaetocnema hortensis*			0	0	11	48	3	5
Other beetle	Chrysomelidae	*Chrysolina marginata*	NR	Disturbed-grassland	0	0	1	1	0	0
Other beetle	Chrysomelidae	*Cryptocephalus fulvus*			1	1	3	5	0	0
Other beetle	Chrysomelidae	*Cryptocephalus pusillus*			0	0	0	0	1	1
Other beetle	Chrysomelidae	*Galeruca tanaceti*			11	35	3	10	4	6
Other beetle	Chrysomelidae	*Longitarsus jacobaeae*			1	7	2	2	0	0
Other beetle	Chrysomelidae	*Longitarsus luridus*			0	0	0	0	1	1
Other beetle	Chrysomelidae	*Longitarsus parvulus*			0	0	3	3	3	3

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Other beetle	Chrysomelidae	*Longitarsus pratensis*			2	2	9	48	1	1
Other beetle	Chrysomelidae	*Longitarsus succineus*			0	0	1	1	3	3
Other beetle	Chrysomelidae	*Neocrepidodera ferruginea*			0	0	0	0	1	2
Other beetle	Chrysomelidae	*Phyllotreta nigripes*			0	0	0	0	5	10
Other beetle	Chrysomelidae	*Phyllotreta nodicornis*			0	0	0	0	1	3
Other beetle	Chrysomelidae	*Psylliodes chrysocephala*			2	2	0	0	1	1
Other beetle	Chrysomelidae	*Sermylassa halensis*			2	3	1	2	1	2
Other beetle	Chrysomelidae	*Sphaeroderma testaceum*			0	0	1	1	2	2
Other beetle	Coccinellidae	*Coccinella septempunctata*			1	1	11	22	8	19
Other beetle	Coccinellidae	*Hippodamia variegata*	Nb	Disturbed-grassland	0	0	11	33	10	21
Other beetle	Coccinellidae	*Nephus redtenbacheri*			0	0	0	0	1	1
Other beetle	Coccinellidae	*Scymnus frontalis*			0	0	2	2	1	1
Other beetle	Coccinellidae	*Subcoccinella vigintiquatuorpunctata*			0	0	1	1	0	0
Other beetle	Coccinellidae	*Tytthaspis sedecimpunctata*			1	1	2	2	1	1
Other beetle	Cryptophagidae	*Atomaria fuscata*			0	0	1	1	2	4
Other beetle	Cryptophagidae	*Atomaria linearis*			0	0	14	32	8	21
Other beetle	Cryptophagidae	*Atomaria testacea*			0	0	4	4	0	0
Other beetle	Curculionidae	*Acalles ptinoides*	Nb	Other habitat	0	0	2	8	2	5
Other beetle	Curculionidae	*Cathormiocerus aristatus*	Nb	Disturbed-grassland	0	0	3	6	0	0
Other beetle	Curculionidae	*Ceutorhynchus pallidactylus*			0	0	0	0	1	1
Other beetle	Curculionidae	*Euophryum confine*			0	0	1	1	1	1
Other beetle	Curculionidae	*Hypera diversipunctata*	RDB3	Other habitat	0	0	2	2	0	0
Other beetle	Curculionidae	*Hypera plantaginis*			0	0	2	2	0	0
Other beetle	Curculionidae	*Hypera pollux*			1	2	0	0	0	0
Other beetle	Curculionidae	*Hypera zoilus*			1	1	6	10	0	0
Other beetle	Curculionidae	*Neliocarus faber*	Nb	Disturbed-grassland	1	1	9	9	5	6

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Other beetle	Curculionidae	*Otiorhynchus ovatus*			6	8	6	17	5	8
Other beetle	Curculionidae	*Otiorhynchus singularis*			0	0	0	0	2	2
Other beetle	Curculionidae	*Philopedon plagiatum*			1	1	1	1	3	3
Other beetle	Curculionidae	*Phyllobius virideaeris*			0	0	1	1	2	5
Other beetle	Curculionidae	*Phyllobius viridicollis*			0	0	0	0	1	1
Other beetle	Curculionidae	*Rhinoncus castor*			0	0	10	14	8	55
Other beetle	Curculionidae	*Romualdius angustisetulus*			0	0	1	1	1	1
Other beetle	Curculionidae	*Romualdius bifoveolatus*			3	4	1	3	1	4
Other beetle	Curculionidae	*Sciaphilus asperatus*			0	0	1	1	0	0
Other beetle	Curculionidae	*Sitona hispidulus*			0	0	7	8	0	0
Other beetle	Curculionidae	*Sitona humeralis*			0	0	3	3	1	1
Other beetle	Curculionidae	*Sitona lepidus*			0	0	6	10	1	1
Other beetle	Curculionidae	*Sitona lineatus*			0	0	2	2	2	2
Other beetle	Curculionidae	*Strophosoma melanogrammum*			0	0	0	0	1	1
Other beetle	Curculionidae	*Trachyphloeus scabricul*			8	58	13	180	11	40
Other beetle	Curculionidae	*Trichosirocalus troglodytes*			0	0	2	3	0	0
Other beetle	Curculionidae	*Tychius junceus*			0	0	2	2	1	1
Other beetle	Curculionidae	*Tychius picirostris*			0	0	1	1	0	0
Other beetle	Elateridae	*Adrastus pallens*			1	1	0	0	0	0
Other beetle	Elateridae	*Agriotes obscurus*			6	15	6	14	4	5
Other beetle	Elateridae	*Agriotes pallidulus*			0	0	0	0	2	2
Other beetle	Elateridae	*Agriotes sputator*			5	8	5	13	2	5
Other beetle	Elateridae	*Agrypnus murinus*			12	59	10	26	10	21
Other beetle	Elateridae	*Athous haemorrhoidalis*			3	8	3	4	0	0
Other beetle	Elateridae	*Dalopius marginatus*			0	0	0	0	1	1
Other beetle	Elateridae	*Prosternon tessellatum*			11	48	3	3	1	1

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Other beetle	Elateridae	*Selatosomus aeneus*			1	5	2	2	0	0
Other beetle	Geotrupidae	*Anoplotrupes stercorosus*			0	0	1	9	0	0
Other beetle	Geotrupidae	*Geotrupes spiniger*			1	11	0	0	0	0
Other beetle	Geotrupidae	*Typhaeus typhoeus*			1	4	1	3	3	3
Other beetle	Helophoridae	*Helophorus rufipes*			0	0	0	0	1	1
Other beetle	Histeridae	*Kissister minimus*			1	1	5	28	3	8
Other beetle	Histeridae	*Margarinotus purpurascens*			0	0	0	0	1	1
Other beetle	Histeridae	*Onthophilus punctatus*	NR	Other habitat	0	0	1	1	1	1
Other beetle	Histeridae	*Saprinus aeneus*	NS	Undisturbed-grassland	2	4	0	0	0	0
Other beetle	Hydrophilidae	*Cercyon impressus*			1	1	0	0	0	0
Other beetle	Hydrophilidae	*Cercyon lateralis*			1	1	0	0	0	0
Other beetle	Hydrophilidae	*Cercyon pygmaeus*			1	6	0	0	0	0
Other beetle	Hydrophilidae	*Cryptopleurum minutum*			1	2	0	0	0	0
Other beetle	Hydrophilidae	*Megasternum concinnum*			3	4	3	3	0	0
Other beetle	Hydrophilidae	*Megasternum immaculatum*			0	0	1	1	0	0
Other beetle	Hydrophilidae	*Sphaeridium lunatum*			1	1	0	0	0	0
Other beetle	Kateretidae	*Brachypterus urticae*			1	1	0	0	0	0
Other beetle	Latridiidae	*Corticaria impressa*			0	0	1	1	0	0
Other beetle	Latridiidae	*Corticarina minuta*			0	0	5	7	4	15
Other beetle	Latridiidae	*Cortinicara gibbosa*			1	1	0	0	0	0
Other beetle	Latridiidae	*Enicmus transversus*			1	1	1	1	0	0
Other beetle	Leiodidae	*Agathidium convexum*			0	0	0	0	1	1
Other beetle	Leiodidae	*Agathidium laevigatum*			2	2	3	5	0	0
Other beetle	Leiodidae	*Agathidium marginatum*	Notable	Undisturbed-grassland	4	5	2	2	0	0
Other beetle	Leiodidae	*Catops grandicollis*			1	1	0	0	0	0
Other beetle	Leiodidae	*Catops nigricans*			2	2	0	0	1	1

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Other beetle	Leiodidae	*Choleva angustata*			0	0	3	4	1	1
Other beetle	Leiodidae	*Choleva jeanneli*			1	2	0	0	0	0
Other beetle	Leiodidae	*Hydnobius punctatus*	Notable	Unknown	0	0	1	1	0	0
Other beetle	Leiodidae	*Leiodes longipes*	RDBI	Undisturbed-grassland	1	1	0	0	0	0
Other beetle	Leiodidae	*Liocyrtusa vittata*			0	0	1	1	1	1
Other beetle	Leiodidae	*Ptomaphagus subvillosus*			1	1	0	0	0	0
Other beetle	Leiodidae	*Sciodrepoides watsoni*			1	1	0	0	1	1
Other beetle	Mordellidae	*Mordellistena parvula*	NS	Undisturbed-grassland	0	0	1	2	0	0
Other beetle	Phalacridae	*Olibrus corticalis*			0	0	0	0	1	1
Other beetle	Scarabaeidae	*Aphodius ater*			1	2	0	0	0	0
Other beetle	Scarabaeidae	*Aphodius coenosus*	NS	Undisturbed-grassland	0	0	1	1	1	1
Other beetle	Scarabaeidae	*Aphodius contaminatus*			0	0	1	1	2	2
Other beetle	Scarabaeidae	*Aphodius depressus*			1	6	0	0	0	0
Other beetle	Scarabaeidae	*Aphodius distinctus*	NS	Undisturbed-grassland	0	0	9	15	3	5
Other beetle	Scarabaeidae	*Aphodius erraticus*			1	2	0	0	0	0
Other beetle	Scarabaeidae	*Aphodius haemorrhoidalis*			1	3	2	3	1	1
Other beetle	Scarabaeidae	*Aphodius ictericus*	NS	Undisturbed-grassland	0	0	1	3	4	9
Other beetle	Scarabaeidae	*Aphodius prodromus*			2	2	4	4	2	2
Other beetle	Scarabaeidae	*Aphodius rufipes*			1	1	0	0	0	0
Other beetle	Scarabaeidae	*Aphodius rufus*			1	7	0	0	0	0
Other beetle	Scarabaeidae	*Aphodius sphacelatus*			1	1	1	1	0	0
Other beetle	Scarabaeidae	*Aphodius sticticus*			0	0	1	1	0	0
Other beetle	Scarabaeidae	*Euheptaulacus villosus*	NS	Disturbed-grassland	0	0	0	0	7	32
Other beetle	Scarabaeidae	*Omaloplia ruricola*	NS	Undisturbed-grassland	0	0	0	0	2	2
Other beetle	Scarabaeidae	*Onthophagus joannae*			2	5	3	5	2	2
Other beetle	Scarabaeidae	*Onthophagus similis*			5	38	2	3	0	0

Group	Family	Species$^{a\ b}$	Status^{c}	Habitat classification^{d}	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Other beetle	Scarabaeidae	*Phyllopertha horticola*			6	13	4	15	3	8
Other beetle	Scraptiidae	*Anaspis maculata*			0	0	0	0	1	1
Other beetle	Scydmaenidae	*Neuraphes angulatus*			0	0	1	1	1	2
Other beetle	Scydmaenidae	*Stenichnus collaris*			1	1	3	4	1	1
Other beetle	Scydmaenidae	*Stenichnus scutellaris*			1	1	3	4	2	6
Other beetle	Silphidae	*Silpha atrata*			2	2	0	0	0	0
Other beetle	Silphidae	*Silpha tristis*			2	11	2	2	0	0
Other beetle	Silphidae	*Thanatophilus sinuatus*			0	0	0	0	1	1
Other beetle	Tenebrionidae	*Cteniopus sulphureus*			1	1	0	0	0	0
Other beetle	Tenebrionidae	*Isomira murina*			4	8	0	0	1	2
Other beetle	Tenebrionidae	*Melanimon tibialis*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Acrotona exigua*			4	4	9	103	7	384
Staphylinid	Staphylinidae	*Acrotona muscorum*			2	7	10	24	7	21
Staphylinid	Staphylinidae	*Aleochara bipustulata*			0	0	17	90	14	44
Staphylinid	Staphylinidae	*Aleochara intricata*			3	6	0	0	0	0
Staphylinid	Staphylinidae	*Aleochara lanuginosa*			1	1	0	0	0	0
Staphylinid	Staphylinidae	*Aleochara spadicea*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Alevonota gracilenta*	RDB	Undisturbed-grassland	2	2	3	3	1	1
Staphylinid	Staphylinidae	*Aloconota gregaria*			0	0	7	11	17	36
Staphylinid	Staphylinidae	*Amischa analis*			13	72	18	106	16	54
Staphylinid	Staphylinidae	*Amischa decipiens*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Amischa nigrofusca*			0	0	3	3	2	2
Staphylinid	Staphylinidae	*Anotylus insecatus*	Notable	Other habitat	0	0	0	0	1	1
Staphylinid	Staphylinidae	*Anotylus nitidulus*			1	1	6	7	14	51
Staphylinid	Staphylinidae	*Anotylus rugosus*			0	0	14	30	14	35
Staphylinid	Staphylinidae	*Anotylus sculpturatus*			0	0	4	7	5	5

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Staphylinid	Staphylinidae	*Anthobium unicolor*			0	0	1	1	0	0
Staphylinid	Staphylinidae	*Atheta xanthopus*			1	1	0	0	1	1
Staphylinid	Staphylinidae	*Badura macrocera*			1	5	0	0	1	1
Staphylinid	Staphylinidae	*Bledius opacus*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Bolitobius castaneus*			2	4	0	0	0	0
Staphylinid	Staphylinidae	*Chaetida longicornis*			1	1	0	0	0	0
Staphylinid	Staphylinidae	*Datomicra canescens*			0	0	2	2	1	1
Staphylinid	Staphylinidae	*Dinaraea angustula*			0	0	3	5	5	40
Staphylinid	Staphylinidae	*Drusilla canaliculata*			10	93	11	143	12	183
Staphylinid	Staphylinidae	*Falagrioma thoracica*			1	7	0	0	2	4
Staphylinid	Staphylinidae	*Gabrius appendiculatus*			0	0	1	1	0	0
Staphylinid	Staphylinidae	*Gabrius nigritulus*			0	0	2	3	2	2
Staphylinid	Staphylinidae	*Gabrius osseticus*	Nb	Other habitat	5	7	3	3	10	22
Staphylinid	Staphylinidae	*Geostiba circellaris*			1	1	2	2	1	9
Staphylinid	Staphylinidae	*Gyrohypnus angustatus*			0	0	8	14	8	12
Staphylinid	Staphylinidae	*Heterothops dissimilis*	RDBK	Other habitat	1	1	3	3	1	1
Staphylinid	Staphylinidae	*Ischnosoma splendidum*			9	38	8	26	3	3
Staphylinid	Staphylinidae	*Lamprinodes saginatus*			5	8	2	3	3	3
Staphylinid	Staphylinidae	*Lathrobium fulvipenne*			0	0	1	1	0	0
Staphylinid	Staphylinidae	*Lesteva longoelytrata*			0	0	0	0	2	2
Staphylinid	Staphylinidae	*Liogluta alpestris*			3	3	18	81	18	170
Staphylinid	Staphylinidae	*Liogluta longiuscula*			0	0	0	0	1	2
Staphylinid	Staphylinidae	*Lobrathium multipunctum*			1	1	2	3	5	8
Staphylinid	Staphylinidae	*Medon castaneus*	RDBI	Other habitat	0	0	1	1	1	1
Staphylinid	Staphylinidae	*Megalinus glabratus*			0	0	1	1	0	0
Staphylinid	Staphylinidae	*Metopsia clypeata*			0	0	1	1	0	0

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Staphylinid	Staphylinidae	*Microdota amicula*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Microdota minuscula*			0	0	1	1	0	0
Staphylinid	Staphylinidae	*Micropeplus staphylinoides*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Mycetoporus angularis*			1	1	0	0	0	0
Staphylinid	Staphylinidae	*Mycetoporus clavicornis*			0	0	0	0	2	2
Staphylinid	Staphylinidae	*Mycetoporus lepidus*			2	7	4	25	5	51
Staphylinid	Staphylinidae	*Mycetoporus piceolus*	NS	Disturbed-grassland	0	0	0	0	1	1
Staphylinid	Staphylinidae	*Mycetoporus punctus*			2	2	0	0	0	0
Staphylinid	Staphylinidae	*Mycetoporus rufescens*			2	2	0	0	0	0
Staphylinid	Staphylinidae	*Nehemitropia lividipennis*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Ochthephilum fracticorne*			0	0	1	1	1	1
Staphylinid	Staphylinidae	*Ocypus aeneocephalus*			15	97	18	233	14	68
Staphylinid	Staphylinidae	*Ocypus brunnipes*			0	0	10	12	6	16
Staphylinid	Staphylinidae	*Ocypus olens*			6	28	15	78	16	124
Staphylinid	Staphylinidae	*Olophrum piceum*			0	0	1	1	1	1
Staphylinid	Staphylinidae	*Omalium caesum*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Ontholestes murinus*			1	1	0	0	0	0
Staphylinid	Staphylinidae	*Othius angustus*			8	13	9	28	18	357
Staphylinid	Staphylinidae	*Othius laeviusculus*			1	3	15	64	5	13
Staphylinid	Staphylinidae	*Othius subuliformis*			0	0	4	7	12	21
Staphylinid	Staphylinidae	*Ousipalia caesula*			0	0	0	0	1	4
Staphylinid	Staphylinidae	*Oxypoda brachyptera*			0	0	3	3	2	2
Staphylinid	Staphylinidae	*Oxypoda brevicornis*			0	0	3	3	2	2
Staphylinid	Staphylinidae	*Oxypoda ferruginea*			3	4	4	16	9	63
Staphylinid	Staphylinidae	*Oxypoda vittata*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Oxytelus laqueatus*			1	1	0	0	0	0

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Staphylinid	Staphylinidae	*Pella limbata*			3	14	5	13	8	30
Staphylinid	Staphylinidae	*Philhygra malleus*			1	1	0	0	0	0
Staphylinid	Staphylinidae	*Philhygra palustris*			1	1	4	9	5	6
Staphylinid	Staphylinidae	*Philonthus carbonarius*			9	20	7	21	2	2
Staphylinid	Staphylinidae	*Philonthus cognatus*			0	0	1	1	1	1
Staphylinid	Staphylinidae	*Philonthus concinnus*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Philonthus cruentatus*			1	1	0	0	0	0
Staphylinid	Staphylinidae	*Philonthus debilis*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Philonthus lepidus*	RDBK	Disturbed-grassland	3	7	8	160	5	58
Staphylinid	Staphylinidae	*Philonthus varians*			1	1	0	0	0	0
Staphylinid	Staphylinidae	*Phloeocharis subtilissima*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Platydracus stercorarius*			15	56	9	21	4	9
Staphylinid	Staphylinidae	*Platystethus arenarius*			1	1	0	0	0	0
Staphylinid	Staphylinidae	*Proteinus ovalis*			0	0	0	0	2	2
Staphylinid	Staphylinidae	*Pselaphus heisei*			0	0	1	2	0	0
Staphylinid	Staphylinidae	*Quedius boops*			2	2	2	2	3	4
Staphylinid	Staphylinidae	*Quedius cinctus*			0	0	0	0	1	1
Staphylinid	Staphylinidae	*Quedius levicollis*			5	7	12	28	13	20
Staphylinid	Staphylinidae	*Quedius nigriceps*			0	0	1	1	0	0
Staphylinid	Staphylinidae	*Quedius nigrocaeruleus*	Nb	Other habitat	0	0	2	2	0	0
Staphylinid	Staphylinidae	*Quedius persimilis*			5	9	2	2	6	8
Staphylinid	Staphylinidae	*Quedius schatzmayri*			1	1	0	0	0	0
Staphylinid	Staphylinidae	*Quedius semiaeneus*			0	0	14	63	7	29
Staphylinid	Staphylinidae	*Quedius semiobscurus*			9	14	12	29	15	36
Staphylinid	Staphylinidae	*Rugilus erichsonii*			3	5	4	7	0	0
Staphylinid	Staphylinidae	*Sepedophilus marshami*			0	0	1	1	0	0

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
Staphylinid	Staphylinidae	*Sepedophilus nigripennis*			3	3	1	2	1	2
Staphylinid	Staphylinidae	*Stenus brunnipes*			3	5	2	2	3	3
Staphylinid	Staphylinidae	*Stenus clavicornis*			0	0	1	1	4	7
Staphylinid	Staphylinidae	*Stenus nanus*			0	0	1	3	0	0
Staphylinid	Staphylinidae	*Stenus ochropus*			0	0	1	1	1	2
Staphylinid	Staphylinidae	*Sunius melanocephalus*	Notable	Undisturbed-grassland	6	13	6	13	11	29
Staphylinid	Staphylinidae	*Sunius propinquus*			0	0	1	1	0	0
Staphylinid	Staphylinidae	*Tachyporus atriceps*			2	4	1	2	1	1
Staphylinid	Staphylinidae	*Tachyporus dispar*			3	9	1	1	0	0
Staphylinid	Staphylinidae	*Tachyporus nitidulus*			0	0	1	1	1	1
Staphylinid	Staphylinidae	*Tachyporus pusillus*			5	8	6	14	3	4
Staphylinid	Staphylinidae	*Tachyporus scitulus*	RDBK	Disturbed-grassland	3	7	7	17	4	6
Staphylinid	Staphylinidae	*Tachyporus tersus*			12	50	6	18	2	4
Staphylinid	Staphylinidae	*Tasgius ater*			0	0	1	1	2	2
Staphylinid	Staphylinidae	*Tasgius melanarius*			2	2	3	4	1	1
Staphylinid	Staphylinidae	*Tasgius morsitans*			2	2	1	1	0	0
Staphylinid	Staphylinidae	*Tasgius winkleri*			1	1	0	0	0	0
Staphylinid	Staphylinidae	*Tinotus morion*			1	3	0	0	0	0
Staphylinid	Staphylinidae	*Xantholinus elegans*			3	3	10	48	11	96
Staphylinid	Staphylinidae	*Xantholinus gallicus*			0	0	5	11	6	40
Staphylinid	Staphylinidae	*Xantholinus laevigatus*			0	0	3	7	2	5
Staphylinid	Staphylinidae	*Xantholinus linearis*			13	43	19	298	20	494
Staphylinid	Staphylinidae	*Xantholinus longiventris*			1	1	7	7	3	10
True bug	Anthocoridae	*Orius laevigatus*			0	0	0	0	1	1
True bug	Anthocoridae	*Orius niger*			0	0	0	0	1	1
True bug	Aphrophoridae	*Neophilaenus exclamationis*			6	10	0	0	1	1

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
True bug	Aphrophoridae	*Neophilaenus lineatus*			1	1	0	0	0	0
True bug	Aphrophoridae	*Philaenus spumarius*			1	1	1	1	0	0
True bug	Berytidae	*Berytinus minor*			1	1	0	0	0	0
True bug	Ceratocombidae	*Ceratocombus coleoptratus*			0	0	1	1	0	0
True bug	Cicadellidae	*Agallia venosa*			10	49	3	6	0	0
True bug	Cicadellidae	*Anoscopus albifrons*			15	197	17	135	10	26
True bug	Cicadellidae	*Anoscopus serratulae*			3	5	2	4	1	1
True bug	Cicadellidae	*Aphrodes makarovi*			3	4	8	16	2	2
True bug	Cicadellidae	*Arocephalus punctum*			2	3	0	0	1	1
True bug	Cicadellidae	*Arthaldeus pascuellus*			1	3	0	0	0	0
True bug	Cicadellidae	*Deltocephalus pulicaris*			5	23	5	13	1	1
True bug	Cicadellidae	*Doratura stylata*			16	89	19	116	11	24
True bug	Cicadellidae	*Errastunus ocellaris*			0	0	0	0	1	1
True bug	Cicadellidae	*Eupelix cuspidata*			5	8	3	3	0	0
True bug	Cicadellidae	*Eupteryx aurata*			0	0	0	0	1	1
True bug	Cicadellidae	*Eupteryx notata*			3	4	2	2	0	0
True bug	Cicadellidae	*Euscelis incisus*			10	18	14	55	2	2
True bug	Cicadellidae	*Graphocraerus ventralis*			0	0	2	7	1	2
True bug	Cicadellidae	*Hardya melanopsis*			5	8	2	2	0	0
True bug	Cicadellidae	*Macustus grisescens*			2	3	0	0	1	1
True bug	Cicadellidae	*Megophthalmus scabripennis*			11	20	4	5	2	3
True bug	Cicadellidae	*Ophiola decumanus*	Nb	Disturbed-grassland	0	0	0	0	2	3
True bug	Cicadellidae	*Psammotettix cephalotes*			0	0	3	3	1	1
True bug	Cicadellidae	*Psammotettix confinis*			1	1	4	7	1	1
True bug	Cicadellidae	*Psammotettix nodosus*			1	1	4	4	5	11
True bug	Cicadellidae	*Psammotettix alienus*	RDBK	Disturbed-grassland	0	0	0	0	2	2

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
True bug	Cicadellidae	*Recilia coronifera*			2	3	0	0	0	0
True bug	Cicadellidae	*Rhytistylus proceps*			16	111	17	65	2	2
True bug	Cicadellidae	*Sardius argus*			3	3	0	0	0	0
True bug	Cicadellidae	*Turrutus socialis*			14	237	17	151	7	8
True bug	Cicadellidae	*Ulopa reticulata*			0	0	1	10	0	0
True bug	Cicadellidae	*Verdanus abdominalis*			1	1	0	0	0	0
True bug	Cydnidae	*Legnotus picipes*	NS	Disturbed-grassland	0	0	1	1	0	0
True bug	Delphacidae	*Conomelus anceps*			1	1	0	0	0	0
True bug	Delphacidae	*Ditropis pteridis*			0	0	0	0	1	1
True bug	Delphacidae	*Hyledelphax elegantulus*			1	3	0	0	1	1
True bug	Delphacidae	*Kosswigianella exigua*			7	13	2	2	0	0
True bug	Delphacidae	*Ribautodelphax angulosus*	Nb	Undisturbed-grassland	1	3	1	1	0	0
True bug	Lygaeidae	*Gastrodes grossipes*			0	0	1	1	0	0
True bug	Lygaeidae	*Heterogaster urticae*			1	1	0	0	0	0
True bug	Lygaeidae	*Lamproplax picea*			1	1	0	0	0	0
True bug	Lygaeidae	*Macrodema micropterum*			0	0	1	2	0	0
True bug	Lygaeidae	*Megalonotus chiragra*			1	1	0	0	0	0
True bug	Lygaeidae	*Megalonotus praetextatus*	Nb	Disturbed-grassland	0	0	1	2	1	1
True bug	Lygaeidae	*Nysius huttoni*			0	0	1	1	0	0
True bug	Lygaeidae	*Plinthisus brevipennis*			11	22	9	35	6	12
True bug	Lygaeidae	*Scolopostethus affinis*			0	0	0	0	1	1
True bug	Lygaeidae	*Scolopostethus decoratus*			0	0	1	3	0	0
True bug	Microphysidae	*Myrmedobia coleoptrata*	Nb	Other habitat	0	0	1	1	1	1
True bug	Miridae	*Chlamydatus pulicarius*	Nb	Undisturbed-grassland	0	0	1	3	0	0
True bug	Miridae	*Chlamydatus pullus*			0	0	1	1	1	1
True bug	Miridae	*Chlamydatus saltitans*			0	0	1	1	0	0

Group	Family	Species[a b]	Status[c]	Habitat classification[d]	C occur	C abun	SC occur	SC abun	DC occur	DC abun
True bug	Miridae	*Lygus rugulipennis*			0	0	2	2	6	9
True bug	Miridae	*Rhabdomiris striatellus*			1	1	0	0	0	0
True bug	Miridae	*Stenodema laevigata*			0	0	1	1	0	0
True bug	Miridae	*Systellonotus triguttatus*	Nb	Disturbed-grassland	0	0	1	1	0	0
True bug	Miridae	*Trigonotylus caelestialum*			0	0	0	0	1	1
True bug	Nabidae	*Himacerus boops*			0	0	1	2	1	1
True bug	Nabidae	*Himacerus major*			1	1	0	0	0	0
True bug	Nabidae	*Nabis ferus*			0	0	0	0	4	4
True bug	Pentatomidae	*Aelia acuminata*			2	2	0	0	0	0
True bug	Pentatomidae	*Podops inuncta*			1	1	0	0	0	0
True bug	Pentatomidae	*Zicrona caerulea*			1	1	0	0	0	0
True bug	Reduviidae	*Coranus subapterus*			0	0	1	1	0	0
True bug	Thyreocoridae	*Thyrecoris scarabaeoides*	NS	Disturbed-grassland	0	0	1	1	0	0
True bug	Tingidae	*Acalypta parvula*			16	75	15	36	2	4
True bug	Tingidae	*Agramma laetum*			4	12	6	8	0	0
True bug	Tingidae	*Derephysia foliacea*			1	1	0	0	0	0
True bug	Tingidae	*Kalama tricornis*			2	6	10	40	1	1

[a] Some specimens were not identifiable to species level. These species are not recognised in the table, but the following summary gives the genus of these specimens, and the number of specimens effected per genus. Where a specimen was identifiable to a species subset or aggregate, or considered to be a potential species (but not confirmed), its possible identity is given in parenthesis: *Chthonolasius* spp. 1, *Calathus* spp. 1, *Harpalus* (*tardus*) 1, *Nebria* (*brevicollis/salina*) 3, *Oulema* (*melanopus/rufocyanea*), *Megasternum* (*immaculatum/concinnum*) 9, *Choleva* spp. 7, *Leiodes* spp. 2, *Leiodes* (*obesa*) 2, *Leiodes* (*rufipennis*) 2, *Mordellistena* spp. 1, *Anotylus* (*sculpturatus/mutator*) 5, *Gabrius* spp. 6, *Mocyta* (*fungi* agg.) 1, *Mycetoporus* (*clavicornis* agg.) 2, *Proteinus* (*olalis/brachypterus*) 1, *Quedius* (*boops* agg.) 99, *Stenus* (*clavicornis/providus*) 1, *Tachyporus* spp. 4, *Orius* spp. 1, *Aphrodes* spp. 2, *Macrosteles* spp. 3, *Psammotettix* spp. 21, *Cixius* spp. 1, *Delphacid* spp. 4, *Muellerianella* spp. 2, *Nysius* (*ericae/thyme*) 1, *Orthops* spp. 1, *Psallus* spp. 1.

[b] Species names follow Duff (2012), Bantock and Botting (2018), and Else et al (2016).

[c] Status definitions: Nationally Rare (NR), Nationally Scarce (NS), or older definitions of Red Data Book (RDB), Nationally Notable (Na, Nb).

[d] Habitat classifications were informed by *a prior* knowledge of species habitat, micro habitat and ecological process requirements from a systematic regional biodiversity audit (Dolman et al 2012) and other sources (see below).

Literature cited (from Table S.2.2(a) only)

Bantock, T., Botting, J. 2018. British Bugs: an online identification guide to UK Hemiptera. Available from: http://www.britishbugs.org.uk/ (accessed December 2018).

Duff, A.G. (2012) Checklist of Beetles of the British Isles. 2nd edition. Iver, Pemberley Books.

Else, G., Bolton, B., Broad, G. (2016) Checklist of British and Irish Hymenoptera - aculeates (Apoidea, Chrysidoidea and Vespoidea). Biodiversity Data Journal 4: e8050. doi:10.3897/BDJ.4.e8050.

Table S.2.2(b). The habitat and ecological process requirements of rare, scarce and threatened species identified in the sampling programme, and their subsequent habitat classification (disturbed-grassland, undisturbed-grassland, and other habitat).

Species	Management guild[a]	Habitat classification
Acalles ptinoides	Closed-canopy mesic woodland - with detritus[2]	Other habitat
Agathidium marginatum	Open mesic habitat[2]	Undisturbed-grassland
Alevonota gracilenta	Open mesic habitat - light disturbance[2]	Undisturbed-grassland
Amara consularis	Open mesic habitat - heavy disturbance[2]	Disturbed-grassland
Amara equestris	Open mesic habitat - light disturbance[2]	Undisturbed-grassland
Amara fulva	Open mesic habitat - light disturbance[2]	Undisturbed-grassland
Amara montivaga	Open mesic habitat – heavy disturbance[7]	Disturbed-grassland
Anotylus insecatus	Subterranean[2]	Other habitat
Aphanisticus pusillus	Open mesic habitat - well vegetated[2]	Undisturbed-grassland
Aphodius coenosus	Open mesic habitat - with dung/carrion[12]	Undisturbed-grassland
Aphodius distinctus	Open mesic habitat - with detritus[2]	Undisturbed-grassland
Aphodius ictericus	Open mesic habitat - with dung/carrion[12]	Undisturbed-grassland
Byrrhus arietinus	Open seasonally wet habitat - moderate vegetation[2]	Other habitat
Calathus ambiguus	Open mesic habitat - heavy disturbance[2]	Disturbed-grassland
Catapion pubescens	Open mesic habitat - short vegetation (heavy grazing)[2]	Disturbed-grassland
Cathormiocerus aristatus	Open mesic habitat - short vegetation and bare ground[8]	Disturbed-grassland
Chlamydatus pulicarius	Open mesic habitat - light disturbance[2]	Undisturbed-grassland
Chrysolina marginata	Open mesic habitat - short vegetation (heavy grazing)[2]	Disturbed-grassland
Dyschirius politus	Open xeric habitat - short vegetation and bare ground [7]	Disturbed-grassland
Euheptaulacus villosus	Open xeric habitat - short and medium vegetation (heavy grazing)[2]	Disturbed-grassland
Gabrius osseticus	Open wet or damp habitat - with detritus[2]	Other habitat
Harpalus pumilus	Open mesic habitat - heavy disturbance[2]	Disturbed-grassland

Species	Management guild[a]	Habitat classification
Heterothops dissimilis	Open to closed canopy woodland - with detritus/fungi[2]	Other habitat
Hippodamia variegata	Open mesic habitat - heavy disturbance[11]	Disturbed-grassland
Hydnobius punctatus	Unknown	Unknown
Hypera diversipunctata	Open seasonally wet woodland[2]	Other habitat
Legnotus picipes	Open xeric habitat - short vegetation and bare ground [1]	Disturbed-grassland
Leiodes longipes	Open mesic habitat - with fungi[3]	Undisturbed-grassland
Licinus depressus	Open mesic habitat - light disturbance[2]	Undisturbed-grassland
Medon castaneus	Open wet to dry habitat – underground mammal burrows[2,6]	Other habitat
Megalonotus praetextatus	Open xeric habitat - disturbed and undisturbed (juxtaposition)[2]	Disturbed-grassland
Mordellistena parvula	Open mesic habitat[2]	Undisturbed-grassland
Mycetoporus piceolus	Open mesic habitat - short vegetation and bare ground [3,12]	Disturbed-grassland
Myrmedobia coleoptrata	Open mesic woodland[2]	Other habitat
Myrmica karavajevi	Open mesic habitat - light disturbance[2]	Undisturbed-grassland
Myrmica schencki	Open mesic habitat - short vegetation and bare ground [2]	Disturbed-grassland
Neliocarus faber	Open mesic habitat - short vegetation (heavy grazing)[2]	Disturbed-grassland
Omaloplia ruricola	Open mesic habitat[2]	Undisturbed-grassland
Onthophilus punctatus	Subterranean[2]	Other habitat
Ophiola decumanus	Open mesic habitat - short vegetation and bare ground [3,12]	Disturbed-grassland
Ophonus laticollis	Open mesic habitat - heavy disturbance[2]	Disturbed-grassland
Panagaeus bipustulatus	Open mesic habitat[2]	Undisturbed-grassland
Philonthus lepidus[b]	Open mesic habitat - short vegetation and bare ground[3,10,12]	Disturbed-grassland
Psammotettix alienus	Open mesic habitat – heavy disturbance[9]	Disturbed-grassland
Quedius nigrocaeruleus	Open to closed canopy woodland - with detritus/fungi[2]	Other habitat
Ribautodelphax angulosus	Open mesic habitat[3,12]	Undisturbed-grassland
Saprinus aeneus	Open mesic habitat - with dung/carrion[4]	Undisturbed-grassland
Sunius melanocephalus	Open mesic habitat - with detritus[2]	Undisturbed-grassland

Species	Management guild[a]	Habitat classification
Syntomus truncatellus	Open mesic habitat[7]	Undisturbed-grassland
Systellonotus triguttatus	Open xeric habitat - short vegetation and bare ground[2]	Disturbed-grassland
Tachyporus scitulus	Open mesic habitat - short vegetation and bare ground [5]	Disturbed-grassland
Thyrecoris scarabaeoides	Open mesic habitat - short vegetation (heavy grazing)[3]	Disturbed-grassland

[a] *Management guild ass*ignment (cross-taxa species groups with similar requirements) was informed by autecological information collected from systematic regional Biodiversity Audit and alternative sources for species not considered by auditing (see numbered superscripts for source identity). Species with insufficient autecological information were not classified.

[b] Autecological information collected through biodiversity auditing (Dolman et al. 2012) grouped *Philonthus lepidus* (which comprised 27% of all priority species records) into the 'open mesic habitat' guild, classifying it as undisturbed-grassland associated, but alternative sources associate this species with 'open mesic habitat with short vegetation and bare ground' (Lane pers comm, Staniec and Pietrykowska-Tudruj 2011, Webb et al. 2018), classifying it as disturbed-grassland associated. Here we classified *P. lepidus* as disturbance associated; however, reclassifying the species as undisturbed-grassland associated does not alter the inference of treatment effects from our disturbed-grassland and undisturbed-grassland invertebrate richness analyses.

Literature cited (from Table S.2.2(b) only)

1. Bantock, T. and Botting, J. (2018). British bugs: an online identification guide to UK Hemiptera. https://www.britishbugs.org.uk (accessed on 17/12/2018).

2. Dolman, P.M., Panter C.J. and Mossman H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology*. 49. 986-997.

3. Lane, pers comm.

4. Lane, S. (2017). A review of the status of the beetles of Great Britain. The clown beetles and false clown beetles - Histeridae and Sphaeritidae. Natural Englnad commissioned report, NECR235.

5. Lane, S., in prep. A review of the status of the beetles of Great Britain: The Tachyporinae (Staphylinidae) beetles. Natural England commissioned report.

6. Lott, D.A. and Anderson, R. (2011). The staphylinidae (rove beetles) of Britian and Ireland parts 7 & 8: Oxporinae, steninae, Euaesthetinae, Pseudopsinae, Paederinae, Staphylininae. Royal Entomological Society, London.

7. Luff, M.L. (2007). The Carabidae (ground Beetles) of Britain and Ireland. Royal Entomological Society, London.

8. Morris, M.G. (1997). Broad-nosed weevils Coleoptera: Curculionidae (Entiminae). Royal Entomological Society, London.

9. Nickel, H. (2003). The leafhoppers and planthoppers of Germany (Hemiptera, Auchenorrhyncha): patterns and strategies in a highly diverse group of phytophagous insects. Pensoft series faunistica No 28. Pensoft Publishers, Sofia-Moscow wt Goecke & Evers, Keltern.

10. Staniec, B. and Pietrykowska-Tudruj, E. (2011). A description of the mature larva of Philonthus lepidus (Gravenhorst, 1802) - a stenotopic species of rove-beetle. *Polish Journal of Entomology*. 80. 33-46.

11. Roy, H., Brown, P. and Lewington, R. (2018). Field guide to the ladybirds of Great Britain and Ireland. London, Bloomsbury.

12. Webb, J., et al. (2018). Pantheon - database version 3.7.6. http://www.brc.ac.uk/pantheon/ (accessed December 2018).

Table S.2.3. Model simplification, combining vegetation strata categories from full models with all fixed factors included. Analyses consider: a) vegetation structure, separately examining vegetation height and bare ground cover; b) the abundance of each of five bird of conservation concern; c) the richness and abundance of all invertebrates and priority (rare, scarce or threatened) invertebrates, separately, for each of five groups (carabids, staphylinids, other beetles, true bugs, and ants); and d) priority invertebrate species richness, separately for two groups that were *a priori* classified as dependent on either physically disturbed, or undisturbed, grassland habitats (see Table S.2.2). For each model, the degrees of freedom (*df*), Akaike's information criterion with small-sample bias adjustment (AIC_c), and the difference in AICc value relative to the best model (ΔAIC_c) are shown.

Analysis	Response metric	AIC_c	ΔAIC_c	*df*	Vegetation strata levels^{a}			
					Young acid grass-heath	Intermediate grass-heath	Ancient acid grass-heath	Calcareous grass-heath
a) Vegetation structure	Vegetation height	21.6^{C}	0	98	(A) 2.09 ± 0.05^{b}	(B) 0.20 ± 0.05	(B) 0.20 ± 0.05	(A) 2.09 ± 0.05^{b}
		25.1	3.5	96	(A) 2.07 ± 0.06^{b}	(B) 0.22 ± 0.07	(C) 0.21 ± 0.07	(D) 0.02± 0.01
	Bare ground cover	504.9^{C}	0	98	(A) -0.64 ± 0.24^{b}	(A) -0.64 ± 0.24^{b}	(B) -0.25 ± 0.06	(A) -0.64 ± 0.24^{b}
		506.7	1.8	96	(A) -0.59 ± 0.24^{b}	(B) -0.07 ± 0.06	(C) -0.29 ± 0.06	(D) -0.08± 0.05
b) Woodlark (*Lullula arborea*)	Abundance	157.8^{C}	0	98	(A) -3.24 ± 0.89^{b}	(B) 2.04 ± 0.82	(B) 2.04 ± 0.82	(B) 2.04 ± 0.82
		162.1	4.3	96	(A) -3.26 ± 0.88^{b}	(B) 2.22 ± 0.89	(C) 2.04 ± 0.90	(D) 1.86± 0.89
b) Eurasian curlew (*Numenius arquata*)	Abundance	166.9^{C}	0	98	(A) -2.46 ± 0.67^{b}	(B) 1.11 ± 0.59	(B) 1.11 ± 0.59	(B) 1.11 ± 0.59
		170.5	3.6	96	(A) -2.42 ± 0.66^{b}	(B) 0.87 ± 0.70	(C) 1.38 ± 0.66	(D) 0.98± 0.66
b) Northern lapwing (*Vanellus vanellus*)	Abundance	124.8^{C}	0	98	(A) -2.70 ± 0.71^{b}	(A) -2.70 ± 0.71^{b}	(A) -2.70 ± 0.71^{b}	(B) -0.95± 0.62
		127.8	3.0	96	(A) -2.86 ± 0.78^{b}	(B) -0.12 ± 0.57	(C) 0.47 ± 0.49	(D) -0.82± 0.68
b) Common linnet (*Linaria cannabina*)	Abundance	114.0	NA	96	(A) -1.28 ± 0.77^{b}	(B) -0.31 ± 0.89	(C) 0.31 ± 0.83	(D) -34.1± 52.4+e7
b) Yellowhammer (*Emberiza citronella*)	Abundance	67.7	0	98	(A) -2.08 ± 0.50^{b}	(A) -2.08 ± 0.50^{b}	(B) 1.16 ± 0.63	(A) -2.08 ± 0.50^{b}
		71.6	3.9	96	(A) -1.97 ± 0.75^{b}	(B) 0.24 ± 1.00	(C) 1.06 ± 0.84	(D) -0.67± 1.23

Analysis	Response metric	AIC_c	ΔAIC_c	*df*	Vegetation strata levels[a]			
					Young acid grass-heath	Intermediate grass-heath	Ancient acid grass-heath	Calcareous grass-heath
c) Carabids	Richness (all species)	287.8[C]	NA	49	(A) 3.84 ± 5.82[b]	(B) 0.40 ± 1.12	(C) -0.43 ± 1.10	(D) -1.44 ± 1.10
	Abundance (all species)	250.9[C]	0	51	(A) 4.26 ± 4.21[b]	(A) 4.26 ± 4.21[b]	(B) -1.79 ± 0.65	(A) 4.26 ± 4.21[b]
		255.3	4.6	49	(A) 4.97 ± 4.35[b]	(B) -0.60 ± 0.84	(C) -2.25 ± 0.83	(D) -0.72 ± 0.83
	Richness (priority species)	157.0[C]	0	51	(A) 2.16 ± 1.89[b]	(A) 2.16 ± 1.89[b]	(B) -1.03 ± 0.35	(A) 2.16 ± 1.89[b]
		161.5	4.5	49	(A) 1.81 ± 1.90[b]	(B) 0.24 ± 0.31	(C) -0.90 ± 0.41	(D) -0.07 ± 0.32
	Abundance (priority species)	245.4[C]	0	51	(A) 0.78 ± 2.11[b]	(A) 0.78 ± 2.11[b]	(B) -1.21 ± 0.33	(A) 0.78 ± 2.11[b]
		250.0	4.6	49	(A) 1.18 ± 2.16[b]	(B) -0.30 ± 0.33	(C) -1.36 ± 0.39	(D) -0.11 ± 0.32
c) Staphylinids	Richness (all species)	250.9[C]	NA	51	(A) 2.56 ± 0.45[b]	(B) 0.00 ± 0.01	(C) -0.02 ± 0.08	(D) -0.13 ± 0.09
	Abundance (all species)	258.5[C]	0	51	(A) 3.16 ± 4.54[b]	(B) -1.64 ± 0.73	(B) -1.64 ± 0.73	(B) -1.64± 0.73
		258.8	0.3	50	(A) 2.22 ± 4.53[b]	(B) -1.26 ± 0.77	(B) -1.26 ± 0.77	(C) -2.35 ± 0.86
		261.3	2.8	49	(A) 2.39 ± 4.59[b]	(B) -1.08 ± 0.88	(C) -1.44 ± 0.87	(D) -2.35 ± 0.87
	Richness (priority species)	180.2[C]	NA	49	(A) 1.48± 1.57[b]	(B) -0.09 ± 0.32	(C) -0.05 ± 0.31	(D) 0.09 ± 0.30
	Abundance (priority species)	314.8[C]	0	51	(A) 1.42 ± 2.21[b]	(B) -1.23 ± 0.32	(B) -1.23 ± 0.32	(B) -1.23 ± 0.32
		315.1	0.3	50	(A) 2.36 ± 2.21[b]	(B) -1.48 ± 0.35	(B) -1.48 ± 0.35	(C) -0.94 ± 0.39
		317.0	2.2	49	(A) 2.89 ± 2.21[b]	(B) -1.33 ± 0.40	(C) -1.72 ± 0.40	(D) -0.94 ± 0.38
c) Other beetles	Richness (all species)	108.3[C]	0	51	(A) 1.13 ± 1.16[b]	(A) 1.13 ± 1.16[b]	(B) -0.61 ± 0.16	(B) -0.61 ± 0.16
		112.5	4.2	49	(A) 1.16 ± 1.22[b]	(B) -0.16 ± 0.23	(C) -0.61 ± 0.23	(D) -0.77 ± 0.23
	Abundance (all species)	470.1[C]	NA	49	(A) 2.24 ± 1.12[b]	(B) -0.05 ± 0.21	(C) -0.31 ± 0.21	(D) -0.30 ± 0.21
	Richness (priority species)	162.4[C]	0	51	(A) -2.87 ± 1.88[b]	(A) -2.87 ± 1.88[b]	(B) -0.44 ± 0.27	(A) -2.87 ± 1.88[b]
		166.1	3.7	49	(A) -2.50 ± 1.94[b]	(B) -0.31 ± 0.28	(C) -0.61 ± 0.30	(D) -0.26 ± 0.27
	Abundance (priority species)	246.6[C]	NA	49	(A) -2.20 ± 1.72[b]	(B) -0.05 ± 0.29	(C) -0.32 ± 0.30	(D) -0.08 ± 0.28

Analysis	Response metric	AIC_c	ΔAIC_c	*df*	Vegetation strata levels[a]			
					Young acid grass-heath	Intermediate grass-heath	Ancient acid grass-heath	Calcareous grass-heath
c) True bugs	Richness (all species)	254.8[C]	0	51	(A) 6.53 ± 4.27[b]	(B) 1.52 ± 0.68	(A) 6.53 ± 4.27[b]	(A) 6.53 ± 4.27[b]
		258.5	3.7	49	(A) 5.61 ± 4.47[b]	(B) 1.54 ± 0.86	(C) 0.52 ± 0.85	(D) -0.51 ± 0.85
	Abundance (all species)	205.9[C]	0	51	(A) 3.34 ± 2.76[b]	(B) 1.24 ± 0.44	(A) 3.34 ± 2.76[b]	(A) 3.34 ± 2.76[b]
		210.7	4.8	49	(A) 3.14 ± 2.92[b]	(B) 1.19 ± 0.56	(C) 0.09 ± 0.56	(D) -0.27 ± 0.55
	Richness (priority species)	72.8[C]	0	51	(A) -6.35 ± 4.60[b]	(A) -6.35 ± 4.60[b]	(A) -6.35 ± 4.60[b]	(B) -1.48 ± 1.04
		77.5	4.7	49	(A) -6.84 ± 4.67[b]	(B) 0.42 ± 0.68	(C) 0.05 ± 0.71	(D) -1.33 ± 1.12
	Abundance (priority species)	94.8[C]	0	51	(A) -7.07 ± 5.39[b]	(A) -7.07 ± 5.39[b]	(A) -7.07 ± 5.39[b]	(B) -1.16 ± 0.91
		99.4	4.6	49	(A) -6.42 ± 5.49[b]	(B) 0.31 ± 0.82	(C) -0.45 ± 0.88	(D) -1.17 ± 1.01
c) Ants	Richness (all species)	225.0[C]	0	51	(A) 3.56 ± 3.46[b]	(B) 0.90 ± 0.46	(B) 0.90 ± 0.46	(A) 3.56 ± 3.46[b]
		229.6	4.6	49	(A) 3.15 ± 3.46[b]	(B) 1.14 ± 0.66	(C) 1.24 ± 0.66	(D) 0.54 ± 0.66
	Richness (priority species)	80.3[C]	0	50	(A) -0.01 ± 3.50[b]	(A) -0.01 ± 3.50[b]	(B) -0.78 ± 0.65	(C) -1.80± 1.04
		82.9	2.9	49	(A) -0.12 ± 3.64[b]	(B) 0.06 ± 0.60	(C) -0.75 ± 0.73	(D) -1.77± 1.08
d) Disturbed-grassland invertebrate species	Richness	186.8[C]	0.5	51	(A) -1.01 ± 1.63[b]	(A) -1.01 ± 1.63[b]	(B) -0.80 ± 0.28	(A) -1.01 ± 1.63[b]
		186.3	0	50	(A) -0.48 ± 1.71[b]	(B) -0.40 ± 0.24	(C) -0.92 ± 0.29	(A) -0.48 ± 1.71[b]
		188.5	2.2	49	(A) -0.37 ± 1.72[b]	(B) -0.46 ± 0.27	(C) -0.99 ± 0.31	(D) -0.14± 0.23
d) Undisturbed-grassland invertebrate species	Richness	192.3[C]	0	51	(A) 1.17 ± 1.40[b]	(A) 1.17 ± 1.40[b]	(B) -0.65 ± 0.23	(A) 1.17 ± 1.40[b]
		195.5	3.2	49	(A) 1.09 ± 1.41[b]	(B) 0.08 ± 0.22	(C) -0.69 ± 0.27	(D) -0.22± 0.23

[a] Shading and letters denote combined categories; coefficients and standard error of individual categories and combined categories are given. Where all levels were initially similar no combination was attempted.

[b] Model Intercept.

[C] The model taken forward for subsequent model selection (Table S.2.4).

Table S.2.4. Candidate models that consider: a) each of vegetation height and bare ground cover, b) the abundance of each of five birds of conservation concern, c) the richness and abundance of all invertebrates and priority (rare, scarce or threatened) invertebrates, separately, for each of five groups (carabids, staphylinids, other beetles, true bugs, and ants), and d) priority invertebrate species richness, separately for two groups that were *a priori* classified as dependent on either physically disturbed, or undisturbed, grassland habitats (see Table S.2.2). Models examine fixed effects of treatment, vegetation strata (parenthesis denote the number of categories within this fixed effect, see Table S.2.3 for category identity), and number of trap days (for invertebrate analyses only). For each candidate model the degrees of freedom (*df*), Akaike's information criterion with small-sample bias adjustment (AIC_c), and the difference in AICc value compared to the most parsimonious model (ΔAIC_c) are shown. Bold type denotes the selected model from each candidate set.

Candidate model	*df*	AIC_c	ΔAIC_c
a) Vegetation height			
Treatment + vegetation strata (2)	98	19.7	0.0
Treatment	99	33.9	14.2
Vegetation strata (2)	100	205.4	185.7
Intercept only	101	208.5	188.8
a) Bare ground cover			
Treatment + vegetation strata (4)	96	50.9	0.0
Treatment	99	52.8	1.8
Intercept only	101	143.5	92.6
Vegetation strata (4)	98	144.0	93.1
b) Woodlark (*Lullula arborea*) abundance			
Treatment + vegetation strata (2)	98	157.8	0.0
Vegetation strata (2)	100	158.5	0.7
Treatment	99	163.2	5.4
Intercept only	101	164.0	6.16
b) Eurasian curlew (*Numenius arquata*) abundance			
Vegetation strata (2)	100	165.4	0.0
Intercept only	101	166.6	1.2
Treatment + vegetation strata (2)	98	166.9	1.4
Treatment	99	168.4	3.0
b) Northern lapwing (*Vanellus vanellus*) abundance			
Treatment + vegetation strata (2)	98	124.8	0.0
Treatment	99	125.6	0.9
Vegetation strata (2)	100	131.0	6.2
Intercept only	101	132.0	7.3
b) Yellowhammer (*Emberiza citronella*) abundance			
Treatment + vegetation strata (2)	98	67.7	0.0
Vegetation strata (2)	100	68.4	0.6
Treatment	99	68.8	1.0
Intercept only	101	69.9	2.1

Candidate model	*df*	AIC$_c$	ΔAIC$_c$
b) Common linnet (*Linaria cannabina*) abundance			
Vegetation strata (4)	98	109.5	0.0
Intercept only	101	111.4	1.8
Treatment + vegetation strata (4)	96	114.0	4.4
Treatment	99	115.6	6.0
c) Carabid richness (all species)			
Treatment	53	283.1	0.0
Trap days + treatment	52	283.5	0.6
Traps days	54	286.2	3.2
Intercept only	55	286.5	3.4
Treatment + vegetation strata (4)	50	287.3	4.3
Trap days + Treatment + vegetation strata (4)	49	287.8	4.8
Traps days + vegetation strata (4)	51	290.3	7.2
Vegetation strata (4)	52	290.4	7.4
c) Carabid abundance (all species)			
Treatment + vegetation strata (2)	52	249.6	0.0
Vegetation strata (2)	54	250.8	1.3
Traps days + treatment + vegetation strata (2)	51	250.9	1.4
Traps days + vegetation strata (2)	53	252.0	2.4
Treatment	53	256.0	6.5
Traps days + treatment	52	256.2	6.7
Intercept only	55	257.3	7.7
Trap days	54	257.4	7.9
c) Carabid richness (priority species)			
Treatment + vegetation strata (2)	52	155.0	0.0
Trap days + treatment + vegetation strata (2)	51	157.0	2.0
Vegetation strata (2)	54	157.9	2.8
Trap days + vegetation strata (2)	53	160.1	5.1
Treatment	53	163.4	8.4
Intercept only	55	165.4	10.4
Trap days + treatment	52	165.7	10.7
Trap days	54	167.3	12.2
c) Carabid abundance (priority species)			
Treatment + vegetation strata (2)	52	243.0	0.0
Trap days + treatment + vegetation strata (2)	51	245.4	2.4
Vegetation strata (2)	54	249.2	6.2
Trap days + vegetation strata (2)	53	250.2	7.3
Treatment	53	253.2	10.2
Trap days + treatment	52	254.8	11.8
Trap days	54	257.8	14.9
Intercept only	55	258.8	15.8
c) Staphylinid richness (all species)			
Treatment	53	352.2	0.0
Trap days + treatment	52	354.5	2.3
Treatment + vegetation strata (4)	50	355.6	3.4
Trap days + treatment + vegetation strata (4)	49	358.1	5.9
Intercept only	55	380.5	28.3
Trap days	54	382.3	30.0
Vegetation strata (4)	52	382.5	30.3
Trap days + vegetation strata (4)	51	384.6	32.4

Candidate model	*df*	AIC$_c$	ΔAIC$_c$
c) Staphylinid abundance (all species)			
Treatment + vegetation strata (2)	52	257.3	0.0
Trap days + Treatment + vegetation strata (2)	51	258.5	1.2
Treatment	53	260.7	3.4
Trap days + treatment	52	261.3	4.0
Vegetation strata (2)	54	284.6	27.3
Trap days + vegetation strata (2)	53	286.8	29.6
Intercept only	55	289.3	32.0
Trap days	54	291.5	34.2
c) Staphylinid richness (priority species)			
Intercept only	55	168.4	0.0
Trap days	54	169.8	1.3
Treatment	53	171.2	2.8
Trap days + treatment	52	173.0	4.6
Vegetation strata (4)	52	174.8	6.3
Trap days + vegetation strata (4)	51	176.2	7.7
Treatment + vegetation strata (4)	50	178.2	9.8
Trap days + treatment + vegetation strata (4)	49	180.2	11.7
c) Staphylinid abundance (priority species)			
Treatment + vegetation strata (2)	52	312.3	0.0
Vegetation strata (2)	54	312.4	0.1
Trap days + vegetation strata (2)	53	314.6	2.3
Trap days + treatment + vegetation strata (2)	51	314.8	2.4
Treatment	53	322.5	10.2
Trap days + treatment	52	324.4	12.1
Intercept only	55	328.4	16.0
Trap days	54	329.8	17.5
c) Other beetles richness (all species)			
Trap days + treatment + vegetation strata (2)	51	108.3	0.0
Treatment + vegetation strata (2)	52	109.9	1.6
Trap days + vegetation strata (2)	53	118.4	10.1
Trap days + treatment	52	119.9	11.6
Vegetation strata (2)	54	121.0	12.7
Treatment	53	121.7	13.4
Trap days	54	127.7	19.4
Intercept only	55	130.4	22.1
c) Other beetles abundance (all species)			
Treatment	53	464.8	0.0
Trap days + treatment	52	465.7	0.9
Trap days	54	468.2	3.4
Treatment + vegetation strata (4)	50	468.5	3.7
Intercept only	55	469.7	4.9
Trap days + treatment + vegetation strata (4)	49	470.1	5.3
Trap days + vegetation strata (4)	51	471.2	6.4
Vegetation strata (4)	52	471.8	7.0
c) Other beetles richness (priority species)			
Treatment + vegetation strata (2)	52	162.0	0.0
Traps days + treatment + vegetation strata (2)	51	162.4	0.4
Treatment	53	162.8	0.7
Trap days + treatment	52	162.9	0.9
Vegetation strata (2)	54	176.2	14.2
Trap days + vegetation strata (2)	53	177.5	15.4
Intercept only	55	178.0	15.9
Trap days	54	178.6	16.6

Candidate model	*df*	AIC_c	ΔAIC_c
c) Other beetle abundance (priority species)			
Treatment	53	240.2	0.0
Trap days + treatment	52	240.9	0.7
Treatment + vegetation strata (4)	50	245.4	5.2
Trap days + treatment + vegetation strata (4)	49	246.6	6.4
Intercept only	55	261.4	21.2
Trap days	54	263.4	23.2
Vegetation strata (4)	52	266.1	25.9
Trap days + vegetation strata (4)	51	268.4	28.2
c) True bug richness (all species)			
Treatment + vegetation strata (2)	52	254.1	0.0
Trap day + treatment + vegetation strata (2)	51	254.9	0.8
Treatment	53	256.6	2.6
Trap days + treatment	52	257.6	3.5
Trap days + vegetation strata (2)	53	311.6	57.5
Trap days	54	313.1	59.0
Vegetation strata (2)	54	314.0	60.0
Intercept only	55	315.3	61.2
c) True bugs abundance (all species)			
Treatment + vegetation strata (2)	52	205.4	0.0
Trap days + treatment + vegetation strata (2)	51	205.9	0.5
Treatment	53	210.8	5.4
Trap days + treatment	52	211.6	6.2
Trap days + vegetation strata (2)	53	261.1	55.7
Vegetation strata (2)	54	263.9	58.5
Trap days	54	264.1	58.7
Intercept only	55	266.5	61.1
c) True bug richness (priority species)			
Vegetation strata (2)	54	70.8	0.0
Treatment + vegetation strata (2)	52	71.2	0.4
Intercept only	55	71.7	0.9
Treatment	53	71.9	1.2
Trap days + vegetation strata (2)	53	72.4	1.7
Trap days + treatment + vegetation strata (2)	51	72.8	2.0
Trap days	54	73.4	2.6
Traps days + treatment	52	73.5	2.8
c) True bug abundance (priority species)			
Intercept only	55	89.0	0.0
Vegetation strata (2)	54	89.7	0.7
Trap days	54	90.7	1.7
Trap days + vegetation strata (2)	53	91.4	2.3
Treatment	53	92.3	3.3
Treatment + vegetation strata (2)	52	93.2	4.1
Trap days + treatment	52	94.0	5.0
Trap days + treatment + vegetation strata (2)	51	94.8	5.8
c) Ant richness (all species)			
Treatment + vegetation strata (2)	52	222.5	0.0
Treatment	53	224.4	1.9
Trap days + treatment + vegetation strata (2)	51	225.0	2.5
Trap days + treatment	52	226.6	4.1
Intercept only	55	246.7	24.1
Trap days	54	247.4	24.9
Vegetation strata (2)	54	248.0	25.5
Trap days + vegetation strata (2)	53	249.1	26.6

Candidate model	*df*	AIC_c	ΔAIC_c
c) Ant richness (priority species)			
Vegetation strata (3)	53	75.6	0.0
Intercept only	55	76.9	1.3
Trap days + vegetation strata (3)	52	77.4	1.7
Treatment + vegetation strata (3)	51	78.0	2.3
Trap days	54	78.6	3.0
Treatment	53	78.7	3.0
Trap days + treatment + vegetation strata (3)	50	80.3	4.6
Trap days + treatment	52	80.8	5.2
d) Disturbed-grassland species richness			
Treatment + vegetation strata (2)	52	184.8	0.0
Trap days + treatment + vegetation strata (2)	51	186.8	2.0
Treatment	53	192.8	8.0
Trap days + treatment	52	194.3	9.5
Vegetation strata (2)	54	195.6	10.8
Trap days + vegetation strata (2)	53	197.8	13.0
Intercept only	55	205.2	20.4
Trap days	54	207.1	22.3
d) Undisturbed-grassland species richness			
Vegetation strata (2)	54	187.8	0.0
Trap days + vegetation strata (2)	52	189.8	2.0
Treatment + vegetation strata (2)	53	189.9	2.1
Trap days + treatment + vegetation strata (2)	51	192.3	4.5
Intercept only	55	194.6	6.9
Trap days	54	196.0	8.2
Treatment	53	197.0	9.2
Trap days + treatment	52	199.0	11.2

Table S.2.5. Parameter estimates from best-supported models that consider: a) each of vegetation height and bare ground cover, b) the abundance of each of five birds of conservation concern, c) the richness and abundance of all invertebrates and priority (rare, scarce or threatened) invertebrates, separately, for each of five groups (carabids, staphylinids, other beetles, true bugs, and ants), and d) priority invertebrate species richness, separately for two groups that were *a priori* classified as dependent on either physically disturbed, or undisturbed, grassland habitats (see Table S.2.2). Models examine the fixed effects of treatment and vegetation strata, and the continuous co-variate of number of trap days (for invertebrate analyses only), where these variables were retained through model selection (see Table S.2.4 for selection between competing candidate models). For each model, coefficients, standard errors, and 95% Confidence Intervals are shown (CI).

Parameter^{a,b}	Coefficient	SE	Lower 95% CI	Upper 95% CI
a) Vegetation height *n,ln*				
Intercept (treatment = control, vegetation strata = young & calcareous pooled)	1.42	0.05	1.32	1.52
Treatment - deep-cultivated	-1.33	0.06	-1.45	-1.21
Treatment - shallow-cultivated	-1.11	0.06	-1.24	-0.99
Vegetation strata – intermediate & ancient-acid pooled	0.21	0.05	0.11	0.31
a) Bare ground cover *b,nt*				
Intercept (treatment = control)	-4.42	1.54	-9.90	-2.37
Treatment - deep-cultivated	7.51	1.76	4.89	13.17
Treatment - shallow-cultivated	4.70	1.58	2.50	10.21
b) Woodlark (*Lullula arborea*) abundance *nb,nt*				
Intercept (vegetation strata = young grass-heath)	-2.71	0.78	-4.59	-1.34
Vegetation strata – intermediate, ancient-acid, & calcareous pooled	2.10	0.83	0.62	4.04
b) Eurasian curlew (*Numenius arquata*) abundance *nb,nt*				
Intercept only	-0.96	0.23	-1.41	-0.51

Parameter[a,b]	Coefficient	SE	Lower 95% CI	Upper 95% CI
b) Northern lapwing (*Vanellus vanellus*) abundance *p,nt*				
Intercept (treatment = control)	-2.89	0.71	-4.68	-1.76
Treatment - deep-cultivated	1.70	0.77	0.36	3.57
Treatment - shallow-cultivated	1.96	0.76	0.67	3.81
b) Yellowhammer (*Emberiza citronella*) abundance *p,nt*				
Intercept (vegetation strata = young, intermediate & calcareous pooled)	-2.76	0.45	-3.79	-1.99
Vegetation strata – ancient-acid grass-heath	1.23	0.63	-0.05	2.51
b) Common linnet (*Linaria cannabina*) abundance *nb,nt*				
Intercept only	-1.45	0.36	-2.13	-0.70
c) Carabid richness (all species) *n,nt*				
Intercept (treatment = control)	11.38	0.72	9.96	12.79
Treatment - deep-cultivated	0.28	0.97	-1.62	2.17
Treatment - shallow-cultivated	2.42	0.97	0.53	4.32
c) Carabid abundance (all species) *n,sq*				
Intercept (vegetation strata = young, intermediate & calcareous pooled)	9.45	0.34	8.78	10.11
Vegetation strata – ancient-acid grass-heath	-1.99	0.66	-3.28	-0.70
c) Carabid richness (priority species) *p,nt*				
Intercept (treatment = control, vegetation strata = young, intermediate & calcareous pooled)	0.94	0.18	0.57	1.28
Treatment - deep-cultivated	-0.72	0.28	-1.28	-0.18
Treatment - shallow-cultivated	-0.51	0.26	-1.03	0.00
Vegetation strata – ancient-acid grass-heath	-0.98	0.34	-1.71	-0.37
c) Carabid abundance (priority species) *nb,nt*				
Intercept (treatment = control, vegetation strata = young, intermediate & calcareous pooled)	1.43	0.23	0.99	1.89
Treatment - deep-cultivated	-0.80	0.32	-1.44	-0.16
Treatment - shallow-cultivated	0.25	0.29	-0.32	0.81

Parameter[a,b]	Coefficient	SE	Lower 95% CI	Upper 95% CI
Vegetation strata – ancient-acid grass-heath	-1.23	0.33	-1.91	-0.59
c) Staphylinid richness (all species) *p,nt*				
Intercept (treatment = control)	2.68	0.07	2.55	2.80
Treatment - deep-cultivated	0.43	0.08	0.27	0.59
Treatment - shallow-cultivated	0.37	0.08	0.22	0.53
c) Staphylinid abundance (all species) *n,sq*				
Intercept (treatment = control, vegetation strata = young grass-heath)	7.99	0.85	6.33	9.67
Treatment - deep-cultivated	4.85	0.77	3.35	6.36
Treatment - shallow-cultivated	3.00	0.76	1.51	4.50
Vegetation strata – intermediate, ancient-acid, & calcareous pooled	-1.73	0.73	-3.15	-0.31
c) Staphylinid richness (priority species) *p,nt*				
Intercept only	0.45	0.11	0.24	0.65
c) Staphylinid abundance (priority species) *nb,nt*				
Intercept (vegetation strata = young grass-heath)	2.74	0.29	2.22	3.37
Vegetation strata – intermediate, ancient-acid, & calcareous pooled	-1.56	0.34	-2.16	-0.82
c) Other beetles richness (all species) *n,sq*				
Intercept (treatment = control, vegetation strata = young & intermediate pooled)	3.4	0.18	3.05	3.75
Treatment - deep-cultivated	-0.01	0.20	-0.41	0.39
Treatment - shallow-cultivated	0.69	0.20	0.29	1.09
Vegetation strata – ancient-acid & calcareous pooled	-0.62	0.16	-0.95	-0.31
c) Other beetles abundance (all species) *nb,nt*				
Intercept (treatment = control)	3.4	0.14	3.10	3.65
Treatment - deep-cultivated	-0.32	0.19	-0.70	0.04
Treatment - shallow-cultivated	0.25	0.19	-0.13	0.61

Parameter^{a,b}	Coefficient	SE	Lower 95% CI	Upper 95% CI
c) Other beetles richness (priority species) *p,nt*				
Intercept (treatment = control)	-0.47	0.32	-1.16	0.09
Treatment - deep-cultivated	1.06	0.36	0.40	1.81
Treatment - shallow-cultivated	1.35	0.35	0.71	2.09
c) Other beetles abundance (priority species) *nb,nt*				
Intercept (treatment = control)	-0.21	0.31	-0.85	0.36
Treatment - deep-cultivated	1.62	0.35	0.97	2.33
Treatment - shallow-cultivated	1.68	0.35	1.03	2.39
c) True bug richness (all species) *n,nt*				
Intercept (treatment = control, vegetation strata = young, ancient-acid & calcareous pooled)	11.84	0.59	10.69	13.00
Treatment - deep-cultivated	-7.54	0.74	-9.00	-6.09
Treatment - shallow-cultivated	-2.31	0.74	-3.77	-0.87
Vegetation strata – intermediate grass-heath	1.50	0.68	0.16	2.83
c) True bug abundance (all species) *n,sq*				
Intercept (treatment = control, vegetation strata = young, ancient-acid & calcareous pooled)	7.05	0.38	6.31	7.81
Treatment - deep-cultivated	-4.74	0.48	-5.68	-3.80
Treatment - shallow-cultivated	-1.30	0.48	-2.24	-0.36
Vegetation strata – intermediate grass-heath	1.23	0.44	0.36	2.09
c) True bug richness (priority species) *p,nt*				
Intercept only	-1.39	0.27	-1.96	-0.90
c) True bug abundance (priority species) *nb,nt*				
Intercept only	-1.03	0.33	-1.67	-0.38

Parameter^{a,b}	Coefficient	SE	Lower 95% CI	Upper 95% CI
c) Ant richness (all species) *n,nt*				
Intercept (treatment = control)	3.75	0.43	2.91	4.59
Treatment - deep-cultivated	3.25	0.57	2.12	4.37
Treatment - shallow-cultivated	2.05	0.57	0.93	3.17
c) Ant richness (priority species) *p,nt*				
Intercept only	-1.23	0.25	-1.79	-0.80
d) Disturbed-grassland species richness *p,nt*				
Intercept (treatment = control, vegetation strata = young, intermediate & calcareous pooled)	0.06	0.27	-0.52	0.55
Treatment - deep-cultivated	0.95	0.30	0.38	1.59
Treatment - shallow-cultivated	1.02	0.30	0.47	1.66
Vegetation strata – ancient-acid grass-heath	-0.81	0.28	-1.40	-0.30
d) Disturbed-grassland species richness *p,nt*				
Intercept (vegetation strata = young, intermediate & calcareous pooled)	1.07	0.09	0.88	1.23
Vegetation strata – ancient-acid grass-heath	-0.64	0.22	-1.11	-0.21

[a] For vegetation strata, categories were pooled in some models (see Table S.2.3). Where the fixed effect of treatment was retained differences between category means (deep-cultivated, shallow-cultivated, control) were assessed by Tukey pairwise comparisons (reported in Fig. 2.3).

[b] The italicized text after each model title denotes the error term (n = normal, b = binominal, p = Possion, nb = negative binomial), and whether the response variable was transformed (nt = not transformed, ln = natural log transformed, sq = square root transformed).

References

Clarke, R.T., Liley, D., Sharp, J.M. & Green, R.E. (2013). Building development and roads: implications for the distribution of Stone curlews across the Brecks. *PLOS ONE,* 8(8), e72984.

Diemont, W.H. (1994). Effects of removal of organic matter on the productivity of heathlands. *Journal of Vegetation Science,* 5(3), 409-414.

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology,* 49, 986-997.

Dolman, P.M. & Sutherland, W.J. (1992). The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology,* 29(2), 402-413.

Dolman, P.M. & Sutherland, W.J. (1994). The use of soil disturbance in the management of Breckland grass heaths for nature conservation. *Journal of Environmental Management,* 41(2), 123-140.

ESRI (2011). ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Farrell, L. (1989). The different types and importance of British heaths. *Botanical Journal of the Linnean Society,* 101, 291-299.

Green, R.E. (2013). Potential for improved management of stone-curlew plots on arable farmland. *Unpublished report*.

Green, R.E. & Griffiths, G.H. (1994). Use of preferred nesting habitat by stone curlews Burhinus oedicnemus in relation to vegetation structure. *Journal of Zoology,* 233(3), 457-471.

Green, R.E., Tyler, G.A. & Bowden, C.G.R. (2000). Habitat selection, ranging behaviour and diet of the stone curlew (*Burhinus oedicnemus*) in southern England. *Journal of Zoology,* 250(2), 161-183.

Heil, G.W. & Bruggink, M. (1987). Competition for nutrients between *Calluna vulgaris* (L.) Hull and *Molinia caerulea* (L.) Moench. *Oecologia,* 73(1), 105-107.

Heil, G.W. & Diemont, W.H. (1983). Raised nutrient levels change heathland into grassland. *Vegetatio,* 53(2), 113-120.

Hill, M., O., Preston, C., D. & Roy, D., B. (2004). *Attributes of British and Irish plants: status, size, life history, geography and habitats*. Centre for Ecology & Hydrology, Cambridgeshire.

Holt, C.A., Fuller, R.J. & Dolman, P.M. (2010). Experimental evidence that deer browsing reduces habitat suitability for breeding Common Nightingales *Luscinia megarhynchos*. *Ibis,* 152(2), 335-346.

Johnston, A. (2009). Demographic analsis of the impact of conservation action on Stone-curlew populations. PhD thesis. Cambridge: University of Cambridge.

Marsden, K. (2017). The effect of ground disturbance on soil nutrients on lowland grass heaths in Breckland, East Anglia. Master's Thesis. Norwich: University of East Anglia.

NSRI (2014). National soil map of England and Wales - NATMAP, 1:250,000 Scale, Cranfield University, Bedfordshire. http://www.landis.org.uk (accessed July 2014).

Panter, C.J., Mossman, H.L. & Dolman, P.M. (2013). *Stanford Training Area (STANTA) biodiversity audit to support grass heath management*. University of East Anglia, Norwich.

Rodwell (1992). *British Plant Communities. Volume 3: Grasslands and Montane Vegetation*. Cambridge University Press, Cambridge.

Sheail, J. (1979). Documentary evidence of the changes in the use, management and appreciation of the grass-heaths of Breckland. *Journal of Biogeography,* 6(3), 277-292.

Sibbett, N. (2007). *Historical changes in land-use, Brettenham Heath*. Natural England unpublished report.

Webb, N.R. (1986). *Heathlands (New Naturalist)*. Collins, Glasgow.

Webb, N.R. (1998). The traditional management of European heathlands. *Journal of Applied Ecology,* 35(6), 987-990.

Chapter 3

Experimental evidence that ground-disturbance benefits Woodlark *Lullula arborea*

Robert W. Hawkes[a], Jennifer Smart[b,c], Andy Brown[d], Helen Jones[b], and Paul M. Dolman[a]

[a]*School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK*

[b]*RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK*

[c]*School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK*

[d]*Natural England, Suite D Unex House Bourges Boulevard, Peterborough, PE1 1NG, UK*

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Abstract

To determine whether ground-disturbance increased Woodlark *Lullula arborea* abundance, we examined responses over three years to four treatments varying in establishment method (shallow- or deep-cultivated) and complexity (homogenous or ‘complex-mosaics’ comprising fallow and recently-cultivated subplots), plus controls, replicated across the UK’s largest lowland grass-heath. Abundance increased through the study, and was higher on plots closer to woodland and across all treatments. Within complex-mosaics, Woodlark preferentially used recently-cultivated subplots over one- or two-year-old fallows. Regardless of treatment detail, providing suitable foraging habitat within *c*. 45 m of woodland, through annual ground-disturbance, can increase Woodlark abundance within lowland grass-heaths characterised by closed swards.

Keywords: Conservation management, grass-heath, lowland heathland, semi-natural habitat

3.1 Introduction

Management interventions for birds have been extensively tested in farmland and woodland (e.g. Siriwardena *et al.* 2007; Holt, Fuller & Dolman 2014), but other lowland semi-natural habitats have received less attention. While many studies use observed relationships between species and habitat composition to inform management (van den Berg, Bullock, Clarke, Langston & Rose 2001; Border, Henderson, Redhead & Hartley 2017), experiments that test multiple treatments across different habitats are needed to support best practice (Buckingham, Atkinson & Rook 2004).

The Woodlark's *Lullula arborea* global population is concentrated in Europe (SPEC 2; Burfield & Van Bommel 2004) where it is protected under Annex 1 of the EC Birds Directive (EC 1979). Although the British population underwent a partial recovery during the late 20th century (Conway *et al.* 2009), declines in some areas have resumed and the species is classified as Threatened (Stanbury *et al.* 2017). Most territories in Britain are associated with lowland heathland or plantation forestry (67 % and 32 % respectively, Conway *et al.* 2009), where the species uses taller vegetation for nesting (Mallord, Dolman, Brown & Sutherland 2007a) and bare-open foraging areas (Bowden 1990; Mallord, Dolman, Brown & Sutherland 2007b). Declines may be linked to the cessation of dynamic processes (e.g. rabbit grazing, turf/litter removal, episodic-cultivation) which historically created early-successional mosaics within lowland heathland. Although the importance of bare ground is known, it is not clear whether treatments that open-up closed swards promote population recovery, nor whether disturbance treatment or habitat type matters.

We assessed the effects of ground-disturbance on Woodlark as an integral part of an extensively replicated, multi-taxa, landscape-scale experiment in the UK's largest lowland grass-heath (involving 102 plots, totalling 248 ha, within 3,850 ha of grass-heath). We examined territory numbers (hereafter 'abundance') and habitat use across four treatments, differing in establishment method (shallow- or deep-cultivated) and complexity (annually treated 'homogenous plots'; or 'complex-mosaic plots', comprising subplots varying in age and disturbance frequency), while controlling for vegetation type, year and landscape features. We *a priori* predicted that: (1) complex-mosaics would support the greatest increase in abundance, and (2) recently-cultivated subplots would be preferred within complex-mosaics.

3.2 Methods

3.2.1 Study site

The study was carried out from 2015-2017 on the Stanford Military Training Area (STANTA; 0°76'E, 52°51'N, 3,500 ha), Bridgham Heath (0°83'E, 52°44'N, 150 ha) and Brettenham Heath (0°83'E, 52°43'N, 200 ha), in Eastern England (Fig. S.3.1; for site details, see Appendix S.3.1).

3.2.2 Experimental design

Across these sites, 66 replicate 2 ha plots (33 deep-cultivated, 33 shallow-cultivated) and 36 uncultivated controls were established in early 2015 (for treatment details, see Appendix S.3.2). Treatments were repeated in early 2016 and 2017, maintaining 26 as 2 ha homogenous plots (13 deep-cultivated, 13 shallow-cultivated) treated annually in the same location, and diversifying 40 as complex-mosaics (20 deep-cultivated, 20 shallow-cultivated), again cultivating 2 ha each year, but half-overlapping and half first-time-cultivation, building up a rotational mosaic of subplots that varied in frequency of, and time since, cultivation. Each complex-mosaic comprised three 1 ha subplots in 2016 and four 1 ha subplots in 2017, that included fallowed (in 2016 one-year-old; in 2017 both one- and two-year-old), first-time-cultivated, and annually-cultivated (Fig. 3.1). All homogenous and complex-mosaic plots received 2 ha of ground-disturbance treatment each year, representing similar cost; but while homogenous plots remained 2 ha in area, complex-mosaics increased to 3 ha in 2016 and 4 ha by 2017. To account for differences in treatment extent between designs and years, monitoring consistently examined a 4 ha area centred on the plot (whether homogenous, complex-mosaic or control), but including sufficient untreated grass-heath to complete 4 ha.

Plots were located in grass-heath, often excluding, but close to (95% within 16m), scattered trees or scrub (*Ulex europaeus*). Potential for unexploded ordnance precluded placing ground-disturbance plots in the central ‘impact area’ of STANTA, restricting treatments to the outer areas of this site and Bridgham and Brettenham Heath (Fig. S.3.1). Control plots were also located in these areas (*n* = 16), and the impact area (*n* = 20). Potential plot locations were mapped based on: (1) underlying soil type (National Soil Resources Institute, Cranfield University), (2) age since last cultivation (Sheail 1979), and (3) indicator plant composition before treatment (Table S.3.1). Using this information, and within constraints of ordnance, plots were allocated randomly to four vegetation strata: (1) calcareous grass-heath of any age (hereafter ‘calcareous grass-heath’), (2) young grass-heath, (3) intermediate grass-heath, and (4) ancient acid grass-heath (Table S.3.2). Treatments and controls (five groups) were distributed similarly with respect to Latitude and Longitude (Kruskal-Wallis, $H = 2.65$, $P = 0.62$; $H = 1.23$, $P = 0.87$, respectively; $n = 102$); but due to aggregated distributions of soil types and grass-heath ages, vegetation strata (four groups) was not (Latitude, $H = 19.26$, $P < 0.001$; Longitude, $H = 47.19$, $P < 0.001$; $n = 102$).

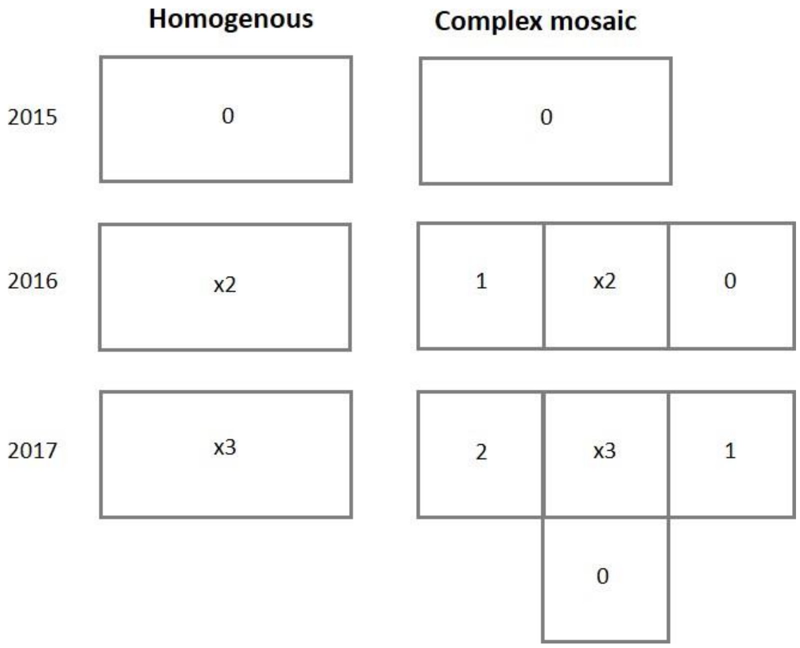

Figure 3.1. Development of homogenous and complex-mosaic plots over three years (2015-2017). Numbers denote the age/disturbance frequency of each plot/subplot; 0: first-time-cultivated; 1: one-year-old fallow; 2: two-year-old fallow; x2 and x3: annually-cultivated in each of two and three consecutive years, respectively. See Figure S2 for example photographs and % bare ground estimates for each complex-mosaic sub-treatment in 2017.

3.2.3 Territory mapping and subplot use

In each year, three 40-minute visits were made to each 4 ha plot between 14 March and 26 June (days between visits: mean 24 ± 11 sd) between dawn and 11:00 during still, dry mornings (Beaufort wind force < 4). During each visit, we recorded Woodlark location and behaviour, initially scanning from a vehicle positioned > 100 m away, followed by walking through each plot's edge and centre. For complex-mosaics, we also recorded the number of registrations on each subplot; multiple subplots used by the same individual were included as separate registrations. Observations were restricted to vehicles on 20 of 936 plot-visits (3 in 2015, 10 in 2016, 7 in 2017; affecting 4 treatment replicates, but not controls) to minimise disturbance to Eurasian Stone-curlew *Burhinus oedicnemus*; on these occasions, vehicles were repositioned during visits to maximise coverage.

Territories were subsequently identified across the three visits, for each year, following Conway *et al.* (2009). We recognised territories with registrations (on, or singing above, the plot) from at least two separate visits, but excluded males apparently drawn in to interact briefly with a resident bird.

3.2.4 Data analysis

Separate analyses considered abundance per plot-year: (1) across all three years (2015-2017; with all treated plots classified as homogeneous in 2015, then homogenous or complex-mosaic thereafter), and (2) during the last two years (2016-2017), when complex-mosaics had accrued (though only in 2017 were all subplots available). Generalised Linear Mixed Models (GLMM), with Poisson error and log-link, considered fixed effects of treatment (5 categories: control, cultivation-method x homogenous vs complex-mosaic), vegetation strata (4 categories), and year (2 or 3 categories), with plot identity as a random factor. Distance from plot edge to the nearest woodland (> 0.5 ha) (potential refuge, Schaefer & Vogel 2000) and Thetford Forest (Fig. S.3.1) (potential population source, Wright, Hoblyn, Sutherland & Dolman 2007), were both entered as covariates.

For occupied complex-mosaics in 2017 only, we related the maximum number of registrations (over three visits) per subplot to sub-treatment (4 categories: first-time-cultivated, annually-cultivated, one-year or two-year fallow), in a GLMM with Poisson error, that incorporated fixed effects of cultivation-method (2 categories: shallow- vs deep-cultivation) and vegetation strata, with plot identity as a random factor.

For parsimony, initial categories within vegetation strata, treatment, and sub-treatment variables were combined if: (i) parameter estimates were initially similar, and (ii) their combination did not reduce model performance (Akalike's Information Criterion corrected for small sample size, AICc, either reduced, or increased ≤ 2; Burnham & Anderson 2002). First, vegetation strata categories were examined within abundance analyses (2015-2017 and 2016-2017) and subplot models that incorporated all other variables. Next, treatment and sub-treatment categories were simplified where possible, within 2016-2017 abundance and 2017 subplot models. Treatment categories were not combined in 2015-2017 abundance models as complex-mosaics were not present every year; thus combined categories would have been confounded with year. Following simplification, for each analysis, the set of candidate models comprising all possible variable combinations were examined using package 'lme4' (Bates, Maechler, Bolker & Walker 2017). Models were accepted as best if ΔAICc (difference in AICc) relative to all other candidate models was > 2. Where more than one model lay within 2 AICc, we used multi-model inference to estimate model-averaged coefficients, unconditional standard errors, and 95% confidence intervals across those competing models < 2 ΔAICc, accounting for their Akaike weights (following Burnham & Andserson 2002), using the package 'MuMIn' (Barton 2018). Candidate variables were deemed to be supported if confidence intervals of the model-averaged parameter did not span zero. Spatial autocorrelation of modelled residuals were examined by Moran's I, separately for each year, using the package 'Ape' (Paradis, Claude & Strimmer 2004). All models were run in R (R Core Team 2015).

3.3 Results

In 2015, 2016 and 2017, 10, 25 and 39 territories were associated with plots, respectively; all occupied plots were within 45 m of woodland. Initial simplification of vegetation strata in abundance models (2015-2017 and 2016-2017) supported combining calcareous with intermediate and young grass-heath (retaining ancient acid as distinct), whilst simplification in 2017 subplot models combined calcareous with intermediate and ancient acid grass-heath (retaining young grass-heath as distinct; Table S.3.3). Subsequent simplification of 2016-2017 abundance models combined all ground-disturbance treatments: cultivation-method x homogenous/complex-mosaic, simplified to treated vs. control (though models retaining complex-mosaics/homogenous were similar; $\Delta AIC_c = 1.9$; Table S.3.3). Simplification of 2017 subplot models combined first-time- with annually-cultivated (hereafter 'recently-cultivated'), and one-year-old with two-year-old fallows (hereafter 'fallows'; Table S.3.3).

Multi-model inference was undertaken for both abundance analyses (2015-2017 and 2016-2017) as there were several candidate models where < 2 ΔAICc (Table S.3.4). For 2015-2017, abundance increased with year, and was higher on all treated plots (compared to controls) and plots closer to woodland (Fig. 3.2 & Table S.3.5). Multi-model inference from 2016-2017 was similar (though treatment categories were combined in this model), but with no support for a difference between the two years (Table S.3.5). Although vegetation strata and distance to Thetford Forest were included in averaged models (2015-2017 and 2016-2017), neither effect was supported (Table S.3.5). Predictions from the 2016-2017 model showed a higher abundance on treatment plots in 2017, on calcareous, intermediate or young grass-heath, 18 m from woodland (median plot-woodland distance), compared to controls (treatment, 0.59, 95% CI 0.37–0.81; control, 0.15, 95% CI 0.03–0.27), whilst plots double this distance from woodland (36 m) had a lower abundance (treatment, 0.36, 95% CI 0.18–0.53; control, 0.09, 95% CI 0.01–0.17; Fig. 3.3). Model averaged residuals from the 2015-2017 analyses were spatially autocorrelated (although only in 2017, where Moran's I was small but significant; Moran's I = 0.04, $P = 0.009$), suggesting some variation attributable to a spatially correlated factor not considered in the modelling; nevertheless, we consider inference robust, as treatments and controls were distributed randomly in the landscape and balanced across vegetation strata (Table S.3.2), and effects of treatment and distance to woodland were consistent with the 2016-2017 model (where there was no spatial autocorrelation).

In 2017, Woodlark were recorded on 21/40 complex-mosaic plots. The best supported model (Table S.3.4), showed more registrations in recently-cultivated than fallow subplots (Fig. 3.4 & Table S.3.6), and on calcareous, intermediate and ancient acid grass-heath (cultivation-method was not supported). Model residuals were not spatially autocorrelated.

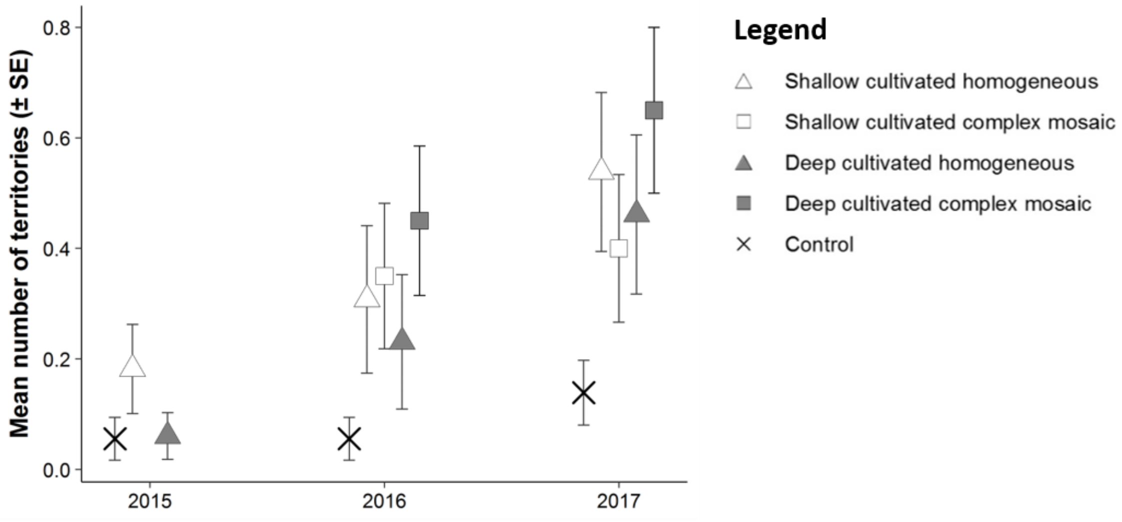

Figure 3.2. Mean (± se) number of Woodlark territories per plot (*n* = 102) for ground-disturbance treatments and controls in each of 2015, 2016 and 2017.

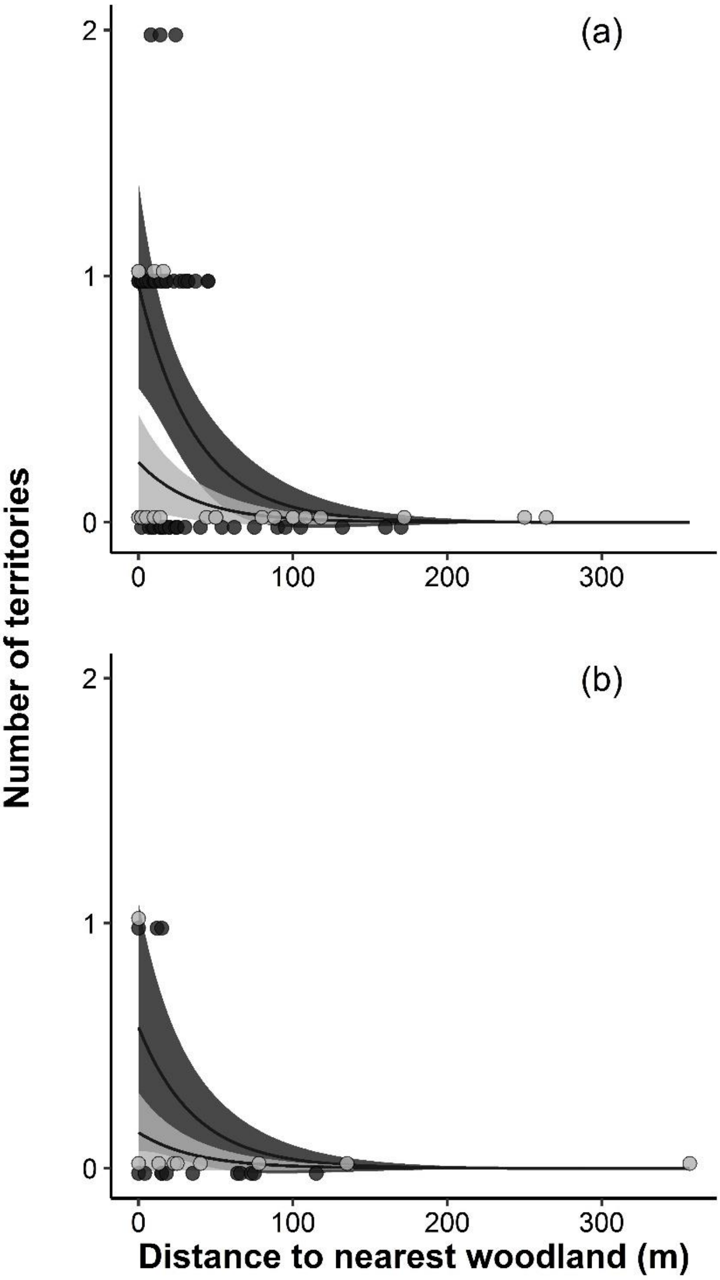

Figure 3.3. Predicted Woodlark *Lullula arborea* abundance in 2017 (the final year of the experiment) across treated (dark grey, *n* = 66) and control (light grey, *n* = 36) plots in relation to distance to the nearest woodland, for (a) calcareous, intermediate and young grass-heath and (b) ancient acid grass-heath. Predictions are based on multi-model inference (Table S.3.5). Lines and shading represent predicted means and 95% confidence intervals, respectively. Circles show individual data points.

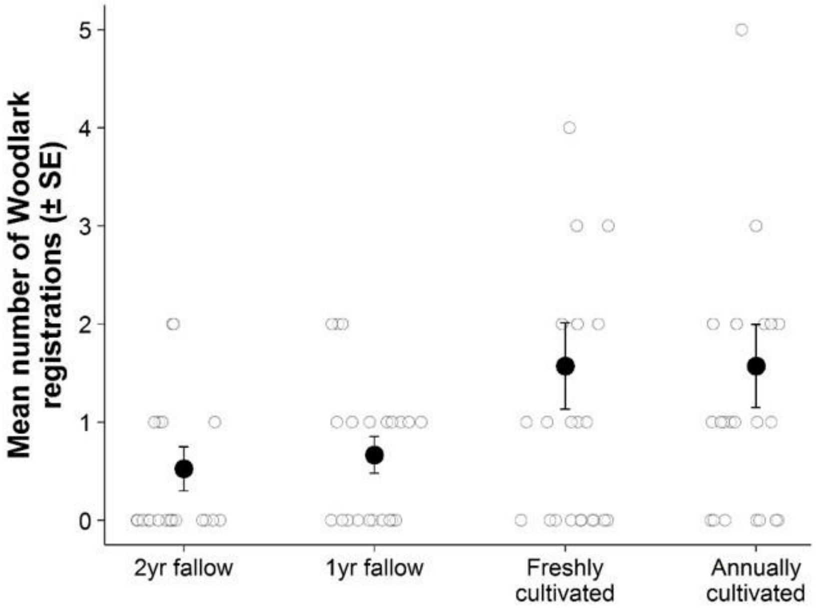

Figure 3.4. Mean number of Woodlark registrations per sub-treatment (filled symbol) across 84 subplots from 21 occupied complex-mosaic plots in 2017 (11 deep-cultivated, 10 shallow-cultivated). Bars represent ± se, unfilled circles show individual data points.

3.4 Discussion

Through an extensively replicated landscape-scale experiment, we have demonstrated that Woodlark responded positively to all ground-disturbance treatments, preferred plots closer to woodland, and selected recently-cultivated subplots within complex-mosaic treatments. Previous research has shown Woodlark require bare-open areas for foraging (Bowden 1990; Sitters *et al.* 1996; Mallord *et al.* 2007b; Arlettaz *et al.* 2012), but as far as we are aware, this is the first time numbers have been influenced experimentally through mechanical interventions.

Contrary to our *a priori* prediction, when all treatment combinations were available (2016-2017), abundance was greater on both ‘shallow and deep-cultivated treatments’ and ‘homogenous and complex-mosaic plots’, compared to controls, but these treatments did not differ from each other. This might be because: (i) both cultivation-methods created suitable foraging habitat, and (ii) recent-cultivation in a matrix of fallows (complex-mosaics) offers little by way of additional resource to recent-cultivation in a matrix of grass-heath (homogenous plots). Within complex-mosaics, their preference for the barer recently-cultivated subplots (Fig. S.3.2) is consistent with a study from Switzerland, which showed *c*. 50% ground vegetation cover is optimal for foraging Woodlark (Arlettaz *et al.* 2012).

The increase from 2015-2017 was attributed to cumulative colonisation as individuals discovered treated plots, consistent with adult fidelity and the known scale of natal dispersal (e.g. up to 11 km; Bowden & Green 1992). We are confident this accumulation of territories was not due to the increasing size and complexity of the complex-mosaics, as abundance was similar between treatments.

Consistent with evidence from Iberia, where colonisation of previously open habitats by woody vegetation benefitted Woodlark (Sirami, Brotons & Martin 2007), our results demonstrated a preference for plots close to woodland. Schaefer and Vogel (2000) explored the ecological function of field-forest ecotones for Woodlark, and showed birds fly towards forest when disturbed, stating 'on closer examination of anti-predation strategies it became clear that forest edge is not a factor of woodlark-territories, but the habitat of that species.' In Britain, Woodlark are regarded as a species of open-heath and clear-fell forestry; however, their association with woodland edge is important.

3.5 Conservation recommendations

Our experiment suggests that ground-disturbance could represent an important conservation prescription for Woodlark within other lowland grass-heaths. Since all treatments involved annual disturbance, and given their preference for recently-cultivated subplots, annual-cultivation may be necessary (although methods which retain bare ground for longer may require less frequent intervention), regardless of establishment method (complex-mosaic or homogenous; shallow-cultivated or deep-cultivated). Interventions should be within *c*. 45 m of woodland, but this may deter other potential beneficiaries that prefer open habitats (e.g. Stone-curlew, Johnston 2009).

Although Woodlark responded positively to all treatments, the multi-taxa consequences of this management are unclear, although autoecological information indicates it will benefit many scarce species (Dolman, Panter & Mossman 2012; Pedley, Franco, Pankhurst & Dolman 2013). We thus advise caution in using a single ground-disturbance prescription until the wider results of our experiment are available.

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Reference

Arlettaz, R., Maurer, M.L., Mosimann-Kampe, P., Nusslé, S., Abadi, F., Braunisch, V. & Schaub, M. (2012). New vineyard cultivation practices create patchy ground vegetation, favouring Woodlarks. *Journal of Ornithology,* 153(1), 229-238.

Barton, K. (2018). Multi-Model Inference. *R package Version 1.42.1*. available at: https://cran.r-project.org/web/packages/MuMIn/ (accessed 23 September 2018).

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2017). Linear mixed-effects models using 'Eigen' and S4. *R package Version 1.1-1.5*. Available at: https://cran.r-project.org/web/packages/lme4/ (accessed May 2018).

Border, J.A., Henderson, I.G., Redhead, J.W. & Hartley, I.R. (2017). Habitat selection by breeding Whinchats *Saxicola rubetra* at territory and landscape scales. *Ibis,* 159(1), 139-151.

Bowden, C. (1990). Selection of foraging habitats by Woodlarks (*Lullula arborea*) nesting in pine plantations. *Journal of Applied Ecology,* 27, 410.

Bowden, C.G.R. & Green, R.E. (1992). The Ecology and management of Woodlarks on pine plantations in the Thetford and Sandlings forests. Unpublished RSPB report. Sandy.

Buckingham, D.L., Atkinson, P. & Rook, A.J. (2004). Testing solutions in grass-dominated landscapes: A review of current research. *Ibis,* 146, 163-170.

Burfield, I. & Van Bommel, F. (2004). *Birds in Europe: population, estimates, trends and conservation status*. Birdlife International, Cambridge.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York.

Conway, G., Wotton, S., Henderson, I., Eaton, M., Drewitt, A. & Spencer, J. (2009). The status of breeding Woodlarks *Lullula arborea* in Britain in 2006. *Bird Study,* 56(3), 310-325.

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology,* 49, 986-997.

Holt, C.A., Fuller, R.J. & Dolman, P.M. (2014). Exclusion of deer affects responses of birds to woodland regeneration in winter and summer. *Ibis,* 156(1), 116-131.

Johnston, A. (2009). Demographic analsis of the impact of conservation action on Stone-curlew populations. PhD thesis. Cambridge: University of Cambridge.

Mallord, J.W., Dolman, P.M., Brown, A. & Sutherland, W.J. (2007a). Nest-site characteristics of Woodlarks *Lullula arborea* breeding on heathlands in southern England: are there consequences for nest survival and productivity? *Bird Study,* 54(3), 307-314.

Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. (2007b). Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology,* 44(1), 185-195.

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics,* 20(2), 289-290.

Pedley, S.M., Franco, A.M.A., Pankhurst, T. & Dolman, P.M. (2013). Physical disturbance enhances ecological networks for heathland biota: A multiple taxa experiment. *Biological Conservation,* 160, 173-182.

R Core Team (2015). *R: a language and environment for statistical computing. Version 3.2.2*. R Foundation for Statistical Computing, Vienna.

Schaefer, T. & Vogel, B. (2000). Why do Woodlarks need field-forest ecotones? — An analysis of possible factors. *Journal of Ornithology,* 141(3), 335-344.

Sheail, J. (1979). Documentary evidence of the changes in the use, management and appreciation of the grass-heaths of Breckland. *Journal of Biogeography,* 6(3), 277-292.

Sirami, C., Brotons, L. & Martin, J. (2007). Vegetation and songbird response to land abandonment: From landscape to census plot. *Diversity and Distributions,* 13, 42-52.

Siriwardena, G.M., Stevens, D.K., Anderson, G.Q.A., Vickery, J.A., Calbrade, N.A. & Dodd, S. (2007). The effect of supplementary winter seed food on breeding populations of farmland birds: evidence from two large-scale experiments. *Journal of Applied Ecology,* 44(5), 920-932.

Sitters, H.P., Fuller, R.J., Hoblyn, R.A., Wright, M.T., Cowie, N. & Bowden, C.G.R. (1996). The Woodlark *Lullula arborea* in Britain: population trends, distribution and habitat occupancy. *Bird Study,* 43(2), 172-187.

Stanbury, A., Brown, A., Eaton, M., Aebischer, N., Gillings, S., Hearn, R., Noble, D., Stroud, D. & Gregory, R. (2017). The risk of extinction for birds in Great Britain. *British Birds,* 110, 502-517.

van den Berg, L.J.L., Bullock, J.M., Clarke, R.T., Langston, R.H.W. & Rose, R.J. (2001). Territory selection by the Dartford warbler (*Sylvia undata*) in Dorset, England: the role of vegetation type, habitat fragmentation and population size. *Biological Conservation,* 101(2), 217-228.

Wright, L.J., Hoblyn, R.A., Sutherland, W.J. & Dolman, P.M. (2007). Reproductive success of Woodlarks *Lullula arborea* in traditional and recently colonized habitats. *Bird Study,* 54, 315-323.

Chapter 3

Supplementary material

Appendix S.3.1. Site information

Appendix S.3.2. Treatments

Figure S.3.1. Study site

Figure S.3.2. Complex-mosaic subplots

Table S.3.1. Plant indicators

Table S.3.2. Strata

Table S.3.3. Model simplification

Table S.3.4. Candidate models

Table S.3.5. Abundance models

Table S.3.6. Subplot model

Appendix S.3.1

This study was carried out on the Stanford Military Training Area (STANTA), Bridgham Heath, and Brettenham Heath National Nature Reserve, in Eastern England (Fig. S.3.1). These sites are integral to the Breckland Special Protection Area (SPA) designated under the EC Birds Directive (EC 1979) to protect internationally important Woodlark *Lullula arborea*, European Nightjar *Caprimulgus europaeus* and Eurasian Stone-curlew *Burhinus oedicnemus* populations**.**

The Breckland biogeographic region of Eastern England has a semi-continental climate, sandy, nutrient-poor soils and a land use history characterised by intensive grazing of heathland and warrens (particularly on plateau and interfluves) and arable cultivation with extended fallow periods (Dolman & Sutherland 1992). Historically, although some episodes of arable intakes from heath or reversion of exhausted fields to grazing land occurred through the Medieval period, in response to fluctuation in population density and economies, many heaths were relatively long-lived within the landscape and persisted uncultivated until the 1800s (Dolman, Panter & Mossman 2010; Dolman, Panter & Mossman 2012). Thus some remaining grass-heaths may not have been cultivated for many centuries. Following widespread conversion of heathland to arable during parliamentary enclosures, subsequent large-scale abandonment of arable (in two main phases, the latter 19th century and then after creation of the military training area) allowed spontaneous regeneration of fallows that developed into grass-heath of varying age (Farrell 1989). Historic land use records from the Tithe Survey of 1846, the Ordnance Surveys of 1883 and 1904 and the Land Utilization Survey of 1932, allowed us to classify grass-heath age (i.e. time since last cultivation) since 1846. For the Stanford Training Area (STANTA) these land use records are summarised by Sheail (1979), and for Bridgham and Brettenham Heath these records were held by the Norfolk Historic Environment team.

Across the study sites the synergistic influences of soil (acidic brown sand, calcareous sand, and rendzina), historic land use and contrasting grass-heath age (young, 86 – 114 years; intermediate, 115 – 171 years, and ancient ≥ 171 years), have shaped plant assemblages that span ecological gradients. Composition varies from calcareous grass-heath on shallower rendzina (e.g. *Festuca ovina, Hieracium pillosela, Thymus praecox/pulegioides* calcareous grassland), through assemblages characterized by sporadic presence of calcareous species and more nutrient-demanding species such as *Holcus* spp., creeping thistle *Cirsium arvense*, and nettle *Urtica dioica* predominant on grasslands developed following arable use (including deep ploughing) until 1900-1940; areas of intermediate age cultivated earlier during the 19th century (that were often 'marled' through surface application of chalk rubble to ameliorate soil acidity); through to grass-heath on acidic podzols not cultivated since at least 1846 and typically dominated by *Deschampsia flexuosa* and *Calluna vulgari*a. Older heath is characterised by an accumulation of organic litter, areas of *Ulex europaeus*, or bracken *Pteridium aquilinum*, and swards dominated by large, mature tussocks of *Deschampsia flexuosa* (considered indicative of higher nutrient states and a phase shift from mineral soil dwarf-shrub to nutrient-impacted grass-dominated states; Heil & Diemont 1983; Heil & Bruggink 1987; Rodwell 1992; Diemont 1994). We stratified experimental treatments and controls across four vegetation strata, based on vegetation composition prior to treatment (see Table S.3.1), between: (1) calcareous grass-heath of any age, (2) young grass-heath, (3) intermediate grass-heath, and (4) ancient acid grass-heath (see Table S.3.2 for classification criteria)

From the early Medieval period, grass-heaths in Breckland were partitioned between sheep-walks and areas of intensively managed rabbit *Oryctolagus cuniculus* warren (Sheail 1979). Although sheep numbers declined in the 19th century, rabbit numbers remained high until the mid-20th Century, and recovered following myxomatosis (Dolman & Sutherland 1992). STANTA supported populations of shingle nesting or short-sward species including Common Ringed Plover, *Charadrius hiaticula* and Northern Wheatear *Oenanthe oenanthe* into the mid-20th century and 1980's respectively (Dolman & Sutherland 1992). In the early 1980's, bulldozing of warrens and intensive rabbit control substantially reduced rabbit numbers (Panter, Mossman & Dolman 2013). Sheep management comprises a hefted system, with relatively low-density (approximately one ewe per ha) and supplementary feeding, and does not exert the grazing pressure of previous centuries. Bracken on STANTA is managed annually by mechanical cutting and aerial herbicide application.

On Bridgham and Brettenham heath sheep grazing has been established since 1990 (Bridgham) and 1982 (Brettenham), following a period of little conservation management, including stock removal, during the 1970's and 1980's. During this period scrub regenerated across both sites (predominately birch *Betula pendula*) and bracken predominated over most of Bridgham (Levett pers. comm. & Sibbett 2007); though since the 1990's targeted scrub removal has occurred, and bracken has been managed annually on Brettenham by mechanical cutting and periodically on Bridgham by herbicide treatment (though bracken is now treated with herbicide annually on Brettenham since 2016, and cut annually on Bridgham since 2010).

STANTA, Bridgham and Brettenham now support long-established, relatively high-biomass (roots, litter and above ground vegetation) closed acidic grassland. Rabbit numbers have declined further over the past two decades, resulting in a loss of bare ground and increased sward height (Panter *et al.* 2013). Localised areas of heavy rabbit grazing were present on Brettenham and Bridgham during this study (2015-2017), but away (at least 200 m) from treatment and control plots.

Appendix S.3.2

Two cultivation methods where trialled here; shallow- and deep-cultivation. Shallow-cultivations were created with a rotary rotovator, which broke up and turned the top 10-13 cm of the surface leaving bare soil interspersed with chunks of turf. Following usual conservation management practice, shallow-cultivated plots were immediately retreated with a second pass if the first pass failed to create sufficient exposed substrate. Deep-cultivations were created with an agricultural plough, which inverted soil and vegetation to 25-28 cm leaving a bare mineral surface.

In each year (2015-2017) cultivation occurred between December and March, with the exception of the shallow-cultivated plots in 2015, which were established in January on Brettenham heath (3 plots), and in April (25 plots) and May (5 plots) on STANTA and Bridgham heath due to a delay imposed by equipment procurement. Since most shallow-cultivated plots were established during the 2015 Woodlark *Lullula arborea* survey period, we left at least one week between plot establishment and the first survey to allow for territory settlement.

Four plots (two shallow-cultivated and two deep-cultivated) were located within areas of dense *Calluna vulgaris*; these were topped with a tractor-mounted flail prior to disturbance. Following usual practice, plots with regenerating *Cirsium arvense*, *Cirsium vulgare* or *Urtica dioica* were topped (in 2015 and 2016) or treated with a herbicide weed wipe (in 2017). Weed management always occurred in late June and July after Woodlark surveys were complete.

For the complex-mosaic plots, which comprised of overlapping subplots varying in age and disturbance frequency in 2016 and 2017 (see Fig. 3.1), archaeological restriction or landscape barriers meant some subplots were smaller than 1 ha (mean subplot area: 0.97 ha ± 0.05 sd). However, subplot size was similar across sub-treatment categories (4 levels; Kruskal-Wallis $H = 3.5$, $P = 0.32$, *df* error = 157).

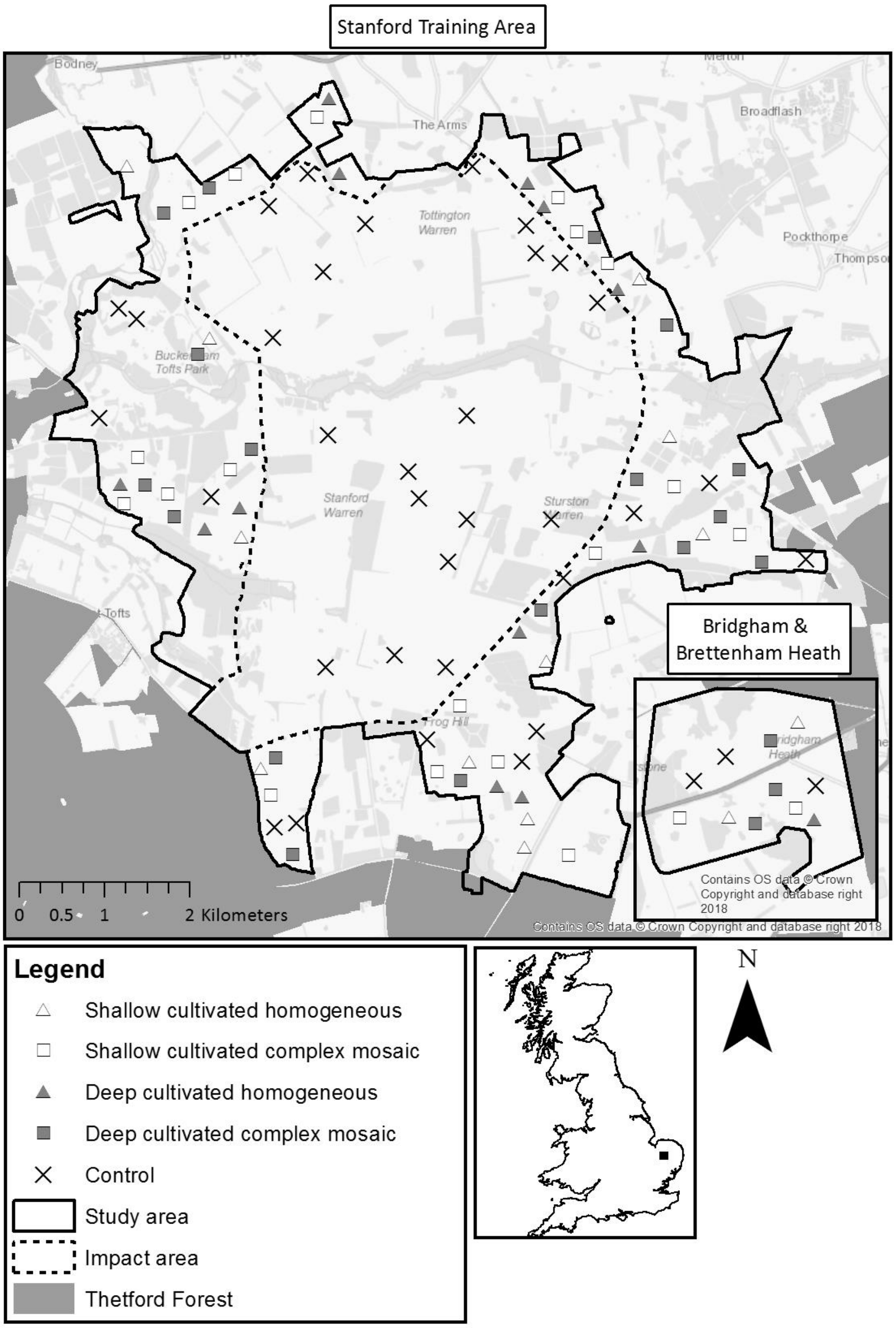

Figure S.3.1. Locations of treatment and control plots (n = 102) within the Stanford Training Area, Bridgham and Brettenham heaths, showing the impact area (where ground-disturbance was precluded). Complex-mosaics occurred in 2016 and 2017, but were homogenous in 2015. Insert shows the location of the study area.

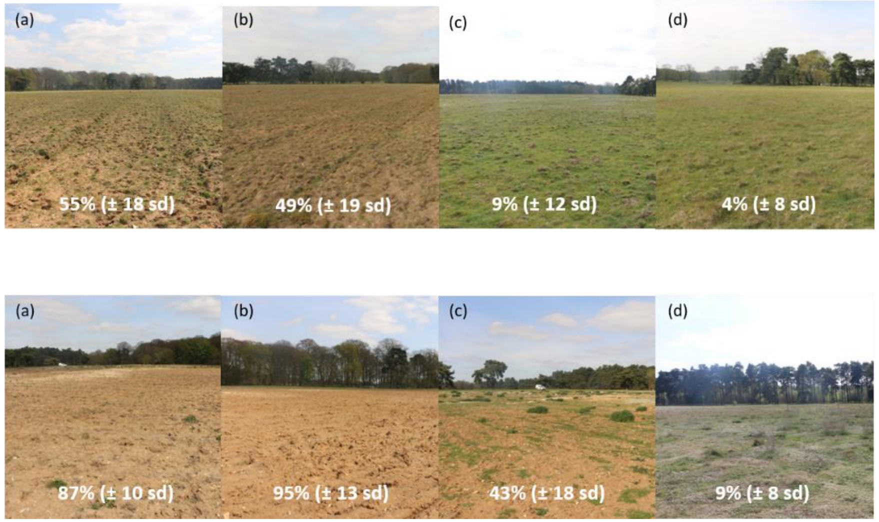

Figure S.3.2. Images of shallow-cultivated (upper row) and deep-cultivated (lower row) complex-mosaic plots, showing all sub-treatments present in April 2017 (when all combinations had accrued). Letters denote sub-treatment identity across both cultivation methods: (a) disturbed in each of three consecutive years (annually-cultivated), (b) first-time-cultivated, (c) one-year-old fallow and (d) two-year-old fallow. The mean % bare cover for each sub-treatment is given at the foot of each photo; estimates were calculated from all subplots (160 subplots from 40 complex-mosaics) in June 2017 along two parallel 100 m transects (30-33 m apart) per subplot, recording incidence of bare substrate (tallying 0-42 whether the tip of a dowel, diameter 25 mm, at each point covered over 50% bare substrate) at each of 42 evenly spaced points, 21 points per transect. Combining of sub-treatment categories to give recently-cultivated subplots (a and b, shallow- and deep-cultivated, combined) and fallow subplots (c and d, shallow- and deep-cultivated, combined) (see Table S.3.3 for combination criteria) gave an average of 71% (± 25 sd) and 16% (± 20 sd) bare substrate cover across the recently-cultivated and fallow subplots, respectively.

Table S.3.1. Vascular plant indicator species associated with acidiphilous or calcicolous grass heath, recorded during baseline surveys to inform the vegetation strata attributable to each plot (see Table S.3.2).

Influence	Indicator species
Acidophilous	*Calluna vulgaris* (2), *Galium saxatile* (3), *Rumex acetosella* (4), *Teucrium scorodonia* (4)
Calcicolous	*Thymus* spp (6-8), *Pilosella officinarum* (7), *Galium verum* (6)

Parentheses denote Ellenberg indicator scores for soil reaction: 1= extremely acidic, 5 = mildly acidic, 9 = alkaline (Hill, Preston & Roy 2004)

Table S.3.2. Vegetation strata categories, their definition, and number of replicate ground-disturbance and control plots per strata. Grass-heath ages are taken from (Sheail 1979) based on the Tithe Survey of 1846, the Ordnance Surveys of 1883 and 1904 and the Land Utilization Survey of 1932.

Strata group	Definition	Number of replicate plots				
		Control	Deep-cultivated complex mosaic	Shallow-cultivated complex mosaic	Deep-cultivated homogenous	Shallow-cultivated homogenous
Calcareous grass-heath of any age	Grass-heath of any age (Sheail 1979) located on well-drained brown calcareous sands or rendzinas (soil association codes: 0521 and 0343f, respectively, Cranfield University 2018)	9	5	5	4	4
Young grass-heath	Young grass-heath (arable between 1904-1932, <114 years old) located on acidic brown sands (soil association code: 0554b), with evidence of historic soil amelioration through ‘marling’ (both acidiphilous and calcareous vascular plant indicators present, see Table S.3.1)	10	6	5	6	5
Intermediate grass-heath	Mostly intermediate aged grass-heath (arable at 1846 but not by 1904, 115-171 years old, 16 plots), but some ancient grass-heath (no evidence of cultivation since at least 1846, > 171 years old, 4 plots), located on acidic brown sands, with evidence of historic soil amelioration through ‘marling’	8	4	5	1	2
Ancient acid grass-heath	Mostly ancient grass-heath (20 plots), but some intermediate aged grass-heath (3 plots), located on acidic brown sands, with no evidence of historic soil amelioration through marling (infrequent calcareous indicator plants). Two plots were mapped as rendzinas and one plot as deep permeable peaty sands affected by groundwater (soil association code: 0861b); however, their plant community and soil pH were characteristic of this strata (confirmed through indicator plant and soil surveys; Marsden 2017)	9	5	5	2	2

Table S.3.3. Model simplification, combining categories within fixed effects, for Woodlark *Lullula arborea* territories (abundance, 2015-2017 and 2016-2017) per plot, or registrations (2017) per subplot. Categories were simplified for: (a) vegetation strata (across each of the three analyses: 2015-2017 abundance, 2016-2017 abundance, 2017 subplots), (b) treatment (2016-2017 abundance analysis, only) and (c) sub-treatment (2017 subplot analysis, only), from full models with all variables included. For each model the degrees of freedom (*df*), Akaike's information criterion with small-sample bias adjustment (AIC$_c$), and the difference in AICc value relative to the best model (ΔAIC$_c$) are shown. Shading denotes merged categories and coefficients and standard error are given.

a) Combining vegetation strata categories across each of the three analyses

AIC$_c$	ΔAIC$_c$	*df*	Vegetation strata levels			
			Young grass-heath	Calcareous grass-heath	Intermediate grass-heath	Ancient acid grass-heath
2015-2017 abundance models						
315.2	0	295	-2.64 ± 0.45*			-0.59 ± 0.34
319.1	3.9	293	-2.84 ± 0.54*	0.23 ± 0.35	0.26 ± 0.38	-0.40 ± 0.43
2016-2017 abundance models						
247.1	0	194	-1.82 ± 0.42*			-0.72 ± 0.38
251.6	4.5	192	-1.81 ± 0.52*	0.04 ± 0.37	0.01 ± 0.40	-0.74 ± 0.47
2017 subplot models						
209.3	0	77	-1.60 ± 0.48*	0.71 ± 0.36		
213.9	4.6	75	-1.58 ± 0.48*	0.79± 0.34	0.67 ± 0.39	0.54 ± 0.54

b) Combining treatment categories in the 2016-2017 abundance analysis**

AIC_c	ΔAIC_c	*df*	Treatment levels				
			Control	Deep-cultivated complex mosaic	Shallow-cultivated complex mosaic	Deep-cultivated homogenous	Shallow-cultivated homogenous
342.8	0	197	-1.84 ± 0.42*	1.36± 0.40			
344.7	1.9	196	-1.84 ± 0.42*	1.42 ± 0.41		1.26 ± 0.44	
247.1	4.3	194	-1.84 ± 0.41*	1.64 ± 0.43	1.17 ± 0.46	1.19 ± 0.51	1.33 ± 0.49

c) Combining sub-treatment categories in the 2017 subplot analysis**

AIC_c	ΔAIC_c	*df*	Sub-treatment levels			
			Two-year-old fallow	One-year-old fallow	First-time-cultivated	Annually-cultivated
206.6	0	79	-1.28 ± 0.39*		0.74 ± 0.26	
209.3	2.7	77	-1.60 ± 0.48*	0.56 ± 0.44	0.97 ± 0.42	1.14 ± 0.41

* Reference level (model intercept)

** Vegetation strata categories were merged in these models (following a)

Table S.3.4. Candidate models relating: (a) the number of Woodlark *Lullula arborea* territories (abundance) per plot (*n* = 102) for three years (2015-2017), to treatment, year, vegetation strata, distance to the nearest woodland (dist wood) and distance to Thetford Forest (dist forest) (n.b. treatment only contained three levels in 2015 as complex-mosaic treatments were yet to accrue), (b) abundance per plot for two years (2016 and 2017, when complex-mosaic treatments had accrued) to the same predictors, and (c) the number of registrations per subplot within occupied complex-mosaics, in 2017 only, to sub-treatment, cultivation-method and vegetation strata. For each candidate model the degrees of freedom (*df*), Akaike's information criterion with small-sample bias adjustment (AIC_c), the difference in AICc value compared to the most parsimonious model (ΔAIC_c), and the model weight (w_i) are shown. For simplicity, only models with < 10 ΔAIC_c are presented.

Candidate model	*df*	AIC_c	ΔAIC_c	w_i
a) 2015-2017 abundance models[1]				
Treatment + vegetation strata + year + dist wood	296	314.7	0.0	0.33
Treatment + year + dist wood	297	315.2	0.5	0.25
Treatment + vegetation strata + year + dist wood + dist forest	295	315.2	0.5	0.25
Treatment + year + dist wood + dist forest	296	316.3	1.6	0.14
Vegetation strata + year + dist wood + dist forest	299	321.5	6.8	0.01
Year + dist wood + dist forest	300	322.2	7.5	0.01
Vegetation strata + year + dist wood	300	322.6	7.9	0.01
Year + dist wood	301	322.6	7.9	0.01
b) 2016-2017 abundance models[1,3]				
Treatment + vegetation strata + year + dist wood + dist forest	197	242.8	0.0	0.27
Treatment + vegetation strata + dist wood + dist forest	198	243.8	0.9	0.17
Treatment + vegetation strata + year + dist wood	198	244.4	1.6	0.13
Treatment + year + dist wood + dist forest	198	244.5	1.6	0.12
Treatment + year + dist wood	199	244.9	2.1	0.10
Treatment + vegetation strata + dist wood	199	245.4	2.5	0.08
Treatment + dist wood + dist forest	199	245.4	2.6	0.08
Treatment + dist wood	200	245.9	3.1	0.06
c) 2017 subplot models[2,4]				
Sub-treatment + vegetation strata	80	204.5	0.0	0.53
Sub-treatment + vegetation strata + cultivation-method	79	206.6	2.1	0.19
Sub-treatment	81	206.8	2.3	0.17
Sub-treatment + cultivation-method	80	208.6	4.1	0.07
Vegetation strata	81	211.6	6.5	0.02
Vegetation strata + cultivation-method	80	213.0	8.4	0.01
Intercept only	82	213.3	8.8	0.01

The following categories were combined within categorical fixed effects (Table S.3.3): [1] vegetation strata: calcareous with intermediate and young grass-heath, vs ancient acid grass-heath; [2]vegetation strata: calcareous with intermediate and ancient acid grass-heath, vs young grass-heath; [3]treatment: all treatment plots combined, vs control plots; [4]sub-tratment: first-time-cultivated with annually-cultivated, and one-year-old fallow with two-year-old fallow

Table S.3.5. Parameter estimates from Generalised Linear Models relating: (a) the number of Woodlark *Lullula arborea* territories (abundance) per plot (*n* = 102) for three years (2015-2017), to treatment, vegetation strata, year, distance to the nearest woodland, and distance to Thetford Forest (n.b. treatment only contained three levels in 2015 as complex-mosaic treatments were yet to accrue), and (b) abundance per plot (*n* = 102), for 2016 and 2017, when complex-mosaic treatments had accrued, to the same predictors. For both analyses (2015-2017, and 2016-2017) coefficients, standard errors, and 95% Confidence Intervals (CI) were derived from multimodel inference across all competing models within 2 AICc (Akaike's information criterion with small-sample bias adjustment) of the most parsimonious, weighted by their AICc score (see Table S.3.4). Effects of candidate variables were deemed to be supported if confidence intervals of the model-averaged parameter did not span zero, bold type denotes these cases.

Parameter	Coefficient	SE	Lower 95% CI	Upper 95% CI
a) 2015-2017 abundance model*				
Intercept	-2.68	0.46	-3.58	-1.77
Treatment - Deep-cultivated complex-mosaic plots[1]	**1.45**	**0.40**	**0.67**	**2.24**
Treatment - Deep-cultivated homogenous plots[1]	**1.00**	**0.47**	**0.08**	**1.92**
Treatment - Shallow-cultivated complex-mosaic plots[1]	**1.25**	**0.41**	**0.45**	**2.05**
Treatment - Shallow-cultivated homogenous plots[1]	**1.21**	**0.45**	**0.32**	**2.09**
Vegetation strata – Ancient acid grass-heath[2]	-0.33	0.38	-1.08	0.42
Year – 2016[3]	**0.91**	**0.37**	**0.18**	**1.65**
Year – 2017[3]	**1.36**	**0.35**	**0.66**	**2.06**
Distance to nearest woodland	**-0.02**	**0.01**	**-0.04**	**-0.01**
Distance to Thetford Forest	-0.07	0.13	-0.34	0.19

Parameter	Coefficient	SE	Lower 95% CI	Upper 95% CI
b) 2016-2017 abundance model*				
Intercept	-1.79	0.43	-2.63	-0.94
Treatment – All treated plots combined[1]	**1.37**	**0.40**	**0.58**	**2.17**
Vegetation strata - Ancient acid grass-heath[2]	-0.54	0.43	-1.39	0.30
Year – 2017[4]	0.33	0.29	-0.24	0.91
Distance to nearest woodland	**-0.03**	**0.01**	**-0.04**	**-0.01**
Distance to Thetford Forest	-0.24	0.19	-0.62	0.13

*For parsimony, vegetation strata categories were combined in both models (a & b), and treatment categories were combined in (b) (Table S.3.3).
Reference categories for fixed factors are; [1]control plots, [2] young, intermediate and calcareous grass-heath combined, [3]2015, [4]2016

Table S.3.6. Best supported model relating the number of registrations per subplot, within occupied complex-mosaic plots (2017 only, *n* = 84 subplots, across 21 complex-mosaic plots) to sub-treatment and vegetation strata. Coefficients, standard errors, and 95% Confidence Intervals (CI) are shown. See Table S.3.4 for selection from candidate models. For parsimony, vegetation strata and sub-treatment categories were combined (Table S.3.3).

Parameter	Coefficient	SE	Lower 95% CI	Upper 95% CI
Intercept	-1.23	0.38	-2.06	-0.55
Sub-treatment – First-time-cultivated and annually-cultivated subplots combined[1]	0.74	0.26	0.24	1.26
Vegetation strata – intermediate, ancient acid, and calcareous grass-heath combined[2]	0.72	0.36	0.05	1.49

Reference categories for fixed factors are; [1]one- and two-year-old fallow sub-treatments combined, [2]yound grass-heath

References

Cranfield University (2018). The soils guide. Available at: www.landis.org.uk. Cranfield University, UK.

Diemont, W.H. (1994). Effects of removal of organic matter on the productivity of heathlands. *Journal of Vegetation Science,* 5(3), 409-414.

Dolman, P.M., Panter, C. & Mossman, H.L. (2010). *Securing biodiversity in Breckland: guidance for conservation and research. First report of the Breckland biodiversity audit*. University of East Anglia, Norwich.

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology,* 49, 986-997.

Dolman, P.M. & Sutherland, W.J. (1992). The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology,* 29(2), 402-413.

Farrell, L. (1989). The different types and importance of British heaths. *Botanical Journal of the Linnean Society,* 101, 291-299.

Heil, G.W. & Bruggink, M. (1987). Competition for nutrients between *Calluna vulgaris* (L.) Hull and *Molinia caerulea* (L.) Moench. *Oecologia,* 73(1), 105-107.

Heil, G.W. & Diemont, W.H. (1983). Raised nutrient levels change heathland into grassland. *Vegetatio,* 53(2), 113-120.

Hill, M., O., Preston, C., D. & Roy, D., B. (2004). *Attributes of British and Irish plants: status, size, life history, geography and habitats*. Centre for Ecology & Hydrology, Cambridgeshire.

Marsden, K. (2017). The effect of ground disturbance on soil nutrients on lowland grass heaths in Breckland, East Anglia. Master's Thesis. Norwich: University of East Anglia.

Panter, C.J., Mossman, H.L. & Dolman, P.M. (2013). *Stanford Training Area (STANTA) biodiversity audit to support grass heath management*. University of East Anglia, Norwich.

Rodwell (1992). *British Plant Communities. Volume 3: Grasslands and Montane Vegetation*. Cambridge University Press, Cambridge.

Sheail, J. (1979). Documentary evidence of the changes in the use, management and appreciation of the grass-heaths of Breckland. *Journal of Biogeography,* 6(3), 277-292.

Sibbett, N. (2007). *Historical changes in land-use, Brettenham Heath*. Natural England unpublished report.

Chapter 4

Effects of experimental land management on habitat use by Eurasian Stone-curlews

Robert W. Hawkes[a], Jennifer Smart[b,c], Andy Brown[d], Rhys Green[e], Helen Jones[b], and Paul M. Dolman[a]

[a]School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

[b]RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

[c]School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

[d]Natural England, Suite D Unex House Bourges Boulevard, Peterborough, PE1 1NG, UK

[e]Department of Zoology, University of Cambridge, Conservation Science Group, Cambridge, CB2 3EJ, UK

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Abstract

Effective conservation is often informed by focal species studies to identify beneficial land management interventions. For nocturnal or cryptic species, quantifying the use by individually-marked animals of habitats modified by interventions can allow unbiased assessment of their efficacy and identify other important habitats. Here, using a landscape-scale experiment, we examine whether interventions intended to create nesting habitat for the largely nocturnal Eurasian Stone-curlew *Burhinus oedicnemus* within semi-natural grassland also provide foraging habitat. GPS loggers were fitted to five adult Stone-curlews during the breeding season within an extensive area of semi-natural grassland (3,850 ha, hereafter 'grassland'), surrounded by a mosaic of arable cropland (total study area 118,600 ha). The largely closed-sward grassland was diversified by experimental ground-disturbance plots (the intervention) prior to this study. We used the GPS fixes to identify 1,881 foraging locations (510 during breeding and 1,371 post-breeding) across the grassland and surrounding landscape. Most foraging locations were close to the nest-site during breeding (90% within 1 km) or day-roost during post-breeding (90% within 5 km), but birds travelled up to 4.1 km from these sites during breeding and 13 km post-breeding. Stone-curlews were two- (by night) or three-times (by day) more likely to select disturbed-grassland over unmodified grassland for foraging during breeding, and approximately fifteen times more likely to do so post-breeding. Spring-sown crops and pig fields or manure heaps were also selected over grassland for nocturnal foraging. Given that central place foraging occurs in this species, conservation efforts that promote breeding attempts through ground-disturbance should ensure suitable foraging habitat is near the nest (< 1 km). Creating multiple areas of disturbed-ground close to the edge of large grassland blocks can provide a network of nesting and foraging habitats, whilst allowing access to foraging habitats on the surrounding arable farmland.

Keywords: telemetry, foraging, roosting, GPS-tracking, resource selection, movement ecology

4.1 Introduction

Effective conservation often depends upon land management interventions. This approach has been particularly effective when the design of the interventions is informed by knowledge of the target species' ecology and their efficacy is subsequently tested (e.g. Peach, Lovett, Wotton & Jeffs 2001; O'Brien, Green & Wilson 2006; Bretagnolle *et al.* 2011). Whilst many studies have appraised land management interventions by comparing the abundance of the target species (e.g. territorial males or nest site location) on treated areas to unmodified controls (e.g. Bright *et al.* 2015; Daskalova, Phillimore, Bell, Maggs & Perkins 2019), the inconspicuous behaviours of certain species are often overlooked (e.g. nocturnal foraging). Instead, accurate tracking data combined with well-replicated land management experiments can provide a more rigorous and unbiased test of intervention efficacy for nocturnal or cryptic species. Tracking can also provide insights into how intervention areas should be distributed to facilitate access to other important habitats.

Land management interventions are critical to the effective conservation of the migratory and largely nocturnal Eurasian Stone-curlew *Burhinus oedicnemus* (hereafter, 'Stone-curlew'), which suffered widespread declines across Europe during the 20th century (Tucker & Heath 1994). In Western Europe, Stone-curlews occupy sparsely-vegetated ground in spring-sown crops and semi-natural dry grassland or dwarf-shrub heathland (hereafter collectively 'semi-natural grassland') with open and short swards produced by grazing and physical disturbance (Green, Tyler & Bowden 2000). The UK's Stone-curlew population declined for much of the 20th Century, but has been subject to an intensive conservation programme and has partly recovered (Evans & Green 2007). This programme was informed by detailed study of the species breeding ecology and habitat use across semi-natural grassland and cropland (Green *et al.* 2000). 'Rescue' interventions were used to protect nests and chicks from crop-management operations and thereby counteract the low breeding success of crop-nesting Stone-curlews. To reduce dependence on individual nest-protection, 'safe' suitable (bare-open, cultivated) uncropped nesting plots (1 - 2 ha) are provided within arable farmland and semi-natural grassland. Although these efforts have led to a partial population recovery (Fig. S.4.1), declines would resume if rescue interventions were to cease (Johnston 2009).

Reducing the reliance of Stone-curlew conservation on resource-intensive rescue interventions, by increasing the proportion of breeding attempts on semi-natural grassland and nest plots, is considered a high priority in the UK (Johnston 2009) and a possible conservation measure elsewhere (Gaget, Fay, Augiron, Villers & Bretagnolle 2019). The number of plots on arable farmland is limited by the number of landowners willing to undertake this management, and the availability of agri-environment scheme funding to compensate for the loss of crop production. However, in semi-natural grasslands managed as nature reserves or for military training, plot creation does not cause significant loss of revenue because extensive livestock management is primarily for conservation objectives.

Mechanical ground disturbance of semi-natural grassland provides suitable Stone-curlew nesting habitat (Johnston 2009; Hawkes *et al.* 2019b), but it is unclear whether such management also provides suitable foraging habitat and whether other habitats are also utilised. To investigate this, we tracked adult Stone-curlews during the breeding season in a large (3,850 ha) block of semi-natural grassland which had been diversified by experimental ground-disturbance treatments (66 plots, 172 ha). First, we assessed the selection of habitats across disturbed-grassland, undisturbed-grassland and farmland habitats in the surrounding landscape for foraging (separately during diurnal breeding, nocturnal breeding and post-breeding). Next, to determine whether the type of ground-disturbance is important, we also examined foraging site selection among subplots that differed in disturbance frequency or time since treatment.

4.2 Methods

4.2.1 Study area

The study was carried out in 2016 in the Breckland region of Eastern England, which is characterized by sandy soils, a semi-continental climate, and varied landcover comprising mixed farmland, plantation forestry, and semi-natural grassland. Breckland held an estimated 207 pairs of breeding Stone-curlews in 2016 (an estimated 58% of the UK population, Fig. S.4.1). This study focused on three semi-natural grassland sites (the Stanford Training Area, STANTA, 52°51’N, 0°76’E, 3500 ha; Bridgham Heath 52°44’N, 0°83’E, 150 ha; and Brettenham Heath, 52°43’N, 0°83’E, 200 ha) (see Appendix S.4.1 for additional details) but also extended across a wider landscape of grassland and arable cropland encompassing the home ranges of tracked birds (118,600 ha, Fig. 4.1). Although this study occurred over a single year, the weather was typical of previous years (Appendix S.4.1).

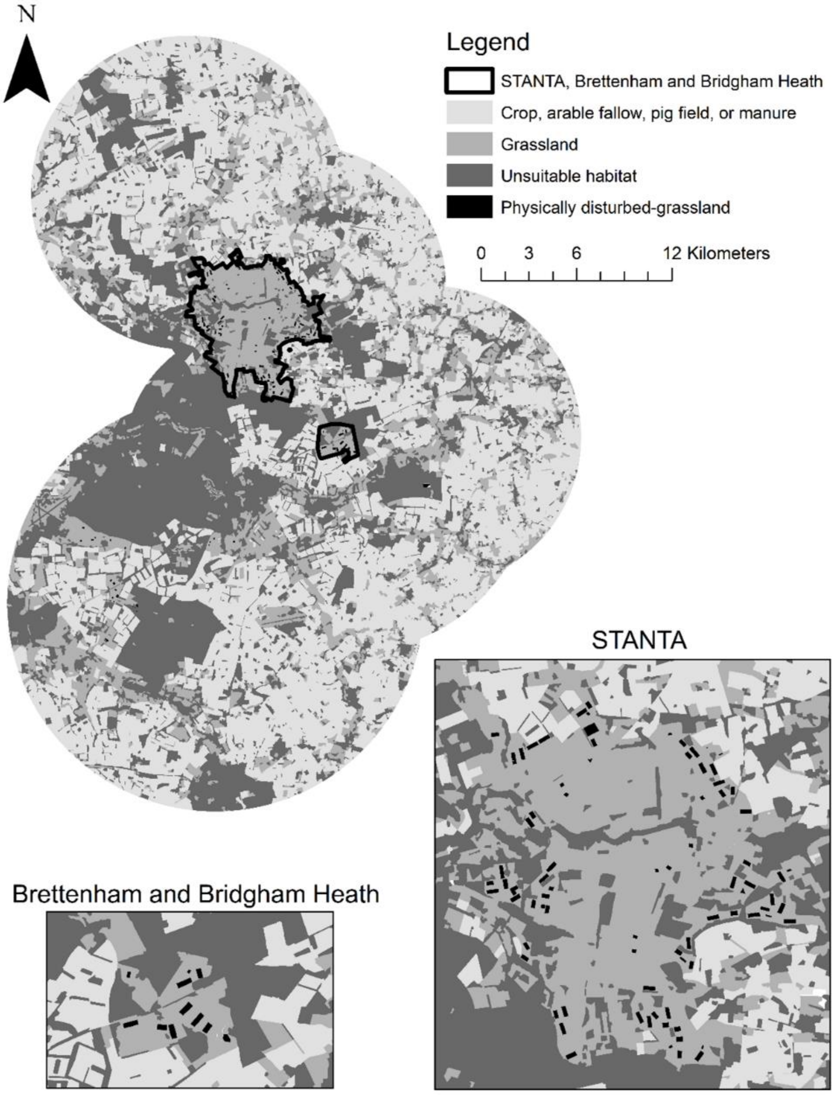


Figure 4.1. Distribution of arable, grassland, physically-disturbed grassland plots and unsuitable habitats across the 118,600 ha study landscape (of Breckland, Eastern England), across which we tracked five adult Eurasian Stone-curlews *Burhinus oedicnemus* and sampled habitat availability. For visual simplicity, crops (seven categories, see Table 4.1), arable fallows, and 'pig fields or manure heaps' are combined. Unsuitable habitat comprised woodland, freshwater, wet or seasonally wet habitats, and urban landcover, all of which Stone-curlews are known to avoid. Inserts show the three semi-natural grassland sites where experimental ground-disturbance was applied.

4.2.2 Ground-disturbance plots

In early 2015 (January to early May), 66 replicate 2-ha ground-disturbance plots (33 shallow-cultivated, created with a rotary-rotovator; 33 deep-cultivated, created with an agricultural plough) were established across the three areas of semi-natural grassland (Fig. 4.1). Treatments were repeated in late 2015 / early 2016 (early November 2015 to late February 2016), maintaining 26 as 2-ha 'homogenous' plots (same area disturbed in both years) and diversifying 40 as 3-ha 'complex-mosaic' plots. A complex mosaic plot comprised: half (1 ha) of the initial 2-ha plot left undisturbed in winter 2015 / 2016 ('fallow'); half of the initial plot on which the ground-disturbance was repeated in winter 2015 / 2016 ('repeat cultivated'); and an adjacent 1-ha area of unmodified grassland cultivated for the first time in winter 2015 / 2016 ('first-time cultivated').

4.2.3 Stone-curlew capture and monitoring

Between March and July 2016, all ground-disturbance plots were searched for Stone-curlews approximately every ten days. During each visit, we scanned the plot from a vehicle located over 100 m away. Five pairs were located (one in each of Bridgham and Brettenham Heath, and three in STANTA). Following Green *et al.* (2000), one individual from each pair was trapped before dawn with a small elastic-powered clap net baited with a tethered beetle prior to breeding (n = 3) or by day with a cage trap on the nest (n = 2) between 20th April – 12th June. We fitted solar-powered 'nanoFix Geo' GPS tags (PathTrack Ltd, Otley, UK) measuring 41 x 12 x 10 mm (LxWxH) plus an external whip antenna and weighing 5.2 g (about 1.5% of the body weight) (see Appendix S.4.1 for attachment details). Tags were configured to record GPS fixes (accurate to approximately ± 15 m) once every hour (71% of fixes) when fully charged, or once every two or three hours (25% and 4% of fixes, respectively) when battery voltage was low. GPS data were routinely downloaded to a remote base station through a UHF radio connection until the tag either dropped off (n = 4) or ceased functioning (n = 1).

Tagged birds were visited at least once a week to establish their status as pre-breeding, incubation-phase, chick-phase, or post-breeding (after nest or brood loss). Once a nest was located, eggs were weighed and their length and breadth measured to calculate the predicted hatch date (Day 2003). Three days prior to hatching, and thereafter until brood failure, visits were more frequent (every three days) to determine whether the eggs had hatched, and if so, whether the chick(s) were alive.

4.2.4 Landcover categorisation

We used the Centre of Ecology and Hydrology *Land Cover Map 2015* (LCM2015) (Rowland *et al.* 2017) to map semi-natural grassland, improved grassland, and arable fields across the study area in ArcGIS V.10 (ESRI 2011), and to identify landcovers known to be unsuitable for Stone-curlews (woodland, freshwater, wet or seasonally wet habitat and urban). Informed by prior information about Stone-curlew foraging habitat preferences (Green *et al.* 2000), we combined semi-natural grassland with improved grassland (hereafter collectively 'grassland'). Next, based on field-based surveys carried out across part of the study area (13,480 ha; Fig. S.4.2) and satellite images obtained from the European Space Agency Copernicus Sentinel-2 satellite (available at; https://scihub.copernicus.eu/dhus/#/home), we mapped: i) experimental ground-disturbance plots and areas of physically-disturbed grassland outwith the experiment (hereafter collectively 'disturbed-grassland'); ii) outdoor pig fields; and iii) cultivated Stone-curlew nest plots within arable crops. Lastly, we mapped locations of manure heaps, which are typically left alongside fields, by field-based surveys. We buffered each heap by 30 m (maximum observed radius, plus 15 m GPS error) and combined them with pig fields to give a 'pig fields or manure heaps' category.

To determine the crop identity within each arable field, we used the 2016 Crop Map for England (CROME, Rural Payments Agency 2019), a dataset comprised of 0.41 ha cells classified by remote sensing as a crop type or a non-crop landcover category. The most frequent category within each field determined its identity, resulting in 14 initial crop categories (Table 4.1), four non-crop categories (grassland and uncropped fallow fields; and two categories excluded from analysis: woodland and freshwater) plus cases where identity was not resolved (classified as 'unidentified field'). Next, supported by prior information on Stone-curlew habitat preferences (Green *et al.* 2000), crop types with similar sowing dates, vegetation structure and profile (i.e. raised versus flat beds) were merged, producing eight categories (Table 4.1). Remotely sensed uncropped fallow fields were combined with Stone-curlew nest plots within arable crops to give an 'arable fallow' category, as both were characteristically bare.

To examine the accuracy of this simplified crop classification, we undertook cross-validation for 561 arable fields across 6,565 ha (Fig. S.4.2) against their ground-truthed identity established from a field-based survey conducted between April and July. This led us to combine autumn cereals with spring cereals (now 'cereals'), and omit field beans, peas and linseed entirely from further analysis owing to high misclassification (Table S.4.1). Finally, to improve the classification accuracy of remotely sensed arable fallows, which field-based surveys showed were frequently 'vegetable or root crops' (Table S.4.1), and to determine the identity of remotely sensed unidentified fields, which were mostly arable fallows or 'vegetable or root crops', we visually inspected each of these fields using Sentinel-2 imagery; classifying as 'vegetable or root crops' where a crop was present in June or August (this was unlikely to be any other crop, Table S.4.1), and otherwise as arable fallow.

Table 4.1. Landcover and crop categories included (Y) and omitted (-) from analyses of Eurasian Stone-curlew *Burhinus oedicnemus* foraging-site selection (separately during breeding and post-breeding; DF = diurnal foraging model, NF = nocturnal foraging model). Initial crop categories [autumn-sown (A), spring-sown (S), or both (B)] were combined according to phenology and structure and further merged (denoted by shading) following cross-validation against a sample of ground-truthed fields (n = 561, Table S.4.1). Omitted categories were known to be unsuitable for Stone-curlews (Table S.4.2), frequently misclassified by remote sensing (crop categories only; judged from cross-validation, Table S.4.1), or used too infrequently to reliably model resource selection (judged separately for each analysis, Table S.4.2).

Initial categories	Categories merged by phenology and structure	Final categories	Categories included in analysis		
			Breeding		Post-breeding
			DF	NF	NF
Grassland[a]	Grassland	Grassland	Y	Y	Y
Disturbed-grassland[b,c]	Disturbed-grassland	Disturbed-grassland	Y	Y	Y
Sugar beet (S)[d] Maize (S)[d]	Sugar beet or maize (S)	Sugar beet or maize (S)	Y	Y	Y
Pig field or manure heaps[b,c]	Pig field or manure heaps	Pig field or manure heaps	-	Y	Y
Carrot (S)[d] Onions (S)[d] Parsnips (S)[d] Cabbage (S)[d] Potatoes (S)[d]	Vegetable or root crops (S)	Vegetable or root crops (S)	-	Y	Y
Arable fallows[b,c,d,e]	Arable fallows	Arable fallows	-	-	Y
Barely (S)[d] Wheat (S)[d]	Cereals (S)	Cereals (B)	-	Y	Y
Barely (A)[d] Wheat (A)[d] Rye (A)[d]	Cereals (A)				
Field beans (B)[d]	Field beans (B)	Field beans (B)	-	-	-
Linseed (S)[d]	Linseed (S)	Linseed (S)	-	-	-
Rape (A)[d]	Rape (A)	Rape (A)	-	-	-
Peas (S)[d]	Peas (S)	Peas (S)	-	-	-

Landcover was identified from: [a] = the Center of Ecology and Hydrology Land Cover Map 2015 (Rowland *et al.* 2017); [b] = satellite images (obtained from the Sentinel-2, available at; https://scihub.copernicus.eu/dhus/#/home); [c] = field-based surveys (see Fig. S.4.2); and [d] = remote sensing (obtained from the Crop Map for England, Rural Payments Agency, 2019). [e]Arable fallows comprised Eurasian Stone-curlew nest plots within arable crops[b,c] and arable fields left uncropped[d].

4.2.5 Classifying locations

GPS fixes (hereafter, 'locations') were classified by breeding stage as: pre-breeding, incubation (hereafter 'breeding'), chick-phase, or post-breeding, and as diurnal (after sunrise, before sunset) or nocturnal (after sunset, before sunrise). Pre-breeding and chick-phase locations were not considered subsequently because tracking was over a short period (pre-breeding, 35 days across three individuals; chick-phase, 10 days across two).

For locations identified during the breeding period, we excluded those within 50 m of the nest (where individuals mostly incubated or loafed, confirmed by field observations), whilst those >50 m from the nest were classified as foraging trips. For locations identified during the post-breeding period, when foraging is almost entirely conducted at night, the fix closest in time to 16:00 (per bird, per day) was classified as the day-roost; definition of the day-roost location by this fix is justified as movement during the day was minimal (median displacement between fixes closest in time to 12:00 versus 16:00 hrs = 32 m, interquartile range IQR 16 – 92 m). All retained breeding (diurnal and nocturnal) and nocturnal post-breeding locations were assumed to represent foraging locations. Post-breeding foraging locations were paired with the day-roost from that day (locations before midnight) or the previous day (locations after midnight). Finally, we omitted foraging locations from landcover categories that were: i) known to be unsuitable for Stone-curlews (Table S.4.2), ii) frequently misclassified by remote sensing (Table S.4.1), or iii) used too infrequently to reliably model (<2% for each of diurnal breeding, nocturnal breeding, and nocturnal post-breeding foraging locations; Table S.4.2). These categories were omitted from subsequent analysis (Table 4.1).

4.2.6 Analysis of resource selection, movement behavior and subplot use

To investigate resource selection, we compared habitat at used locations with availability at the scale of each individuals' home-range (third order selection; Johnson 1980). To control for central place foraging when sampling habitat availability (Fig. 4.2), we paired each foraging location with four random locations positioned the same distance from the nest-site (during breeding) or day-roost (post-breeding), but in random directions. By constraining random locations this way, the modelled sample represented used and unused sites equally available for the same travel investment.

We used Generalized Estimating Equations (GEE) from the package 'geepack' (Halekoh, Højsgaard & Yan 2006) with a binomial response variable (used locations, random locations) and logit link to model: i) foraging-site selection during breeding (separate models considered diurnal and nocturnal locations, as response to human disturbance, Taylor, Green & Perrins 2007, anti-predator vigilance, and prey availability, may all differ between day and night); and ii) nocturnal foraging-site selection post-breeding. GEEs are suited to resource selection analyses because they model robust standard error estimates that account for repeated observations of the same individual by replacing the assumption of independence with a defined correlation structure (Koper & Manseau 2009). For each model, habitat was entered as a fixed effect (see Table 4.1 for categories), with undisturbed grassland set as the reference category and locations (used/random) clustered by bird identity to control for repeat observations from the same individual. An interaction between date and habitat was not considered because the start and end of each tracking period varied considerably (Fig. S.4.3); thus date would have been confounded with individual. We selected an autoregressive correlation structure for every model (after assessing model fit by comparing the quasilikelihood information criterion of models with an autoregressive, exchangeable, or independent correlation structure, following Pan 2001), which assumes correlations between locations decrease progressively with time; though importantly, GEEs are still reliable with mis-specified correlation structures (Hardin & Hilbe 2002; Dormann *et al.* 2007; Koper & Manseau 2009). Following usual practice (e.g. Keating & Cherry 2004; Hebblewhite *et al.* 2005) we evaluated the probability of selection of each habitat relative to grassland (model intercept) using odds ratios derived from the beta coefficients. Habitat categories were considered to be selected similarly to grassland when their odds ratio Confidence Interval (CI) overlapped one, and similarly to another habitat when CIs overlapped. All analysis was undertaken in R (R Core Team 2015).

Following Boyce, Vernier, Nielsen and Schmiegelow (2002), we validated each model through a *k*-fold cross-validation, at each iteration withholding 20% of both used and available data (randomly, pooling data across individuals) while using the rest to develop a new cross-validation set (the trained model, producing five sets). For each set (trained model), we examined the Spearman's rank correlation between ten equal-sized categories of odds ratio 'scores' (hereafter 'bins'; 0-10, increasing from the lowest to highest score) and the area-adjusted frequency of each bin (for a detailed overview, see Roberts *et al.* 2017). A significant ($P < 0.05$) positive correlation between area-adjusted scores and odd ratio bins (i.e. the area-adjusted frequency increases progressively with bin rank) across all sets, indicates a model with good predicative performance (Boyce *et al.* 2002).

To determine whether Stone-curlews travelled further from the nest- or roost-site to forage within certain habitats, we used linear mixed models from the package 'lme4' (Bates, Maechler, Bolker & Walker 2017). Separately for diurnal breeding, nocturnal breeding and nocturnal post-breeding, distance traveled to each foraging location (log transformed) was included as the dependent variable, with habitat type as a categorical fixed effect (see Table 4.1 for categories) and bird identity as a random effect. Habitat category means were compared by Tukey's pairwise comparison in the package 'multcomp' (Hothorn, Bretz & Westfall 2008).

We examined the use of treated plots in greater detail, separately for foraging locations during breeding (pooling diurnal and nocturnal) and nocturnal post-breeding, considering only those plot mosaics with at least one location during the relevant period. We excluded homogenous plots because only one treatment type was available. We calculated the number of locations within each subplot (three categories: first-time cultivated, repeat cultivated, and fallow), but discarded 18 breeding-period foraging locations from one individual to avoid over-inflating subplot use on the plot where they nested (but retaining their locations from other plots, and all post-breeding locations). Whether frequency of use of the three subplot categories differed from a uniform distribution was examined using Fisher's exact tests, separately for deep- and shallow-cultivated complex-mosaics. Where overall subplot use differed significantly from uniform (Fisher's exact $P < 0.05$), we performed three pair-wise comparisons (Fisher's exact tests) with Bonferroni adjusted correction for multiple tests (MacDonald & Gardner 2000).

4.3 Results

Three male and two female adult Stone-curlews were tracked for a mean duration of 84 days (range: 67 – 103 days). During the breeding period, 287 diurnal (37 - 101 per individual) and 223 nocturnal (39 - 75 per individual) foraging locations were recorded across four individuals (three males and one female from a different pair, from one breeding attempt each). Note, the greater number of diurnal locations was attributable to the longer period of diurnal tracking (daylength ranged from 14 - 17 hours). Two bred on disturbed-grassland, and the other two on an arable crop (one on each of sugar beet and maize) immediately adjacent to grassland and close to disturbed-grassland (120 m and 350 m, respectively). Post-breeding, 1371 nocturnal foraging locations (110-476 per individual) were recorded across all five individuals. During each period, 96% (during breeding) and 94% (post-breeding) of foraging locations were within 100 m of another foraging location (from the same individual, from the same period). However, omitting one individual that was only tracked post- breeding, just 17% of post-breeding foraging locations were within 100 m of a breeding period foraging location (from the same individual). Each individuals breeding and post-breeding home range either completely or partially overlapped, but the latter was always larger (Fig. S.4.4).

4.3.1 Breeding foraging-site selection

During breeding, 90% of foraging locations were within 1 km of the nest (the furthest was 4.1 km, Fig. 4.2). Birds travelled further to forage at night (nocturnal foraging, median distance traveled = 523 m, IQR 157 – 842 m; diurnal foraging, 109 m, IQR 68 – 305 m; Mann-Whitney, $P < 0.001$). The most distant nocturnal foraging locations were on ‘pig fields or manure heaps’ (Fig. 4.3). Diurnally, three habitats had enough foraging locations (>2%) for analysis of habitat selection (Table 4.1), but ‘cereals’, ‘pig fields or manure heaps’, rape, arable fallows and ‘vegetable or root crops’ were rarely used and therefore excluded (Table S.4.2). Nocturnally, individuals foraged across a greater range of habitats, but rape and arable fallows were again excluded because of sparse data.

Accounting for central place foraging when sampling habitat availability, breeding Stone-curlews were two- to three-times more likely to select disturbed-grassland over grassland for both nocturnal (odds ratio = 1.9, 95% CI: 1.2 – 3.4, Table 4.2) or diurnal foraging (odds ratio = 3.4, 95% CI: 1.3 – 8.9). Nocturnally and diurnally, 'sugar beet or maize' was also preferred relative to unmodified grassland and was selected with similar preference to disturbed-grassland. Nocturnally, Stone-curlews were ten-times more likely to select 'pig fields or manure heaps' over grassland (odds ratio = 10.0, 95% CI: 3.9 – 27.4), which they also selected over every remaining habitat except 'sugar beet or maize'. Neither 'cereals' nor 'vegetable or root crops' were selected relative to grassland, either diurnally or nocturnally. Model validation (*k*-fold cross-validation) showed the predictive performance of the nocturnal model was good (Fig. S.4.5). For the diurnal model, there was no positive correlation between the area-adjusted scores and odds ratio bins for two of the five trained sets, attributable to the low number of habitat categories considered by this model (Table 4.1); nevertheless, because every set gave similar inference, we consider the overall model robust.

4.3.2 Post-breeding foraging-site selection

Post-breeding, 90% of foraging locations were within 5 km of the day-roost (the furthest was 13 km, Fig. 4.2). Birds travelled further to forage than they did at night during breeding (nocturnal foraging post-breeding, median distance traveled = 1267 m, IQR 351 – 2662 m; Mann-Whitney, $P < 0.001$). Seven habitats contained enough nocturnal foraging locations for inclusion in analysis of habitat selection (Table 4.1); but rape was rarely used and therefore excluded (Table S.4.2).

Accounting for central place foraging, post-breeding Stone-curlews were approximately 15-times more likely to select either disturbed-grassland (odds ratio = 14.3, 95% CI: 7.5 – 26.8) or arable fallows (odds ratio = 15.8, 95% CI: 7.8 – 31.5) than undisturbed grassland for foraging (Table 4.2); both were also preferred relative to every crop. 'Pig fields or manure heaps' was also selected relative to undisturbed grassland, to a similar degree as disturbed-grassland and arable fallows, and above two of the three considered crops ('cereals' and 'vegetable or root crops', but not 'sugar beet or maize'). 'Sugar beet or maize' and 'vegetable or root crops' (but not 'cereals') were selected over grassland. The predictive performance of this model was good (Fig. S.4.5).

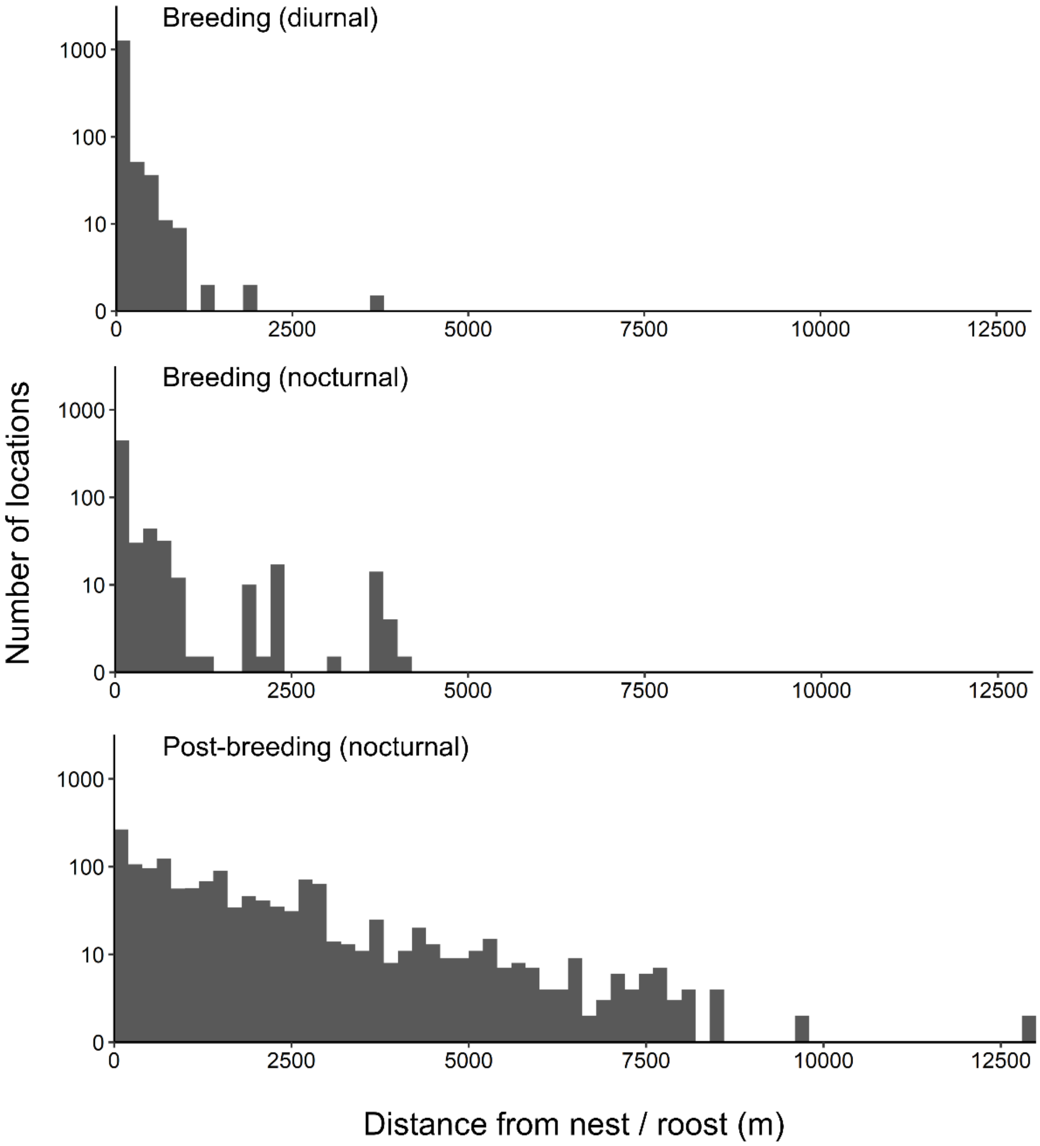


Figure 4.2. Distribution of breeding (diurnal and nocturnal) and post-breeding (nocturnal only) locations from tracked Eurasian Stone-curlews, relative to the breeding period nest-site (n = 4 adults) or post-breeding day-roost (n = 5 adults) respectively. In subsequent analysis, locations less than 50 m from the nest-site (but not the day-roost) were excluded to avoid over-representing periods of inactivity. We also excluded breeding and post-breeding locations that were: i) within habitats known to be unsuitable for Stone-curlews (Table S.4.2); ii) frequently misclassified by remote sensing (Table S.4.1); or iii) used too infrequently to reliably model resource selection (Table S.4.2).

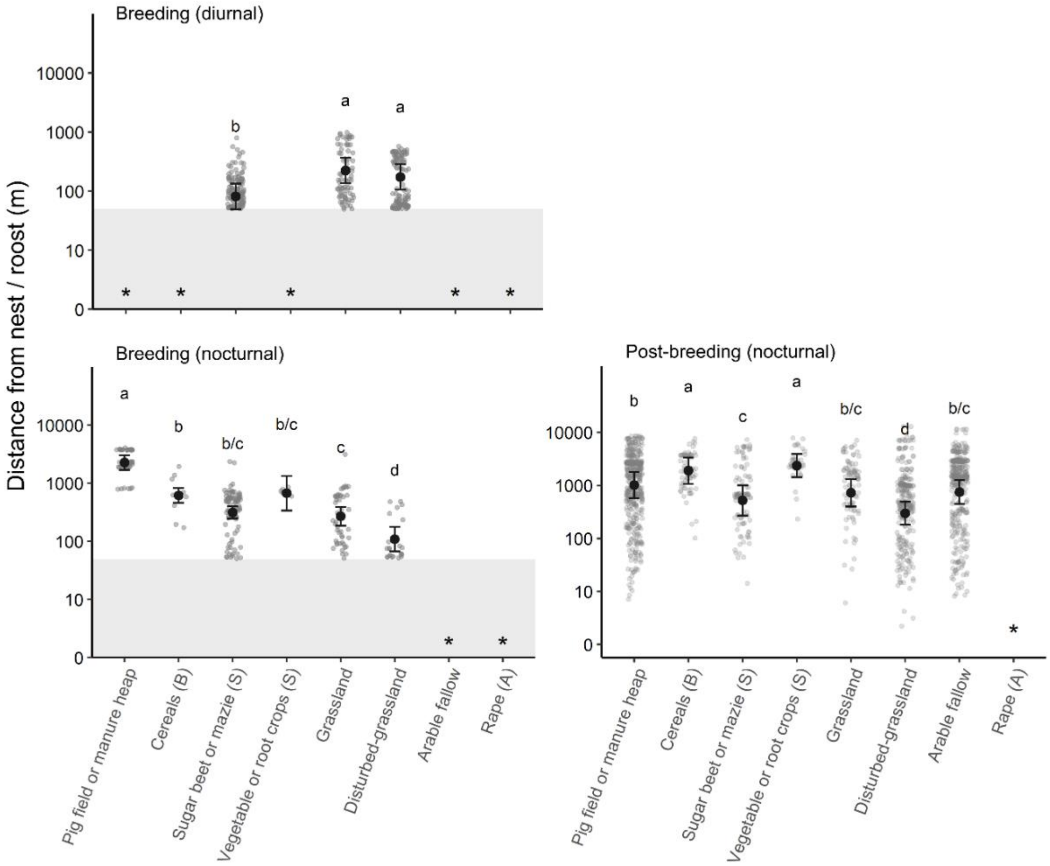
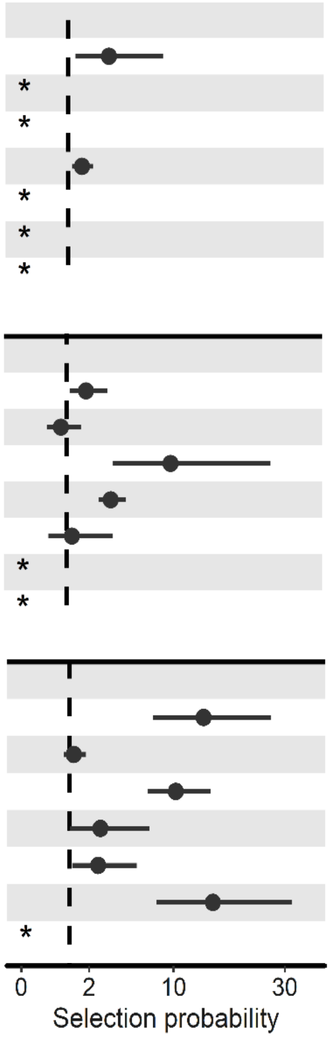


Figure 4.3. Distance travelled by Eurasian Stone-curlews from their nest-site or day-roost, for diurnal breeding, nocturnal breeding and nocturnal post-breeding foraging locations in different habitats. Shown are individual foraging locations (grey circles) and estimated means (black circles, bars represent 95% CIs) from linear mixed models including the fixed effect of habitat (see Table 4.1 for included categories); means that share a superscript do not differ significantly (Tukeys pairwise comparisons p > 0.05). Asterisks denote habitats omitted from analysis as they were used too infrequently to model reliably (Table S.4.2). For crop categories, letters in parentheses denote whether it was autumn-sown (A), spring-sown (S), or both (B). For the breeding period panels, shading represents the first 50 m from the nest where locations were excluded to avoid over-representing periods of inactivity.

Table 4.2. Eurasian Stone-curlew foraging site (separately for diurnal breeding, nocturnal breeding and nocturnal post-breeding locations) utilisation, showing odds ratios (± 95% CI) of each habitat relative to undisturbed grassland (reference category) estimated from Generalized Estimating Equations with a binomial response and habitat entered as a fixed effect (Table 4.1). Categories for which the lower CI is greater than one (dashed line) are preferred to grassland; those marked * were omitted from that model because they were never or rarely used (Table S.4.2). For crop categories, the letters in parenthesis denotes whether it was autumn-sown (A), spring-sown (S), or included both (B). The number of used and random locations within each habitat category are also shown.



Landcover	Coefficient odds ratios (± 95% CIs)	No. used locations	No. random location
Breeding diurnal			
Grassland (intercept)		76 (27%)	544 (48%)
Disturbed-grassland	3.4 (1.3, 8.9)	102 (36%)	180 (16%)
Cereals (B)	NA	NA	NA
Pig field or manure heap	NA	NA	NA
Sugar beet or maize (S)	1.7 (1.2, 2.3)	109 (40%)	424 (37%)
Vegetable or root crops (S)	NA	NA	NA
Arable fallows	NA	NA	NA
Rape (A)	NA	NA	NA
Breeding nocturnal			
Grassland (intercept)		46 (20%)	428 (48%)
Disturbed-grassland	1.9 (1.2, 3.4)	23 (10%)	94 (11%)
Cereals (B)	0.8 (0.4, 1.7)	12 (6%)	129 (15%)
Pig field or manure heap	10.0 (3.9, 27.4)	49 (22%)	32 (4%)
Sugar beet or maize (S)	3.7 (2.8, 5.0)	87 (38%)	172 (19%)
Vegetable or root crops (S)	1.2 (0.4, 3.9)	6 (3%)	37 (4%)
Arable fallows	NA	NA	NA
Rape (A)	NA	NA	NA
Post-breeding nocturnal			
Grassland (intercept)		90 (7%)	1989 (36%)
Disturbed-grassland	14.3 (7.5, 26.8)	257 (19%)	298 (5%)
Cereals (B)	1.2 (0.8, 1.8)	62 (5%)	1093 (20%)
Pig field or manure heap	10.2 (6.9, 15.5)	450 (33%)	714 (13%)
Sugar beet or maize (S)	2.7 (1.0, 7.1)	96 (7%)	691 (13%)
Vegetable or root crops (S)	2.5 (1.1, 5.8)	43 (3%)	321 (6%)
Arable fallows	15.8 (7.8, 31.5)	373 (27%)	378 (7%)
Rape (A)	NA	NA	NA

4.3.3 Subplot selection

Stone-curlews were recorded foraging in four complex-mosaic plots during breeding (all shallow-cultivated, none deep-cultivated). Post-breeding, foraging was recorded in eight (six shallow-cultivated, two deep-cultivated) complex-mosaic plots. Within the shallow-cultivated complex-mosaics, breeding-period foraging locations were uniformly distributed across all subplot types (Fisher's exact test P > 0.47); however, post-breeding, first-time cultivated and repeat-cultivated subplots both held more foraging locations than fallows (Table 4.3). Within deep-cultivated complex-mosaics, first-time cultivated subplots held more post-breeding foraging locations than fallows or repeat-cultivated subplots.

Table 4.3. Eurasian Stone-curlew utilization of cultivation subplots (FC = first-time cultivated, RC = repeat cultivated, FL =one-year-old fallow), showing number of foraging locations during breeding and post-breeding, separately for shallow-cultivated and deep-cultivated complexes. Separately for complex type and breeding/post-breeding, subplot categories that share a superscript do not differ significantly (pairwise Fisher's exact tests, p < 0.05, after Bonferroni correction). NA denotes cases where no locations were recorded.

	Shallow-cultivated complex mosaics			Deep-cultivated complex mosaics		
	FC	RC	FL	FC	RC	FL
Breeding foraging locations	22^a	15^a	12^a	NA	NA	NA
Post-breeding foraging locations	48^a	21^a	0^b	41^a	1^b	0^b

4.4 Discussion

Our study showed that physically-disturbing semi-natural grassland to create nesting plots safe from arable farming operations also provided foraging habitat strongly selected by Stone-curlews. Pig fields, manure heaps and sparse spring-sown crops were also selected across the wider landscape. Stone-curlews are known to select bare and open habitats (Green *et al.* 2000; Caccamo, Pollonara, Emilio & Giunchi 2011), but this is the first study to demonstrate that creating bare or sparsely vegetated ground through rotational physical ground-disturbance increases foraging opportunities.

The only previous study to track Stone-curlews in the UK found that short semi-natural grassland (<5 cm) provided suitable foraging habitat (Green *et al.* 2000). However, in this study, conducted in the same region three decades later, semi-natural grassland was not preferred. Over the intervening period rabbit populations have collapsed, with a concurrent reduction in very short grassland (<2 cm) (Appendix S.4.1). We are confident that sward growth, which is known to reduce nest habitat quality (Green & Griffiths 1994; Bealey, Green, Robson, Taylor & Winspear 1999), also explains why unmodified grassland was rarely used for foraging.

Relative to undisturbed grassland, Stone-curlews were two- or three-times more likely to select disturbed-grassland for foraging whilst breeding (nocturnally and diurnally, respectively), and nearly fifteen times more likely post-breeding. This increase in the importance of disturbed-grassland as the season progressed probably occurred because sward and crop growth (see Fig. S.4.6 for sward growth) renders grassland and most arable habitats unsuitable later in the season, limiting foraging to habitats that stay bare and short for longer. Arable fallows were used to a similar extent as disturbed-grassland post-breeding, probably because they too were sparsely vegetated later in the season. Interestingly, an additional supplementary analysis, which assessed the selection of day-roost sites across all five tagged individuals (Appendix S.4.2), showed that disturbed grassland and arable fallows also provide suitable roosting habitat; corroborating the findings from the foraging site selection models. We suspect that ground disturbance improved foraging and roosting opportunities because it provides better visibility of prey (an important feature for nocturnal waders, Martin 1990), higher densities of some prey (Hawkes *et al.* 2019b), and camouflage (Green *et al.* 2000).

Thus far we have established that physical disturbance of closed-sward grassland improved foraging opportunities, but does cultivation detail matter? Within our experimental complex-mosaics, foraging locations were evenly distributed across shallow-cultivated subplots during breeding. However, post-breeding, Stone-curlews preferred to forage within first-time cultivated and repeat cultivated subplots relative to one-year-old fallows in the shallow-cultivated mosaics, and within the first-time cultivated subplots over fallows in the deep-cultivated mosaics. This is consistent with evidence from Spain, where recently-tilled fields are more likely to be occupied by Stone-curlew than older fallows (Sanz-Pérez *et al.* 2019). Within the shallow-cultivated mosaics, it is possible that subplot detail became important post-breeding because the fallows supported short vegetation early but not later in the season, in contrast to the consistently short and sparse repeat-cultivated and first-time cultivated subplots (Fig. S.4.6). Another explanation for a lack of selection during the breeding period could be that the initial structural suitability of repeat cultivated and first-time cultivated subplots (Fig. S.4.6) was offset by a reduction in invertebrate prey following cultivation. Pitfall trapping data (Hawkes, unpublished data) suggests that by the post-breeding period the abundance of some important invertebrate groups have recovered (e.g. Carabidae and Scarabaeidae), or at least partially recovered (e.g. Araneae and Silphidae), on the repeat and first-timed cultivated subplots. However, we lacked data to confirm whether an initial decline occurred post-cultivation.

Stone-curlews did not exclusively feed in disturbed-grassland, with ‘pig fields or manure heaps’ and ‘sugar beet or maize crops’ also important. During breeding, Stone-curlews used a greater range of habitats at night (when birds are most active, Green *et al.* 2000), including ‘pig fields or manure heaps’, which was then selected over disturbed-grassland and nearly every other habitat. Post-breeding, ‘pig fields or manure heaps’ were again important for foraging (and roosting, Appendix S.4.2). Green et al (2000) did not find a preference for pig fields, and manure heaps were only selected over other habitats later in the season; however pig fields were scarce in the landscape when this initial research occurred, with few opportunities to test their utilization. Manure heaps, which Stone-curlews utilise for foraging by hunting around the base and climbing the sides (Green pers. obs.), have been documented as an important foraging resource in other Stone-curlew populations (Giannangeli, de Sanctis, Manginelli & Medina 2004;

Caccamo *et al.* 2011), attributed to the high densities of prey they likely contain. Pig fields were probably selected for the same reason.

Although pig fields clearly provided foraging opportunities, they are considered to have a detrimental impact on semi-natural habitats through local atmospheric deposition of ammonia (Chesterton 2009). Experimental work has shown that the addition of nutrients results in the loss of characteristic lichens, annuals, reduced diversity and dominance of perennial grasses in Breckland grass-heath (Davy & Bishop 1984), chalk grassland (Bobbink 1991) and dunes (Boorman & Fuller 1982). Eutrophication of nutrient-poor ecosystems occurs close to poultry and other intensive animal units (Berendse, Laurijsen & Okkerman 1988; Pitcairn *et al.* 1998). Given nutrient deposition poses a significant threat to this habitat, we do not advocate the establishment of new pig units close to grassland. It is unclear whether manure heaps also pose a similar threat, but this would need to be established before they are advocated as a possible conservation tool.

Consistent with Green *et al.* (2000), our results also show that ‘sugar beet or maize’, both of which were characteristically bare and open early in the season, were selected during breeding; whilst ‘cereals’ and rape, which comprised a denser and generally taller crop, were avoided. Foraging selection post-breeding was similar, though disturbed-grassland and arable fallows were selected over every crop category. Although during this period the ‘vegetable or root crops’ category was selected over grassland for foraging, this is attributable to a single part-fallowed field which contained 22/43 post-breeding foraging locations within this category. Although we did not measure invertebrate prey within farmland habitats, previous work has shown that abundance varies across taxa according to crop type (for example, Myriapoda are more abundant in sugar beet, whilst Araneae are more abundant in spring-sown cereal; Green *et al.* 2000). However, whilst we suspect that prey availability was the main reason why Stone-curlew utilised manure heaps and pig fields, we agree with Green *et al.* (2000) that crop selection is probably influenced predominantly by vegetation structure.

4.5 Conclusions

Although our study only considered a limited number of tracked individuals, the precise tracking data, combined with our experimental manipulations, provides a highly informative assessment of intervention efficacy for this nocturnal and difficult to study species. We conclude that interventions which open-up closed swards increase create suitable foraging habitat, which all individuals strongly selected relative to its availability. Since recently-cultivated ground was selected over fallows during the post-breeding period, annual ground disturbance is probably necessary to maintain suitable habitat throughout the season. Shallow-cultivation may offer a better long-term solution, as the repeat cultivated subplots in the deep-cultivated mosaics were rarely used. Grassland ground-disturbance plots also benefit many other priority species (Dolman & Sutherland 1992; Hawkes, Smart, Brown, Jones & Dolman 2019a; Hawkes *et al.* 2019b).

Consistent with the only other assessments of Stone-curlew movement behavior during the breeding season (Green *et al.* 2000; Caccamo *et al.* 2011), most foraging activity was centered on the nest-site or day-roost. However, in our study, individuals traveled up to 4.1 km (during breeding) and 13 km (post-breeding), further than previously reported. It is possible that the two earlier studies, which used VHF radio tags and manual tracking, overlooked infrequent distant foraging trips. Given central place foraging, conservation strategies aiming to improve nesting habitat through ground-disturbance should ensure sufficient foraging habitat is near to nesting plots (during breeding, 90% of foraging locations were within 1 km of the nest). Targeting interventions close to favoured farmland habitats (e.g. pig fields and sugar beet or maize) is not viable, because these rotate around the landscape. Instead, creating extensive areas of disturbed ground within permanent semi-natural grassland adjacent to farmland will create suitable foraging habitat, whilst allowing access to these other habitats. Here, breeding Stone-curlews accessed ‘sugar beet or maize’ and ‘pig fields or manure heaps’ up to 2.4 km and 4.1 km from the nest-site, respectively (Fig. 4.3). Finally, further work is needed to establish whether habitat selection influences breeding performance; however, this would require a large sample of individuals tracked over multiple years.

This study demonstrates that examining spatial habitat use can inform management options and strategies and offers important insight into how land management interventions can be effectively targeted. Whilst costly management options are increasingly based on prior knowledge of the target species ecological requirements, we argue that they can be more efficient if examined in the context of target species resource use within post-intervention landscapes.

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References

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2017). Linear mixed-effects models using 'Eigen' and S4. *R package Version 1.1-1.5*. Available at: https://cran.r-project.org/web/packages/lme4/ (accessed May 2018).

Bealey, C.E., Green, R.E., Robson, R., Taylor, C.R. & Winspear, R. (1999). Factors affecting the numbers and breeding success of Stone Curlews *Burhinus oedicnemus* at Porton Down, Wiltshire. *Bird Study,* 46(2), 145-156.

Berendse, F., Laurijsen, C. & Okkerman, P. (1988). The acidifying effect of ammonia volatilized from farm-manure on forest soils. *Ecological Bulletins,* (39), 136-138.

Bobbink, R. (1991). Effects of nutrient enrichment in Dutch chalk grassland. *Journal of Applied Ecology,* 28(1), 28-41.

Boorman, L.A. & Fuller, R.M. (1982). Effects of added nutrients on dune swards grazed by rabbits. *Journal of Ecology,* 70, 345-355.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002). Evaluating resource selection functions. *Ecological Modelling,* 157(2), 281-300.

Bretagnolle, V., Villers, A., Denonfoux, L., Cornulier, T., Inchausti, P. & Badenhausser, I. (2011). Rapid recovery of a depleted population of Little Bustards *Tetrax tetrax* following provision of alfalfa through an agri-environment scheme. *Ibis,* 153(1), 4-13.

Bright, J.A., Morris, A.J., Field, R.H., Cooke, A.I., Grice, P.V., Walker, L.K., Fern, J. & Peach, W.J. (2015). Higher-tier agri-environment scheme enhances breeding densities of some priority farmland birds in England. *Agriculture, Ecosystems & Environment,* 203(Supplement C), 69-79.

Caccamo, C., Pollonara, E., Emilio, B.N. & Giunchi, D. (2011). Diurnal and nocturnal ranging behaviour of Stone-curlews *Burhinus oedicnemus* nesting in river habitat. *Ibis,* 153(4), 707-720.

Chesterton, C. (2009). *Environmental impacts of land management*. Natural England Research Report, NERR030.

Daskalova, G.N., Phillimore, A.B., Bell, M., Maggs, H.E. & Perkins, A.J. (2019). Population responses of farmland bird species to agri-environment schemes and land management options in Northeastern Scotland. *Journal of Applied Ecology,* 56(3), 640-650.

Davy, A.J. & Bishop, G.F. (1984). Response of *Hieracium Pilosella* in Breckland grass-heath to inorganic nutrients. *Journal of Ecology,* 72(1), 319-330.

Day, T.C.F. (2003). The effects of disturbance from roads on stone curlews in southern England. PhD Thesis, University of Cambridge

Dolman, P.M. & Sutherland, W.J. (1992). The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology,* 29(2), 402-413.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, D.W., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography,* 30(5), 609-628.

ESRI (2011). ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Evans, A.D. & Green, R.E. (2007). An example of a two-tiered agri-environment scheme designed to deliver effectively the ecological requirements of both localised and widespread bird species in England. *Journal of Ornithology,* 148(2), 279-286.

Gaget, E., Fay, R., Augiron, S., Villers, A. & Bretagnolle, V. (2019). Long-term decline despite conservation efforts questions Eurasian Stone-curlew population viability in intensive farmlands. *Ibis,* 161, 359-371.

Giannangeli, L., de Sanctis, A., Manginelli, R. & Medina, F.M. (2004). Seasonal variation of the diet of the Stone Curlew *Burhinus oedicnemus distinctus* at the island of La Palma, Canary Islands. *Ardae,* 92(2), 175-184.

Green, R.E. & Griffiths, G.H. (1994). Use of preferred nesting habitat by stone curlews Burhinus oedicnemus in relation to vegetation structure. *Journal of Zoology,* 233(3), 457-471.

Green, R.E., Tyler, G.A. & Bowden, C.G.R. (2000). Habitat selection, ranging behaviour and diet of the stone curlew (*Burhinus oedicnemus*) in southern England. *Journal of Zoology,* 250(2), 161-183.

Halekoh, U., Højsgaard, S. & Yan, J. (2006). The R Package geepack for Generalized Estimating Equations. *Journal of Statistical Software,* 15(2), 1-11.

Hardin, J.W. & Hilbe, J.M. (2002). *Generalized Estimating Equations*. Chapman & Hall, London.

Hawkes, R.W., Smart, J., Brown, A., Jones, H. & Dolman, P.M. (2019a). Experimental evidence that ground-disturbance benefits Woodlark *Lullula arborea*. *Ibis,* 161, 447-452.

Hawkes, R.W., Smart, J., Brown, A., Jones, H., Lane, S., Wells, D. & Dolman, P.M. (2019b). Multi-taxa consequences of management for an avian umbrella species. *Biological Conservation,* 236, 192-201.

Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E. & Paquet, P.C. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology,* 86(8), 2135-2144.

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal,* 50(3), 346-363.

Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology,* 61(1), 65-71.

Johnston, A. (2009). Demographic analsis of the impact of conservation action on Stone-curlew populations. PhD Thesis, University of Cambridge

Keating, K.A. & Cherry, S. (2004). Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management,* 68, 774-789.

Koper, N. & Manseau, M. (2009). Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. *Journal of Applied Ecology,* 46(3), 590-599.

MacDonald, P.L. & Gardner, R.C. (2000). Type I error rate comparisons of post hoc procedures for I x J chi-square tables. *Educational and Psychological Measurement,* 60(5), 735-754.

Martin, G.R. (1990). *Birds by night*. T. & A.D. Poyser, London.

O'Brien, M., Green, R.E. & Wilson, J. (2006). Partial recovery of the population of Corncrakes *Crex crex* in Britain, 1993–2004. *Bird Study,* 53(3), 213-224.

Pan, W. (2001). Akaike's information criterion in generalized estimating equations. *Biometrics,* 57(1), 120-125.

Peach, W.J., Lovett, L.J., Wotton, S.R. & Jeffs, C. (2001). Countryside stewardship delivers cirl buntings (*Emberiza cirlus*) in Devon, UK. *Biological Conservation,* 101(3), 361-373.

Pitcairn, C.E.R., Leith, I.D., Sheppard, L.J., Sutton, M.A., Fowler, D., Munro, R.C., Tang, S. & Wilson, D. (1998). The relationship between nitrogen deposition, species composition and foliar nitrogen concentrations in woodland flora in the vicinity of livestock farms. *Environmental Pollution,* 102(1, Supplement 1), 41-48.

R Core Team (2015). R: a language and environment for statistical computing. Version 3.2.2. R Foundation for Statistical Computing, Vienna.

Roberts, D.R., Bahn, V., Ciuti, S., Boyce, M.S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J.J., Schröder, B., Thuiller, W., Warton, D.I., Wintle, B.A., Hartig, F. & Dormann, C.F. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography,* 40(8), 913-929.

Rowland, C.S., Morton, R.D., Carrasco, L., McShane, G., O'Neil, A.W. & Wood, C.M. (2017). Land Cover Map 2015 (vector, GB). NERC environmental information data centre. Available at: https://doi.org/10.5285/6c6c9203-7333-4d96-88ab-78925e7a4e73 (accessed 27 June 2019).

Rural Payments Agency (2019). Crop Map For England (CROME). Available at: https://data.gov.uk/dataset/6f316b8b-ae74-489c-ba3c-c2325a9c16a1/crop-map-of-england-crome-2016-complete (accessed 27 June 2019).

Sanz-Pérez, A., Giralt, D., Robleño, I., Bota, G., Milleret, C., Mañosa, S. & Sardà-Palomera, F. (2019). Fallow management increases habitat suitability for endangered steppe bird species through changes in vegetation structure. *Journal of Applied Ecology,* 56, 2166-2175.

Taylor, E.C., Green, R.E. & Perrins, J. (2007). Stone-curlews *Burhinus oedicnemus* and recreational disturbance: developing a management tool for access. *Ibis,* 149(s1), 37-44.

Tucker, G.M. & Heath, M.F. (1994). *Birds in Europe: their conservation status*. BirdLife International, Cambridge.

Chapter 4

Supplementary material

Appendix S.4.1. Study area, climate and method details

Appendix S.4.2. Day-roost site selection

Figure S.4.1. UK Stone-curlew population

Figure S.4.2. Ground-truthed area

Figure S.4.3. Daily number of foraging locations throughout the tracking period

Figure S.4.4. Breeding and post-breeding home ranges and foraging locations

Figure S.4.5. Cross-validating foraging- and roost-site selection models

Figure S.4.6. Grassland and complex-mosaic plot vegetation

Table S.4.1. Validating crop classification accuracy

Table S.4.2. Number of foraging and roost locations per habitat

Appendix S.4.1

Study area details

Within Breckland, large areas of farmland and semi-natural grassland constitute part of the +39,000 ha Breckland Special Protection Area (SPA) designated under the EC Birds Directive (EC 1979, 79/409/EEC), because of the internationally important populations of Eurasian Stone-curlew *Burhinus oedicnemus* and two other bird species (European Nightjar *Caprimulgus europaeus* and Woodlark *Lullula arborea*). Here, the highest densities of breeding Stone-curlews occur in semi-natural grassland with very short (<2 cm) vegetation because of grazing and disturbance by European rabbits *Oryctolagus cuniculus* and grazing by livestock (Green, Tyler & Bowden 2000). Some of these grasslands are on nature reserves, but most are within a large military training area (the Stanford Training Area, STANTA). During the 1980s, these grasslands were characteristically bare and open with very short swards (Green & Griffiths 1994); however, since then, rabbit populations have collapsed, along with a concurrent reduction in short grassland where declines have been particularly severe (deduced from surveys of habitat structure and rabbit activity between 1998-2013, Panter, Mossman & Dolman 2013). Similar rabbit declines have occurred on Brettenham and Brigham Heath, with remnant populations confined to a few localized areas (R.H. pers. obs.) In 2016 (i.e. during the present study), the mean sward height across the three semi-natural grassland sites (STANTA, Bridgham Heath, and Brettenham Heath) was 4.2 cm ± 1.6 SD in April / early May and 6.3 cm ± 2.0 in June / early July (see Fig. S.4.5 for grassland survey details).

On STANTA (the largest of the three sites) grazing management comprises a low-density hefted sheep grazing system (approximately one ewe per ha) supported by supplementary feeding, which does not exert the grazing pressure of previous centuries. Bracken is managed annually by mechanical cutting and aerial herbicide application. Bridgham and Brettenham Heath are grazed at a similar density (but within compartments), with bracken managed annually through mechanical cutting on Bridgham Heath and herbicide spray on Brettenham Heath (though on Bridgham heath was managed with herbicide spray prior to 2010 and Brettenham Heath was managed with mechanical cutting prior to 2016)

Climate

Based on daily weather records from a nearby weather station (Santon Downham, 0°671E, 52°459N), the climate during the study period (March to August 2016) was typical of previous years (assessed through two-sample t-tests; comparing the maximum daily temperature during 2016 to 2013, 2014 and 2015 combined, separately for each month). However, April was cooler ($t = 3.5$, $df = 117$, $p = <0.001$) and August was warmer ($t = -2.9$, $df = 122$, $p = <0.01$). Records were provided by Met Office (2019).

GPS tag attachment

The tag was attached to a patch of muslin gauze (60 x 25 mm). The base of the tag and the surrounding fringe of gauze were attached to the bird's back (the skin and feathers over the dorsal synsacrum) with cyanoacrylate glue after swabbing with acetone to remove oils. The posterior margin of the gauze patch was positioned carefully so the bird was not prevented from accessing it's preen gland. Tagged birds carried unique combinations of colour rings so that they could be identified individually through a telescope.

Appendix S.4.2

To investigate selection of post-breeding day-roost sites, we compared habitat at used day-roost locations (derived from five tracked adult Eurasian Stone-curlews *Burhinus oedicnemus*) with availability within each individuals home range. First, consistent with our approach for the foraging locations, we omitted day-roost locations from landcover categories that were: i) known to be unsuitable for Stone-curlews (woodland, freshwater, wet or seasonally wet habitats, and urban; Table S.4.2), ii) frequently misclassified by remote sensing (peas, field beans, and linseed; Table S.4.1), or iii) used too infrequently to reliably model (<2% of day-roost locations; 'cereals' and rape; Table S.4.2). These categories were omitted from subsequent analysis. Next, to sample habitat availability, we paired each used location with four random locations positioned anywhere within a Minimum Convex Polygon containing all roost locations of that individual. Then, following the same approach as our foraging site selection analyses, we used Generalized Estimating Equations (GEE) from the package ‘geepack’ (Halekoh, Højsgaard & Yan 2006) with a binomial response variable (used locations, random locations) and logit link to model day-roost site selection. Habitat was entered as a fixed effect (six categories, including: undisturbed grassland, disturbed-grassland, ‘sugar beet or maize’, ‘pig field or manure heaps’, ‘vegetable or root crops’, arable fallows), with undisturbed grassland set as the reference category and locations (used/random) clustered by bird identity to control for repeat observations from the same individual. Last, evaluation of resource selection and subsequent model cross validation followed the same approach/procedure as the foraging-site selection models (see methods). All modelling was run in R (R Core Team 2015).

Results

Post-breeding, 244 day-roost locations were recorded across all five individuals (ranging from 37 – 65 locations per individual) from 50 roost sites (a roost site was defined as single day-roost location, or a cluster of day-roost locations, that are at least 100 m from any other location). Tracked Stone-curlews rarely roosted in ‘cereals’ or rape crops (Table S.4.2); both habitats were omitted from analysis of roosting habitat selection. Stone-curlews were over a hundred-times more likely to roost in disturbed grassland (odds ratio = 134.3, 95% CI: 66.7 – 270.4), and fifty-times more likely to roost in arable fallows (odds ratio = 49.4, 95% CI: 18.2 – 134.3), relative to undisturbed grassland. Both were also selected over every crop (‘sugar beet or maize’, odds ratio = 4.5, 95% CI: 1.3 – 16.5; vegetable or root crops, odds ratio = 1.8, 95% CI: 0.2 – 16.5), and disturbed-grassland (but not arable fallows) was also selected over ‘pig fields or manure heaps’ (odds ratio = 18.2, 95% CI: 6.7 – 49.4). Stone-curlews were more likely to roost in ‘pig fields or manure heaps’ and ‘sugar beet or maize’ than undisturbed grassland, but these were not selected over ‘vegetable or root crops’. The predictive performance of this model was good (Fig. S.4.5).

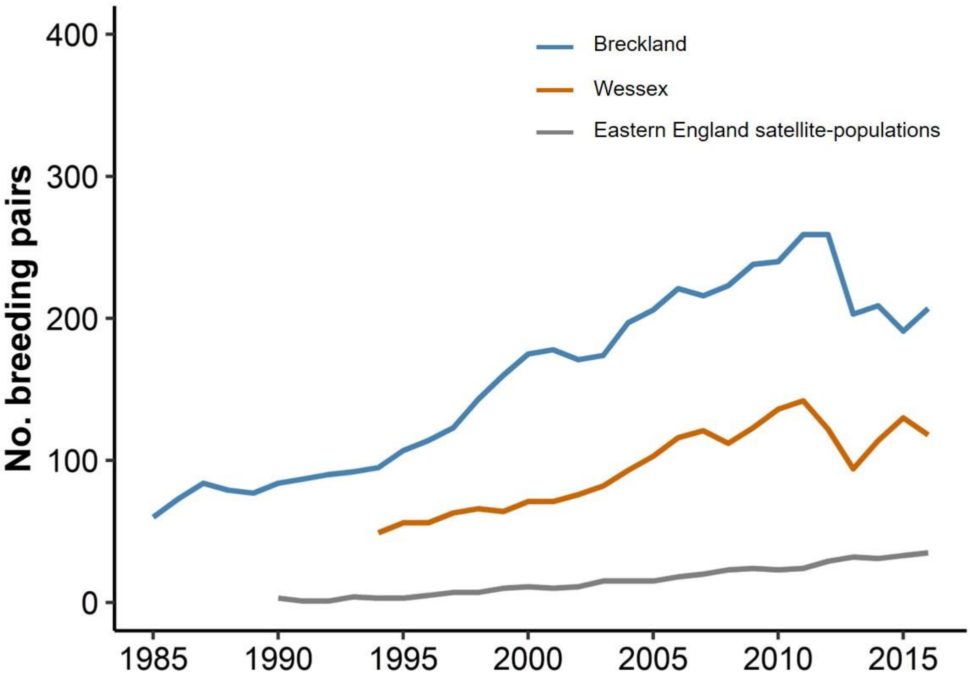

Figure S.4.1. The number of Eurasian Stone-curlew *Burhinus oedicnemus* breeding pairs in the UK between 1985 and 2016. Population totals are shown for the two main sub-populations (Breckland in the East of England, data presented here shows 1985-2016; and Wessex in southern England, 1994-2016) plus other small satellite populations in Eastern England (Cambridgeshire, North West Norfolk, and the Suffolk coast, collectively 'Eastern England satellite-populations', 1990-2016). For visual simplicity, we have combined satellite-populations in Southern England (Oxfordshire, Hampshire and Devon) with 'Wessex'. The data presented here was collected by RSPB fieldworks, with additional information provided by other land owners and organisations that also monitor Stone-curlews (for a detailed overview of the survey methods used, see Green & Griffiths 1994). Because access restrictions prohibited a complete survey within some sub-populations, the annual totals include every confirmed pair plus an estimated number of 'missed' pairs per sub-population (n.b. the estimated area relative to the surveyed area was small, thus any inaccuracies are minor).

Figure S.4.2. Distribution of arable, grassland, physically-disturbed grassland and unsuitable habitats across the 118,600 ha of Breckland, Eastern England, in which we tracked five adult Eurasian Stone-curlews *Burhinus oedicnemus* and sampled habitat availability. The highlighted area shows the extent of the 13,480 ha within which a field-based ground-truth survey confirmed: (1) crop species identity within each arable field (comprising 6,565 ha of cropped or fallow habitat); (2) the location of outdoor pig units (fields totaling 619 ha) and manure heaps (n = 97); and (3) within 6,296 ha of grassland, any areas of disturbed-grassland (outwith our experimental plots). For visual simplicity, crops (seven categories, see Table 4.1), arable fallows, pig fields and manure heaps are combined. Unsuitable habitat comprise woodland, freshwater, wet or seasonally wet habitats, and urban landcover, all of which Stone-curlews are known to avoid. Inserts show the three semi-natural grassland sites where experimental ground-disturbance was applied.

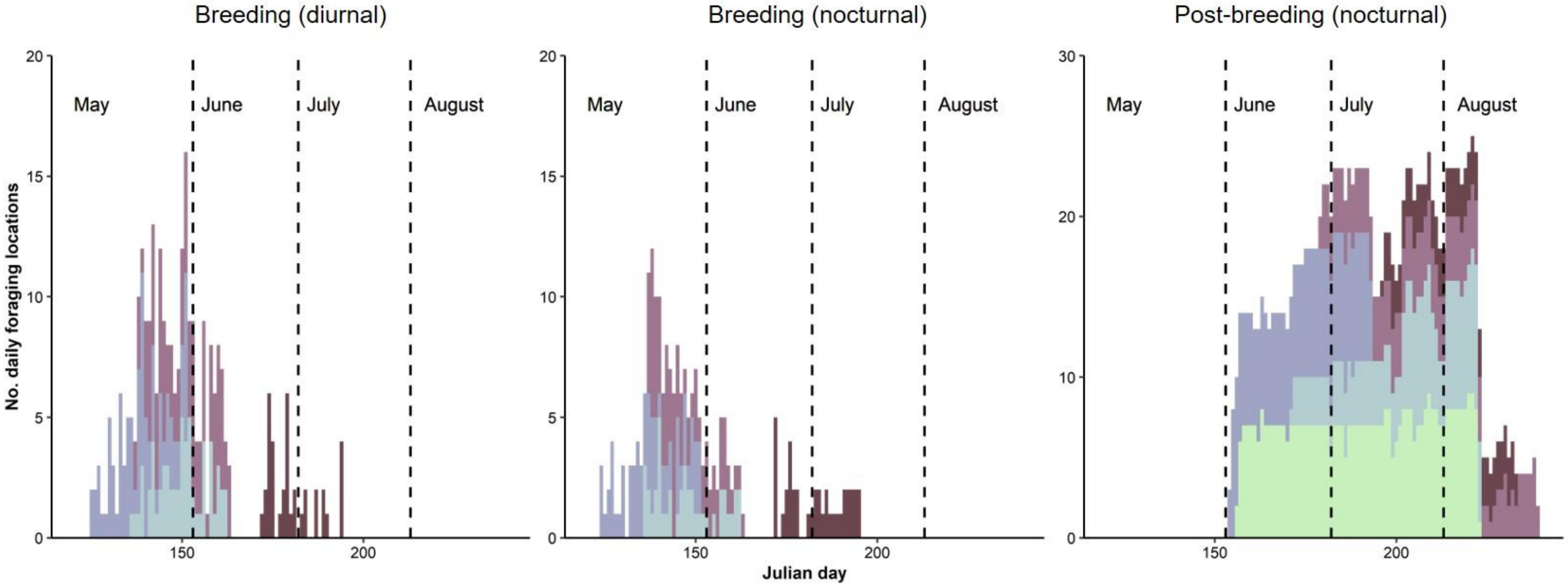

Figure S.4.3. Daily number of foraging locations from adult Eurasian Stone-curlews *Burhinus oedicnemus* tracked during breeding (reported separately for diurnal and nocturnal locations; n = 4 birds) and post-breeding (nocturnal locations only; n = 5 birds). Colours represent unique individuals.

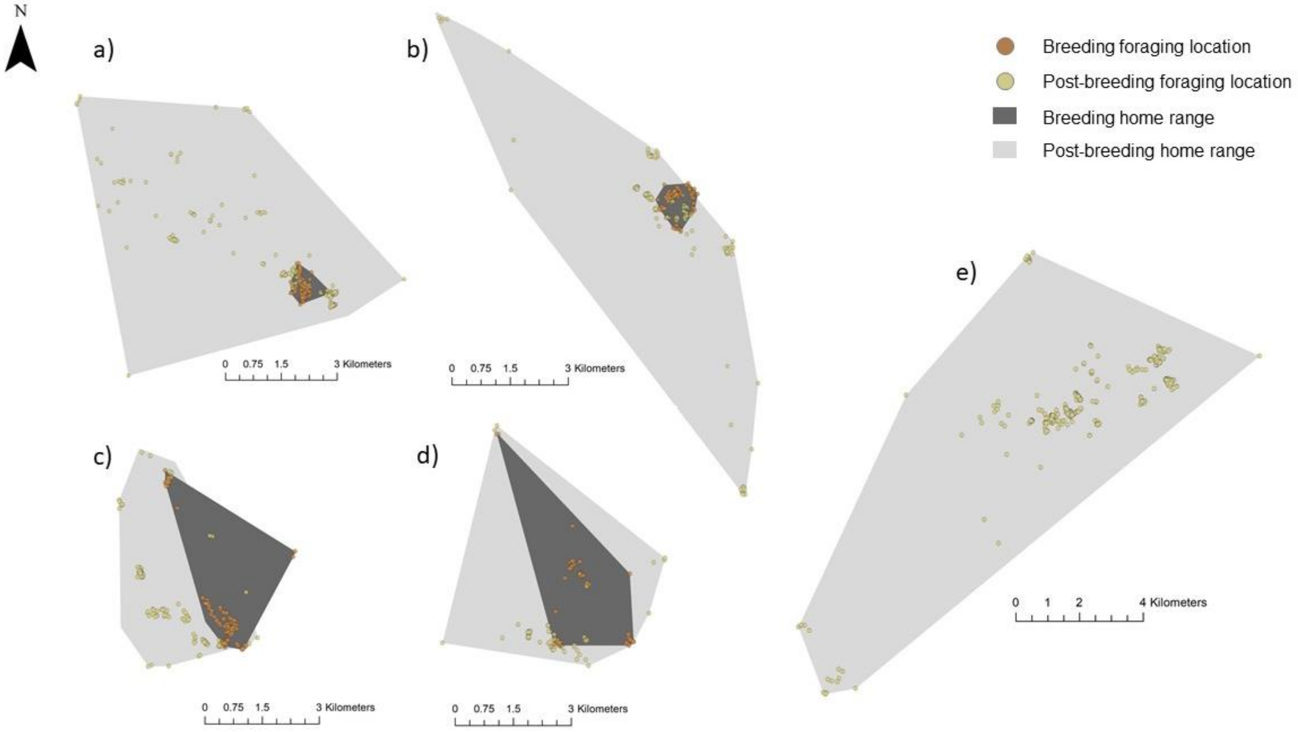

Figure S.4.4. The home range (Minimum Convex Polygon) and individual foraging locations of five adult Eurasian Stone-curlews *Burhinus oedicnemus*, shown separately for the breeding and post-breeding period. Note, one individual (e) was only tracked during the post-breeding period. We excluded foraging locations less than 50 m from the nest-site (but not the day-roost) to avoid over-representing periods of inactivity. We also excluded breeding and post-breeding locations that were: i) within habitats known to be unsuitable for Stone-curlews (Table S.4.2); ii) frequently misclassified by remote sensing (Table S.4.1); or iii) used too infrequently to reliably model resource selection (Table S.4.2).

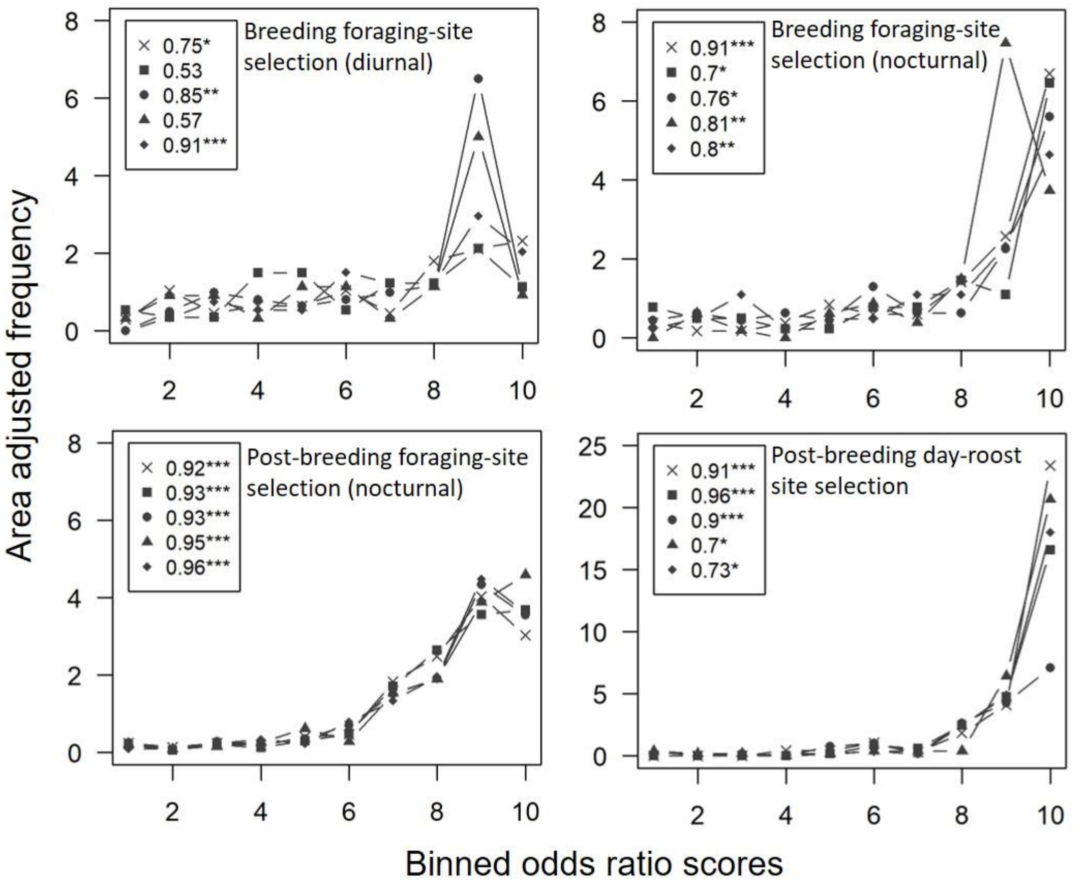

Figure S.4.5. Area-adjusted frequency of binned odds ratio scores (ranked lowest to highest, and assigned to ten categories, 0-10) of cross-validated Eurasian Stone-curlew *Burhinus oedicnemus* use, derived from separate models examining forging-site selection during breeding (considering diurnal and nocturnal foraging separately), foraging-site selection post-breeding (nocturnal locations only), and day-roost site selection post-breeding. Frequency values for individual cross-validation sets (n = 5, per model) are shown with unique symbols. Spearman's rank correlations (rho) between the area-adjusted frequency and bin rank for each set are given in each panel (asterixis denote coefficient significance; * p < 0.05, ** p < 0.01, *** p < 0.001).

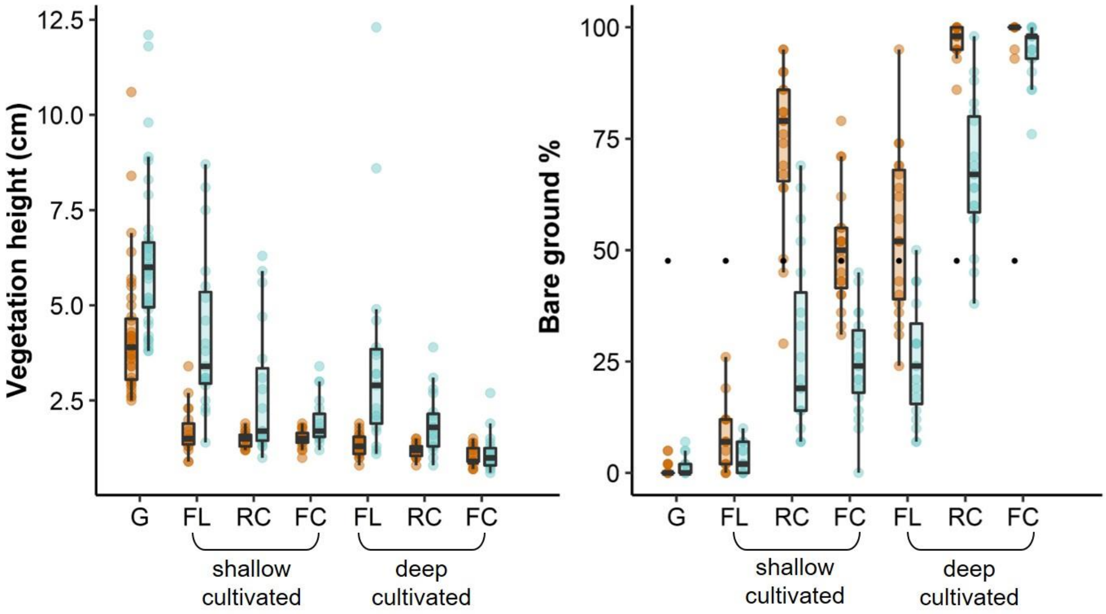

Figure S.4.6. Vegetation height and bare ground cover within one-year-old fallow (FL), repeat cultivated (RC) and first-time cultivated (FC) subplots, across 40 shallow-cultivated and deep-cultivated complex-mosaic plots (20 shallow-cultivated, 20 deep-cultivated; total = 120 subplots), plus 39 uncultivated grassland controls (G), within three semi-natural grassland sites where Eurasian Stone-curlews *Burhinus oedicnemus* were caught. Within each subplot and grassland control, vegetation height was assessed in April or early May (orange) and then again June or early July (blue) using a sward stick (diameter 90 mm, weight 250 g; following Green & Griffiths 1994) at 42 points distributed evenly along two parallel 100m transects (placed 30–33m apart). We also assessed whether bare substrate covered over 50% at each point (tip of the sward stick dowel, 25mm diameter), giving incidence from 0 to 42. Filled circles show the mean vegetation height (from the 42 sward stick measurements) and estimated bare ground cover (bare ground incidence, 0 – 42, converted to % cover) for each subplot and grassland control. Box plots show the median (central line) and the interquartile range (box) and whiskers show the range of data points within x 1.5 of the interquartile range, relative to the lower and upper quartile.

Table S.4.1. Cross-validation of remote-sensed land-cover categories by ground truthing. Accuracy (percentage of fields correctly classified) of remote sensing classification (from the 2016 Crop Map for England; Rural Payments Agency 2019) is shown for arable fallows, non-crop landcover (grassland and woodland), simplified crop categories (following initial merger based on prior knowledge of Eurasian Stone-curlew *Burhinus oedicnemus* suitability and similarities in sow date, vegetation structure and soil profile, see Table 4.1), and fields where the identity was not resolved (unidentified field), using ground-truth data from 561 arable fields (6,565 ha, Fig. S.4.2) from surveys undertaken between April and early July 2016. Autumn- and spring-sown cereals were merged to improve classification accuracy (initial autumn- and spring-sown cereals were correctly classified in 47% and 63% cases, respectively). Sample sizes (number of fields in each data set) are given in parentheses.

	Ground-truthed identity												
Remote sensed crop or non-crop identity		Rape (16)	Cereal (261)	Sugar beet or maize (117)	Vegetable or root crops (112)	Arable fallow (26)	Field beans (10)	Linseed (1)	Pea (5)	Grass fodder (7)	Lucerne (6)	**% of CROME crop correctly classified**	**Validation outcome**
	Rape (18)	16	2	0	0	0	0	0	0	0	0	**89%**	Carried forward to analysis
	Cereal (240)	0	232	1	5	1	0	0	1	0	0	**97%**	
	Sugar beet or maize (125)	0	2	96	24	2	0	1	0	0	0	**77%**	
	Vegetable or root crops (32)	0	0	1	31	0	0	0	0	0	0	**97%**	
	Arable fallow (32)	0	5	1	20	6	0	0	0	0	0	**19%**	Examined further to improve accuracy^{a}
	Unidentified field (26)	0	0	3	10	13	0	0	0	0	0	**NA**	Examined further to establish identity^{a}
	Field bean (17)	0	0	11	5	1	0	0	0	0	0	**0%**	Excluded from analysis owing to poor accuracy
	Linseed (1)	0	0	1	0	0	0	0	0	0	0	**0%**	
	Pea (32)	0	0	2	16	0	10	0	4	0	0	**13%**	
	Grassland* (33)	0	20	0	1	1	0	0	0	7	4	**NA**	Arable fields misclassified as non-arable. No further action taken
	Woodland* (5)	0	0	1	0	2	0	0	0	0	2	**NA**	

	Ground-truthed identity												
		Rape (16)	Cereal (261)	Sugar beet or maize (117)	Vegetable or root crops (112)	Arable fallow (26)	Field beans (10)	Linseed (1)	Pea (5)	Grass fodder (7)	Lucerne (6)	**% of CROME crop correctly classified**	**Validation outcome**
	% ground-truth crop correctly classified by CROME	**100%**	**89%**	**82%**	**28%**	**23%**	**0%**	**0%**	**80%**	**100%**	**33%**		

[a] Using satellite data derived from Sentinel 2 (see methods) we manually examined every field (across the entire study area, Fig. 4.1) classified by CROME as arable fallow or unidentified landcover, to establish whether a crop was present in June or August; these fields were then visually classified as ‘vegetable or root crops’ (where present; this was unlikely to be any other crop, Table S.4.1) or as arable fallow (where no crop was visible).

Table S.4.2. Distribution of GPS fixes from five adult Eurasian Stone-curlews *Burhinus oedicnemus* across 15 landcover categories, reported separately for foraging locations (diurnal and nocturnal breeding, and nocturnal post-breeding) and post-breeding day-roost locations (see Appendix S.4.1 for day-roost site selection analysis). Results are reported before and after we excluded landcover categories that were either frequently misclassified by remote sensing (see Table S.4.1), or *a priori* considered unsuitable for Stone-curlew (woodland, freshwater, wet or seasonally wet habitat and urban); or were infrequently used (<2% of fixes). Shading denotes excluded categories.

Landcover	**Foraging locations**						**Day-roost locations**	
	Diurnal breeding		**Nocturnal breeding**		**Nocturnal post-breeding**			
	Before exclusions	**After exclusions**	**Before exclusions**	**After exclusions**	**Before exclusions**	**After exclusions**	**Before exclusions**	**After exclusions**
Field beans	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	12 (0.8%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Peas	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	24 (1.7%)	0 (0.0%)	9 (3.5%)	0 (0.0%)
Linseed	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Arable fallow	0 (0.0%)	0 (0.0%)	3 (1.3%)	0 (0.0%)	373 (25.8%)	373 (27.2%)	58 (22.7%)	58 (23.8%)
Grassland	76 (25%)	76 (26.5%)	46 (19.8%)	46 (20.4%)	90 (6.2%)	90 (6.6%)	13 (5.1%)	13 (5.3%)
Disturbed-grassland	102 (33.6%)	102 (36.3%)	23 (10.0%)	23 (10.2%)	257 (17.8%)	257 (18.7)	82 (32.2%)	82 (33.6%)
Rape	0 (0.0%)	0 (0.0%)	2 (0.9%)	0 (0.0%)	1 (0.1%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Pig field or manure heap[a]	4 (1.3%)	0 (0.0%)	49 (21.1%)	49 (21.7%)	450 (31.2%)	450 (32.8%)	59 (23.1%)	59 (24.2%)
Cereals	5 (1.6%)	0 (0.0%)	12 (5.2%)	12 (5.8%)	62 (4.3%)	62 (4.5%)	2 (0.8%)	0 (0.0%)
Sugar beet or maize	109 (35.9%)	109 (40.0%)	87 (37.5%)	87 (38.1%)	96 (6.6%)	96 (7.0%)	27 (10.6%)	27 (11.1%)
Vegetable or root crops	0 (0.0%)	0 (0.0%)	6 (2.6%)	6 (2.7%)	43 (3.0%)	43 (3.1%)	5 (2.0%)	5 (2.0%)
Woodland	8 (2.6%)	0 (0.0%)	4 (1.7%)	0 (0.0%)	34 (2.4%)	0 (0.0%)	0 (0.0%)	0 (0.0%)

	Foraging locations						**Day-roost locations**	
	Diurnal breeding		**Nocturnal breeding**		**Nocturnal post-breeding**			
	Before exclusions	**After exclusions**	**Before exclusions**	**After exclusions**	**Before exclusions**	**After exclusions**	**Before exclusions**	**After exclusions**
Urban	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	1 (0.1%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Freshwater	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	1 (0.1%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Wet or seasonally wet habitat	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Total no. fixes	**304**	**287**	**232**	**223**	**1444**	**1371**	**255**	**244**

References

Green, R.E. & Griffiths, G.H. (1994). Use of preferred nesting habitat by stone curlews Burhinus oedicnemus in relation to vegetation structure. *Journal of Zoology,* 233(3), 457-471.

Green, R.E., Tyler, G.A. & Bowden, C.G.R. (2000). Habitat selection, ranging behaviour and diet of the stone curlew (*Burhinus oedicnemus*) in southern England. *Journal of Zoology,* 250(2), 161-183.

Halekoh, U., Højsgaard, S. & Yan, J. (2006). The R Package geepack for Generalized Estimating Equations. *Journal of Statistical Software,* 15(2), 1-11.

Met Office (2019). Met Office MIDAS open: UK land surfacestations data (1853-current). Centre for Environmental Data Analysis.

Panter, C.J., Mossman, H.L. & Dolman, P.M. (2013). *Stanford Training Area (STANTA) biodiversity audit to support grass heath management*. University of East Anglia, Norwich.

R Core Team (2015). R: a language and environment for statistical computing. Version 3.2.2. R Foundation for Statistical Computing, Vienna.

Rural Payments Agency (2019). Crop Map For England (CROME). Available at: https://data.gov.uk/dataset/6f316b8b-ae74-489c-ba3c-c2325a9c16a1/crop-map-of-england-crome-2016-complete (accessed 27 June 2019).

Chapter 5

Experimental evidence that novel land management interventions inspired by history enhance biodiversity

Robert W. Hawkes[a], Jennifer Smart[b,c], Andy Brown[d], Helen Jones[b], Steve A. Lane[e], Colin Lucas[f], James McGill[g], Nick Owens[h], Amanda Ratier Backes[i], Jon R. Webb[d], Doreen Wells[j], and Paul M. Dolman[a]

[a] School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

[b] RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

[c] School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

[d] Natural England, Suite D, Unex House, Bourges Boulevard, Peterborough, PE1 1NG, UK

[e] 5 Lancaster Way, East Winch, King's Lynn, PE32 1NY, UK

[f] 49 Mill Road, Beccles, NR34 9UT, UK

[g] 13 Cresswell Avenue, Taunton, TA2 6LS, UK

[h] 22 Springfield Close, Weybourne, Holt, NR25 7TB, UK

[i] Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

[j] 1 Cobden Terrace, Great Yarmouth, NR30 1BT, UK

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Photo credit: Annabelle Horton

Abstract

1. Within semi-natural habitats, knowledge of priority species requirements and landscape history encourages novel forms of management incorporating physical-disturbance and spatio-temporal variability. Despite strong justification for implementing such management, multi-taxa experimental confirmation is needed.
2. Informed by a bio-regional analysis of priority species requirements and historical land-use, we examined responses of vascular plants (hereafter 'plants'); spiders; true bugs; ground, rove and 'other' beetles; bees and wasps; ants; and true flies, to deep- and shallow-cultivation across an extensive closed-sward grassland (3,850 ha). Treatments and controls were replicated across 61 plots (20 shallow-cultivated, 20 deep-cultivated, 21 control), with treatments accumulating over three years to create 4 ha complexes comprising: repeat cultivation, first-time cultivation, one-year fallow and two-year fallow. Sampling gave 132,251 invertebrates from 878 species and 28,846 plant observations from 167 species.
3. Across all taxa, both treatments increased richness of non-priority species and doubled richness of priority species (rare, scarce or threatened).
4. Non-priority plant, ground beetle, rove beetle and true bug richness were greater on both treatments than controls, and non-priority other beetle, bee and wasp, ant and true fly richness were greater with deep-cultivation. Priority spider, ground beetle, other beetle, and true bug richness were greater on both treatments than controls, and priority plant richness was greater with deep-cultivation. Across most taxonomic groups, numbers of unique species (either of non-priority or priority species) were similar between treatments and controls.
5. Those priority dry-open habitat invertebrates *a priori* predicted to require greater intensity of disturbance responded more strongly to treatments than those associated with little or no disturbance.
6. *Synthesis and applications.* Our landscape-scale experiment confirmed the considerable biodiversity value of interventions inspired by history and informed by the ecological requirements of priority biota. Since treatments and controls each supported unique species, a combination of management interventions would support the widest range of species. Crucially, the intended recipients responded particularly well, suggesting bio-regional analysis of priority species

requirements across multiple taxa could successfully inform interventions within other systems.

Keywords: biodiversity audit, grassland, heterogeneity, landscape-scale, lowland heathland, multi-taxa, physical disturbance, semi-natural habitat

5.1 Introduction

Across Europe, conservation tends to focus on semi-natural habitats shaped by a long history of human management (Ratcliffe 1977; EC 1992), yet priority plants (Hülber *et al.* 2017) and invertebrates (Seibold *et al.* 2019) continue to disappear from such areas. Within surviving remnants, land management often mimics perceptions of historic (pre-industrial c 1200 – 1750) practices on the assumption that this will support assemblages that persisted through human activity (Wright, Lake & Dolman 2012). Such interventions are usually justified with reference to the ecology of a taxonomically-biased species-subset (Clark & May 2002; Griffiths & Dos Santos 2012), or a belief that mimicking historic management will support regional biota (Fuller, Williamson, Barnes & Dolman 2017). Although many interpretations of ‘traditional’ management are based on incomplete historical records and are potentially suboptimal for threatened biodiversity, confidence in alternative approaches requires evidence. A new emphasis on ‘re-wilding’ (Pettorelli *et al.* 2018) and a progressive shift from biodiversity conservation for its intrinsic value (DEFRA 2007) toward ecosystem service provision (DEFRA 2018), further increase the need for approaches which can quantify and predict biodiversity responses to landscape-scale interventions. Biodiversity Audits (Dolman, Panter & Mossman 2012) provide a tool to quantify and characterise the shared habitat, resource and ecological requirements of a diverse range of priority species, but whilst such analyses support the importance of historical management to priority biota (Dolman *et al.* 2012), there is a pressing need for multi-taxa experimental confirmation.

Crucially, perceptions and implementation of ‘traditional management’ tend to be simplified and homogenised (Fuller *et al.* 2017). Historical management was instead characterised by biomass removal and physical disturbance through complex multi-layered land-use, varying temporally and spatially both within sites and across landscapes (Linnell, Kaczensky, Wotschikowsky, Lescureux & Boitani 2015; Fuller *et al.* 2017). Synthesising autecological knowledge (Dolman *et al.* 2012) with a detailed understanding of these historic land-use complexities (Linnell *et al.* 2015; Fuller *et al.* 2017) inspires novel interventions (hereafter, ‘enhanced management’), often with an emphasis on physical-disturbance, grazing, nutrient removal, spatio-temporal variability, early-successional habitats and structural complexity (Fuller *et al.* 2017). This might involve near-accurate replication of specific pre-industrial practices (e.g. coppicing, Merckx *et al.* 2012) or the use of large herbivores to create and maintain dynamic mosaics (consistent with some principles of rewilding, Van Klink & WallisDeVries 2018); but in other circumstances it may be appropriate to adopt new approaches that provide the resources needed by the widest range of species.

Despite recent calls for strategies that deploy novel forms of enhanced management (Linnell *et al.* 2015; Fuller *et al.* 2017), this approach is untested. Specifically, it is unclear whether target priority species are able to colonise newly-established suitable habitats (Thomas 1994) and whether benefits of management are offset by the loss of other species intolerant of the intervention. In addition, modern techniques offer interventions that differ from historical methods, while accelerated succession (from increased rates of nitrogen-deposition, Tipping *et al.* 2019; Ridding *et al.* 2020) may reduce the duration and colonisation of suitable micro-habitats, such that more severe interventions may be beneficial (Härdtle, Niemeyer, Niemeyer, Assmann & Fottner 2006; Pedley, Franco, Pankhurst & Dolman 2013), but this requires assessment of how efficacy varies with intensity. Last, most tests of intervention efficacy within semi-natural habitats focus either on vegetation structure as a proxy for biodiversity, or on single species or a limited subset of taxa (e.g. Lepidoptera, Goodenough & Sharp 2016; or birds, Żmihorski, Pärt, Gustafson & Berg 2016). Given that semi-natural habitats are especially valued for their diverse assemblages (Ratcliffe 1977), robust multi-taxa studies are needed to reliably assess the effectiveness of conservation strategies.

Here, we test the multi-taxa consequences of enhanced management interventions across a mosaic of semi-natural lowland dry-grassland and heathland (hereafter ‘grassland’). We selected grassland because conservation practices have long emphasised the role of grazing (Wells 1969; Bakker, De Bie, Dallinga, Tjaden & De Vries 1983) but there is increasing realisation that the needs of many priority species may be better met by temporally and spatially dynamic physical-disturbance than by promoting temporal stability and uniform prescriptions (e.g. Pywell *et al.* 2007; Cameron & Leather 2011; Pedley *et al.* 2013; Hawkes *et al.* 2019b). Land-use history (Fuller *et al.* 2017) justifies creating overlapping mosaics of cultivations that vary in disturbance age and frequency, that are more likely to benefit priority grassland species (Dolman *et al.* 2012).

To examine the effects of such management on grassland biodiversity, we conducted a well-replicated, landscape-scale experiment across one of the UK’s most extensive grasslands (3,850 ha). The selected interventions focussed on two methods of promoting structural complexity through ground-disturbance (shallow- or deep-cultivation), built up over a three-year period to create 40 physically-disturbed complexes (totalling 160 ha). We quantified responses across nine taxonomic groups, comparing treatments to generalised management - areas of grassland managed with light grazing and limited or no ground disturbance. We considered the effects of treatment on species richness (hereafter 'richness') and assemblage composition, separately for non-priority and priority species overall (pooling across taxa) and for each taxonomic group. We also tested whether species whose autecology suggests an association with physically-disturbed dry-open habitat (the intended recipients) responded more strongly to treatment than those thought to require no or lighter disturbance.

5.2 Methods

5.2.1 Study area

The experiment was carried out in Breckland, a biogeographical region of Eastern England characterised by a semi-continental climate and sandy soils, that hosts over 2,000 priority plant and invertebrate species (26% of all UK priority species, Dolman *et al.* 2012). Of these, 400 (64% of all dry-open habitat priority species) are believed to require heavy grazing and/or physical ground-disturbance, conditions characteristic of pre-industrial regional land-use. We attempted to provide the resources required by these species by implementing complex, ground-disturbance interventions across the lightly sheep-grazed grasslands of the Stanford Military Training Area (STANTA) (52°51'N, 0°76'E, 3500 ha), Bridgham Heath (52°44'N, 0°83'E, 150 ha) and Brettenham Heath (52°43'N, 0°83'E, 200 ha) (for further study area details, see Hawkes *et al.* 2019b; and map in Fig. S.5.1).

5.2.2 Experimental treatments

In early 2015, 40 2-ha ground-disturbance plots (20 shallow-cultivated using a rotary rotovator; 20 deep-cultivated using an agricultural plough) and 21 4-ha uncultivated generalised management plots (hereafter 'controls') were located in grassland mostly excluding, but sometimes close to, scattered trees or scrub (for establishment method and management details, see Hawkes, Smart, Brown, Jones & Dolman 2019a). Treatment was repeated in the winters of 2015-2016 and 2016-2017, each year cultivating 2-ha with half (1-ha) overlapping a central repeatedly-treated sub-plot, and half (1-ha) first-time-cultivation, so that in the final year (2017) each complex contained four 1-ha subplots, comprising: 1-year fallowed, 2-year fallowed, first-time-cultivated, and repeatedly-cultivated (see Fig. S.5.2).

Treatment complexes and control plots were restricted to the outer areas of STANTA, plus Bridgham and Brettenham Heath, owing to risks from unexploded ordnance in the STANTA 'impact area' (see Fig. S.5.1). Within this constraint, treatments and controls were randomly (but evenly) allocated across four grassland strata (following Hawkes *et al.* 2019a), based on soil, age since cultivation, and plant composition: calcareous grassland of any age; young grassland (≤110 years old); intermediate grassland (111-167 years old) and ancient-acid grassland (≥168 years old) (see Table S.5.1 for details). Treatments and controls were distributed across the study area, but vegetation strata were aggregated due to distributions of soil types and grassland ages (Hawkes *et al.* 2019b).

5.2.3 Responses to treatment

Responses to treatment were assessed in 2017. Invertebrates were sampled across all 40 treatment complexes and 21 control plots, and vascular plants (hereafter 'plants') across 32 complexes (16 shallow-cultivated, 16 deep-cultivated) and 16 controls (randomly selected, constrained to vegetation strata) due to resource constraints. For each sampled treatment complex all four 1-ha subplots (which differed markedly in vegetation structure, Fig. S.5.3) were sampled, for controls a central 1 ha plot was sampled (as vegetation structure was uniform throughout each plot). All sampled subplots or plots had a similar trapping deployment (see below); greater sampling intensity in each complex than each control was accounted for by rarefaction (see analysis). We could not sample four 1-ha subplots for each control without severely curtailing replication of treatment complexes (that were more heterogeneous) owing to sample identification.

Eight invertebrate groups were sampled using pitfall traps [spiders (Araneae); ground beetles (Carabidae); rove beetles (Staphylinidae); other beetles (Coleoptera, excluding Carabidae and Staphylinidae); true bugs (Hemiptera, excluding aphids); ants (Formicidae); bees and wasps (Aculeata, excluding ants)] and pan traps [true bugs; bees and wasps; true flies (Diptera, resolved for: Asilidae, Rhagionidae, Stratiomyidae, Syrphidae, Tabanidae, Therevidae, Tipulidae)]. In each sampled control plot and treatment subplot six pitfall traps (each 11 cm deep, 8 cm diameter, covered by 12 mm x 12 mm mesh, with 50 ml of 33% propylene glycol) were deployed, set 15 m apart in a central 15 m x 30 m grid, for seven consecutive days, separately in each of May/June, July/August, and September. Four yellow pan traps (each 4 cm deep, 15 cm diameter, set at ground level, covered with 30 mm x 40 mm mesh, with 150 ml of water with a few drops of unscented detergent) were deployed once in each control plot and treatment subplot, in a central 15 m x 15 m grid, for three consecutive days, between 1 July and 26 August. Including redeployments (replacement sets following failure of more than half the aggregate expected trap-days, per treatment subplot or control plot, in a trapping round), 96% (pitfall traps) and 94% (pan traps) of all trap deployments were successful (considered active for the whole exposure period). Additional trapping details are in Appendix S.5.1 of supplementary materials. Plant incidence was sampled from 16 quadrats (1 m x 1 m) distributed evenly (11-14 m apart) along two parallel 100 m transects (30-33 m apart) in each control plot and treatment subplot (giving frequency per species, 0-16), between 10 April and 7 July. For analyses, data were pooled across months (pitfall traps only) and sampling methods (pitfall traps, pan traps and quadrats) giving one composite sample per control plot (n=21) or treatment subplot (n=160, nested within 20 deep- and 20 shallow-cultivated complexes).

Most sampled taxa were identified to species level, the few unresolved plants (0.3%), spiders (<0.1%), ground, rove and other beetles (<0.1%, 3.5%, 1.0%), true bugs (3.7%), and bees and wasps (0.9%) were not considered further. Priority species were identified as those recognised as: (i) Threatened (IUCN Critically Endangered, Endangered and Vulnerable) or Near Threatened in Great Britain; or (ii) Nationally Rare (NR) and Nationally Scarce (NS), or the older designations of Red Data Book (RDB) and Nationally Notable (Na, Nb). Others were classified as ‘non-priority’ species.

5.2.4 Data analysis

We used sample-based rarefaction (re-scaled to the number of individuals, using the Mao Tau function) from the package 'iNEXT' (Chao *et al.* 2014) to calculate cumulative richness for each of the two cultivation treatments and the controls (hereafter, collectively 'regimes'). We compared overall richness (pooling across all nine taxa) and also the richness of each taxon, separately for non-priority and priority species, between regimes. As the number of individuals sampled differed among regimes, following Chao *et al.* (2014) we compared richness estimates at a base sample size (hereafter 'BSS') set as the smaller of: twice that of the regime with the smallest sample size, or the regime with the largest sample size. For comparison, each regime was subsequently extrapolated (observed richness < BSS) or rarefied (observed richness > BSS) to the BSS. As extrapolation is unreliable beyond double the original sample size (Chao *et al.* 2014), setting the BBS to the largest sample size was inappropriate. Consistent with other studies (e.g. Schall *et al.* 2018), we also set the BSS to the smallest sample size (classical rarefaction) to ensure robustness of findings. Richness estimates were considered to differ between regimes when pairwise 95% CIs obtained from 200 bootstrapping replications, did not overlap (Chao *et al.* 2014). Finally, because comparisons of overall non-priority and priority species richness considered eight complexes (four deep-cultivated, four shallow-cultivated) and five controls that lacked plant data, we tested whether removing these samples entirely from both of these analyses altered inference.

Irrespective of relative richness, regimes may support distinctive assemblages, or unique species not recorded in any other regime. We quantified the percentage of the species-pool supported within each regime, and the percentage of the species-pool unique to the regime, separately for non-priority and priority species, for the overall assemblage and each taxon, using Euler diagrams (in package 'Eulerr': Larsson 2019). To simultaneously consider plant and invertebrate samples, we omitted the five controls and eight complexes sampled only for invertebrates. To control for the greater level of sampling effort in the treatment complexes we undertook 200 iterations, each resampling all 16 control plots and 16 subplots from each treatment regime (of 64 available per treatment regime, resampling independently of complex-identity), drawing one per (four) sub-treatment x (four) vegetation strata combination per iteration. For each metric regimes were compared through pair-wise comparisons with Bonferroni correction across the three contrasts (i.e. at least 199 of the 200 iterations showed larger values for one regime).

To establish whether enhanced management increased the richness of the intended recipients, we used two existing species-classifications based on autecological information. The first, available as an online tool (Pantheon, Webb *et al.* 2018), classifies invertebrate species on a composite ecological gradient of increasing disturbance intensity (hereafter 'habitat guilds'). We used this to classify those non-priority and priority invertebrates associated only with dry-open habitats ('open-habitat' in Pantheon; excluding those associated with wet/shaded habitats, and those whose broad ecological requirements were unknown) as requiring 'tall swards and scrub', 'short swards without exposed sand' (hereafter, 'short swards'), or 'short sward with exposed sand' (hereafter, 'short swards and bare ground'); excluding those with unknown or undifferentiated structural requirements. The second (of priority invertebrates only) considers a two-way classification, independently, of grazing intensity and physical disturbance (Dolman *et al.* 2012) (hereafter, 'management guilds') and was used to classify only those priority invertebrates associated with dry-open habitats (as above) as requiring no/light/heavy physical-disturbance and either no/light grazing (hereafter, 'no grazing') or heavy grazing; excluding those with unknown or undifferentiated requirements for physical-disturbance and grazing (see Table S.5.2). Plants, although classified in management guilds, were omitted for consistency with habitat guild analyses. Next, for each guild, we compared overall invertebrate richness between regimes using rarefaction, separately for non-priority (habitat guilds) and priority (habitat or management guilds) species.

5.3 Results

Sampling gave 28,846 plant observations from 150 non-priority and 12 priority species, and 132,251 invertebrates (121,968 from pitfall traps, 10,283 from pan traps) from 708 non-priority and 170 priority species (see Table S.5.3 for species and Table S.5.4 for numbers sampled per invertebrate group); including a new species to Britain (see thesis Appendix A). For non-priority and priority species overall, and separately for spiders, ground beetles, rove beetles, other beetles, true bugs, ants, true flies, and plants, sample-based rarefaction approached the asymptote within each regime (Fig. 5.1, Fig. 5.2), indicating sampling had effectively captured their diversity. Although non-priority and priority bees and wasps approached the asymptote on both treatment regimes, they were uncommon on, and therefore insufficiently sampled from, controls.

5.3.1 Overall treatment consequences

For non-priority species, overall richness was greater on both treatments (deep-cultivated: 610 species, 95% CI 600-620; shallow-cultivated: 554, 542-565) than controls (445, 416-474), while deep-cultivation supported more species than shallow-cultivation (Fig. 5.1a). Both treatments supported a larger percentage of the overall non-priority species-pool (deep-cultivation: 77%, 74-80%; shallow-cultivation: 71%, 67-75%) than controls (56%, 54-58%; Fig. 5.1b). Relative to the species-pool deep-cultivation also supported a greater percentage of unique non-priority species (17% relative to the species-pool, 14-20%) than either shallow-cultivation (10%, 8-12%) or controls (8%, 6-9%).

For priority species, overall richness on both treatments (deep-cultivation: 114 species, 110-120 95% CI; shallow-cultivation: 107, 102-112) was approximately double that of controls (60: 49-70) (deep- and shallow-cultivation did not differ) (Fig. 5.1a). Consequently, both treatments supported double the percentage of the overall priority species-pool (deep-cultivated: 65%, CI 57-71%; shallow-cultivated: 65%, 59-72%) than controls (overall assemblage: 38%, 35-41%). For rarefaction of those priority species with a GB IUCN threat status (from 42% of priority invertebrates and 92% of priority plants assessed; see Table S.5.3), both treatments contained more Threatened or Near-Threatened species (deep-cultivated, 8: 7-10; shallow-cultivated: 6, 5-6) than controls (2: 1-3) (Fig. S.5.4). Relative to the species-pool both treatments supported a greater percentage of unique priority species (deep-cultivated: 23%, 17-28%; shallow-cultivated: 20%, 14-26%) than controls (9%, 6-12%; Fig. 5.1b). For all rarefaction analyses, lowering the BSS to the smallest sample size (Table S.5.5), or removing the subset of treatment complexes and control plots that lacked plant data, did not affect inference.

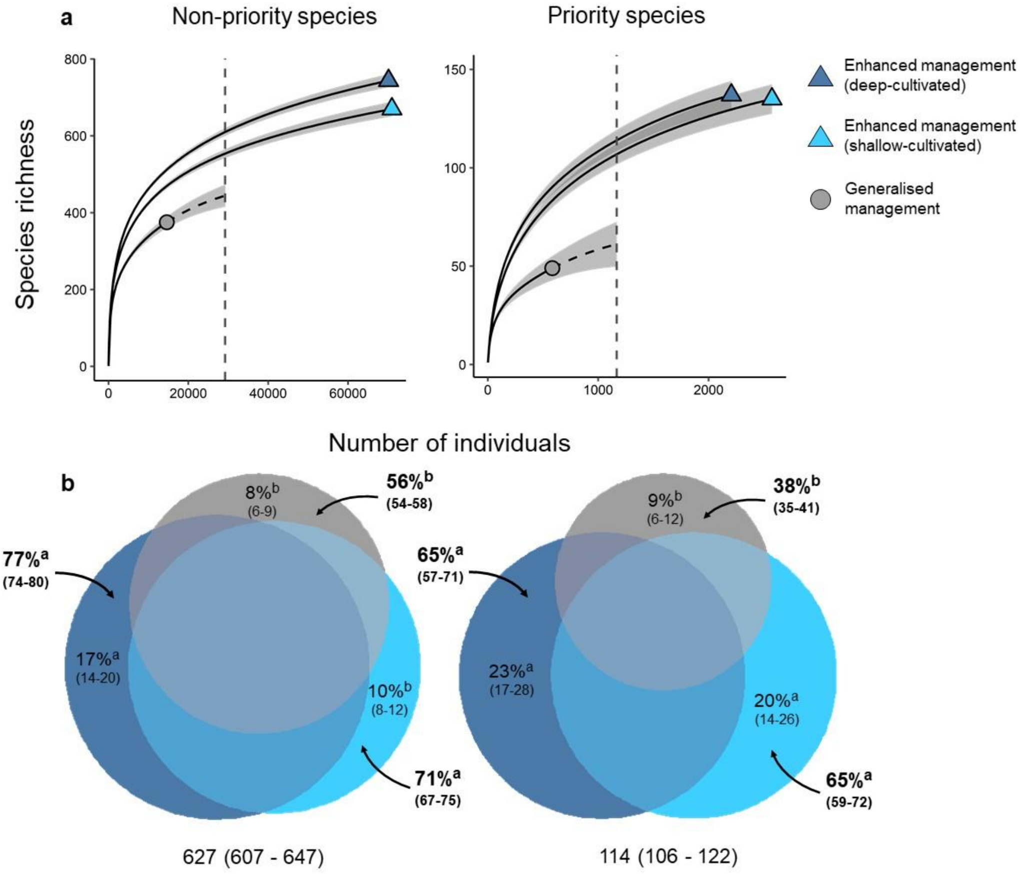

Figure 5.1. Composition of non-priority and priority species pooled across nine taxonomic groups, in shallow- or deep-cultivated treatments (enhanced management) and controls (generalised management). Panel (a) shows sampled-based rarefaction rescaled to numbers of individuals for each regime; symbols and solid lines denote observed and interpolated richness respectively, dashed lines extrapolate to the base sample size (twice the smallest sample size: vertical dashed line), shading represents 95% CI bounds. Panel (b) shows the mean and 95% CI of total richness across all regimes (reported below each Euler diagram), and the percentage of this species pool recorded within (outer bold values) and unique to (values within Euler sets) each regime, based on 200 resampling iterations each comprising 16 subplots per treatment and all 16 control plots; regimes that share a superscript do not differ (based on pairwise comparisons with Bonferonni correction). Diagrams also illustrate the proportion of species shared between regimes (see Table S.5.6 for percentages).

5.3.2 Taxa-specific treatment consequences

For non-priority species, richness was greater on treatments than controls for eight (deep-cultivation: plants; ground beetles; rove beetles; other beetles; true bugs; bees and wasps; ants; true flies) and four (shallow-cultivation: plants; ground and rove beetles; true bugs) of the nine taxonomic groups (Fig. 5.2). Deep-cultivation supported greater richness than shallow-cultivation for five groups (plants; other beetles; true bugs; bees and wasps; true flies). Treatments supported a greater percentage of the overall non-priority species-pool than controls for six (deep-cultivation: plants; ground, rove and other beetles; bees and wasps; true flies) or five (shallow-cultivation: plants; ground, rove and other beetles; bees and wasps) groups (Fig. 5.3). Treatments held more unique non-priority species than controls, respectively for three groups (deep-cultivation: ground beetles; other beetles; bees and wasps) or one group (shallow-cultivation: ground beetles), while controls did not hold more unique non-priority species for any group.

For priority species, richness was greater on treatments than controls for five (deep-cultivation: plants; spiders; ground beetles; other beetles; true bugs) or four (shallow-cultivation: spiders; ground beetles; other beetles; true bugs) of the seven groups considered (ants and true flies were omitted) (Fig. 5.2). Deep-cultivation contained more priority ground beetles but fewer priority true bugs than shallow-cultivation. Treatments supported a greater percentage of the overall priority species-pool than controls for four groups (deep-cultivation: ground beetles; other beetles; true bugs; bees and wasps, shallow-cultivation: spiders; ground beetles; other beetles; true bugs) (Fig. 5.3). Treatments only held more unique priority species than controls for one group (deep-cultivation: ground beetles; shallow-cultivation: other beetles), while controls did not hold more unique non-priority species for any group.

Lowering the BSS to the smallest sample size affected inference for four of 16 rarefaction analyses (non-priority other beetles; non-priority ants; non-priority true flies; priority rove beetles; Table S.5.5). In three of these cases, non-significant differences became significant (reflecting narrower CIs without extrapolation), therefore we consider inference from extrapolation to twice the lowest sample size conservative.

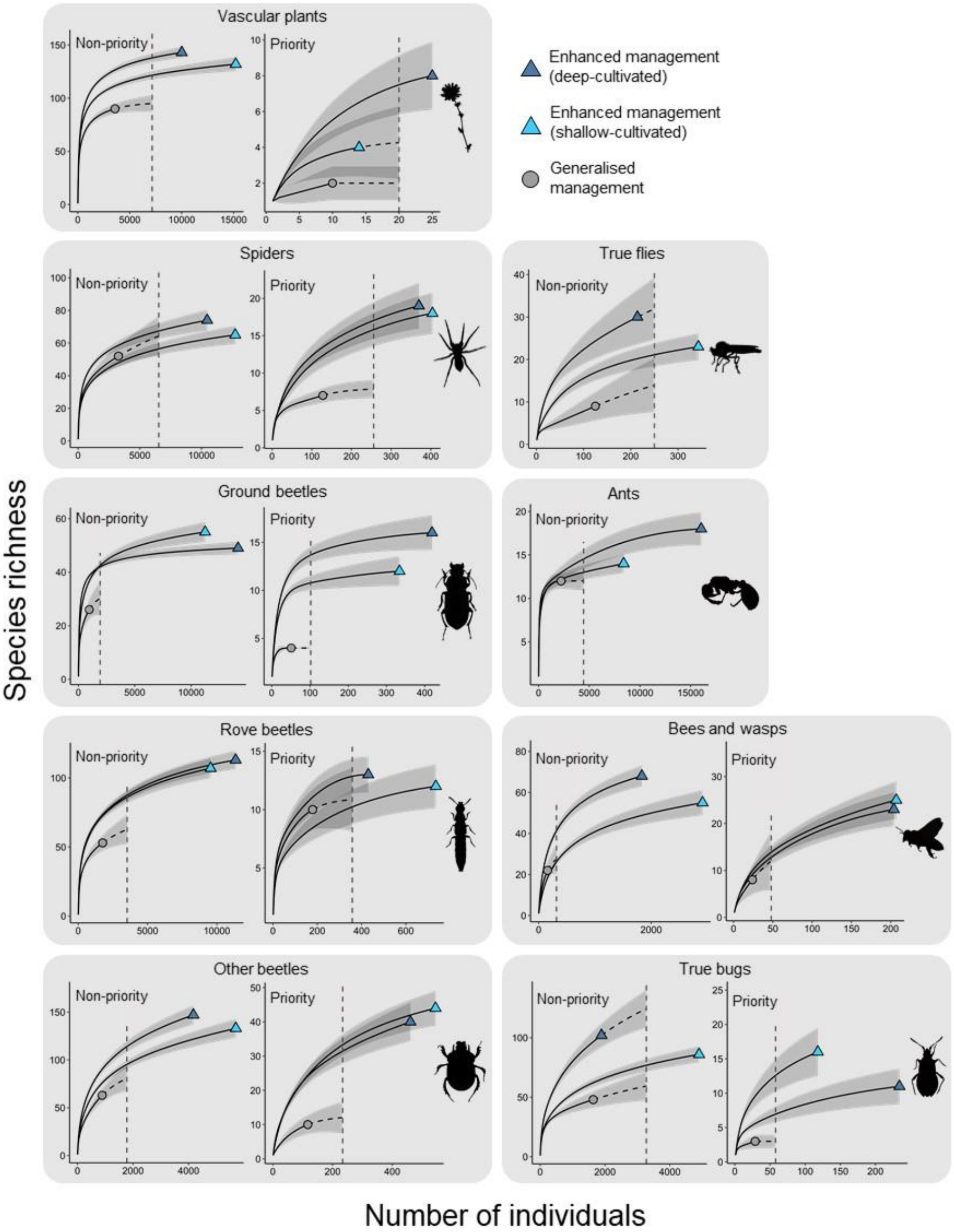

Figure 5.2. Richness of non-priority and priority species within each of nine taxonomic groups, in shallow- or deep-cultivated treatments (enhanced management) and controls (generalised management). Shown are sample-based rarefactions rescaled to numbers of individuals, symbols and solid lines denote interpolated and observed richness respectively, dashed lines extrapolate to the base sample size (twice the smallest sample size: vertical dashed line); shading represents 95% CIs. Ants and true flies, were not subjected to rarefaction owing to limited numbers of priority species (four per group, across all regimes).

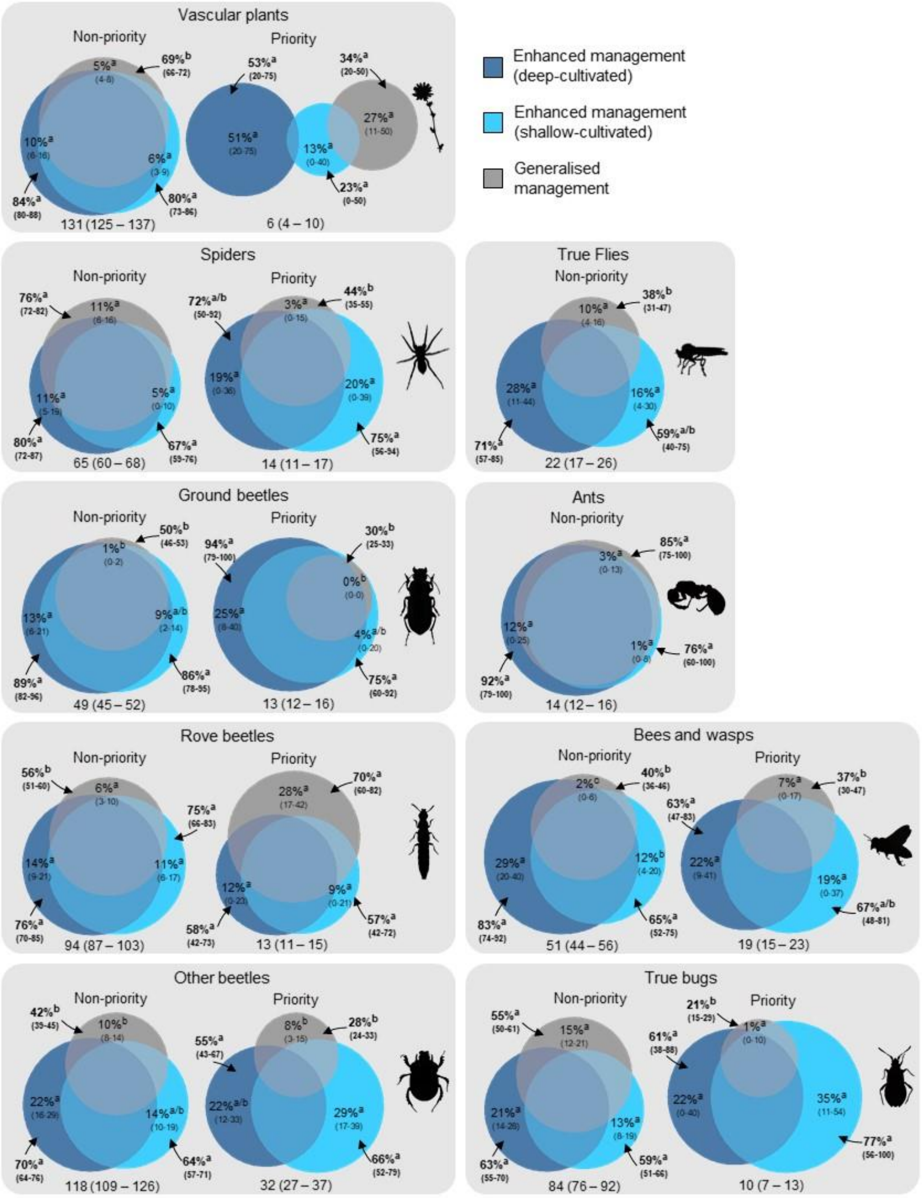

Figure 5.3. Representation of non-priority and priority species in shallow- or deep-cultivated treatments (enhanced management) and generalised management (controls), for each of nine taxonomic groups. Shown are the mean and 95% CI of overall richness across regimes (reported below each Euler diagram) and the percentage of this species pool recorded within (outer bold values) and unique to (values within Euler sets) each regime, based on 200 resampling iterations each comprising 16 subplots per treatment and all 16 control plots; regimes that share a superscript do not differ (based on pairwise comparisons with Bonferonni correction). Diagrams also illustrate the proportion of species shared between regimes (see Table S.5.6 for percentages). For ants and true flies, limited numbers of priority species prohibited separate examination.

5.3.3 Habitat and management guilds

Of the 708 non-priority and 170 priority invertebrate species, 551 non-priority and 135 priority species were associated with dry-open habitats (76 and 14 were associated with wet/shaded habitats, while broad ecological requirements of 81 and 21 were unknown); of these 518 (94 %) and 123 (91 %) were classified among the three habitat guilds (Table S.5.3) (the remainder had unknown or undifferentiated structural requirements). For non-priority species, richness of the 346 'tall sward and scrub' associated species was greater on both treatments than controls; richness of the 94 'short sward' species was similar between regimes, and for the 78 'short sward and bare ground' species richness was greater for one treatment (deep-cultivation) than controls (Fig. 5.4). For priority species, for the 35 'tall sward and scrub' associated species richness was greater on one treatment (shallow-cultivation), for the 33 'short sward' species neither treatment; in contrast for the 55 'short sward and bare ground' species richness was nearly three times greater on both treatments than on controls.

Of the 135 dry-open priority invertebrate species, 105 (78 %) were classified into five management guilds (Table S.5.3; 25 had unknown or undifferentiated requirements for grazing and disturbance and 5 were classified as wet/shaded associated). Response to treatment was progressively greater for management guilds with more intense requirements (Fig. 5.4): for the 15 priority species requiring 'no physical-disturbance and no grazing', richness was similar across treatments and controls; for those requiring either 'no physical-disturbance and heavy grazing' (17 species) or 'light physical-disturbance and no grazing' (15 species), richness was greater for shallow-cultivation or both treatments (respectively) than controls; for those requiring 'heavy physical-disturbance and no grazing' (33 species), richness on both treatments was double that on controls; while for priority species requiring 'heavy physical-disturbance and heavy grazing' (25 species), richness on both treatments was three times that on controls. Lowering the BBS to the smallest sample size affected inference for one of the six habitat guild analyses ('short sward' associated non-priority species, again providing greater frequency of significant contrasts) and none of the five management guild analyses (Table S.5.5).

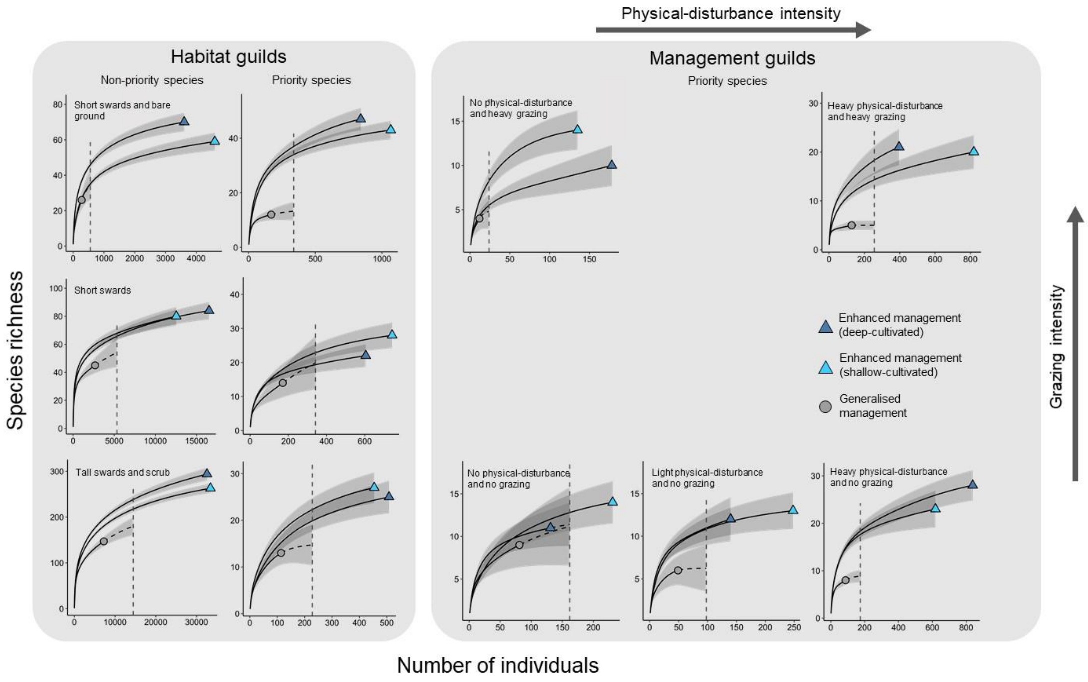

Figure 5.4. Response to management for invertebrate guilds with differing habitat and management requirements. Left panels consider species classified between three habitat guilds (from the Pantheon database) on a composite gradient with increasing disturbance intensity: from long swards and scrub, through short sward, to short sward with bare ground, separately for non-priority and priority species. Right panels (priority species only) consider classification between five management guilds (from biodiversity auditing) in relation to two independent gradients of grazing and physical disturbance intensity. For each habitat or management guild, sample-based rarefaction (rescaled to numbers of sampled individuals) contrasts richness between shallow- or deep-cultivated treatments (enhanced management) and controls (generalised management). Symbols and solid lines denote interpolated and observed richness respectively, dashed lines represent richness extrapolated to the base sample size (twice the smallest sample size: vertical dashed line); shading represents 95% CIs.

5.4 Discussion

Through the largest multi-taxa land management experiment yet conducted in a European grassland, we quantified consequences of management interventions inspired by history and informed by systematic, cross-taxa analysis of the requirements of priority species. Sampling over 130,000 invertebrates and 28,000 plant observations showed that using physical-disturbance to enhance the structural complexity of grassland otherwise managed solely by grazing, increased the overall richness of non-priority and priority species. Consistent with our prediction, priority species considered to require greater intensity of disturbance responded most strongly to treatments.

Treatments increased structural complexity (Fig. S.5.3) and supported a greater overall richness of non-priority and priority species than controls, consistent with well-established benefits of habitat heterogeneity (Stein, Gerstner & Kreft 2014). More surprising was the magnitude of response - especially of priority species - which nearly doubled in richness with treatment. This was probably attributable to the range of conditions within each complex; ranging from recent cultivations with extensive bare ground, which support the warmer conditions required by some species (Krämer, Kämpf, Enderle, Poniatowski & Fartmann 2012); to regenerating fallows, which provide important resources for herbivores and granivores (Woodcock & Pywell 2010). Juxtaposition of cultivation sub-treatments (fallows, fresh- and repeated-cultivation) within complexes may have further increased richness through complementarity of sub-treatments for species dependent on contrasting micro-habitats. Irrespective, in practice it would be less efficient and more costly to create an equivalent set of independent, but isolated, sub-treatment plots.

Whilst the overall richness of non-priority and priority species was considerably greater on either treatment than controls, responses to establishment method varied across taxa and according to species status. This is unsurprising, given that each treatment supported a distinct set of conditions (Fig. S.5.3). For example, priority ground beetles responded more to deep-cultivation, probably because some important ruderal food plants (e.g. *Chenopodium album*) were more abundant on this treatment (Table S.5.3; most priority ground beetles were granivores); whilst priority true bugs responded more to shallow-cultivation, probably because many require the taller structures and plant resources. Notably, priority bee and wasp richness was similar across regimes, even though most were classified as requiring short swards and bare ground (Fig. S.5.5); as these were uncommon on controls, greater pan trap sampling effort may have revealed differences. Additionally, pan traps may have sampled large numbers of commuting individuals and not just local foragers, which may also explain the lack of response among priority bees and wasps. Last, given responses varied considerably across taxa, our study demonstrates the value of multi-taxa sampling when evaluating the biodiversity consequence of management intervention.

Treatment effects on richness (relative to the control) were greater for priority than non-priority spiders, ground beetles, other beetles (both treatments), plants (deep-cultivation only), and true bugs (shallow-cultivation only). For each of these groups (excluding plants, where we did not examine habitat associations) those species associated with 'short sward' or 'short sward and bare ground' comprised a greater proportion of the total for priority species than for non-priority species (Fig. S.5.5), which may explain why priority species responded more strongly to treatment. As treatments were optimised to inferred cross-taxa requirements of the largest number of priority species (Dolman *et al.* 2012), it is encouraging that benefits from treatments were much greater for priorities than non-priorities across most groups.

In contrast to the response of multiple taxa to treatment complexes in this study, an earlier assessment in the first summer following initial treatment showed priority species richness increased for only one group (other beetles) (Hawkes *et al.* 2019b). The greater response after three years of treatment may be due to greater structural complexity of fully developed complexes against relatively homogenous freshly cultivated plots during the first year, but also the progressive colonisation and establishment of species since initial treatment, as rare and scarce species can accumulate over time (Kirmer *et al.* 2008). While priority species were able to accrue to this extent in just over two years, it may take longer for treated areas to realise their full potential (Rydgren *et al.* 2020).

Across most taxonomic groups, all regimes supported a similar proportion of unique non-priority and priority species. This demonstrates that, whilst treatment may increase richness across most taxonomic groups, no single treatment can deliver the resource requirements to maximise beta diversity (as emphasised by Fuller *et al.* 2017). To cater for the broadest range of species, efforts to implement enhanced management should adopt a range of strategies, comprising different establishment methods while also retaining some untreated habitat. Even for treatments designed to enhance structural heterogeneity, heterogeneity in treatments is required.

We predicted that dry-open habitat species associated with heavy disturbance would respond more strongly to treatment than those associated with no or light disturbance. For priority invertebrate species, those *a priori* thought to be associated with the heaviest forms of disturbance responded most strongly to treatment, regardless of whether these were classified along a single composite disturbance gradient (habitat guilds) or on independent gradients of grazing intensity and physical disturbance (management guilds). This confirms the importance of prevailing historic management to extant priority species (Fuller *et al.* 2017) and the success of the Biodiversity Audit approach in targeting enhanced management interventions appropriate to the ecological requirements of priority species (Dolman *et al.* 2012). For non-priority invertebrates, while those apparently associated short swards and bare ground responded positively to treatments, so did those associated with tall swards and scrub – again reflecting structural complexity of treatment complexes.

Whilst this experiment focused on mechanical interventions, other approaches which create and maintain bare-open microhabitats and structural complexity may be effective. More natural processes, such as the use of wild boar *Sus scrofa* or large herbivores, can promote dynamic mosaics with resulting benefits for some priority species and taxa (De Schaetzen, Van Langevelde & WallisDeVries 2018; Garrido *et al.* 2019). Nonetheless, maintenance of high habitat complexity in many low nutrient systems may best be achieved through intensive interventions, especially where increased rates of atmospheric nutrient deposition have accelerated vegetation growth (Härdtle *et al.* 2006).

5.5 Synthesis and applications

Fuller *et al.* (2017) argued that a better appreciation of the complexity and intensity of historical management, combined with knowledge of priority species requirements, encourages novel forms of enhanced intervention within cultural landscapes. Through an unprecedented landscape-scale biodiversity experiment, we confirm that restoring structural complexity and nested heterogeneity to grassland, through cultivation-and-fallow complexes built up over three years, both increased non-priority species richness and, crucially, doubled priority species richness. To maximise overall beta diversity (cumulative richness), complexity should be created through a range of establishment methods, as shallow- or deep-cultivation each supported unique species. To further inform subsequent management, it will be useful to examine whether certain sub-treatments (fallow ages, repeated or first-time disturbance) within these complexes were more beneficial, and what extent of such management is optimal.

Given the intended recipients responded most strongly to our interventions, we argue that systematic analysis of the relative frequency of species with contrasting resource requirements, across the full complement of priority species, can also inform management strategies and prescriptions in other biogeographical regions. Where biodiversity is well-characterised and autecological knowledge strong (e.g. much of Europe) we recommend such regional Biodiversity Audits, synthesised with a detailed understanding of historic land-use, to better inform conservation interventions.

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References

Bakker, J.P., De Bie, S., Dallinga, J.H., Tjaden, P. & De Vries, Y. (1983). Sheep-grazing as a management tool for heathland conservation and regeneration in the Netherlands. *Journal of Applied Ecology,* 20(2), 541-560.

Cameron, K.H. & Leather, S.R. (2011). Heathland management effects on carabid beetle communities: the relationship between bare ground patch size and carabid biodiversity. *Journal of Insect Conservation,* 16(4), 523-535.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. & Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs,* 84(1), 45-67.

Clark, J.A. & May, R.M. (2002). Taxonomic bias in conservation research. *Science,* 297(5579), 191-192.

De Schaetzen, F., Van Langevelde, F. & WallisDeVries, M.F. (2018). The influence of wild boar (*Sus scrofa*) on microhabitat quality for the endangered butterfly *Pyrgus malvae* in the Netherlands. *Journal of Insect Conservation,* 22(1), 51-59.

DEFRA (2007). *Conserving Biodiversity - The UK Approach.* DEFRA, London.

DEFRA (2018). *A Green Future: Our 25 Year plan to improve the environment*. DEFRA, London.

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology,* 49, 986-997.

EC (1992). *Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora.* European Commission, Brussels.

Fuller, R.J., Williamson, T., Barnes, G. & Dolman, P.M. (2017). Human activities and biodiversity opportunities in pre-industrial cultural landscapes: relevance to conservation. *Journal of Applied Ecology,* 54(2), 459-469.

Garrido, P., Mårell, A., Öckinger, E., Skarin, A., Jansson, A. & Thulin, C.-G. (2019). Experimental rewilding enhances grassland functional composition and pollinator habitat use. *Journal of Applied Ecology,* 56(4), 946-955.

Goodenough, A.E. & Sharp, M.H. (2016). Managing calcareous grassland for the declining Duke of Burgundy *Hamearis lucina* butterfly: effects of grazing management on Primula host plants. *Journal of Insect Conservation,* 20(6), 1087-1098.

Griffiths, R.A. & Dos Santos, M. (2012). Trends in conservation biology: Progress or procrastination in a new millennium? *Biological Conservation,* 153, 153-158.

Härdtle, W., Niemeyer, M., Niemeyer, T., Assmann, T. & Fottner, S. (2006). Can management compensate for atmospheric nutrient deposition in heathland ecosystems? *Journal of Applied Ecology,* 43(4), 759-769.

Hawkes, R.W., Smart, J., Brown, A., Jones, H. & Dolman, P.M. (2019a). Experimental evidence that ground-disturbance benefits Woodlark *Lullula arborea*. *Ibis,* 161, 447-452.

Hawkes, R.W., Smart, J., Brown, A., Jones, H., Lane, S., Wells, D. & Dolman, P.M. (2019b). Multi-taxa consequences of management for an avian umbrella species. *Biological Conservation,* 236, 192-201.

Hülber, K., Moser, D., Sauberer, N., Maas, B., Staudinger, M., Grass, V., Wrbka, T. & Willner, W. (2017). Plant species richness decreased in semi-natural grasslands in the Biosphere Reserve Wienerwald, Austria, over the past two decades, despite agri-environmental measures. *Agriculture, Ecosystems & Environment,* 243, 10-18.

Kirmer, A., Tischew, S., Ozinga, W.A., Von Lampe, M., Baasch, A. & Van Groenendael, J.M. (2008). Importance of regional species pools and functional traits in colonization processes: predicting re-colonization after large-scale destruction of ecosystems. *Journal of Applied Ecology,* 45(5), 1523-1530.

Krämer, B., Kämpf, I., Enderle, J., Poniatowski, D. & Fartmann, T. (2012). Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability. *Journal of Insect Conservation,* 16(6), 857-865.

Larsson, J. (2019). eulerr: area-proportional euler and venn diagrams with ellipses. R package version 5.1.0. Available at: https://cran.r-project.org/package=eulerr (accessed on 05/01/2020).

Linnell, J.D.C., Kaczensky, P., Wotschikowsky, U., Lescureux, N. & Boitani, L. (2015). Framing the relationship between people and nature in the context of European conservation. *Conservation Biology,* 29(4), 978-985.

Merckx, T., Feber, R.E., Hoare, D.J., Parsons, M.S., Kelly, C.J., Bourn, N.A.D. & Macdonald, D.W. (2012). Conserving threatened Lepidoptera: Towards an effective woodland management policy in landscapes under intense human land-use. *Biological Conservation,* 149(1), 32-39.

Pedley, S.M., Franco, A.M.A., Pankhurst, T. & Dolman, P.M. (2013). Physical disturbance enhances ecological networks for heathland biota: A multiple taxa experiment. *Biological Conservation,* 160, 173-182.

Pettorelli, N., Barlow, J., Stephens, P.A., Durant, S.M., Connor, B., Schulte to Bühne, H., Sandom, C.J., Wentworth, J. & du Toit, J.T. (2018). Making rewilding fit for policy. *Journal of Applied Ecology,* 55(3), 1114-1125.

Pywell, R.F., Bullock, J.M., Tallowin, J.B., Walker, K.J., Warman, E.A. & Masters, G. (2007). Enhancing diversity of species-poor grasslands: An experimental assessment of multiple constraints. *Journal of Applied Ecology,* 44(1), 81-94.

Ratcliffe, D. (1977). *A Nature Conservation Review: Volume 1: The Selection of Biological Sites of National Importance to Nature Conservation in Britain*. Cambridge University Press, New York.

Ridding, L.E., Bullock, J.M., Pescott, O.L., Hawes, P., Walls, R., Pereira, M.G., Thacker, S.A., Keenan, P.O., Dragosits, U. & Pywell, R.F. (2020). Long-term change in calcareous grassland vegetation and drivers over three time periods between 1970 and 2016. *Plant Ecology*.

Rydgren, K., Auestad, I., Halvorsen, R., Hamre, L.N., Jongejans, E., Töpper, J.P. & Sulavik, J. (2020). Assessing restoration success by predicting time to recovery—But by which metric? *Journal of Applied Ecology,* 57(2), 390-401.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Schulze, E.-D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T. & Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology,* 55(1), 267-278.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S. & Weisser, W.W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature,* 574, 671-674.

Stein, A., Gerstner, K. & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters,* 17(7), 866-880.

Thomas, C.D. (1994). Extinction, colonization, and metapopulations: environmental tracking by rare species. *Conservation Biology,* 8(2), 373-378.

Tipping, E., Davies, J.A.C., Henrys, P.A., Jarvis, S.G., Rowe, E.C., Smart, S.M., Le Duc, M.G., Marrs, R.H. & Pakeman, R.J. (2019). Measured estimates of semi-natural terrestrial NPP in Great Britain: comparison with modelled values, and dependence on atmospheric nitrogen deposition. *Biogeochemistry,* 144(2), 215-227.

Van Klink, R. & WallisDeVries, M.F. (2018). Risks and opportunities of trophic rewilding for arthropod communities. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 373(1761).

Webb, J., Heaver, D., Lott, D., Dean, H.J., van Breda, J., Curson, J., Harvey, M.C., Gurney, M., Roy, D.B., van Breda, A., Drake, M., Alexander, K.N.A. & Foster, G. (2018). Pantheon - database version 3.7.6. Available at: http://www.brc.ac.uk/pantheon/ (accessed on 17/12/2018).

Wells, T.C.E. (1969). Botanical aspects of conservation management of chalk grasslands. *Biological Conservation,* 2(1), 36-44.

Woodcock, B.A. & Pywell, R.F. (2010). Effects of vegetation structure and floristic diversity on detritivore, herbivore and predatory invertebrates within calcareous grasslands. *Biodiversity and Conservation,* 19(1), 81-95.

Wright, H.L., Lake, I.R. & Dolman, P.M. (2012). Agriculture—a key element for conservation in the developing world. *Conservation Letters,* 5(1), 11-19.

Żmihorski, M., Pärt, T., Gustafson, T. & Berg, Å. (2016). Effects of water level and grassland management on alpha and beta diversity of birds in restored wetlands. *Journal of Applied Ecology,* 53(2), 587-595.

Chapter 5

Supplementary material

Appendix S.5.1. Invertebrate sampling detail

Figure S.5.1. Study area

Figure S.5.2. Examples of treated and untreated grassland

Figure S.5.3. Vegetation structure of regimes

Figure S.5.4. Richness of GB Threatened and Near Threatened species

Figure S.5.5. Invertebrate habitat associations

Figure S.5.6. Pan traps

Table S.5.1. Sampling across vegetation strata

Table S.5.2. Management guilds

Table S.5.3. Species list

Table S.5.4. Invertebrate sample sizes

Table S.5.5. Richness of non-priority and priority species

Table S.5.6. Species uniqueness and overlap between regimes

Appendix S.5.1

Pan traps were used to further sample true bugs, bees and wasps, and true flies (see methods for specification and deployment details) in addition to samples obtained by pitfall trapping. To minimise interference by livestock, a steel wire mesh (size 400 mm x 400 mm, mesh 30 mm x 40 mm, bent to produce a concaved two-sided cage; see Fig. S.5.6) was added over pan traps (%13 of all deployed) on those plots where livestock density appeared high when traps were being established. To determine whether this mesh impeded invertebrate capture rates, we deployed six pan traps (three with and three without the mesh; hereafter 'mesh traps' and 'no mesh traps', respectively) along two parallel transects (three traps spaced 15 m apart along each transect that were also 15 m apart; mesh and no mesh traps were allocated randomly to individual positions) in the centre of each of five randomly selected deep-cultivated fallow subplots (either one- or two-year old fallows). Traps were deployed for two consecutive days in early July 2017, and invertebrates were identified to species level. Trap data were subsequently pooled to give one composite sample per category (mesh traps or no mesh traps) per subplot, providing five pairs of samples. Sampling gave 57 bee and wasp from 26 species, 31 true flies from 8 species, and 147 true bugs from 26 species. The additional mesh protection did not reduce capture rates (abundance) across any of these groups (Wilcoxon Signed Rank Test; bees and wasps, $V = 7$, $P = 1.00$, $df = 9$; true flies, $V = 0$, $P = 0.10$, $df = 9$; true bugs, $V = 5$, $P = 0.63$, $df = 9$).

For pitfall trapping rounds and pan trapping, trap efficiency (e.g. trap failure due to being removed, dislodged, trampled, emptied, filled with sand, etc.) was assessed on collection, we calculated the cumulative number of 'trap-days' for each control plot and treatment subplot (separately for each pitfall trapping round, and for pan traps), with successful traps considered active for the whole exposure period, partially-successful traps for half the exposure period (partially dislodged/trampled pitfall traps for partially emptied pan traps), and failed traps inactive for the whole exposure period (completely removed, destroyed by trampling, completed emptied, or filled with sand). Where the total number of trap-days per control plot or treatment subplot was less than half the intended period (pitfall traps, 21/42 days; pan traps, 6/12 days), samples were discarded and a replacement set of traps deployed immediately. Including redeployments, 96% (pitfall traps) and 94% (pan traps) of all trap deployments were successful; thus any differences in capture rates, attributable to slight variations in exposure period, were considered negligible.

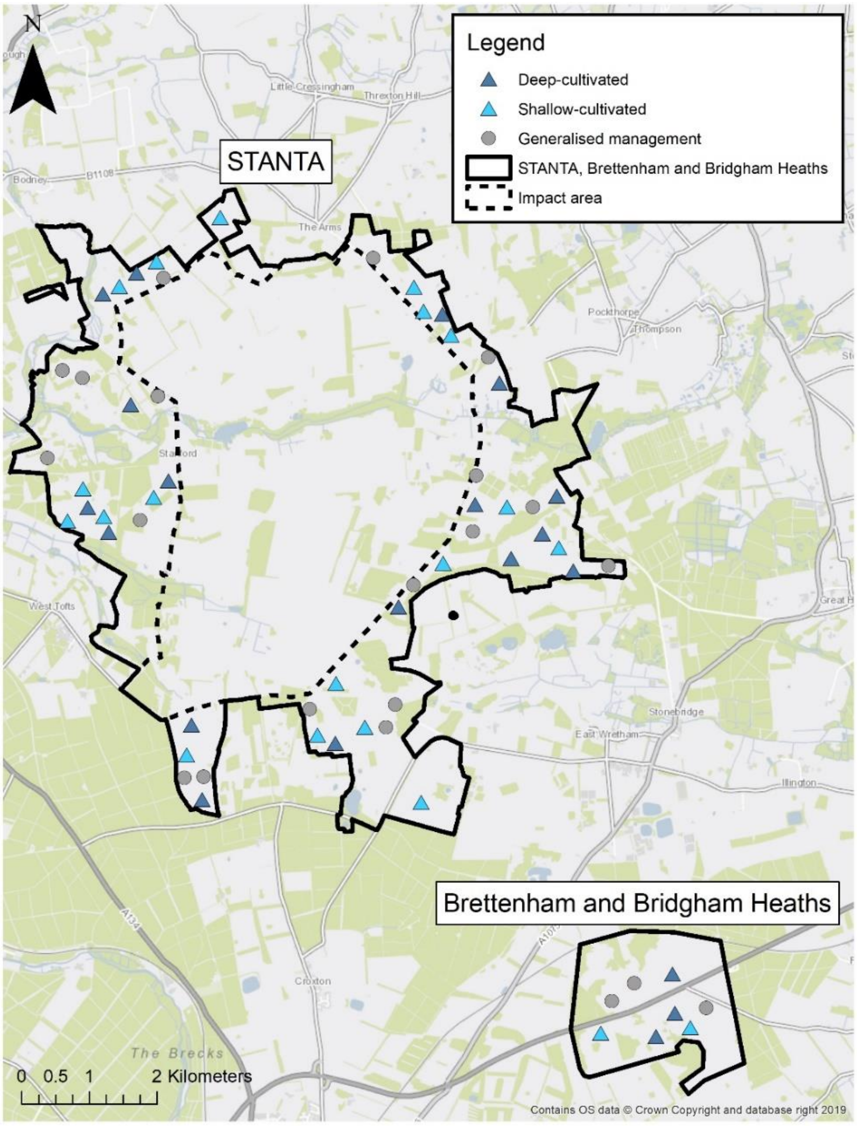

Figure S.5.1. Study area, showing location of control plots (generalised management) and the shallow- and deep-cultivated complexes across three study sites (the Stanford Training Area, Bridgham Heath and Brettenham Heath) and the impact area boundary (within which ground disturbance plots were precluded due to unexploded ordinance).

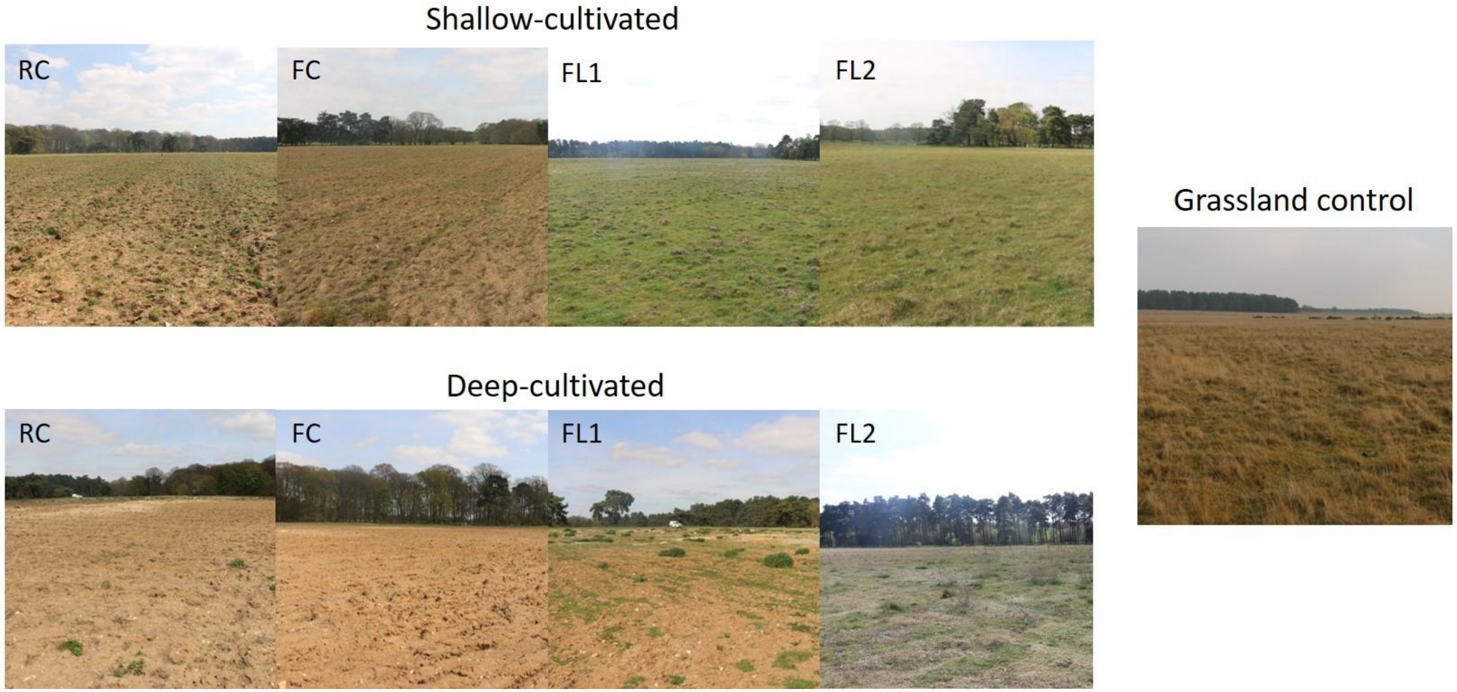

Figure S.5.2. Examples of treated and untreated grassland, showing repeatedly-cultivated (RC), freshly-cultivated (FC), one-year fallow (FL1), and two-year fallow (FL2) subplots within one deep-cultivated and within one shallow-cultivated complex, and one uncultivated grassland control plot at April 2017. Mean vegetation height and bare-ground cover across the 40 complexes (20 deep-cultivated and 20 shallow-cultivated, comprising 160 subplots) and 21 grassland controls, are presented in Supplementary Materials Fig. S.5.3.

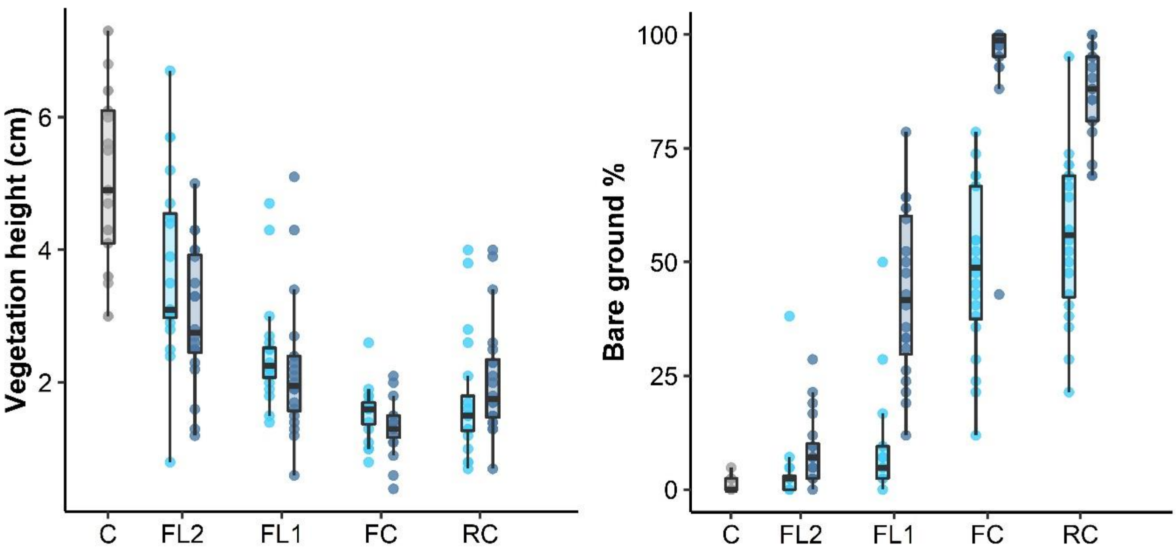

Figure S.5.3. Vegetation structure of regimes, showing height and percentage incidence of bare ground within two-year fallow (FL2), one-year fallow (FL1), freshly-cultivated (FC), and repeatedly-cultivated (RC) subplots, from 20 deep-cultivated (dark blue) and 20 shallow-cultivated (light blue) complexes (four subplots per complex, totalling 160 subplots), plus 21 uncultivated grassland controls (C) (see Fig. S.5.1 for the study area map). Within each subplot and grassland control, vegetation height was assessed once in June or early July using a sward stick (diameter 90 mm, weight 250 g; following Green & Griffiths 1994) at 42 points distributed evenly along two parallel 100m transects (placed 30–33m apart). Whether bare substrate covered over 50% of each point (tip of the sward stick dowel, 25mm diameter), was recorded giving incidence from 0 to 42. Filled circles show means for each subplot or grassland control, for each category box plots show the median (thick internal line), interquartile range (box) and the range of data points within x 1.5 of the interquartile range (whiskers), relative to the lower and upper quartile. See Supplementary Materials Fig. S.5.2 for photographs of examples of each subplot category.

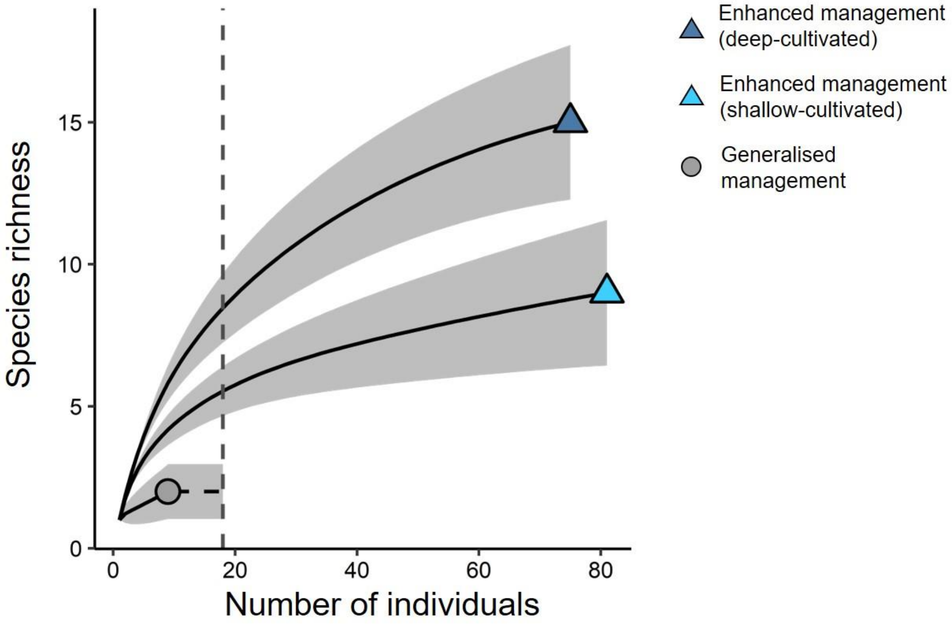

Figure S.5.4. Richness of GB Threatened and Near Threatened species, considering priority species classified as GB Critically Endangered, Endangered ,Vulnerable or Near Threatened (based upon red list guidelines developed by the International Union for Conservation of Nature, IUCN) across nine taxonomic groups (though only considering species with a UK IUCN threat status, see Table S.5.3), comparing shallow- and deep-cultivated treatments and generalised management (controls). Shown are sample-based rarefactions rescaled to numbers of sampled individuals, symbols denote observed richness, solid and dashed lines represent interpolated and extrapolated (restricted to the base sample size) richness respectively; shading represents 95% CI bounds. The vertical dashed line denotes the base sample size, where richness was compared (twice the smallest sample size).

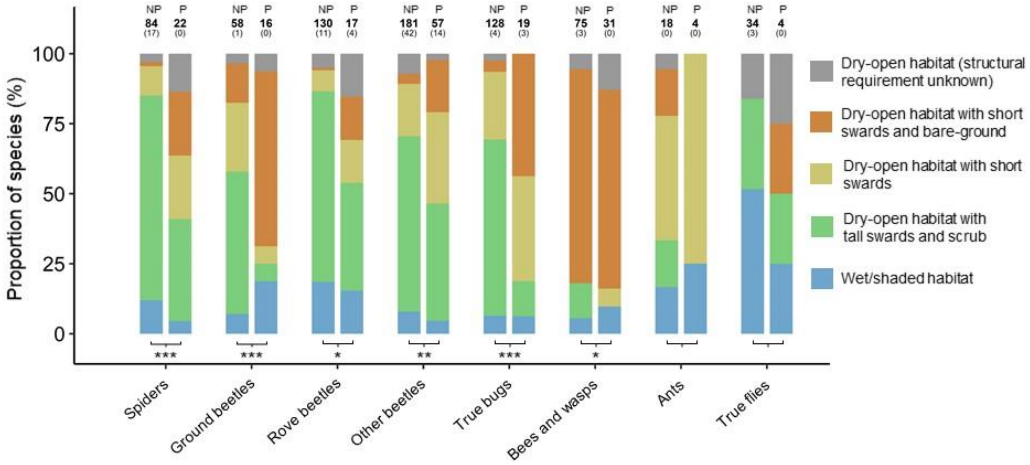

Figure S.5.5. Invertebrate habitat associations, showing the proportion of non-priority (NP) and priority species (P) associated with wet/shaded habitat, dry-open habitat with tall swards and scrub, dry-open habitat with short swards, and dry-open habitat with short swards and bare-ground (classified by the Pantheon database, Webb *et al.* 2018), separately for eight invertebrate groups (pooling across treatments and controls). Stacked bars also show the proportion of dry-open habitat species with unknown structural requirements. * denotes invertebrate groups where the relative distribution across the four habitat categories differs between non-priority and priority species (excluding dry-open habitat species with unknown structural requirements: Fisher's Exact: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$). The number of unclassified species (habitat association unknown, shown in parentheses) and total richness (number of species across the five guilds, plus unclassified species; bold type) are reported above each column.

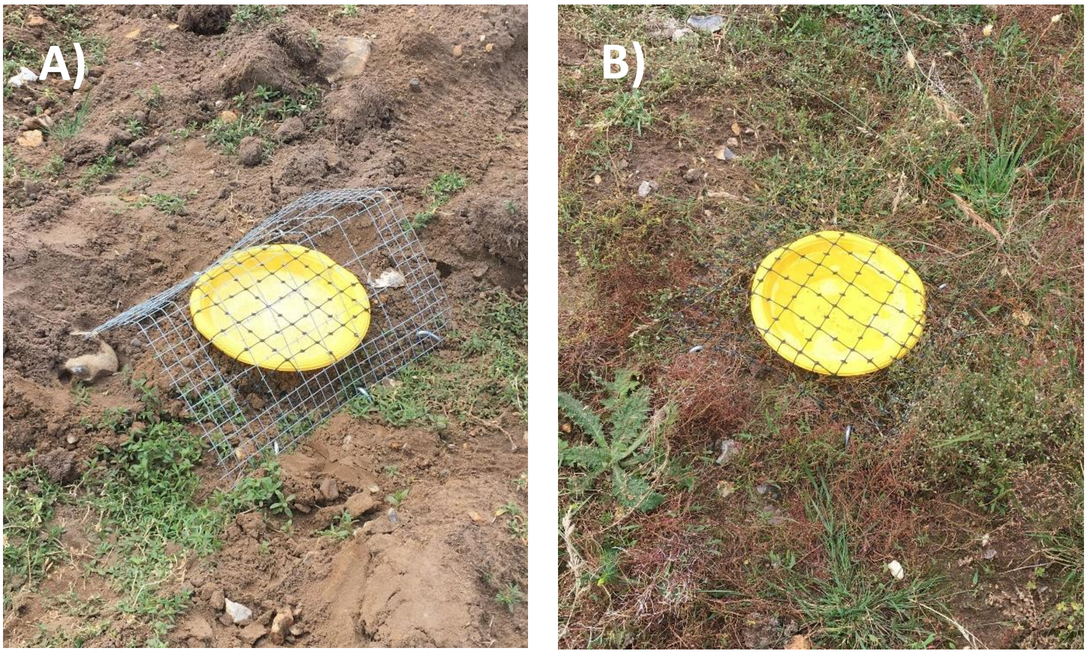

Figure S.5.6. Pan traps with (A) and without (B) an additional layer of mesh protection to minimize inference where livestock densities were high (details are in Appendix S.5.1 in Supporting Information).

Table S.5.1. Sampling across vegetation strata, showing category definitions and the number of replicate deep-cultivated complexes, shallow-cultivated complexes and control plots per strata. For each indicator plant species, Ellenberg indicator scores for soil pH association (ranging from 1 to 9, with 1 = extremely acidic, 5 = mildly acidic, 9 = alkaline, Hill, Preston & Roy 2004) are given in parentheses.

Vegetation strata	**Definition** [a]	**Deep-cultivated complexes**	**Shallow-cultivated complexes**	**Control plots**
Calcareous grassland of any age	Grass-heath of any age (Sheail 1979) located on well-drained brown calcareous sands or rendzinas (soil association codes: 0521 and 0343f, respectively, NSRI 2014)	5	5	6
Young grassland	Young, semi-improved, grass-heath (arable between 1904-1932, ≤110 years old) located on acidic brown sands (soil association code: 0554b), but with evidence of historic soil amelioration through ‘marling’ from presence of both acidiphilous (*Calluna vulgaris* (2), *Rumex acetosella* (4), *Galium saxatile* (3), *Teucrium scorodonia* (4)); and calcareous (*Thymus* spp. (6 - 8), *Pilosella officinarum* (7), *Galium verum* (6)) vascular plant indicators	6	5	5
Intermediate grassland	Mostly intermediate-aged grass-heath (arable at 1846 but reverted by 1904, 111-167 years old, 11 of the 14 plots), but some ancient grass-heath (no cultivation since 1845, ≥168 years old, 3 of 14 plots), located on acidic brown sands, with evidence of historic soil amelioration through ‘marling’	4	5	5
Ancient-acid grassland	Mostly ancient grass-heath (12 plots) located on acidic brown sands, with no evidence of historic marling and calcareous indicator plants infrequent. Three additional plots were also included in this category on the basis of characteristic plant assemblages (confirmed through indicator plant and soil surveys; Marsden 2017) despite being mapped as rendzinas (two plots ≥131 years old) or as deep permeable peaty sands affected by groundwater (soil association code 0861b; one plot ≥131 years old)	5	5	5

[a] Grass-heath ages were based on the Tithe Survey of 1846, the Ordnance Surveys of 1883 and 1904 and the Land Utilization Survey of 1932; for STANTA these were previously overlain and collated by Sheail (1979), the same data sources were used to classify grassland age on Brettenham and Bridgham Heaths (see Hawkes *et al.* 2019).

Table S.5.2. Management guilds. The original guild classification (a priori classified by a regional Biodiversity Audit, Dolman, Panter & Mossman 2012) of all dry-open habitat (mesic and xeric, but not damp) associated priority invertebrates identified during the sampling programme, and their subsequent merger to a two-way classification in terms of grazing intensity and physical disturbance (omitting species attributed to wet/shaded guilds, or dry-open habitat species with unknown or undifferentiated requirements for grazing and physical disturbance) to produce five management guilds.

Original guild	**Management guild classification**
open - mesic	no physical-disturbance and no grazing
open - mesic - moderately vegetated	no physical-disturbance and no grazing
open - mesic - well vegetated	no physical-disturbance and no grazing
open - mesic - lightly disturbed, light grazing	light physical-disturbance and no grazing
open - xeric - light disturbance	light physical-disturbance and no grazing
open - xeric - juxtaposition	heavy physical-disturbance and no grazing
open - mesic - juxtaposition	heavy physical-disturbance and no grazing
open - xeric - heavily disturbed	heavy physical-disturbance and no grazing
open - mesic - heavily disturbed	heavy physical-disturbance and no grazing
open - mesic - dung	no physical-disturbance and heavy grazing
open - xeric - short/moderate vegetation	no physical-disturbance and heavy grazing
open - mesic - sward mosaics	no physical-disturbance and heavy grazing
open - mesic - short vegetation	no physical-disturbance and heavy grazing
open - mesic - disturbance, grazing	heavy physical-disturbance and heavy grazing
open - xeric - disturbance, grazing	heavy physical-disturbance and heavy grazing
mesic - subterranean	unknown / undifferentiated
open and scrub - mesic	unknown / undifferentiated
open and scrub - mesic	unknown / undifferentiated
open - mesic - fungi	unknown / undifferentiated
open - mesic - detritus	unknown / undifferentiated
open - xeric - bare ground, detritus	unknown / undifferentiated
open - xeric - burn	unknown / undifferentiated
open to closed-canopy - detritus/fungi	unknown / undifferentiated
open to closed-canopy – mesic	unknown / undifferentiated
variety of habitats	unknown / undifferentiated
ecological requirements unknown	unknown / undifferentiated
open wood - mesic	wet/shaded
ecotone open - wood	wet/shaded
open - wet or damp - detritus	wet/shaded
open - seasonally wet – moderate vegetation	wet/shaded
open - wet to dry	wet/shaded

Table S.5.3. Species list of all invertebrate and vascular plant species identified across the treatment complexes and control plots, showing their: GB rarity and threat status; status as non-priority (NP) or priority (P) species; broad habitat association (either dry-open habitat, or unknown/wet/shaded); attribution to habitat guild (all dry-open habitat associated invertebrates) and management guild (priority dry-open habitat associated invertebrates only); and abundance (number of individual invertebrates or plant observations) separately from deep-cultivated complexes (DC), shallow-cultivated complexes (SC), and control plots (C).

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
Ants										
Formica fusca	Formicidae	none	not ass	NP	dry-open	SS	not ass	253	214	7
Formica lemani	Formicidae	none	not ass	NP	dry-open	TS & S	not ass	214	236	15
Lasius brunneus	Formicidae	NA	not ass	P	unknown/wet/shaded	not ass	not ass	1	0	0
Lasius flavus	Formicidae	none	not ass	NP	dry-open	SS	not ass	5300	1498	1044
Lasius fuliginosus	Formicidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	3	1	0
Lasius meridionalis	Formicidae	none	not ass	NP	dry-open	SS & BG	not ass	4	1	0
Lasius mixtus	Formicidae	none	not ass	NP	dry-open	SS	not ass	2	0	0
Lasius niger	Formicidae	none	not ass	NP	dry-open	SS	not ass	2037	2419	252
Lasius platythorax	Formicidae	none	not ass	NP	dry-open	SS	not ass	2	0	0
Lasius psammophilus	Formicidae	none	not ass	NP	dry-open	SS & BG	not ass	622	450	67
Lasius sabularum	Formicidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	2	4	2
Lasius umbratus	Formicidae	none	not ass	NP	dry-open	SS	not ass	32	12	3
Myrmica hirsuta	Formicidae	RDB K	not ass	P	dry-open	SS	N_DIS/H_GRZ	1	0	0
Myrmica karavajevi	Formicidae	RDB K	not ass	P	dry-open	SS	L_DIS/N_GRZ	9	9	1
Myrmica lobicornis	Formicidae	none	not ass	NP	dry-open	SS	not ass	163	28	26
Myrmica rubra	Formicidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Myrmica ruginodis	Formicidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	110	110	8

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Myrmica sabuleti	Formicidae	none	not ass	NP	dry-open	SS	not ass	703	238	183
Myrmica scabrinodis	Formicidae	none	not ass	NP	dry-open	TS & S	not ass	6502	3158	606
Myrmica schencki	Formicidae	Nb	not ass	P	dry-open	SS	H_DIS/H_GRZ	21	169	29
Stenamma debile	Formicidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	2	0	0
Tetramorium caespitum	Formicidae	none	not ass	NP	dry-open	SS & BG	not ass	85	24	4
Bees and wasps										
Andrena alfkenella	Andrenidae	RDB 3	not ass	P	dry-open	SS	UNK/UNDIF	3	2	1
Andrena bicolor	Andrenidae	none	not ass	NP	dry-open	SS & BG	not ass	8	4	0
Andrena bimaculata	Andrenidae	Nb	not ass	P	dry-open	SS & BG	UNK/UNDIF	2	0	0
Andrena denticulata	Andrenidae	none	not ass	NP	dry-open	SS & BG	not ass	1	0	0
Andrena dorsata	Andrenidae	none	not ass	NP	dry-open	SS & BG	not ass	54	73	1
Andrena flavipes	Andrenidae	none	not ass	NP	dry-open	SS & BG	not ass	13	12	2
Andrena fuscipes	Andrenidae	none	not ass	NP	dry-open	SS & BG	not ass	1	5	0
Andrena labiata	Andrenidae	Na	not ass	P	dry-open	SS & BG	L_DIS/N_GRZ	1	1	0
Andrena minutula	Andrenidae	none	not ass	NP	dry-open	SS & BG	not ass	2	0	0
Andrena nigriceps	Andrenidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	0	1	0
Andrena ovatula	Andrenidae	none	not ass	NP	dry-open	SS & BG	not ass	5	1	0
Andrena thoracica	Andrenidae	none	not ass	NP	dry-open	SS & BG	not ass	10	7	0
Panurgus banksianus	Andrenidae	none	not ass	NP	dry-open	SS & BG	not ass	0	1	0
Apis mellifera	Apidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	5	6	1
Bombus lapidarius	Apidae	none	not ass	NP	dry-open	TS & S	not ass	11	17	2
Bombus lucorum	Apidae	none	not ass	NP	dry-open	TS & S	not ass	4	1	0
Bombus pascuorum	Apidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	2	1	0
Bombus terrestris	Apidae	none	not ass	NP	dry-open	TS & S	not ass	8	6	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance DC	SC	C
Nomada rufipes	Apidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	0	3	0
Bethylus fuscicornis	Bethylidae	none	not ass	NP	dry-open	TS & S	not ass	1	1	0
Epyris niger	Bethylidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	2	0	0
Chrysis illigeri	Chrysididae	Nb	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	13	16	1
Hedychridium ardens	Chrysididae	none	not ass	NP	dry-open	SS & BG	not ass	6	6	0
Hedychridium roseum	Chrysididae	none	not ass	NP	dry-open	SS & BG	not ass	6	0	0
Hedychrum niemelai	Chrysididae	RDB 3	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	64	79	12
Hedychrum nobile	Chrysididae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	5	3	2
Hylaeus cornutus	Colletidae	Na	not ass	P	unknown/wet/shaded	not ass	not ass	0	1	0
Hylaeus dilatatus	Colletidae	RDB 3	not ass	P	dry-open	UNK/UNDIF	N_DIS/H_GRZ	1	1	0
Astata boops	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	2	0	0
Cerceris arenaria	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	3	2	0
Cerceris quinquefasciata	Crabronidae	RDB 3;Sec 41	not ass	P	dry-open	SS & BG	UNK/UNDIF	7	10	0
Cerceris ruficornis	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	0	3	0
Cerceris rybyensis	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	4	3	2
Crabro cribrarius	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	3	1	0
Crabro peltarius	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	0	1	0
Crossocerus palmipes	Crabronidae	Nb	not ass	P	dry-open	SS & BG	UNK/UNDIF	0	2	0
Crossocerus quadrimaculatus	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	8	0	0
Crossocerus wesmaeli	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	5	0	0
Diodontus minutus	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	18	0	0
Dryudella pinguis	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	1	0	0
Ectemnius continuus	Crabronidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	2	0	0
Harpactus tumidus	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	1	0	0
Lindenius albilabris	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	1	0	0
Mellinus arvensis	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	37	10	1

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Nysson dimidiatus	Crabronidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/H_GRZ	4	7	0
Nysson trimaculatus	Crabronidae	Nb	not ass	P	unknown/wet/shaded	not ass	not ass	35	2	0
Oxybelus uniglumis	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	98	13	1
Tachysphex pompiliformis	Crabronidae	none	not ass	NP	dry-open	SS & BG	not ass	11	11	0
Trypoxylon figulus	Crabronidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	20	1	0
Halictus rubicundus	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	2	4	0
Halictus tumulorum	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	13	13	1
Lasioglossum albipes	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	5	2	1
Lasioglossum brevicorne	Halictidae	RDB 3	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	2	3	1
Lasioglossum calceatum	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	32	30	5
Lasioglossum fulvicorne	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	4	3	1
Lasioglossum lativentre	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	3	1	0
Lasioglossum leucopus	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	96	63	3
Lasioglossum leucozonium	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	20	19	4
Lasioglossum malachurum	Halictidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	1	0	0
Lasioglossum minutissimum	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	11	1	0
Lasioglossum parvulum	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	1	0	0
Lasioglossum punctatissimum	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	31	16	0
Lasioglossum quadrinotatum	Halictidae	Na	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	2	0	0
Lasioglossum sexnotatum	Halictidae	RDB 1	not ass	P	dry-open	UNK/UNDIF	H_DIS/N_GRZ	1	0	0
Lasioglossum villosulum	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	2	2	0
Sphecodes ephippius	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	4	5	0
Sphecodes geoffrellus	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	23	13	0
Sphecodes gibbus	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	0	1	0
Sphecodes longulus	Halictidae	Na	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	0	1	0
Sphecodes miniatus	Halictidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/H_GRZ	2	2	0

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
Sphecodes monilicornis	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	12	7	0
Sphecodes niger	Halictidae	RDB 3	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	0	1	0
Sphecodes pellucidus	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	3	0	0
Sphecodes puncticeps	Halictidae	none	not ass	NP	dry-open	SS & BG	not ass	3	0	0
Sphecodes reticulatus	Halictidae	Na	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	1	0	0
Hoplitis claviventris	Megachilidae	none	not ass	NP	dry-open	TS & S	not ass	2	0	0
Megachile versicolor	Megachilidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	3	0
Osmia bicolor	Megachilidae	Nb	not ass	P	dry-open	SS & BG	wet/shaded	0	1	0
Osmia leaiana	Megachilidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	3	1
Dasypoda hirtipes	Melittidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	2	6	5
Melitta haemorrhoidalis	Melittidae	none	not ass	NP	dry-open	SS & BG	not ass	0	1	0
Myrmosa atra	Melittidae	none	not ass	NP	dry-open	SS & BG	not ass	7	2	0
Anoplius infuscatus	Pompilidae	none	not ass	NP	dry-open	SS & BG	not ass	1	0	0
Anoplius nigerrimus	Pompilidae	none	not ass	NP	dry-open	SS & BG	not ass	22	27	6
Anoplius viaticus	Pompilidae	none	not ass	NP	dry-open	SS & BG	not ass	34	8	1
Aporus unicolor	Pompilidae	Na	not ass	P	dry-open	UNK/UNDIF	H_DIS/H_GRZ	2	1	0
Arachnospila anceps	Pompilidae	none	not ass	NP	dry-open	TS & S	not ass	29	39	5
Arachnospila minutula	Pompilidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	10	19	0
Arachnospila spissa	Pompilidae	none	not ass	NP	dry-open	TS & S	not ass	1	1	0
Arachnospila trivialis	Pompilidae	none	not ass	NP	dry-open	SS & BG	not ass	46	24	0
Caliadurgus fasciatellus	Pompilidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	6	4	0
Episyron rufipes	Pompilidae	none	not ass	NP	dry-open	SS & BG	not ass	1	0	0
Evagetes crassicornis	Pompilidae	none	not ass	NP	dry-open	SS & BG	not ass	35	44	3
Evagetes dubius	Pompilidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/H_GRZ	35	21	0
Priocnemis agilis	Pompilidae	Nb	not ass	P	dry-open	UNK/UNDIF	N_DIS/H_GRZ	0	2	0
Priocnemis confusor	Pompilidae	Nb	not ass	P	dry-open	SS	UNK/UNDIF	0	1	1

								Abundance		
Species[a]	**Family**	**GB rarity[b]**	**GB threat[c,g]**	**Status**	**Broad habitat association[d,g]**	**Habitat guild[e,g]**	**Management guild[f,g]**	**DC**	**SC**	**C**
Priocnemis hyalinata	Pompilidae	Nb	not ass	P	unknown/wet/shaded	not ass	not ass	3	5	1
Priocnemis parvula	Pompilidae	none	not ass	NP	dry-open	SS & BG	not ass	61	46	2
Priocnemis pusilla	Pompilidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	11	13	3
Priocnemis schioedtei	Pompilidae	Nb	not ass	P	dry-open	SS & BG	wet/shaded	2	12	2
Ammophila sabulosa	Sphecidae	none	not ass	NP	dry-open	SS & BG	not ass	1	0	0
Podalonia affinis	Sphecidae	RDB 3	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	10	10	0
Tiphia femorata	Tiphiidae	none	not ass	NP	dry-open	SS & BG	not ass	950	2324	110
Tiphia minuta	Tiphiidae	Nb	not ass	P	dry-open	SS & BG	N_DIS/H_GRZ	1	0	0
Vespula germanica	Vespidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Vespula vulgaris	Vespidae	none	not ass	NP	dry-open	TS & S	not ass	1	1	0
True flies										
Dysmachus trigonus	Asilidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	13	94	38
Eutolmus rufibarbis	Asilidae	NS	LC	P	dry-open	UNK/UNDIF	H_DIS/N_GRZ	15	8	7
Machimus arthriticus	Asilidae	NR	EN	P	dry-open	SS & BG	H_DIS/H_GRZ	13	31	8
Machimus atricapillus	Asilidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	19	14	15
Machimus cingulatus	Asilidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	45	141	66
Rhagio lineola	Rhagionidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	4	2	0
Rhagio tringarius	Rhagionidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	3	8	1
Chloromyia formosa	Stratiomyidae	none	LC	NP	dry-open	TS & S	not ass	12	12	0
Odontomyia angulata	Stratiomyidae	NR	VU	P	unknown/wet/shaded	not ass	not ass	3	0	0
Oplodontha viridula	Stratiomyidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1	1	0
Stratiomys singularior	Stratiomyidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Chrysotoxum elegans	Syrphidae	NS	LC	P	dry-open	TS & S	N_DIS/H_GRZ	0	0	1
Episyrphus balteatus	Syrphidae	none	LC	NP	dry-open	TS & S	not ass	15	4	0
Eristalinus sepulchralis	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	8	1	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Eristalis abusivus	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1	3	0
Eristalis arbustorum	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	3	8	0
Eristalis horticola	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	3	1	0
Eristalis intricarius	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Eristalis tenax	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	23	22	1
Eumerus strigatus	Syrphidae	none	LC	NP	dry-open	TS & S	not ass	8	6	0
Eupeodes corollae	Syrphidae	none	LC	NP	dry-open	TS & S	not ass	20	5	1
Eupeodes luniger	Syrphidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	1	0	0
Helophilus hybridus	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	0	1	1
Helophilus pendulus	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Helophilus trivittatus	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Scaeva pyrastri	Syrphidae	none	LC	NP	dry-open	TS & S	not ass	0	0	1
Sphaerophoria scripta	Syrphidae	none	LC	NP	dry-open	TS & S	not ass	1	6	0
Syritta pipiens	Syrphidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Syrphus ribesii	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	3	2	1
Syrphus vitripennis	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Xylota segnis	Syrphidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Chrysops viduatus	Tabanidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	2	0	0
Hybomitra distinguenda	Tabanidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	10	0	0
Thereva bipunctata	Therevidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	2	4	0
Thereva nobilitata	Therevidae	none	LC	NP	dry-open	TS & S	not ass	9	4	0
Thereva plebeja	Therevidae	none	LC	NP	dry-open	TS & S	not ass	1	2	0
Nephrotoma flavescens	Tipulidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Nephrotoma scurra	Tipulidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	1	0	0

Ground beetles

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
Acupalpus dubius	Carabidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Agonum muelleri	Carabidae	none	LC	NP	dry-open	SS	not ass	29	7	0
Amara aenea	Carabidae	none	LC	NP	dry-open	SS	not ass	1139	1199	4
Amara anthobia	Carabidae	none	LC	NP	dry-open	SS & BG	not ass	0	3	0
Amara apricaria	Carabidae	none	LC	NP	dry-open	SS	not ass	3	2	0
Amara bifrons	Carabidae	none	LC	NP	dry-open	SS	not ass	26	9	0
Amara communis	Carabidae	none	LC	NP	dry-open	TS & S	not ass	0	3	0
Amara convexior	Carabidae	none	LC	NP	dry-open	SS	not ass	201	489	211
Amara equestris	Carabidae	NS	LC	P	dry-open	SS & BG	L_DIS/N_GRZ	45	39	5
Amara eurynota	Carabidae	none	LC	NP	dry-open	SS	not ass	0	2	0
Amara familiaris	Carabidae	none	LC	NP	dry-open	TS & S	not ass	168	40	0
Amara fulva	Carabidae	NS	LC	P	[unknown/wet/shaded]	not ass	not ass	23	0	0
Amara lucida	Carabidae	NS	LC	P	dry-open	SS & BG	L_DIS/N_GRZ	19	18	0
Amara lunicollis	Carabidae	none	LC	NP	dry-open	TS & S	not ass	347	1038	133
Amara montivaga	Carabidae	NS	LC	P	dry-open	SS & BG	H_DIS/N_GRZ	79	59	0
Amara ovata	Carabidae	none	LC	NP	dry-open	SS	not ass	4	1	0
Amara plebeja	Carabidae	none	LC	NP	dry-open	TS & S	not ass	3	1	0
Amara similata	Carabidae	none	LC	NP	dry-open	SS	not ass	7	1	0
Amara tibialis	Carabidae	none	LC	NP	dry-open	SS & BG	not ass	55	111	2
Anisodactylus binotatus	Carabidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Badister bullatus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	10	13	5
Bembidion femoratum	Carabidae	none	LC	NP	[unknown/wet/shaded]	not ass	not ass	293	8	0
Bembidion lampros	Carabidae	none	LC	NP	dry-open	SS	not ass	522	188	2
Bembidion properans	Carabidae	none	LC	NP	dry-open	SS	not ass	104	91	0
Bembidion quadrimaculatum	Carabidae	none	LC	NP	dry-open	SS	not ass	518	40	0
Bradycellus caucasicus	Carabidae	NS	LC	P	dry-open	UNK/UNDIF	N_DIS/N_GRZ	2	1	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Bradycellus harpalinus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	0	4	0
Bradycellus verbasci	Carabidae	none	LC	NP	dry-open	TS & S	not ass	0	3	0
Calathus ambiguus	Carabidae	NS	LC	P	dry-open	SS & BG	H_DIS/N_GRZ	11	2	0
Calathus cinctus	Carabidae	none	LC	NP	dry-open	SS & BG	not ass	29	11	1
Calathus fuscipes	Carabidae	none	LC	NP	dry-open	TS & S	not ass	5467	3938	214
Calathus melanocephalus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	195	208	18
Carabus granulatus	Carabidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Carabus nemoralis	Carabidae	none	LC	NP	dry-open	TS & S	not ass	3	10	4
Carabus problematicus	Carabidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	36	78	23
Carabus violaceus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	86	52	15
Cicindela campestris	Carabidae	none	LC	NP	dry-open	SS & BG	not ass	142	9	0
Curtonotus aulicus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	151	26	0
Dyschirius politus	Carabidae	NS	LC	P	[unknown/wet/shaded]	not ass	not ass	5	0	0
Harpalus affinis	Carabidae	none	LC	NP	dry-open	SS	not ass	320	60	0
Harpalus anxius	Carabidae	NS	LC	P	dry-open	SS & BG	H_DIS/N_GRZ	17	19	0
Harpalus attenuatus	Carabidae	NS	LC	P	dry-open	SS & BG	H_DIS/N_GRZ	33	11	0
Harpalus froelichii	Carabidae	NR;Sec 41	NT	P	dry-open	SS & BG	H_DIS/N_GRZ	2	0	0
Harpalus latus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	28	53	20
Harpalus pumilus	Carabidae	NR	NT	P	dry-open	SS & BG	H_DIS/N_GRZ	17	25	0
Harpalus rubripes	Carabidae	none	LC	NP	dry-open	SS & BG	not ass	70	41	1
Harpalus rufipalpis	Carabidae	none	LC	NP	dry-open	SS & BG	not ass	143	251	1
Harpalus rufipes	Carabidae	none	LC	NP	dry-open	TS & S	not ass	422	283	2
Harpalus smaragdinus	Carabidae	NS	LC	P	dry-open	SS & BG	H_DIS/H_GRZ	95	21	0
Harpalus tardus	Carabidae	none	LC	NP	dry-open	SS	not ass	311	186	6
Laemostenus terricola	Carabidae	none	LC	NP	dry-open	TS & S	not ass	8	8	1
Leistus spinibarbis	Carabidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance DC	SC	C
Licinus depressus	Carabidae	NS	LC	P	dry-open	SS & BG	L_DIS/N_GRZ	9	17	15
Loricera pilicornis	Carabidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	44	12	0
Microlestes minutulus	Carabidae	none	LC	NP	dry-open	SS & BG	not ass	12	14	0
Nebria brevicollis	Carabidae	none	LC	NP	dry-open	TS & S	not ass	331	39	2
Nebria salina	Carabidae	none	LC	NP	dry-open	TS & S	not ass	853	225	1
Notiophilus aquaticus	Carabidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	107	137	1
Notiophilus biguttatus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	34	27	0
Notiophilus palustris	Carabidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Notiophilus substriatus	Carabidae	none	LC	NP	dry-open	SS & BG	not ass	18	12	0
Panagaeus bipustulatus	Carabidae	NS	LC	P	dry-open	SS	N_DIS/N_GRZ	13	11	4
Paradromius linearis	Carabidae	none	LC	NP	dry-open	TS & S	not ass	0	1	0
Poecilus versicolor	Carabidae	none	LC	NP	dry-open	TS & S	not ass	316	1060	140
Pterostichus madidus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	1088	483	118
Pterostichus melanarius	Carabidae	none	LC	NP	dry-open	TS & S	not ass	68	10	1
Pterostichus niger	Carabidae	none	LC	NP	dry-open	TS & S	not ass	45	20	22
Stenolophus teutonus	Carabidae	NS	LC	P	unknown/wet/shaded	not ass	not ass	1	0	0
Stomis pumicatus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	4	4	0
Syntomus foveatus	Carabidae	none	LC	NP	dry-open	SS	not ass	263	718	15
Syntomus truncatellus	Carabidae	NS	LC	P	dry-open	TS & S	N_DIS/N_GRZ	48	111	27
Synuchus vivalis	Carabidae	none	LC	NP	dry-open	TS & S	not ass	14	12	0
Trechus obtusus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	0	1	0
Trechus quadristriatus	Carabidae	none	LC	NP	dry-open	TS & S	not ass	133	2	0
Other beetles										
Notoxus monoceros	Anthicidae	none	LC	NP	dry-open	SS & BG	not ass	1	0	0
Omonadus floralis	Anthicidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	2	0	0

								Abundance		
Species[a]	**Family**	**GB rarity[b]**	**GB threat[c,g]**	**Status**	**Broad habitat association[d,g]**	**Habitat guild[e,g]**	**Management guild[f,g]**	**DC**	**SC**	**C**
Apion haematodes	Apionidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	35	12	0
Apion rubens	Apionidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	0	0	1
Apion rubiginosum	Apionidae	RDB 3	not ass	P	dry-open	UNK/UNDIF	H_DIS/H_GRZ	1	2	0
Catapion pubescens	Apionidae	Nb	not ass	P	dry-open	TS & S	N_DIS/H_GRZ	1	1	0
Ceratapion carduorum	Apionidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Ceratapion gibbirostre	Apionidae	none	not ass	NP	dry-open	TS & S	not ass	2	0	0
Ceratapion onopordi	Apionidae	none	not ass	NP	dry-open	TS & S	not ass	0	2	0
Ischnopterapion loti	Apionidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Oxystoma craccae	Apionidae	none	not ass	NP	dry-open	TS & S	not ass	0	0	1
Oxystoma pomonae	Apionidae	none	not ass	NP	dry-open	TS & S	not ass	0	0	1
Perapion curtirostre	Apionidae	none	not ass	NP	dry-open	TS & S	not ass	1	3	1
Perapion marchicum	Apionidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	16	3	0
Protapion fulvipes	Apionidae	none	not ass	NP	dry-open	TS & S	not ass	13	5	0
Squamapion atomarium	Apionidae	none	not ass	NP	dry-open	SS	not ass	2	2	0
Stenopterapion tenue	Apionidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Taeniapion urticarium	Apionidae	none	not ass	NP	dry-open	SS	not ass	1	0	0
Aphanisticus pusillus	Buprestidae	NS	LC	P	dry-open	SS	N_DIS/N_GRZ	1	4	1
Byrrhus arietinus	Byrrhidae	Nb	not ass	P	dry-open	TS & S	wet/shaded	0	1	0
Byrrhus fasciatus	Byrrhidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	5	7	0
Byrrhus pilula	Byrrhidae	none	not ass	NP	dry-open	SS	not ass	13	19	13
Byrrhus pustulatus	Byrrhidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	13	15	0
Curimopsis maritima	Byrrhidae	none	not ass	NP	dry-open	SS	not ass	3	14	0
Cytilus sericeus	Byrrhidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	5	1	0
Cantharis lateralis	Cantharidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Cantharis rustica	Cantharidae	none	LC	NP	dry-open	TS & S	not ass	27	20	9
Malthodes pumilus	Cantharidae	NS	LC	P	unknown/wet/shaded	not ass	not ass	0	1	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Cassida hemisphaerica	Chrysomelidae	NS	LC	P	dry-open	TS & S	L_DIS/N_GRZ	1	3	0
Cassida prasina	Chrysomelidae	NS	LC	P	dry-open	SS	N_DIS/H_GRZ	0	5	1
Cassida rubiginosa	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	2	0	0
Chaetocnema arida	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	2	10	0
Chaetocnema concinna	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	4	0	0
Chaetocnema hortensis	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	101	286	0
Chrysolina marginata	Chrysomelidae	NR	NT	P	dry-open	SS & BG	N_DIS/H_GRZ	0	7	0
Chrysolina sturmi	Chrysomelidae	NS	LC	P	dry-open	TS & S	H_DIS/H_GRZ	3	0	0
Cryptocephalus fulvus	Chrysomelidae	none	LC	NP	dry-open	SS	not ass	1	12	0
Galeruca tanaceti	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	21	20	6
Lochmaea suturalis	Chrysomelidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	0	0	2
Longitarsus jacobaeae	Chrysomelidae	none	LC	NP	dry-open	SS	not ass	0	0	1
Longitarsus luridus	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	0	2	0
Longitarsus melanocephalus	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	1	5	1
Longitarsus parvulus	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	5	1	0
Longitarsus pellucidus	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Longitarsus pratensis	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	5	73	3
Longitarsus succineus	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	3	2	0
Neocrepidodera ferruginea	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	6	6	0
Neocrepidodera transversa	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	2	0	0
Phyllotreta nigripes	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	16	2	0
Phyllotreta nodicornis	Chrysomelidae	none	LC	NP	dry-open	SS	not ass	7	1	0
Phyllotreta vittula	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Psylliodes chrysocephala	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	5	2	0
Sermylassa halensis	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	1	0	2
Sphaeroderma testaceum	Chrysomelidae	none	LC	NP	dry-open	TS & S	not ass	13	4	0

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
Coccinella septempunctata	Coccinellidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	84	50	2
Harmonia axyridis	Coccinellidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	2	0
Hippodamia variegata	Coccinellidae	Nb	not ass	P	dry-open	TS & S	H_DIS/N_GRZ	226	119	0
Nephus redtenbacheri	Coccinellidae	none	not ass	NP	dry-open	SS	not ass	2	0	1
Platynaspis luteorubra	Coccinellidae	NA	not ass	P	dry-open	TS & S	UNK/UNDIF	0	2	0
Rhyzobius litura	Coccinellidae	none	not ass	NP	dry-open	TS & S	not ass	5	1	0
Scymnus femoralis	Coccinellidae	Nb	not ass	P	dry-open	SS	N_DIS/N_GRZ	0	1	0
Scymnus frontalis	Coccinellidae	none	not ass	NP	dry-open	SS	not ass	19	36	0
Scymnus schmidti	Coccinellidae	Nb	not ass	P	dry-open	SS	UNK/UNDIF	16	22	0
Subcoccinella vigintiquattuorpunctata	Coccinellidae	none	not ass	NP	dry-open	TS & S	not ass	3	1	0
Tytthaspis sedecimpunctata	Coccinellidae	none	not ass	NP	dry-open	TS & S	not ass	3	22	1
Orthoperus brunnipes	Corylophidae	RDB 3	not ass	P	unknown/wet/shaded	not ass	not ass	1	0	0
Atomaria atricapilla	Cryptophagidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Atomaria fuscata	Cryptophagidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	17	1	0
Atomaria linearis	Cryptophagidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	41	7	0
Atomaria nigriventris	Cryptophagidae	Notable	not ass	P	unknown/wet/shaded	not ass	not ass	9	1	0
Atomaria scutellaris	Cryptophagidae	RDB K	not ass	P	unknown/wet/shaded	not ass	not ass	12	4	0
Atomaria testacea	Cryptophagidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	4	5	1
Cryptophagus distinguendus	Cryptophagidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Cryptophagus schmidtii	Cryptophagidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Ephistemus globulus	Cryptophagidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	3	0	0
Acalles ptinoides	Curculionidae	Nb	not ass	P	unknown/wet/shaded	not ass	not ass	4	4	0
Attactagenus plumbeus	Curculionidae	Nb	not ass	P	dry-open	TS & S	N_DIS/N_GRZ	1	0	2
Aulacobaris picicornis	Curculionidae	Nb	not ass	P	dry-open	SS	L_DIS/N_GRZ	2	3	0
Barynotus obscurus	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Brachysomus echinatus	Curculionidae	Nb	not ass	P	dry-open	TS & S	N_DIS/H_GRZ	0	3	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Cathormiocerus aristatus	Curculionidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/H_GRZ	2	6	0
Ceutorhynchus atomus	Curculionidae	Na	not ass	P	dry-open	SS	H_DIS/N_GRZ	1	0	0
Ceutorhynchus contractus	Curculionidae	none	not ass	NP	dry-open	SS	not ass	1	0	0
Ceutorhynchus erysimi	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	10	3	0
Ceutorhynchus pallidactylus	Curculionidae	none	not ass	NP	dry-open	SS	not ass	0	1	0
Charagmus griseus	Curculionidae	none	not ass	NP	dry-open	SS & BG	not ass	3	1	0
Cleonis pigra	Curculionidae	Nb	not ass	P	dry-open	SS & BG	L_DIS/N_GRZ	11	13	0
Euophryum confine	Curculionidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	1	0
Glocianus distinctus	Curculionidae	none	not ass	NP	dry-open	SS	not ass	1	1	0
Glocianus pilosellus	Curculionidae	RDB 2	not ass	P	dry-open	SS	H_DIS/N_GRZ	0	1	0
Glocianus punctiger	Curculionidae	Nb;Sec 41	not ass	P	dry-open	TS & S	N_DIS/N_GRZ	0	2	0
Gronops lunatus	Curculionidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/H_GRZ	4	0	0
Gymnetron melanarium	Curculionidae	Nb	not ass	P	dry-open	TS & S	L_DIS/N_GRZ	0	0	2
Hypera arator	Curculionidae	none	not ass	NP	dry-open	SS	not ass	11	5	0
Hypera dauci	Curculionidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	2	0	0
Hypera diversipunctata	Curculionidae	RDB 3	not ass	P	unknown/wet/shaded	not ass	not ass	9	3	1
Hypera plantaginis	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	1
Hypera postica	Curculionidae	none	not ass	NP	dry-open	SS	not ass	2	0	0
Hypera zoilus	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	5	10	5
Limobius borealis	Curculionidae	Na	not ass	P	dry-open	TS & S	H_DIS/H_GRZ	0	1	0
Mecinus labilis	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	1	2	0
Mecinus pascuorum	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	1	5	0
Mecinus pyraster	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Mogulones asperifoliarum	Curculionidae	none	not ass	NP	dry-open	SS	not ass	1	0	0
Nedyus quadrimaculatus	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	2	1	0
Neliocarus faber	Curculionidae	Nb	not ass	P	dry-open	SS	N_DIS/H_GRZ	7	36	4

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance DC	Abundance SC	Abundance C
Neliocarus nebulosus	Curculionidae	none	not ass	NP	dry-open	SS	not ass	1	0	0
Otiorhynchus ovatus	Curculionidae	none	not ass	NP	dry-open	SS & BG	not ass	15	15	19
Otiorhynchus singularis	Curculionidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	2	7	0
Parethelcus pollinarius	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Philopedon plagiatum	Curculionidae	none	not ass	NP	dry-open	SS	not ass	5	14	1
Phyllobius pyri	Curculionidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	0	1
Phyllobius virideaeris	Curculionidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	7	2
Pityogenes bidentatus	Curculionidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Pityophthorus pubescens	Curculionidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Rhinocyllus conicus	Curculionidae	Nb	not ass	P	dry-open	SS & BG	UNK/UNDIF	11	0	0
Rhinoncus castor	Curculionidae	none	not ass	NP	dry-open	SS & BG	not ass	453	326	0
Rhinoncus pericarpius	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Romualdius angustisetulus	Curculionidae	none	not ass	NP	[unknown/wet/shaded]	not ass	not ass	1	6	0
Romualdius bifoveolatus	Curculionidae	none	not ass	NP	[unknown/wet/shaded]	not ass	not ass	6	11	15
Sitona hispidulus	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	5	5	0
Sitona humeralis	Curculionidae	none	not ass	NP	dry-open	SS	not ass	19	10	0
Sitona lepidus	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	15	13	0
Sitona lineatus	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	12	4	0
Stenocarus ruficornis	Curculionidae	Nb	not ass	P	dry-open	SS	H_DIS/N_GRZ	1	0	0
Strophosoma melanogrammum	Curculionidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	1	0
Trachyphloeus scabricul	Curculionidae	none	not ass	NP	dry-open	SS	not ass	311	1152	196
Trichosirocalus horridus	Curculionidae	Na	not ass	P	dry-open	SS	H_DIS/N_GRZ	1	3	0
Trichosirocalus troglodytes	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	6	21	1
Tychius junceus	Curculionidae	none	not ass	NP	dry-open	SS	not ass	16	42	0
Tychius picirostris	Curculionidae	none	not ass	NP	dry-open	TS & S	not ass	18	19	0
Tychius pusillus	Curculionidae	Nb	not ass	P	dry-open	SS	N_DIS/H_GRZ	6	3	0

								Abundance		
Species[a]	**Family**	**GB rarity[b]**	**GB threat[c,g]**	**Status**	**Broad habitat association[d,g]**	**Habitat guild[e,g]**	**Management guild[f,g]**	**DC**	**SC**	**C**
Tychius quinquepunctatus	Curculionidae	RDB 2	not ass	P	dry-open	SS	L_DIS/N_GRZ	0	1	0
Dermestes murinus	Dermestidae	NS	LC	P	unknown/wet/shaded	not ass	not ass	1	0	0
Agriotes lineatus	Elateridae	none	not ass	NP	dry-open	TS & S	not ass	1	0	1
Agriotes obscurus	Elateridae	none	not ass	NP	dry-open	TS & S	not ass	136	237	23
Agriotes pallidulus	Elateridae	none	not ass	NP	dry-open	TS & S	not ass	2	2	0
Agriotes sputator	Elateridae	none	not ass	NP	dry-open	TS & S	not ass	91	213	15
Agrypnus murinus	Elateridae	none	not ass	NP	dry-open	SS	not ass	449	278	98
Athous haemorrhoidalis	Elateridae	none	not ass	NP	dry-open	TS & S	not ass	30	24	2
Dalopius marginatus	Elateridae	none	not ass	NP	dry-open	TS & S	not ass	2	0	0
Kibunea minuta	Elateridae	none	not ass	NP	dry-open	TS & S	not ass	0	0	1
Prosternon tessellatum	Elateridae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	22	31	27
Selatosomus aeneus	Elateridae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	1	0	2
Stenagostus rhombeus	Elateridae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Lycoperdina succincta	Endomychidae	RDB 2	not ass	P	dry-open	SS	UNK/UNDIF	0	3	0
Anoplotrupes stercorosus	Geotrupidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	0	322	0
Geotrupes spiniger	Geotrupidae	none	LC	NP	dry-open	TS & S	not ass	2	4	0
Odonteus armiger	Geotrupidae	NS	LC	P	dry-open	TS & S	UNK/UNDIF	5	10	1
Typhaeus typhoeus	Geotrupidae	none	LC	NP	dry-open	SS	not ass	15	15	1
Helophorus nubilus	Helophoridae	NS	not ass	P	dry-open	TS & S	UNK/UNDIF	1	1	0
Helophorus porculus	Helophoridae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Helophorus rufipes	Helophoridae	none	not ass	NP	dry-open	TS & S	not ass	12	1	0
Kissister minimus	Histeridae	none	LC	NP	dry-open	SS & BG	not ass	89	481	37
Margarinotus purpurascens	Histeridae	none	LC	NP	dry-open	SS	not ass	158	49	0
Onthophilus punctatus	Histeridae	NR	LC	P	dry-open	TS & S	UNK/UNDIF	2	0	0
Saprinus aeneus	Histeridae	NS	LC	P	dry-open	TS & S	N_DIS/H_GRZ	0	5	0
Saprinus semistriatus	Histeridae	none	LC	NP	dry-open	TS & S	not ass	2	0	0

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
Cercyon pygmaeus	Hydrophilidae	none	not ass	NP	dry-open	TS & S	not ass	1	5	2
Megasternum concinnum	Hydrophilidae	none	not ass	NP	dry-open	TS & S	not ass	177	236	37
Megasternum immaculatum	Hydrophilidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	8	0
Sphaeridium bipustulatum	Hydrophilidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Sphaeridium lunatum	Hydrophilidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Sphaeridium scarabaeoides	Hydrophilidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Brachypterus glaber	Kateretidae	none	not ass	NP	dry-open	TS & S	not ass	54	1	0
Brachypterus urticae	Kateretidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Cartodere bifasciata	Latridiidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	2	1	0
Corticarina minuta	Latridiidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	161	99	0
Cortinicara gibbosa	Latridiidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	8	8	3
Enicmus histrio	Latridiidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	1
Enicmus transversus	Latridiidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	10	10	0
Agathidium laevigatum	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	13	16	3
Agathidium marginatum	Leiodidae	Notable	not ass	P	unknown/wet/shaded	not ass	not ass	10	94	97
Catops chrysomeloides	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Catops nigricans	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	2	1	2
Choleva agilis	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Choleva fagniezi	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Choleva jeanneli	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	4	12	0
Colon appendiculatum	Leiodidae	RDB K	not ass	P	unknown/wet/shaded	not ass	not ass	0	1	0
Leiodes macropus	Leiodidae	RDB K	not ass	P	unknown/wet/shaded	not ass	not ass	0	1	0
Leiodes obesa	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	4	0
Leiodes rufipennis	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	25	29	0
Leiodes triepkii	Leiodidae	RDB K	not ass	P	unknown/wet/shaded	not ass	not ass	0	1	0
Liocyrtusa vittata	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	3	2

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Ptomaphagus medius	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	1	1
Ptomaphagus subvillosus	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	11	25	4
Ptomaphagus varicornis	Leiodidae	RDB K	not ass	P	unknown/wet/shaded	not ass	not ass	2	0	0
Sciodrepoides watsoni	Leiodidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	27	13	2
Rhizophagus dispar	Monotomidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Mordellistena parvula	Mordellidae	NS	LC	P	unknown/wet/shaded	not ass	not ass	1	3	0
Epuraea aestiva	Nitidulidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Glischrochilus hortensis	Nitidulidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	56	8	1
Meligethes aeneus	Nitidulidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	6	0	1
Meligethes lugubris	Nitidulidae	Notable	not ass	P	[unknown/wet/shaded]	not ass	not ass	3	2	2
Meligethes ovatus	Nitidulidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Meligethes planiusculus	Nitidulidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	0	1
Oedemera lurida	Oedemeridae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Oedemera nobilis	Oedemeridae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Olibrus liquidus	Phalacridae	none	not ass	NP	[unknown/wet/shaded]	not ass	not ass	1	0	0
Olibrus pygmaeus	Phalacridae	Nb	not ass	P	[unknown/wet/shaded]	not ass	not ass	1	0	0
Ptenidium nitidum	Ptiliidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Ptenidium pusillum	Ptiliidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	3	0
Aphodius ater	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	3	3	0
Aphodius coenosus	Scarabaeidae	NS	LC	P	dry-open	TS & S	N_DIS/H_GRZ	9	12	0
Aphodius contaminatus	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	5	31	3
Aphodius depressus	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	1	2	0
Aphodius distinctus	Scarabaeidae	NS	LC	P	dry-open	TS & S	UNK/UNDIF	6	7	0
Aphodius foetens	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	1	1	0
Aphodius foetidus	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	6	0	0
Aphodius granarius	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	7	19	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Aphodius ictericus	Scarabaeidae	NS	LC	P	dry-open	TS & S	N_DIS/H_GRZ	35	35	0
Aphodius prodromus	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	5	11	0
Aphodius pusillus	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	5	16	0
Aphodius rufus	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	0	1	0
Aphodius sticticus	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Diastictus vulneratus	Scarabaeidae	NR	VU	P	dry-open	SS & BG	H_DIS/H_GRZ	13	6	0
Euheptaulacus villosus	Scarabaeidae	NS	LC	P	dry-open	SS & BG	N_DIS/H_GRZ	30	3	6
Omaloplia ruricola	Scarabaeidae	NS	LC	P	dry-open	SS	N_DIS/N_GRZ	8	2	0
Onthophagus joannae	Scarabaeidae	none	LC	NP	dry-open	SS	not ass	111	152	22
Onthophagus similis	Scarabaeidae	none	LC	NP	dry-open	TS & S	not ass	273	388	63
Phyllopertha horticola	Scarabaeidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	58	341	161
Neuraphes angulatus	Scydmaenidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	5	5	1
Stenichnus collaris	Scydmaenidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	3	3	5
Stenichnus poweri	Scydmaenidae	RDB K	not ass	P	unknown/wet/shaded	not ass	not ass	1	107	0
Stenichnus scutellaris	Scydmaenidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	2	3	0
Nicrophorus humator	Silphidae	none	not ass	NP	dry-open	TS & S	not ass	4	0	0
Nicrophorus investigator	Silphidae	none	not ass	NP	dry-open	TS & S	not ass	7	2	2
Nicrophorus vespillo	Silphidae	none	not ass	NP	dry-open	TS & S	not ass	370	57	35
Nicrophorus vespilloides	Silphidae	none	not ass	NP	dry-open	TS & S	not ass	4	2	1
Oiceoptoma thoracicum	Silphidae	none	not ass	NP	dry-open	TS & S	not ass	4	0	0
Silpha atrata	Silphidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	27	15	15
Silpha laevigata	Silphidae	none	not ass	NP	dry-open	SS	not ass	49	44	1
Silpha tristis	Silphidae	none	not ass	NP	dry-open	TS & S	not ass	112	98	17
Thanatophilus rugosus	Silphidae	none	not ass	NP	dry-open	TS & S	not ass	44	0	0
Thanatophilus sinuatus	Silphidae	none	not ass	NP	dry-open	TS & S	not ass	29	4	1
Isomira murina	Tenebrionidae	none	LC	NP	dry-open	SS	not ass	6	7	6

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
Nalassus laevioctostriatus	Tenebrionidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	0	0	1
Trixagus dermestoides	Throscidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Rove beetles										
Acrotona exigua	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	253	142	8
Acrotona muscorum	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	25	14	0
Aleochara bilineata	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	652	578	0
Aleochara bipustulata	Staphylinidae	none	not ass	NP	dry-open	SS	not ass	2177	977	1
Aleochara brevipennis	Staphylinidae	Notable	not ass	P	unknown/wet/shaded	not ass	not ass	27	2	0
Aleochara curtula	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	2	0	0
Aleochara intricata	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	4	15	1
Aleochara spadicea	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Aleochara verna	Staphylinidae	RDB K	not ass	P	unknown/wet/shaded	not ass	not ass	27	22	0
Alevonota gracilenta	Staphylinidae	RDB K	not ass	P	dry-open	TS & S	L_DIS/N_GRZ	3	4	2
Aloconota gregaria	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	107	23	2
Amischa analis	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	445	1027	308
Amischa decipiens	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	2	1	0
Amischa forcipata	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	2	1	0
Amischa nigrofusca	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	5	3	0
Anotylus insecatus	Staphylinidae	Notable	not ass	P	unknown/wet/shaded	not ass	not ass	2	0	0
Anotylus nitidulus	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	96	13	0
Anotylus rugosus	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	45	5	0
Anotylus sculpturatus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	37	8	0
Atheta oblita	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	4	1	0
Atheta vaga	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Atheta xanthopus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	31	82	1

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Badura macrocera	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	2	15	3
Bessobia fungivora	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Bisnius pseudoparcus	Staphylinidae	Notable	not ass	P	unknown/wet/shaded	not ass	not ass	0	1	0
Bisnius sordidus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Bledius gallicus	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	3	0	0
Bledius opacus	Staphylinidae	none	not ass	NP	[unknown/wet/shaded]	not ass	not ass	70	2	0
Bolitobius castaneus	Staphylinidae	none	LC	NP	dry-open	SS	not ass	0	1	1
Carpelimus pusillus	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Chaetida longicornis	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1	1	0
Cypha longicornis	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	54	13	0
Datomicra canescens	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	0	3	0
Dilacra pruinosa	Staphylinidae	RDB I	not ass	P	unknown/wet/shaded	not ass	not ass	2	0	0
Dimetrota atramentaria	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	4	14	0
Dinaraea angustula	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	155	90	1
Drusilla canaliculata	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1348	817	555
Falagrioma thoracica	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	12	3	52
Gabrius appendiculatus	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	4	0	0
Gabrius breviventer	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	3	2	0
Gabrius nigritulus	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	5	0	0
Gabrius osseticus	Staphylinidae	Nb	not ass	P	dry-open	SS & BG	wet/shaded	99	60	53
Geostiba circellaris	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	33	125	6
Gyrohypnus angustatus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	34	8	0
Gyrophaena affinis	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Heterothops dissimilis	Staphylinidae	RDB K	not ass	P	unknown/wet/shaded	not ass	not ass	2	7	8
Ischnosoma splendidum	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	46	69	44
Lamprinodes saginatus	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	10	10	6

								Abundance		
Species[a]	**Family**	**GB rarity[b]**	**GB threat[c,g]**	**Status**	**Broad habitat association[d,g]**	**Habitat guild[e,g]**	**Management guild[f,g]**	**DC**	**SC**	**C**
Leptacinus intermedius	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Liogluta alpestris	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	22	11	0
Lobrathium multipunctum	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	26	5	0
Medon castaneus	Staphylinidae	RDB I	not ass	P	dry-open	TS & S	wet/shaded	2	2	0
Megalinus glabratus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	2	5	0
Metopsia clypeata	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Microdota amicula	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	6	0	0
Microdota indubia	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	0	4	1
Microdota liliputana	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	2	0
Microdota minuscula	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	2	14	0
Micropeplus fulvus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Micropeplus staphylinoides	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	3	4	4
Mycetoporus angularis	Staphylinidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	7	12	11
Mycetoporus clavicornis	Staphylinidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	0	1	1
Mycetoporus lepidus	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	238	65	3
Mycetoporus piceolus	Staphylinidae	NS	LC	P	dry-open	SS	H_DIS/H_GRZ	0	0	1
Mycetoporus punctus	Staphylinidae	NS	LC	P	dry-open	UNK/UNDIF	UNK/UNDIF	0	3	3
Mycetoporus rufescens	Staphylinidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	0	0	1
Nehemitropia lividipennis	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Ochthephilum fracticorne	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	3	1
Ocypus aeneocephalus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	89	217	35
Ocypus brunnipes	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	7	9	2
Ocypus fuscatus	Staphylinidae	Nb	not ass	P	dry-open	TS & S	UNK/UNDIF	6	0	2
Ocypus olens	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	810	657	145
Oligota picipes	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	11	0
Omalium excavatum	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	4	1	0

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
Omalium exiguum	Staphylinidae	Notable	not ass	P	dry-open	UNK/UNDIF	UNK/UNDIF	0	1	0
Omalium oxyacanthae	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Ontholestes murinus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Othius angustus	Staphylinidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	586	182	69
Othius laeviusculus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	163	326	7
Othius punctulatus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1	2	0
Othius subuliformis	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	113	65	23
Ousipalia caesula	Staphylinidae	none	not ass	NP	dry-open	SS & BG	not ass	2	27	0
Oxypoda acuminata	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Oxypoda brachyptera	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	128	93	0
Oxypoda brevicornis	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	19	10	0
Oxypoda ferruginea	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	184	577	19
Oxypoda haemorrhoa	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	2	0	0
Oxypoda opaca	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	0	2	0
Oxypoda vittata	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	5	0	0
Pella limbata	Staphylinidae	none	not ass	NP	dry-open	SS	not ass	80	35	26
Philhygra palustris	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	8	0	0
Philonthus carbonarius	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	347	393	17
Philonthus cognatus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1003	312	0
Philonthus concinnus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	0	2	0
Philonthus cruentatus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1	3	0
Philonthus laminatus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	11	1	0
Philonthus lepidus	Staphylinidae	RDB K	not ass	P	dry-open	SS & BG	H_DIS/H_GRZ	109	428	42
Philonthus succicola	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1	1	0
Philonthus tenuicornis	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	2	1	0
Philonthus varians	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	0	3	0

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
Platydracus stercorarius	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	84	195	82
Proteinus laevigatus	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Proteinus ovalis	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Pselaphus heisei	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	7	18	0
Quedius boops	Staphylinidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	33	55	1
Quedius curtipennis	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Quedius levicollis	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	152	161	25
Quedius longicornis	Staphylinidae	Nb	not ass	P	dry-open	TS & S	UNK/UNDIF	2	0	1
Quedius molochinus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	3	2	0
Quedius nigriceps	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	2	1	0
Quedius persimilis	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	89	130	22
Quedius picipes	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1	1	0
Quedius schatzmayri	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	15	18	0
Quedius semiaeneus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	277	455	2
Quedius semiobscurus	Staphylinidae	none	not ass	NP	dry-open	SS	not ass	193	244	31
Rugilus erichsonii	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	9	37	16
Sepedophilus marshami	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	3	4	0
Sepedophilus nigripennis	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	10	4	3
Stenus brunnipes	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	8	5	3
Stenus clavicornis	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	15	17	3
Stenus impressus	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Stenus nanus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	25	27	0
Stenus ochropus	Staphylinidae	none	not ass	NP	dry-open	SS	not ass	17	4	5
Sunius melanocephalus	Staphylinidae	Notable	not ass	P	dry-open	TS & S	UNK/UNDIF	118	83	43
Sunius propinquus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	2	2	0
Tachinus marginellus	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	3	0	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance DC	Abundance SC	Abundance C
Tachinus rufipes	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	3	2	0
Tachyporus atriceps	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	3	2	1
Tachyporus chrysomelinus	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Tachyporus dispar	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	29	29	11
Tachyporus hypnorum	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	18	10	4
Tachyporus nitidulus	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	2	3	0
Tachyporus pusillus	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	117	266	10
Tachyporus scitulus	Staphylinidae	NR	LC	P	dry-open	SS	L_DIS/N_GRZ	31	122	24
Tachyporus solutus	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Tachyporus tersus	Staphylinidae	none	LC	NP	dry-open	TS & S	not ass	82	155	66
Tasgius ater	Staphylinidae	none	not ass	NP	dry-open	SS	not ass	4	2	0
Tasgius melanarius	Staphylinidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	5	1	3
Tasgius morsitans	Staphylinidae	none	not ass	NP	dry-open	SS	not ass	2	3	2
Tasgius winkleri	Staphylinidae	none	not ass	NP	dry-open	SS	not ass	3	1	0
Tinotus morion	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	1	16	1
Trichiusa immigrata	Staphylinidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Xantholinus elegans	Staphylinidae	none	not ass	NP	dry-open	SS	not ass	151	98	23
Xantholinus gallicus	Staphylinidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	39	20	18
Xantholinus laevigatus	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	23	13	0
Xantholinus linearis	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	344	411	76
Xantholinus longiventris	Staphylinidae	none	not ass	NP	dry-open	TS & S	not ass	23	12	1
Spiders										
Tegenaria gigantea	Agelenidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Hypsosinga albovittata	Araneidae	NS	LC	P	dry-open	UNK/UNDIF	N_DIS/N_GRZ	11	8	1
Clubiona diversa	Clubionidae	none	LC	NP	dry-open	TS & S	not ass	1	0	1

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance DC	Abundance SC	Abundance C
Argenna subnigra	Dictynidae	NS	LC	P	dry-open	SS	H_DIS/N_GRZ	245	193	47
Harpactea hombergi	Dysderidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Drassodes cupreus	Gnaphosidae	none	LC	NP	dry-open	TS & S	not ass	5	7	0
Drassodes pubescens	Gnaphosidae	NS	LC	P	dry-open	TS & S	H_DIS/N_GRZ	10	9	6
Drassyllus pusillus	Gnaphosidae	none	LC	NP	dry-open	TS & S	not ass	394	448	153
Haplodrassus signifer	Gnaphosidae	none	LC	NP	dry-open	TS & S	not ass	200	236	31
Micaria pulicaria	Gnaphosidae	none	LC	NP	dry-open	SS	not ass	4	4	0
Micaria silesiaca	Gnaphosidae	NR	NT	P	dry-open	SS & BG	UNK/UNDIF	1	2	0
Trachyzelotes pedestris	Gnaphosidae	none	LC	NP	dry-open	TS & S	not ass	33	11	27
Zelotes electus	Gnaphosidae	NS	LC	P	dry-open	SS & BG	N_DIS/N_GRZ	31	67	19
Zelotes latreillei	Gnaphosidae	none	LC	NP	dry-open	TS & S	not ass	2	5	8
Hahnia montana	Hahniidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	7	3	3
Hahnia nava	Hahniidae	none	LC	NP	dry-open	TS & S	not ass	259	165	270
Araeoncus humilis	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	47	26	0
Bathyphantes gracilis	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	38	42	8
Bathyphantes parvulus	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	1	1	1
Centromerus incilium	Linyphiidae	NS	LC	P	dry-open	TS & S	H_DIS/H_GRZ	1	1	0
Ceratinella brevipes	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	2	0	1
Ceratinella brevis	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	2	1	0
Ceratinella scabrosa	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	0	1	0
Ceratinopsis stativa	Linyphiidae	NS	LC	P	dry-open	TS & S	N_DIS/N_GRZ	8	10	6
Cnephalocotes obscurus	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	11	16	10
Dicymbium nigrum	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Diplostyla concolor	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	2	0	0
Erigone atra	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1305	874	22
Erigone dentipalpis	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	2668	1409	3

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance DC	Abundance SC	Abundance C
Erigone promiscua	Linyphiidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	6	2	0
Erigonella hiemalis	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	0	0	2
Evansia merens	Linyphiidae	NS	LC	P	dry-open	UNK/UNDIF	N_DIS/N_GRZ	3	2	0
Gongylidiellum murcidum	Linyphiidae	NS	VU	P	unknown/wet/shaded	not ass	not ass	0	1	0
Gongylidiellum vivum	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	0	1	0
Meioneta beata	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	78	81	31
Meioneta fuscipalpa	Linyphiidae	NR	VU	P	dry-open	TS & S	H_DIS/H_GRZ	1	0	0
Meioneta rurestris	Linyphiidae	none	LC	NP	dry-open	SS	not ass	45	41	1
Mermessus trilobatus	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	37	27	5
Metopobactrus prominulus	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	1	3	1
Micrargus herbigradus	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	13	1	2
Micrargus subaequalis	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Microlinyphia pusilla	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	7	7	12
Mioxena blanda	Linyphiidae	NR	DD	P	dry-open	SS	UNK/UNDIF	2	0	0
Oedothorax apicatus	Linyphiidae	none	LC	NP	dry-open	SS	not ass	107	3	0
Oedothorax fuscus	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	8	1	0
Oedothorax gibbosus	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	3	1	0
Oedothorax retusus	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	21	2	1
Ostearius melanopygius	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	19	2	0
Palliduphantes ericaeus	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	0	0	1
Palliduphantes insignis	Linyphiidae	NS	LC	P	dry-open	TS & S	UNK/UNDIF	2	2	0
Pelecopsis parallela	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	61	88	1
Peponocranium ludicrum	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	0	1	1
Pocadicnemis juncea	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	15	2	2
Porrhomma pygmaeum	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Savignia frontata	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	3	2	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance DC	SC	C
Stemonyphantes lineatus	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Tapinocyba praecox	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	32	11	26
Tenuiphantes mengei	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	0	0	3
Tenuiphantes tenuis	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	341	381	78
Tiso vagans	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	147	199	149
Typhochrestus digitatus	Linyphiidae	NS	LC	P	dry-open	SS & BG	H_DIS/H_GRZ	1	6	0
Walckenaeria acuminata	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Walckenaeria antica	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	3	6	16
Walckenaeria atrotibialis	Linyphiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	12	5	12
Walckenaeria dysderoides	Linyphiidae	NS	LC	P	dry-open	TS & S	L_DIS/N_GRZ	8	2	0
Walckenaeria monoceros	Linyphiidae	NS	LC	P	dry-open	SS & BG	UNK/UNDIF	2	2	0
Walckenaeria vigilax	Linyphiidae	none	LC	NP	dry-open	TS & S	not ass	0	1	0
Agroeca cuprea	Liocranidae	NR; Sec 41	NT	P	dry-open	SS & BG	L_DIS/N_GRZ	1	0	0
Agroeca proxima	Liocranidae	none	LC	NP	dry-open	UNK/UNDIF	not ass	10	12	1
Phrurolithus festivus	Liocranidae	none	LC	NP	dry-open	TS & S	not ass	25	0	1
Alopecosa barbipes	Lycosidae	none	LC	NP	dry-open	SS	not ass	82	119	8
Alopecosa cuneata	Lycosidae	NS	LC	P	dry-open	SS	H_DIS/H_GRZ	21	87	48
Alopecosa pulverulenta	Lycosidae	none	LC	NP	dry-open	TS & S	not ass	13	31	17
Arctosa leopardus	Lycosidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Arctosa perita	Lycosidae	none	LC	NP	dry-open	SS & BG	not ass	138	3	0
Pardosa monticola	Lycosidae	none	LC	NP	dry-open	TS & S	not ass	2753	5759	1103
Pardosa nigriceps	Lycosidae	none	LC	NP	dry-open	TS & S	not ass	7	5	5
Pardosa palustris	Lycosidae	none	LC	NP	dry-open	SS	not ass	87	493	107
Pardosa prativaga	Lycosidae	none	LC	NP	dry-open	TS & S	not ass	91	34	1
Pardosa pullata	Lycosidae	none	LC	NP	dry-open	TS & S	not ass	475	733	693
Pirata hygrophilus	Lycosidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	4	0	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Trochosa ruricola	Lycosidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	28	14	3
Trochosa terricola	Lycosidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	52	43	43
Xerolycosa nemoralis	Lycosidae	NS	LC	P	dry-open	SS	UNK/UNDIF	16	7	0
Thanatus striatus	Philodromidae	NS	LC	P	dry-open	TS & S	N_DIS/N_GRZ	0	1	0
Pisaura mirabilis	Pisauridae	none	LC	NP	dry-open	TS & S	not ass	2	1	1
Euophrys frontalis	Salticidae	none	LC	NP	dry-open	TS & S	not ass	1	0	1
Heliophanus flavipes	Salticidae	none	LC	NP	dry-open	TS & S	not ass	4	7	1
Talavera aequipes	Salticidae	none	LC	NP	dry-open	SS	not ass	1	2	0
Pachygnatha degeeri	Tetragnathidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	239	342	160
Achaearanea riparia	Theridiidae	NS	LC	P	dry-open	UNK/UNDIF	H_DIS/N_GRZ	2	0	0
Enoplognatha ovata	Theridiidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Enoplognatha thoracica	Theridiidae	none	LC	NP	dry-open	TS & S	not ass	41	50	24
Neottiura bimaculata	Theridiidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Robertus lividus	Theridiidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	10	3	0
Steatoda albomaculata	Theridiidae	NR	LC	P	dry-open	SS	H_DIS/N_GRZ	0	1	0
Steatoda phalerata	Theridiidae	none	LC	NP	dry-open	TS & S	not ass	359	822	147
Ozyptila atomaria	Thomisidae	none	LC	NP	dry-open	TS & S	not ass	4	5	5
Ozyptila praticola	Thomisidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Ozyptila sanctuaria	Thomisidae	none	LC	NP	dry-open	TS & S	not ass	18	54	19
Ozyptila trux	Thomisidae	none	LC	NP	dry-open	TS & S	not ass	1	0	0
Xysticus bifasciatus	Thomisidae	NS	LC	P	dry-open	TS & S	UNK/UNDIF	4	3	1
Xysticus cristatus	Thomisidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	21	32	4
Xysticus erraticus	Thomisidae	none	LC	NP	dry-open	TS & S	not ass	41	42	41
Xysticus kochi	Thomisidae	none	LC	NP	dry-open	SS	not ass	5	8	0
Zora spinimana	Zoridae	none	LC	NP	dry-open	TS & S	not ass	1	0	0

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
True bugs										
Orius laevigatus	Anthocoridae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	1	0	0
Orius niger	Anthocoridae	none	not ass	NP	dry-open	TS & S	not ass	68	23	0
Neophilaenus exclamationis	Aphrophoridae	none	not ass	NP	dry-open	SS	not ass	3	15	20
Berytinus crassipes	Berytidae	none	not ass	NP	dry-open	SS	not ass	0	1	1
Berytinus minor	Berytidae	none	not ass	NP	dry-open	SS	not ass	0	1	1
Berytinus montivagus	Berytidae	none	not ass	NP	dry-open	SS	not ass	0	1	0
Ceratocombus coleoptratus	Ceratocombidae	none	not ass	NP	dry-open	TS & S	not ass	5	5	5
Agallia consobrina	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Anaceratagallia ribauti	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	21	8	0
Anaceratagallia venosa	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	6	30	37
Anoscopus albifrons	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	129	360	278
Anoscopus histrionicus	Cicadellidae	none	not ass	NP	dry-open	SS	not ass	1	0	0
Anoscopus serratulae	Cicadellidae	none	not ass	NP	dry-open	SS	not ass	1	11	0
Aphrodes makarovi	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	79	128	6
Arocephalus languidus	Cicadellidae	1st Brit record	not ass	NP	[unknown/wet/shaded]	not ass	not ass	0	6	0
Arocephalus punctum	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	0	12	18
Arthaldeus pascuellus	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	5	0	1
Cicadella viridis	Cicadellidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	0	1	0
Deltocephalus pulicaris	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	206	555	100
Dikraneura variata	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	0	0	3
Doratura stylata	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	70	275	112
Emelyanoviana mollicula	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	2	0	0
Errastunus ocellaris	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	6	4	0
Eupelix cuspidata	Cicadellidae	none	not ass	NP	dry-open	SS	not ass	1	8	10
Eupteryx atropunctata	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	24	0	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Eupteryx aurata	Cicadellidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	4	0	0
Eupteryx notata	Cicadellidae	none	not ass	NP	dry-open	SS	not ass	36	112	32
Eupteryx stachydearum	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Eupteryx urticae	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	9	0	0
Eupteryx vittata	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Euscelis incisus	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	393	446	59
Forcipata citrinella	Cicadellidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	1	0
Graphocraerus ventralis	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	0	16	0
Hardya melanopsis	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	5	9	70
Hyledelphax elegantula	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	10	5	25
Javesella dubia	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	0	2	1
Kelisia sabulicola	Cicadellidae	none	not ass	NP	dry-open	SS & BG	not ass	2	1	1
Kosswigianella exigua	Cicadellidae	none	not ass	NP	dry-open	SS	not ass	38	81	35
Macropsis fuscula	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	4	1	0
Macrosteles laevis	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	1	4	0
Macrosteles quadripunctulatus	Cicadellidae	NA	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	19	5	0
Macrosteles sexnotatus	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	1	3	0
Macrosteles variatus	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Macustus grisescens	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	0	0	1
Megophthalmus scabripennis	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	56	62	20
Megophthalmus scanicus	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	2	8	3
Ophiola decumana	Cicadellidae	Nb	not ass	P	dry-open	SS	H_DIS/H_GRZ	64	4	0
Platymetopius undatus	Cicadellidae	NA	not ass	P	unknown/wet/shaded	not ass	not ass	0	1	0
Psammotettix alienus	Cicadellidae	RDB K	not ass	P	[unknown/wet/shaded]	not ass	not ass	3	3	0
Psammotettix cephalotes	Cicadellidae	none	not ass	NP	dry-open	SS	not ass	34	194	0
Psammotettix confinis	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	32	107	1

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Psammotettix nodosus	Cicadellidae	none	not ass	NP	dry-open	SS	not ass	153	329	7
Recilia coronifera	Cicadellidae	none	not ass	NP	dry-open	SS	not ass	3	23	11
Rhytistylus proceps	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	4	35	36
Ribautodelphax angulosa	Cicadellidae	Nb	not ass	P	dry-open	TS & S	N_DIS/N_GRZ	5	8	20
Sardius argus	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	12	16	16
Streptanus aemulans	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Streptanus sordidus	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	4	7	0
Turrutus socialis	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	52	1298	432
Ulopa reticulata	Cicadellidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	4	1	2
Verdanus abdominalis	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	1	4	0
Zyginidia scutellaris	Cicadellidae	none	not ass	NP	dry-open	TS & S	not ass	47	50	11
Arenocoris falleni	Coreidae	NS	LC	P	dry-open	SS & BG	H_DIS/H_GRZ	1	0	0
Arenocoris waltlii	Coreidae	NR	CR	P	[unknown/wet/shaded]	not ass	not ass	0	1	0
Ceraleptus lividus	Coreidae	NS	LC	P	dry-open	SS	N_DIS/N_GRZ	0	3	1
Coriomeris denticulatus	Coreidae	none	LC	NP	dry-open	SS	not ass	2	1	0
Spathocera dalmanii	Coreidae	NS	LC	P	dry-open	SS	N_DIS/H_GRZ	0	2	0
Syromastus rhombeus	Coreidae	none	LC	NP	dry-open	SS	not ass	1	2	0
Legnotus picipes	Cydnidae	NS	LC	P	dry-open	SS & BG	H_DIS/H_GRZ	2	23	0
Sehirus luctuosus	Cydnidae	none	LC	NP	dry-open	SS	not ass	2	0	0
Conomelus anceps	Delphacidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Criomorphus albomarginatus	Delphacidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Delphacinus mesomelas	Delphacidae	none	not ass	NP	dry-open	SS	not ass	0	0	1
Dicranotropis hamata	Delphacidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Ditropis pteridis	Delphacidae	none	not ass	NP	dry-open	TS & S	not ass	5	0	0
Javesella pellucida	Delphacidae	none	not ass	NP	dry-open	TS & S	not ass	55	89	15
Xanthodelphax straminea	Delphacidae	none	not ass	NP	dry-open	TS & S	not ass	1	2	0

								Abundance		
Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	DC	SC	C
Calocoris roseomaculatus	Heteroptera	none	not ass	NP	dry-open	SS	not ass	0	3	0
Liocoris tripustulatus	Heteroptera	none	not ass	NP	dry-open	TS & S	not ass	2	0	0
Nabis rugosus	Heteroptera	none	not ass	NP	dry-open	TS & S	not ass	3	4	0
Nysius huttoni	Heteroptera	none	not ass	NP	unknown/wet/shaded	not ass	not ass	11	2	0
Plagiognathus chrysanthemi	Heteroptera	none	not ass	NP	dry-open	SS	not ass	3	9	0
Trapezonotus arenarius	Heteroptera	none	not ass	NP	dry-open	SS	not ass	1	0	0
Trigonotylus ruficornis	Heteroptera	none	not ass	NP	dry-open	TS & S	not ass	0	3	0
Cymus claviculus	Lygaeidae	none	not ass	NP	dry-open	SS & BG	not ass	1	0	0
Drymus ryei	Lygaeidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Drymus sylvaticus	Lygaeidae	none	not ass	NP	dry-open	TS & S	not ass	0	0	1
Heterogaster urticae	Lygaeidae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Megalonotus chiragra	Lygaeidae	none	not ass	NP	dry-open	SS & BG	not ass	2	10	0
Megalonotus dilatatus	Lygaeidae	Nb	not ass	P	dry-open	SS & BG	UNK/UNDIF	0	2	0
Megalonotus praetextatus	Lygaeidae	Nb	not ass	P	dry-open	SS	H_DIS/N_GRZ	49	27	8
Megalonotus sabulicola	Lygaeidae	Nb	not ass	P	dry-open	SS & BG	H_DIS/N_GRZ	2	0	0
Peritrechus geniculatus	Lygaeidae	none	not ass	NP	dry-open	TS & S	not ass	9	6	4
Peritrechus lundii	Lygaeidae	none	not ass	NP	dry-open	TS & S	not ass	3	2	0
Plinthisus brevipennis	Lygaeidae	none	not ass	NP	dry-open	SS	not ass	42	58	57
Scolopostethus affinis	Lygaeidae	none	not ass	NP	dry-open	SS	not ass	1	1	0
Stygnocoris fuligineus	Lygaeidae	none	not ass	NP	dry-open	TS & S	not ass	15	2	1
Stygnocoris sabulosus	Lygaeidae	none	not ass	NP	dry-open	TS & S	not ass	1	2	3
Acetropis gimmerthalii	Miridae	none	not ass	NP	dry-open	TS & S	not ass	0	0	2
Amblytylus nasutus	Miridae	none	not ass	NP	dry-open	TS & S	not ass	2	2	0
Capsodes gothicus	Miridae	none	not ass	NP	dry-open	TS & S	not ass	1	0	1
Capsus ater	Miridae	none	not ass	NP	dry-open	TS & S	not ass	2	3	2
Charagochilus gyllenhalii	Miridae	none	not ass	NP	dry-open	SS	not ass	1	0	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance DC	Abundance SC	Abundance C
Chlamydatus pulicarius	Miridae	Nb	not ass	P	dry-open	TS & S	L_DIS/N_GRZ	0	16	0
Chlamydatus pullus	Miridae	none	not ass	NP	dry-open	SS	not ass	61	134	0
Chlamydatus saltitans	Miridae	none	not ass	NP	dry-open	SS	not ass	4	1	0
Conostethus roseus	Miridae	none	not ass	NP	dry-open	TS & S	not ass	0	2	0
Dicyphus globulifer	Miridae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Hallodapus rufescens	Miridae	none	not ass	NP	dry-open	SS & BG	not ass	0	0	1
Lopus decolor	Miridae	none	not ass	NP	dry-open	TS & S	not ass	4	5	1
Lygocoris pabulinus	Miridae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Lygus rugulipennis	Miridae	none	not ass	NP	dry-open	TS & S	not ass	18	4	0
Megaloceroea recticornis	Miridae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Notostira elongata	Miridae	none	not ass	NP	dry-open	TS & S	not ass	3	0	0
Pithanus maerkelii	Miridae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Polymerus unifasciatus	Miridae	none	not ass	NP	dry-open	SS	not ass	1	1	0
Psallus wagneri	Miridae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Rhabdomiris striatellus	Miridae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Stenodema calcarata	Miridae	none	not ass	NP	dry-open	TS & S	not ass	1	2	0
Stenodema laevigata	Miridae	none	not ass	NP	dry-open	TS & S	not ass	1	0	0
Systellonotus triguttatus	Miridae	Nb	not ass	P	dry-open	SS	H_DIS/H_GRZ	0	1	0
Trigonotylus caelestialum	Miridae	none	not ass	NP	dry-open	TS & S	not ass	1	1	0
Himacerus apterus	Nabidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Himacerus boops	Nabidae	none	not ass	NP	dry-open	TS & S	not ass	4	0	1
Nabis ericetorum	Nabidae	none	not ass	NP	dry-open	UNK/UNDIF	not ass	1	0	0
Nabis ferus	Nabidae	none	not ass	NP	dry-open	TS & S	not ass	10	9	0
Nabis flavomarginatus	Nabidae	none	not ass	NP	dry-open	TS & S	not ass	0	2	0
Nabis limbatus	Nabidae	none	not ass	NP	dry-open	TS & S	not ass	0	1	0
Aelia acuminata	Pentatomidae	none	LC	NP	dry-open	TS & S	not ass	1	6	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Dolycoris baccarum	Pentatomidae	none	LC	NP	dry-open	TS & S	not ass	7	1	0
Palomena prasina	Pentatomidae	none	LC	NP	dry-open	TS & S	not ass	2	0	0
Podops inuncta	Pentatomidae	none	LC	NP	dry-open	SS	not ass	0	1	7
Coranus woodroffei	Reduviidae	none	not ass	NP	[unknown/wet/shaded]	not ass	not ass	0	1	0
Chorosoma schillingi	Rhopalidae	none	LC	NP	dry-open	SS & BG	not ass	0	1	0
Myrmus miriformis	Rhopalidae	none	LC	NP	dry-open	TS & S	not ass	0	1	0
Rhopalus parumpunctatus	Rhopalidae	NS	LC	P	dry-open	SS & BG	H_DIS/H_GRZ	1	1	0
Stictopleurus abutilon	Rhopalidae	none	LC	NP	dry-open	SS	not ass	2	1	0
Salda littoralis	Saldidae	NS	LC	P	unknown/wet/shaded	not ass	not ass	1	0	0
Saldula orthochila	Saldidae	NS	LC	P	dry-open	SS	N_DIS/H_GRZ	87	20	0
Saldula saltatoria	Saldidae	none	LC	NP	unknown/wet/shaded	not ass	not ass	6	0	0
Odontoscelis lineola	Scutelleridae	NS	LC	P	dry-open	SS & BG	H_DIS/H_GRZ	0	1	0
Acalypta parvula	Tingidae	none	not ass	NP	dry-open	SS	not ass	26	105	149
Agramma laetum	Tingidae	none	not ass	NP	dry-open	SS	not ass	1	15	11
Derephysia foliacea	Tingidae	none	not ass	NP	unknown/wet/shaded	not ass	not ass	1	0	0
Kalama tricornis	Tingidae	none	not ass	NP	dry-open	SS	not ass	15	144	26
Tingis ampliata	Tingidae	none	not ass	NP	dry-open	TS & S	not ass	2	0	0
Tingis cardui	Tingidae	none	not ass	NP	dry-open	TS & S	not ass	3	2	0
Vascular plants										
Acer pseudoplatanus	Aceraceae	none	not ass	NP	not ass	not ass	not ass	21	1	2
Anthriscus caucalis	Apiaceae	none	LC	NP	not ass	not ass	not ass	1	4	0
Torilis japonica	Apiaceae	none	LC	NP	not ass	not ass	not ass	2	1	0
Achillea millefolium	Asteraceae	none	LC	NP	not ass	not ass	not ass	99	169	31
Arctium minus	Asteraceae	none	LC	NP	not ass	not ass	not ass	4	1	0
Bellis perennis	Asteraceae	none	LC	NP	not ass	not ass	not ass	6	7	1

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Carduus nutans	Asteraceae	none	LC	NP	not ass	not ass	not ass	1	0	0
Cirsium acaule	Asteraceae	none	LC	NP	not ass	not ass	not ass	1	2	0
Cirsium arvense	Asteraceae	none	LC	NP	not ass	not ass	not ass	241	161	15
Cirsium vulgare	Asteraceae	none	LC	NP	not ass	not ass	not ass	221	123	7
Conysa canadensis	Asteraceae	none	not ass	NP	not ass	not ass	not ass	62	5	0
Crepis capillaris	Asteraceae	none	LC	NP	not ass	not ass	not ass	137	335	19
Filago vulgaris	Asteraceae	none	NT	P	not ass	not ass	not ass	2	0	0
Hypochaeris glabra	Asteraceae	none	VU	P	not ass	not ass	not ass	2	0	0
Hypochaeris radicata	Asteraceae	none	LC	NP	not ass	not ass	not ass	21	93	4
Lactuca serriola	Asteraceae	none	LC	NP	not ass	not ass	not ass	0	0	1
Lactuca virosa	Asteraceae	none	LC	NP	not ass	not ass	not ass	8	0	0
Leontodon autumnalis	Asteraceae	none	not ass	NP	not ass	not ass	not ass	1	14	5
Onopordum acanthium	Asteraceae	none	LC	NP	not ass	not ass	not ass	0	6	0
Pilosella officinarum	Asteraceae	none	LC	NP	not ass	not ass	not ass	43	296	110
Senecio jacobaea	Asteraceae	none	LC	NP	not ass	not ass	not ass	8	16	5
Senecio sylvaticus	Asteraceae	none	LC	NP	not ass	not ass	not ass	5	1	0
Senecio vulgaris	Asteraceae	none	LC	NP	not ass	not ass	not ass	36	39	0
Sonchus asper	Asteraceae	none	LC	NP	not ass	not ass	not ass	7	0	0
Sonchus oleraceaus	Asteraceae	none	LC	NP	not ass	not ass	not ass	36	30	0
Taraxacum officinale	Asteraceae	none	not ass	NP	not ass	not ass	not ass	151	337	63
Cynoglossum officinale	Boraginaceae	none	NT	P	not ass	not ass	not ass	1	0	0
Myosotis ramosissima	Boraginaceae	none	LC	NP	not ass	not ass	not ass	20	43	5
Arabidopsis thaliana	Brassicaceae	none	LC	NP	not ass	not ass	not ass	34	60	2
Arabis hirsuta	Brassicaceae	none	LC	NP	not ass	not ass	not ass	19	54	0
Capsella bursa-pastoris	Brassicaceae	none	LC	NP	not ass	not ass	not ass	19	38	0
Cardamine hirsuta	Brassicaceae	none	LC	NP	not ass	not ass	not ass	2	19	0

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
Coronopus squamatus	Brassicaceae	none	not ass	NP	not ass	not ass	not ass	5	0	0
Erophila verna	Brassicaceae	none	LC	NP	not ass	not ass	not ass	17	43	0
Teesdalia nudicaulis	Brassicaceae	none	NT	P	not ass	not ass	not ass	0	0	1
Campanula rotundifolia	Campanulaceae	none	LC	NP	not ass	not ass	not ass	6	5	7
Arenaria serpyllifolia	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	250	295	7
Cerastium arvense	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	266	276	57
Cerastium fontanum	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	239	345	41
Cerastium glomeratum	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	33	45	0
Cerastium semidecandrum	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	37	119	0
Moehringia trinervia	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	1	0	0
Sagina procumbens	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	12	4	0
Silene latifolia	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	23	12	0
Spergularia rubra	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	4	5	0
Stellaria graminea	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	212	376	93
Stellaria media (agg.?)	Caryophyllaceae	none	LC	NP	not ass	not ass	not ass	21	24	1
Chenopodium album	Chenopodiaceae	none	LC	NP	not ass	not ass	not ass	18	7	0
Convolvulus arvensisvu	Convolvulaceae	none	LC	NP	not ass	not ass	not ass	104	77	3
Sedum acre	Crassulaceae	none	LC	NP	not ass	not ass	not ass	20	31	0
Bryonia dioica	Cucurbitaceae	none	LC	NP	not ass	not ass	not ass	1	0	0
Carex arenaria	Cyperaceae	none	LC	NP	not ass	not ass	not ass	4	11	2
Carex caryophyllea	Cyperaceae	none	LC	NP	not ass	not ass	not ass	33	41	1
Carex divulsa	Cyperaceae	none	LC	NP	not ass	not ass	not ass	22	0	1
Carex hirta	Cyperaceae	none	LC	NP	not ass	not ass	not ass	72	81	27
Carex muricata	Cyperaceae	none	LC	NP	not ass	not ass	not ass	3	12	23
Carex pilulifera	Cyperaceae	none	LC	NP	not ass	not ass	not ass	26	5	12
Pteridium aquilinum	Dennstaedtiaceae	none	LC	NP	not ass	not ass	not ass	156	103	51

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Knautia arvensis	Dipsacaceae	none	LC	NP	not ass	not ass	not ass	0	1	0
Scabiosa columbaria	Dipsacaceae	none	LC	NP	not ass	not ass	not ass	0	1	0
Equisetum arvense	Equisetaceae	none	LC	NP	not ass	not ass	not ass	4	0	0
Calluna vulgaris	Ericaceae	none	LC	NP	not ass	not ass	not ass	10	21	23
Lathyrus linifolius	Fabaceae	none	LC	NP	not ass	not ass	not ass	7	8	5
Lathyrus pratensis	Fabaceae	none	LC	NP	not ass	not ass	not ass	8	1	0
Lotus corniculatus	Fabaceae	none	LC	NP	not ass	not ass	not ass	54	82	43
Medicago lupulina	Fabaceae	none	LC	NP	not ass	not ass	not ass	157	172	11
Medicago minima	Fabaceae	NS	VU	P	not ass	not ass	not ass	9	0	0
Ononis repens	Fabaceae	none	LC	NP	not ass	not ass	not ass	5	0	0
Ornithopus perpusillus	Fabaceae	none	LC	NP	not ass	not ass	not ass	52	21	3
Trifolium arvense	Fabaceae	none	LC	NP	not ass	not ass	not ass	11	4	0
Trifolium campestre	Fabaceae	none	LC	NP	not ass	not ass	not ass	74	59	10
Trifolium dubium	Fabaceae	none	LC	NP	not ass	not ass	not ass	141	180	26
Trifolium micranthum	Fabaceae	none	LC	NP	not ass	not ass	not ass	1	0	0
Trifolium pratense	Fabaceae	none	LC	NP	not ass	not ass	not ass	6	1	0
Trifolium repens	Fabaceae	none	LC	NP	not ass	not ass	not ass	242	515	146
Trifolium striatum	Fabaceae	none	LC	NP	not ass	not ass	not ass	17	14	0
Ulex europaeus	Fabaceae	none	LC	NP	not ass	not ass	not ass	5	3	1
Vicia hirsuta	Fabaceae	none	LC	NP	not ass	not ass	not ass	6	25	33
Vicia lathyroides	Fabaceae	none	LC	NP	not ass	not ass	not ass	22	51	8
Vicia sativa	Fabaceae	none	LC	NP	not ass	not ass	not ass	166	228	99
Vicia tetrasperma	Fabaceae	none	LC	NP	not ass	not ass	not ass	4	5	5
Quercus robur	Fagaceae	none	LC	NP	not ass	not ass	not ass	3	4	3
Ceratocapnos claviculata	Fumariaceae	none	LC	NP	not ass	not ass	not ass	1	1	0
Fumaria muralis	Fumariaceae	none	LC	NP	not ass	not ass	not ass	1	0	0

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance		
								DC	SC	C
Fumaria officinalis	Fumariaceae	none	LC	NP	not ass	not ass	not ass	1	0	0
Fumaria parviflora	Fumariaceae	NS	VU	P	not ass	not ass	not ass	4	0	0
Erodium cicutarium	Geraniaceae	none	LC	NP	not ass	not ass	not ass	43	74	0
Geranium dissectum	Geraniaceae	none	LC	NP	not ass	not ass	not ass	1	7	0
Geranium molle	Geraniaceae	none	LC	NP	not ass	not ass	not ass	170	352	29
Geranium pusillum	Geraniaceae	none	LC	NP	not ass	not ass	not ass	20	42	0
Geranium robertianum	Geraniaceae	none	LC	NP	not ass	not ass	not ass	2	12	0
Luzula campestris	Juncaceae	none	LC	NP	not ass	not ass	not ass	81	390	133
Glechoma hederacea	Lamiaceae	none	LC	NP	not ass	not ass	not ass	68	159	22
Lamium purpureum	Lamiaceae	none	LC	NP	not ass	not ass	not ass	0	5	16
Prunella vulgaris	Lamiaceae	none	LC	NP	not ass	not ass	not ass	5	53	2
Teucrium scorodonia	Lamiaceae	none	LC	NP	not ass	not ass	not ass	16	0	0
Thymus polytrichus	Lamiaceae	none	LC	NP	not ass	not ass	not ass	0	0	4
Thymus pulegioides	Lamiaceae	none	LC	NP	not ass	not ass	not ass	70	150	60
Linium catharticum	Linaceae	none	LC	NP	not ass	not ass	not ass	2	32	5
Epilobium parviflorum	Onagraceae	none	LC	NP	not ass	not ass	not ass	1	0	0
Papaver dubium	Papaveraceae	none	LC	NP	not ass	not ass	not ass	2	0	0
Papaver rhoeas	Papaveraceae	none	LC	NP	not ass	not ass	not ass	15	2	0
Plantago coronopus	Plantaginaceae	none	LC	NP	not ass	not ass	not ass	25	2	0
Plantago lanceolata	Plantaginaceae	none	LC	NP	not ass	not ass	not ass	213	533	101
Plantago major	Plantaginaceae	none	LC	NP	not ass	not ass	not ass	0	1	0
Agrostis capillaris	Poaceae	none	LC	NP	not ass	not ass	not ass	353	533	98
Agrostis stolonifera	Poaceae	none	LC	NP	not ass	not ass	not ass	110	77	66
Agrostis vinealis	Poaceae	none	LC	NP	not ass	not ass	not ass	0	0	2
Aira praecox	Poaceae	none	LC	NP	not ass	not ass	not ass	6	4	7
Anisantha sterilis	Poaceae	none	not ass	NP	not ass	not ass	not ass	23	39	2

								Abundance		
Species[a]	**Family**	**GB rarity[b]**	**GB threat[c,g]**	**Status**	**Broad habitat association[d,g]**	**Habitat guild[e,g]**	**Management guild[f,g]**	**DC**	**SC**	**C**
Anthoxanthum odoratum	Poaceae	none	LC	NP	not ass	not ass	not ass	430	649	227
Arrhenatherum elatius	Poaceae	none	LC	NP	not ass	not ass	not ass	126	226	90
Brachypodium (sylvaticum?)	Poaceae	none	LC	NP	not ass	not ass	not ass	0	2	0
Briza media	Poaceae	none	LC	NP	not ass	not ass	not ass	1	0	3
Bromus hordeaceus	Poaceae	none	LC	NP	not ass	not ass	not ass	183	352	88
Calamagrostis epigejos	Poaceae	none	LC	NP	not ass	not ass	not ass	0	1	0
Cynosurus cristatum	Poaceae	none	LC	NP	not ass	not ass	not ass	0	1	0
Dactylis glomerata	Poaceae	none	LC	NP	not ass	not ass	not ass	44	250	74
Deschampsia cespitosa	Poaceae	none	LC	NP	not ass	not ass	not ass	1	0	0
Deschampsia flexuosa	Poaceae	none	LC	NP	not ass	not ass	not ass	73	131	49
Elytrigia repens	Poaceae	none	LC	NP	not ass	not ass	not ass	20	7	0
Festuca heterophylla	Poaceae	none	not ass	NP	not ass	not ass	not ass	4	15	1
Festuca ovina (agg.?)	Poaceae	none	LC	NP	not ass	not ass	not ass	177	351	137
Festuca pratensis	Poaceae	none	LC	NP	not ass	not ass	not ass	0	1	0
Festuca rubra (agg.?)	Poaceae	none	LC	NP	not ass	not ass	not ass	342	599	117
Helictotrichon pratense	Poaceae	none	LC	NP	not ass	not ass	not ass	78	109	54
Helictotrichon pubescens	Poaceae	none	LC	NP	not ass	not ass	not ass	47	187	83
Holcus lanatus	Poaceae	none	LC	NP	not ass	not ass	not ass	414	587	167
Holcus mollis	Poaceae	none	LC	NP	not ass	not ass	not ass	21	94	9
Hordeum murinum	Poaceae	none	LC	NP	not ass	not ass	not ass	101	85	2
Koeleria macrantha	Poaceae	none	LC	NP	not ass	not ass	not ass	78	297	107
Lolium multiflorum	Poaceae	none	not ass	NP	not ass	not ass	not ass	2	1	0
Lolium perenne	Poaceae	none	LC	NP	not ass	not ass	not ass	48	50	30
Phleum phleoides	Poaceae	NR	LC	P	not ass	not ass	not ass	0	4	9
Phleum pratensis sens.lat.	Poaceae	none	LC	NP	not ass	not ass	not ass	113	333	60
Poa annua	Poaceae	none	LC	NP	not ass	not ass	not ass	68	13	4

Species[a]	**Family**	**GB rarity**[b]	**GB threat**[c,g]	**Status**	**Broad habitat association**[d,g]	**Habitat guild**[e,g]	**Management guild**[f,g]	**Abundance**		
								DC	**SC**	**C**
Poa pratensis sens.lat.	Poaceae	none	LC	NP	not ass	not ass	not ass	93	203	79
Poa trivialis	Poaceae	none	LC	NP	not ass	not ass	not ass	61	49	7
Trisetum flavescens	Poaceae	none	LC	NP	not ass	not ass	not ass	125	269	88
Vulpia bromoides	Poaceae	none	LC	NP	not ass	not ass	not ass	2	0	0
Vulpia ciliata ssp. ambigua	Poaceae	NS	not ass	P	not ass	not ass	not ass	1	0	0
Fallopia convolvulus	Polygonaceae	none	LC	NP	not ass	not ass	not ass	6	2	0
Rumex acetosa	Polygonaceae	none	LC	NP	not ass	not ass	not ass	42	123	51
Rumex acetosella	Polygonaceae	none	LC	NP	not ass	not ass	not ass	614	561	58
Anagallis arvensis	Primulaceae	none	LC	NP	not ass	not ass	not ass	6	3	0
Primula elatior	Primulaceae	NS	NT	P	not ass	not ass	not ass	4	1	0
Ranunculus repens	Ranunculaceae	none	LC	NP	not ass	not ass	not ass	12	15	0
Reseda lutea	Resedaceae	none	LC	NP	not ass	not ass	not ass	102	93	0
Aphanes arvensis (agg.?)	Rosaceae	none	LC	NP	not ass	not ass	not ass	96	103	2
Crataegus monogyna	Rosaceae	none	LC	NP	not ass	not ass	not ass	43	9	1
Filipendula vulgaris	Rosaceae	none	LC	NP	not ass	not ass	not ass	2	0	0
Potentilla reptans	Rosaceae	none	LC	NP	not ass	not ass	not ass	24	20	8
Galium aparine	Rubiaceae	none	LC	NP	not ass	not ass	not ass	20	25	1
Galium parisiense	Rubiaceae	NS	VU	P	not ass	not ass	not ass	2	0	0
Galium saxatile	Rubiaceae	none	LC	NP	not ass	not ass	not ass	144	208	50
Galium verum	Rubiaceae	none	LC	NP	not ass	not ass	not ass	432	478	156
Saxifraga tridactylites	Saxifragaceae	none	LC	NP	not ass	not ass	not ass	30	23	0
Digitalis purpurea	Scrophulariaceae	none	LC	NP	not ass	not ass	not ass	4	1	0
Verbascum pulverulentum	Scrophulariaceae	NS	LC	P	not ass	not ass	not ass	0	2	0
Verbascum thapsus	Scrophulariaceae	none	LC	NP	not ass	not ass	not ass	1	3	0
Veronica arvensis	Scrophulariaceae	none	LC	NP	not ass	not ass	not ass	96	201	4
Veronica chamaedrys	Scrophulariaceae	none	LC	NP	not ass	not ass	not ass	299	575	194

Species[a]	Family	GB rarity[b]	GB threat[c,g]	Status	Broad habitat association[d,g]	Habitat guild[e,g]	Management guild[f,g]	Abundance DC	SC	C
Veronica officinalis	Scrophulariaceae	none	LC	NP	not ass	not ass	not ass	22	21	14
Veronica serpyllifolia	Scrophulariaceae	none	LC	NP	not ass	not ass	not ass	3	9	1
Urtica dioica	Urticaceae	none	LC	NP	not ass	not ass	not ass	341	235	7
Urtica urens	Urticaceae	none	LC	NP	not ass	not ass	not ass	3	0	0
Viola tricolor	Violaceae	none	NT	P	not ass	not ass	not ass	0	7	0

[a] Species names follow Duff (2012), Bantock and Botting (2018), Chandler (2018), Else et al (2016), Hill et al (2004), and Merrett et al (2014).

[b] GB rarity status definitions: Nationally Rare (NR), Nationally Scarce (NS), or older definitions of Red Data Book (RDB), Nationally Notable (Na, Nb).

[c] GB threat status definitions: Least Concern (LC), Near Threatened (NR), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), and Data Deficient (DD).

[d] Broad habitat association: square brackets denote cases where we disagree with the broad habitat association provided by Pantheon. In all 13 cases we are confident the species is 'dry-open' associated (not 'unknown/wet/shaded').

[e] Habitat guild definitions: tall swards and scrub (TS & S), short shorts (SS), short swards and bare ground (SS & BG), and unknown or undifferentiated structural requirements (UNK/UNDIF).

[f] Management guild definitions: no physical-disturbance and no grazing (N_DIS/N_GRZ), light physical-disturbance and no grazing (L_DIS/N_GRZ), heavy physical-disturbance and no grazing (H_DIS/N_GRZ), no physical-disturbance and heavy grazing (N_DIS/H_GRZ), heavy physical-disturbance and heavy grazing (H_DIS/H_GRZ), unknown or undifferentiated requirements for grazing and physical-disturbance (UNK/UNDIF)

[g] 'Not ass' denotes not assessed.

Literature cited (from Table S.5.3 only)

Bantock, T., Botting, J. 2018. British Bugs: an online identification guide to UK Hemiptera. Available from: http://www.britishbugs.org.uk/ (accessed December 2018).

Chandler, P.J. (2018) An Update of the 1998 Checklist of Diptera of the British Isles. Available from: http://www.dipteristsforum.org.uk/documents/BRITISH_ISLES_CHECKLIST.pdf (accessed March 2020)

Duff, A.G. (2012) Checklist of Beetles of the British Isles. 2nd edition. Iver, Pemberley Books.

Else, G., Bolton, B., Broad, G. (2016) Checklist of British and Irish Hymenoptera - aculeates (Apoidea, Chrysidoidea and Vespoidea). Biodiversity Data Journal 4: e8050. doi:10.3897/BDJ.4.e8050.

Hill, M,O., Preston, C,D., Roy, D,B. (2004) *PLANTATT - attributes of British and Irish plants: status, size, life history, geography and habitats*. Centre for Ecology & Hydrology, Abbotts Ripton.

Merrett, P., Russell-Smith, A., Harvey, P. (2014) A Revised Check List of British Spiders, *Arachnology* 16(4), 134-144

Table S.5.4. Invertebrate sample sizes showing number of individuals and species identified within each invertebrate group, separately for non-priority and priority species (see Table S.5.3 for full species list).

Group	**Non-priority species**		**Priority species**	
	Individuals	**Species**	**Individuals**	**Species**
Ants	26,647	18	240	4
Bees and wasps	4,903	75	435	31
True flies	682	34	86	4
Ground beetles	26,382	58	804	16
Other beetles	10,761	181	1,123	57
Rove beetles	22,667	130	1,344	17
True bugs	8,432	128	381	19
Spiders	26,462	84	902	22

Table S.5.5. Richness of non-priority and priority species, reported separately for all species pooled (a; overall richness), each taxon (b), each habitat guild (c), and each management guild (d; priority species only), for shallow-cultivated (SC) and deep-cultivated (DC) treatments and generalised management (controls). Richness estimates (and 95% CIs) were derived from sample-based rarefaction rescaled to numbers of sampled individuals, with the base sample size (BSS, the point on the rarefaction curve where richness estimates are compared) set to: i) twice that of the regime (treatment or control) with the smallest sample size, or the regime with the largest sample size, whichever was smaller ('higher BSS'); and ii) the regime with the smallest sample size ('lower BSS'). Estimates that share a superscript do not differ significantly (95% CIs do not overlap; A-C, highest to lowest). * denotes analyses where inference is consistent between BSS thresholds.

Analysis		**Higher BBS**			**Lower BSS**	
	Control	**SC treatment**	**DC treatment**	**Control**	**SC treatment**	**DC treatment**
a) Overall richness						
Non-priority species*	445 (416-474)^{c}	554 (542-565)^{b}	610 (600-620)^{a}	375 (360-390)^{c}	469 (462-477)^{b}	515 (508-522)^{a}
Priority species*	60 (49-70)^{b}	107 (102-112)^{a}	114 (110-120)^{a}	49 (43-55)^{b}	83 (80-87)^{a}	90 (86-94)^{a}
b) Richness of each taxon						
Plants (non-priority)*	95 (87-103)^{c}	122 (118-125)^{b}	137 (134-142)^{a}	90 (85-95)^{c}	111 (109-114)^{b}	126 (124-129)^{a}
Plants (priority)*	2 (1-3)^{b}	4 (2-6)$^{a/b}$	8 (6-9)^{a}	2 (1-3)^{b}	4 (2-5)$^{a/b}$	6 (5-7)^{a}
Spiders (non-priority)*	64 (52-76)$^{a/b}$	57 (53-60)^{b}	67 (63-72)^{a}	52 (46-58)$^{a/b}$	48 (45-50)^{b}	59 (56-62)^{b}
Spiders (priority)*	8 (7-9)^{b}	16 (14-18)^{a}	17 (14-20)^{a}	7 (6-8)^{b}	12 (11-14)^{a}	13 (12-15)^{a}
Ground beetles (non-priority)*	30 (24-37)^{b}	42 (41-44)^{a}	42 (41-43)^{a}	26 (22-30)^{b}	36 (36-38)^{a}	39 (38-39)^{a}
Ground beetles (priority)*	4 (4-4)^{c}	11 (10-12)^{b}	14 (13-15)^{a}	4 (4-4)^{c}	10 (9-10)^{b}	12 (11-13)^{a}
Rove beetles (non-priority)*	63 (52-73)^{b}	86 (82-91)^{a}	87 (84-91)^{a}	53 (47-59)^{b}	73 (70-76)^{a}	73 (71-76)^{a}
Rove beetles (priority)	11 (8-14)^{a}	10 (9-12)^{a}	13 (11-14)^{a}	10 (8-12)$^{a/b}$	8 (7-10)^{b}	11 (10-12)^{a}
Other beetles (non-priority)	81 (67-94)^{b}	95 (91-99)^{b}	114 (108-119)^{a}	63 (56-70)^{c}	76 (73-79)^{b}	90 (86-94)^{a}
Other beetles (priority)*	12 (7-17)^{b}	33 (30-36)^{a}	31 (28-35)^{a}	10 (7-13)^{b}	24 (22-26)^{a}	24 (22-26)^{a}
True bugs (non-priority)*	59 (47-71)^{c}	77 (72-82)^{b}	124 (108-140)^{a}	48 (41-55)^{c}	62 (59-66)^{b}	97 (88-105)^{a}
True bugs (priority)*	3 (2-4)^{c}	13 (10-15)^{a}	7 (6-8)^{b}	3 (2-4)^{c}	10 (8-11)^{a}	6 (5-6)^{b}
Bees and wasps (non-priority)*	27 (20-35)^{b}	26 (25-28)^{b}	41 (39-43)^{a}	22 (18-26)^{b}	19 (18-20)^{b}	31 (29-32)^{a}
Bees and wasps (priority)*	12 (6-18)^{a}	14 (12-15)^{a}	13 (11-14)^{a}	8 (5-11)^{a}	10 (9-11)^{a}	9 (8-10)^{a}
Ants (non-priority)	12 (11-13)^{b}	13 (12-14)$^{a/b}$	15 (13-16)^{a}	12 (11-13)^{a}	12 (12-13)^{a}	13 (12-14)^{a}
True flies (non-priority)	14 (8-20)^{b}	21 (18-24)^{b}	32 (25-39)^{a}	9 (6-12)^{c}	17 (15-19)^{b}	24 (20-28)^{a}

Analysis		**Higher BBS**			**Lower BBS**	
	Control	**SC treatment**	**DC treatment**	**Control**	**SC treatment**	**DC treatment**
c) Richness within each habitat guild						
Tall swards and scrub (non-priority)*	180 (161-200)^{c}	217 (211-224)^{b}	238 (230-246)^{a}	147 (136-158)^{c}	181 (176-186)^{b}	195 (190-201)^{a}
Tall swards and scrub (priority)*	15 (10-19)^{b}	22 (20-25)^{a}	20 (18-22)$^{a/b}$	13 (10-16)^{b}	18 (16-19)^{a}	15 (14-17)$^{a/b}$
Short swards (non-priority)	54 (44-65)^{a}	68 (64-72)^{a}	66 (63-69)^{a}	45 (39-51)^{b}	60 (57-62)^{a}	57 (55-58)^{a}
Short swards (priority)*	20 (12-28)^{a}	23 (20-25)^{a}	19 (17-22)^{a}	14 (10-18)^{a}	18 (16-20)^{a}	17 (15-18)^{a}
Short swards and bare ground (non-priority)*	35 (26-44)^{b}	35 (34-37)^{b}	46 (44-48)^{a}	26 (21-31)^{b}	26 (25-27)^{b}	37 (36-38)^{a}
Short swards and bare ground (priority)*	13 (10-17)^{b}	34 (32-36)^{a}	37 (34-39)^{a}	12 (10-14)^{b}	28 (27-30)^{a}	30 (28-32)^{a}
d) Richness within each management guild						
No physical-disturbance and no grazing (priority)*	11 (7-16)^{a}	13 (11-15)^{a}	11 (9-14)^{a}	9 (6-12)^{a}	10 (9-12)^{a}	10 (8-12)^{a}
No physical-disturbance and heavy grazing (priority)*	5 (3-7)^{b}	8 (7-9)^{a}	5 (5-6)^{b}	4 (3-5)^{b}	6 (6-7)^{a}	4 (4-5)^{b}
Light physical-disturbance and no grazing (priority)*	6 (4-9)^{b}	11 (10-12)^{a}	11 (9-13)^{a}	6 (4-8)^{b}	9 (8-10)^{a}	9 (8-10)^{a}
Heavy physical-disturbance and no grazing (priority)*	9 (8-10)^{b}	18 (16-19)^{a}	18 (17-20)^{a}	8 (7-9)^{b}	15 (14-16)^{a}	15 (14-16)^{a}
Heavy physical-disturbance and heavy grazing (priority)*	5 (4-6)^{b}	14 (13-16)^{a}	18 (15-21)^{a}	5 (4-6)^{b}	12 (11-13)^{a}	14 (12-16)^{a}

Table S.5.6. Species uniqueness and overlap between regimes. The mean (and 95% CI) percentage of species unique to, or shared between, control plots, shallow-cultivated complexes (SC) and deep-cultivated complexes (DC) are shown for non-priority (NP) and priority species (P), separately for the overall assemblage and for each taxon. This analysis is based on species lists drawn from 200 iterations, each resampling 32 treatment subplots (16 deep- and 16 shallow-cultivated subplots from 64 available in each treatment, resampled independent of plot-complex identity) and all 16 control plots.

Analysis	**Unique to controls**	**Unique to SC complexes**	**Unique to DC complexes**	**Shared between controls and SC complexes**	**Shared between controls and DC complexes**	**Shared between SC and DC complexes**	**Shared between SC and DC complexes and controls**
Overall NP assemblage	8% (6-9%)	10% (8-12%)	17% (14-20%)	5% (3-7%)	4% (3-6%)	17% (15-19%)	39% (37-41%)
Overall P assemblage	9% (6-12%)	20% (14-26%)	23% (17-28%)	6% (3-10%)	3% (1-5%)	20% (15-25%)	19% (15-23%)
Vascular plants NP	5% (4-8%)	6% (3-9%)	10% (6-16%)	4% (2-8%)	4% (2-7%)	15% (12-18%)	55% (51-59%)
Vascular plants P	27% (11-50%)	13% (0-40%)	51% (20-75%)	7% (0-25%)	0% (0-0%)	2% (0-17%)	0% (0-0%)
Spiders NP	11% (6-16%)	5% (0-10%)	11% (5-19%)	4% (0-9%)	10% (5-16%)	8% (3-14%)	51% (45-57%)
Spiders P	3% (0-15%)	20% (0-39%)	19% (0-36%)	6% (0-18%)	4% (0-17%)	17% (0-33%)	32% (21-50%)
Ground beetles NP	1% (0-2%)	9% (2-14%)	13% (6-21%)	2% (0-6%)	1% (0-4%)	29% (22-35%)	46% (42-52%)
Ground beetles P	0% (0-0%)	4% (0-20%)	25% (8-40%)	2% (0-8%)	0% (0-0%)	41% (29-55%)	27% (17-33%)
Rove beetles NP	6% (3-10%)	11% (6-17%)	14% (9-21%)	5% (2-10%)	4% (1-8%)	19% (14-25%)	40% (35-45%)
Rove beetles P	28% (17-42%)	9% (0-21%)	12% (0-23%)	4% (0-17%)	3% (0-13%)	10% (0-23%)	34% (27-42%)
Other beetles NP	10% (8-14%)	14% (10-19%)	22% (16-29%)	5% (2-9%)	3% (1-6%)	22% (17-27%)	23% (19-26%)
Other beetles P	8% (3-15%)	29% (17-39%)	22% (12-33%)	7% (3-15%)	4% (0-10%)	20% (13-29%)	9% (3-17%)
True bugs NP	15% (12-21%)	13% (8-19%)	21% (14-28%)	8% (4-13%)	5% (1-8%)	11% (7-15%)	27% (23-31%)
True bugs P	1% (0-10%)	35% (11-54%)	22% (0-40%)	3% (0-13%)	1% (0-11%)	23% (8-44%)	15% (8-25%)
Bees and wasps NP	2% (0-6%)	12% (4-20%)	29% (20-40%)	2% (0-7%)	5% (0-10%)	19% (11-28%)	30% (24-36%)
Bees and wasps P	7% (0-17%)	19% (0-37%)	22% (9-41%)	10% (0-24%)	3% (0-11%)	21% (10-33%)	17% (9-29%)
Ants NP	3% (0-13%)	1% (0-8%)	12% (0-25%)	4% (0-14%)	9% (0-23%)	2% (0-13%)	69% (53-86%)
True flies NP	10% (4-16%)	16% (4-30%)	28% (11-44%)	3% (0-10%)	3% (0-11%)	18% (6-30%)	22% (12-32%)

References

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology,* 49, 986-997.

Green, R.E. & Griffiths, G.H. (1994). Use of preferred nesting habitat by stone curlews Burhinus oedicnemus in relation to vegetation structure. *Journal of Zoology,* 233(3), 457-471.

Hawkes, R.W., Smart, J., Brown, A., Jones, H., Lane, S., Wells, D. & Dolman, P.M. (2019). Multi-taxa consequences of management for an avian umbrella species. *Biological Conservation,* 236, 192-201.

Hill, M., O., Preston, C., D. & Roy, D., B. (2004). *Attributes of British and Irish plants: status, size, life history, geography and habitats*. Centre for Ecology & Hydrology, Cambridgeshire.

Marsden, K. (2017). The effect of ground disturbance on soil nutrients on lowland grass heaths in Breckland, East Anglia. Master's Thesis. Norwich: University of East Anglia.

NSRI (2014). National soil map of England and Wales - NATMAP, 1:250,000 Scale, Cranfield University, Bedfordshire. http://www.landis.org.uk (accessed July 2014).

Sheail, J. (1979). Documentary evidence of the changes in the use, management and appreciation of the grass-heaths of Breckland. *Journal of Biogeography,* 6(3), 277-292.

Webb, J., Heaver, D., Lott, D., Dean, H.J., van Breda, J., Curson, J., Harvey, M.C., Gurney, M., Roy, D.B., van Breda, A., Drake, M., Alexander, K.N.A. & Foster, G. (2018). Pantheon - database version 3.7.6. Available at: http://www.brc.ac.uk/pantheon/ (accessed on 17/12/2018).

Chapter 6

Multi-taxa experimental evidence informs novel semi-natural grassland management

Robert W. Hawkes[a], Jennifer Smart[b,c], Andy Brown[d], and Paul M. Dolman[a]

[a]*School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK*

[b]*RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK*

[c]*School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK*

[d]*Natural England, Suite D, Unex House, Bourges Boulevard, Peterborough, PE1 1NG, UK*

Abstract

1. Management interventions informed by land-use history and the ecological requirements of priority species can enhance biodiversity. However, to facilitate best practice, there is a pressing need to identify optimal treatments; establish whether treatment efficacy varies according to fine-scale differences in habitat; and evaluate how much management in terms spatial extent is needed to optimise biodiversity gain.
2. Through the largest land management experiment ever attempted in a European semi-natural grassland, we examined responses of vascular plants (hereafter 'plants'); spiders; true bugs; ground, rove and 'other' beetles; bees and wasps; ants; and true flies to eight physical-disturbance treatments that varied in depth (shallow and deep-cultivation) and cultivation frequency or age (repeat-cultivatation, first-time-cultivation, one-year fallow and two-year fallow). Treatments (*n* = 160) and non-intervention controls (*n* = 21) were implemented across an extensive mosaic (3,850 ha) of calcareous, intermediate, and ancient-acid grassland (hereafter, 'soil-vegetation strata'). Sampling gave 132,251 invertebrates from 878 species and 28,846 plant observations from 167 species.
3. Relative to controls, the richness of non-priority species increased in at least one of the treatments for four and five of the groups in the shallow- and deep-cultivations, respectively (shallow: other, ground & rove beetles, bees and wasps; deep: identical to shallow with the addition of plants). In contrast, the one-year-old fallowed deep-cultivation (but not the shallow-cultivated equivalent) was the only treatment which increased priority species richness across multiple taxa (ground & other beetles, true bugs, and bees and wasps). The effect of treatment on richness was always consistent across soil-vegetation strata, regardless of taxonomic group or priority status.
4. For almost all taxonomic groups assemblage composition differed markedly between the repeat- or first-time-cultivation treatments (whether shallow- or deep-cultivated) and controls, and the fallows converged towards controls with age (one- then two-year-old fallows) and depth (deep- than shallow-cultivations). The two-year-old shallow-cultivation fallows overlapped controls for most taxonomic groups.

5. Based on a hypothetical 42-ha grassland block, all four deep-cultivated treatments need to take place across 40% of the landscape to optimise the cumulative richness of non-priority and priority invertebrates. This increases to 60% with the four shallow-cultivated treatments.
6. *Synthesis and applications:* Within dry-grasslands and lowland heaths characterized by closed swards and limited bare ground, we recommend providing a continuity of recently-cultivated and fallowed areas, through shallow- and deep-cultivations, to cater for the widest range of species. To optimise the cumulative richness of non-priority and priority invertebrates, complex management – comprising the full range of treatment combinations - needs to be implemented across 40 – 60% of the landscape. Incorporating this prescription into future agri-environment schemes as a bespoke option would help facilitate this recommendation.

Keywords: agri-environment schemes, best practice, biodiversity, invertebrates, landscape-scale, lowland heath, physical-disturbance, plants

6.1 Introduction

To counteract the ongoing decline and loss of species from semi-natural terrestrial habitats (Hülber *et al.* 2017; Seibold *et al.* 2019), conservation often focuses on arresting or re-setting ecological succession through grazing and biomass removal, partly mimicking past land-uses that created these habitats (Wright, Lake & Dolman 2012). Recent cross-taxa evidence has confirmed that enhanced interventions, inspired by the complexity and changeability of pre-industrial land-use (c. 1200-1750) and informed by the requirements of regional biota, benefit scarce biodiversity (see Chapter 5). However, whilst the activities which characterize historic land-use are broadly understood (Fuller, Williamson, Barnes & Dolman 2017), the details of the underpinning biodiversity responses are often unclear. Moreover, greatly increased rates of eutrophication through atmospheric deposition (Tipping *et al.* 2019; Ridding *et al.* 2020) and reduced biomass removal (especially topsoil removal, Power, Ashmore & Cousins 1998; Härdtle, Niemeyer, Niemeyer, Assmann & Fottner 2006) have altered ecological dynamics in such a way that practices which once sustained large numbers of priority species may no longer be optimal. To facilitate the widespread adoption of enhanced management interventions, multi-taxa land management experiments are needed to identify optimal treatments, determine whether their efficacy varies according to finer-scaled differences within habitats, and establish the spatial extent to which such management should be applied across semi-natural sites.

Whilst numerous studies have successfully appraised interventions by contrasting treated areas to unmodified controls (e.g. Marks, James, Laurence & Sutherland 1992; Pywell *et al.* 2007; Merckx *et al.* 2012), conservationists have called for a shift in research emphasis towards a better understanding of how interventions should be targeted in the landscape and the spatial scales over which they are needed (Wilson, Evans & Grice 2010). To date, most attempts to address this important knowledge gap have focused on birds (e.g. Perkins, Maggs, Watson & Wilson 2011) or pollinators (e.g. Dicks *et al.* 2015) in intensive agricultural systems. For semi-natural habitats -particularly those designated for their conservation value - the potential extent of management is less limited by competing land-use objectives such as crop or livestock production. However, excessive intervention may be unnecessary, or even reduce net benefits by disadvantaging species associated with less interventionist management.

Since semi-natural habitats often comprise a range of fine-scale habitats that vary in vegetation structure and composition (attributable variations in soil type and land-use history, Wells, Sheail, Ball & Ward 1976; Fitter 1982), treatment efficacy may vary across these gradients in such a way that perceived best-practice may be less effective in certain areas. To uncover this detail, treatment replicates need to be distributed across a range of soil-vegetation strata.

Another major limitation of traditional tests of habitat management interventions is their limited taxonomic scope. Most typically focus on a limited number of iconic, flagship, or threatened species (Mikoláš *et al.* 2015; Goodenough & Sharp 2016; Hawkes, Smart, Brown, Jones & Dolman 2019a), or taxa that are more easily identified or at least better-known (e.g. birds, plants, and some invertebrate taxa). Given that cross-taxa congruence varies with study scale (Westgate, Barton, Lane & Lindenmayer 2014) and is typically weaker for rarer species and at local scales (Grenyer *et al.* 2006), it is generally inappropriate to generalise inference beyond monitored species or groups. Congruence also varies along ecological gradients (e.g. management intensity, Manning *et al.* 2015), which raises further doubts about the appropriateness of so-called ‘indicator groups’ as a way of evaluating conservation efficacy. Since semi-natural habitats are valued for their diverse and threatened assemblages (Ratcliffe 1977), multi-taxa experiments are needed to inform best practice as different taxonomic groups are expected to show contrasting responses to management according to their ecology and life history differences (see Chapter 5).

Within semi-natural lowland dry-grassland and heathland (hereafter ‘grassland’), numerous experiments have demonstrated that physical ground-disturbance treatments benefit some target species and assemblages (Dolman & Sutherland 1994; Cameron & Leather 2011; Hawkes *et al.* 2019b). There is evidence that greater levels of disturbance provide greater benefits to specialist species (Pedley, Franco, Pankhurst & Dolman 2013). However, such studies have focused on homogenous, even-aged treatments (Dolman & Sutherland 1994; Cameron & Leather 2011; Pedley *et al.* 2013; Hawkes *et al.* 2019b), which fail to restore the range and diversity of historic conditions (Fuller *et al.* 2017). Recent cross-taxa experimental evidence demonstrates that heterogeneous physical-disturbance complexes, comprising mosaics of treatments that vary in fallow age and disturbance frequency, benefit biodiversity (especially priority species, see Chapter 5).

However, whilst the overall efficacy of this management is known, it is unclear whether certain treatments within these complexes are more effective than others, or whether their efficacy varies with habitat detail. It is also unclear how much of any landscape ought to be disturbed in order to enhance its overall species richness.

To address these critical uncertainties, we devised an extensively replicated experiment across one of the UKs largest grassland sites (see Chapter 5). We compared two methods of promoting structural complexity and nested heterogeneity through ground-disturbance (shallow- or deep-cultivation) developed over three years to create complexes comprising subplots that vary in disturbance age and frequency - providing eight treatments. We examined responses of eight invertebrate groups and of vascular plants to these treatments, relative to areas managed with light grazing and without ground disturbance (controls). We explored effects on species richness (hereafter 'richness') within each taxonomic group, separately for non-priority and priority species, and effects on the species composition within each group. Finally, to determine how much management is needed to maximise overall cumulative richness, we compared different management scenarios, compromising varying amounts (in terms of proportions of overall grassland extent) of shallow or deep-cultivated complexes, to a hypothetical, control-only landscape.

6.2 Methods

6.2.1 Study area

The experiment was carried out in the Breckland biogeographical region of Eastern England. This region is characterised by a semi-continental climate and sandy soils, and hosts over 2,000 priority plant and invertebrate species (26% of all UK priority species, Dolman, Panter & Mossman 2012). Complex physical-disturbance interventions that were informed by historic land-use (Fuller *et al.* 2017) and the requirements of regional priority species (Dolman *et al.* 2012) were implemented across extensive lightly sheep-grazed grasslands of the Stanford Military Training Area (STANTA) (52°51'N, 0°76'E, 3500 ha), Bridgham Heath (52°44'N, 0°83'E, 150 ha) and Brettenham Heath (52°43'N, 0°83'E, 200 ha) (Fig. 6.1). Across these study sites, the synergistic influences of soil (acidic brown sand, calcareous sand, or rendzina), historic land use and contrasting grassland age (young, ≤110 years; intermediate, 111 – 167 years, and ancient ≥168 years), have shaped plant assemblages that span multiple ecological gradients (for details, see Hawkes *et al.* 2019b).

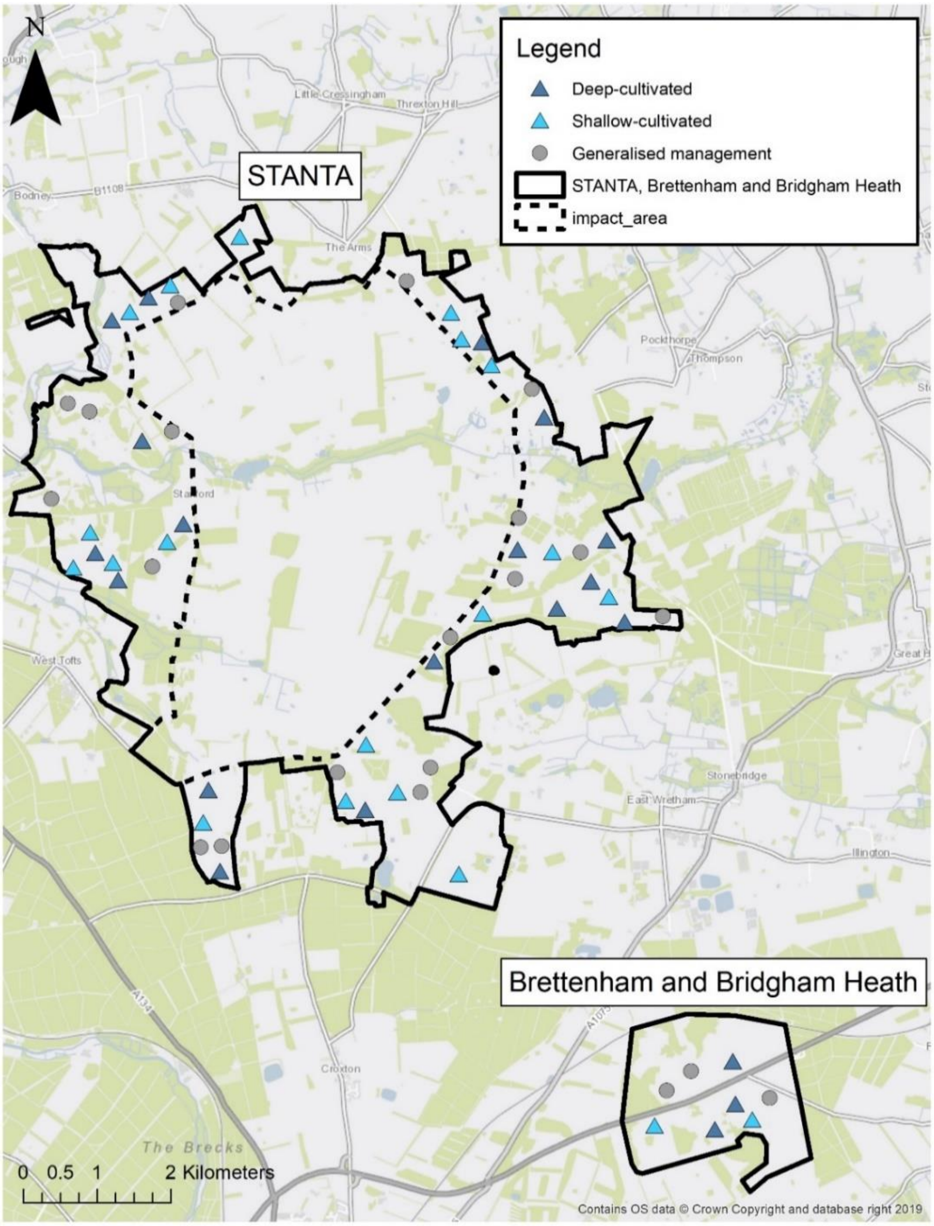

Figure 6.1. Location of control plots and shallow- and deep-cultivated complexes (each containing repeatedly-cultivated, first-time-cultivated, one-year-old fallow, and two-year-old fallow sub-plot treatments) across the three study sites (the Stanford Training Area, Bridgham Heath and Brettenham Heath. The impact area boundary (where physical ground disturbance plots were precluded due to unexploded ordinance) is shown.

6.2.2 Experimental treatments and soil-vegetation strata

Forty 2-ha ground disturbance plots (20 shallow-cultivated, with a rotary rotovator; 20 deep-cultivated, with an agricultural plough) and 21 1-ha non-intervention grassland controls were initially established in grassland mostly excluding, but sometimes close to, scattered trees or scrub (for establishment method details, see Hawkes *et al.* 2019b). Ground disturbance was repeated in the winters of 2015-2016 and 2016-2017, each year cultivating 2-ha with half (1-ha) overlapping a central repeatedly-treated sub-plot, and half (1-ha) first-time-cultivation, so that in the final year (2017) each 'complex' contained four 1-ha treatment subplots, comprising: fallowed (1-year-old and 2-year-old), first-time-cultivated, and repeatedly-cultivated land (Fig. 6.2). Eight treatment categories (four subplot treatments per complex x two establishment methods) plus the controls were analysed.

Complexes and control plots were restricted to the outer areas of STANTA, plus Bridgham and Brettenham Heath, owing to risks from unexploded ordnance in the central STANTA 'impact area' (Fig. 6.1). Within this constraint, complexes and controls were allocated across three soil-vegetation strata, based on soil, age since cultivation, and vascular plant composition, comprising: calcareous grassland, intermediate grassland, and ancient-acid grassland (see Table S.6.1 for treatment/control sample sizes per soil-vegetation strata). Calcareous grassland was characterised by shorter swards (mean height 4.2 cm, 3.7-4.6 95C CI, Hawkes *et al.* 2019b) comprised a mixture of calcicolous and acidophilous plant species developed on rendzina (grassland of any age), or on brown sands following recent arable abandonment (≤110 years old) (see Table S.6.1 for details); intermediate grassland was characterised by taller swards (mean height 5.14 cm, 4.66–5.67 95% CI) with a mixture of calcicolous and acidophilous plants developed on brown sands and was older (111-167 years since cultivation); while ancient-acid grassland (≥168 years since cultivation) was characterised by taller swards with few or no calcicolous plants developed on brown sands. In previous analyses of this experiment (Hawkes *et al.* 2019a; Hawkes *et al.* 2019b), calcareous grassland was sub-divided between 'calcareous' (on rendzina) and 'young' grassland (with pH ameliorated by addition of calcareous marl); their merger here is justified by their similar vegetation structure and plant composition.

Figure 6.2. Schematic of a physically disturbed complex (either deep- or shallow-cultivated) comprising four sub-plot treatments: RC, repeatedly-cultivated; FC, first-time-cultivated; F1, one-year-old fallow; F2, two-year-old fallow. See Chapter 5 for vegetation height and bare ground cover estimates for each treatment.

6.2.3 Responses to treatment

Responses to treatment were assessed in 2017 when all treatment combinations had accumulated. Sampling considered eight invertebrate groups: spiders (Araneae), ground beetles (Carabidae), rove beetles (Staphylinidae), all other beetles (Coleoptera, excluding Carabidae and Staphylinidae), true bugs (Hemiptera, excluding aphids), ants (Formicidae), bees and wasps (Aculeata, excluding ants), and true flies (a subset of Diptera, comprising: Asilidae, Rhagionidae, Stratiomyidae, Syrphidae, Tabanidae, Therevidae, Tipulidae), and vascular plants (hereafter ‘plants’).

Invertebrates were sampled using pitfall traps (spiders, ground beetles, rove beetles, other beetles, true bugs, ants, and bees and wasps) and pan traps (true bugs, bees and wasps, and true flies) within each treatment subplot (*n* = 160, from 40 complexes) and control plot (*n* = 21) – hereafter ‘sampling units’. Six pitfall traps (each 11 cm deep, 8 cm diameter, covered with 12 x 12 mm wire mesh, filled with 50 ml of 33% propylene glycol) were deployed in each sampling unit, set 15 m apart in a central 15 m x 30 m grid, for seven consecutive days, separately in each of three periods (May/June, July/August, and September). Four yellow pan traps (each 4 cm deep, 15.5 cm diameter, set at ground level, covered with 30 x 40 mm plastic mesh, filled with 150 ml of water with a few drops of unscented detergent) were also deployed in sampling units, set 15 m apart in a central 15 m x 15 m grid, for three consecutive days, between 1 July and 26 August (for additional details, see Chapter 5). Upon collection, we calculated the cumulative number of 'trap-days' for each sampling unit (separately for each pitfall trapping round, and for pan traps), with successful traps considered active for the whole exposure period, partially-successful traps for half the exposure period (e.g. partially dislodged, trampled or emptied), and failed traps (e.g. completely removed, destroyed by trampling, completed emptied, or filled with sand) inactive for the whole exposure period. Where aggregate sampling was less than half (<21/42 pitfall-trap-days per period; or <6/12 pan-trap-days), samples were discarded and a new set of traps immediately redeployed. In subsequent analyses, data were pooled across periods (pitfall traps only) and sampling methods (pitfall traps and pan traps) to give one composite sample per sampling unit.

Plant incidence was sampled from 16 quadrats (1 m x 1 m) distributed evenly (11-14 m apart) along two parallel 100 m transects (spaced 30-33 m apart) in each of 144 treatment subplots (from 16 shallow-cultivated and 16 deep-cultivated complexes) and 16 control plots (randomly selected) between 10 April and 7 July (giving frequency per species, 0-16) owing to resource constraints.

Most sampled taxa were identified to species level, the few unidentified plants (0.3%), spiders (<0.1%), ground beetles (<0.1%), rove beetles (3.5%), other beetles (1.0%), true bugs (3.7%), and bees and wasps (0.9%) were not considered further. Priority species were identified as those recognised as: (i) Threatened (IUCN Critically Endangered, Endangered and Vulnerable) or Near Threatened in Great Britain; or (ii) Nationally Rare (NR) and Nationally Scarce (NS), or the older designations of Red Data Book (RDB) and Nationally Notable (Na, Nb), with the remaining species classified as 'non-priority'.

6.2.4 Data analysis

For each invertebrate group, sampling efficiency of treatments (pooling subplots within each treatment category) and controls was assessed by comparing sample-based rarefaction (re-scaled to the number of individuals, using the Mao Tau function), using the package 'iNEXT' (Hsieh, Ma & Chao 2018). All models were run in R (R Core Team 2015).

We used Generalised Linear Mixed Models (GLMMs), to examine the fixed effects of treatment (nine levels) and soil-vegetation strata (three levels) on richness, separately for non-priority and priority species within each taxonomic group. To determine whether the effect of treatment varied according to grassland habitat, we considered an interaction between treatment and soil-vegetation strata. Plot (for controls) or complex (for treated subplots) identity was included as a random effect to control for non-independence of treatment subplots within complexes. To account for slight variation in trap success between treatment subplots and control plots, the total number of pitfall trap days (pooled across sampling rounds) and pan trap days were included as separate random effects for each invertebrate group sampled using that method.

For each analysis the appropriate error term for count data (Poisson or negative binomial) was selected by examining the ratio of deviance / residual degrees of freedom of full (global) models. Candidate models comprising three possible variable combinations (additive effects of treatment, soil-vegetation strata and treatment*strata interaction; additive effects of both treatment and soil-vegetation strata; or of treatment alone) were examined using the package 'lme4' (Bates, Maechler, Bolker & Walker 2017). The top-ranked model was considered 'best' if ΔAICc >2 (Akalike's Information Criterion corrected for small sample size) relative to the next-ranked model (Burnham & Anderson 2002); where competing models were within 2 ΔAICc the most parsimonious was selected, as additional variables lacked strong support (Burnham and Anderson, 2002). Next, where soil-vegetation strata was retained in the selected model, we combined levels within this fixed effect if parameter estimates were similar and their merger did not reduce model performance (change in ΔAICc ≤2 upon combination). Last, the fixed effect of treatment was considered to be supported if the performance of the selected model deteriorated (ΔAICc >2) upon its removal, in these cases category means were compared by Tukey's pairwise comparison using the package 'multcomp' (Hothorn, Bretz & Westfall 2008).

Species composition was compared between treatment categories and controls, separately for each taxonomic group (but pooling non-priority and priority species) by Non-Metric Multidimensional Scaling (NMDS) performed using a Bray–Curtis dissimilarity-matrix of abundance data (square-root transformed with Wisconsin double standardisation, following Clarke & Warwick 2001) using the 'Vegan' package (Oksanen *et al.* 2018). Sampling units with fewer than ten observations for that group were omitted to avoid overrepresenting localities where the assemblage was poorly characterized (a more conservative threshold than previous studies, Hawkes *et al.* 2019b). Model performance was assessed by examining stress (<0.05 excellent; <0.1 good; <0.2 potentially useful; >0.3 close to arbitrary, Clarke & Warwick 2001).

Finally, to determine the proportionate extent of management needed to optimise cumulative richness, we explored a range of scenarios using sample-based rarefaction (scaled to number of samples, using the Mao Tau function); separately of non-priority and priority invertebrate species (pooled across taxa, plants were omitted owing to reduced sampling). First, we resampled all 21 control plots to produce a control-only landscape (0% of landscape managed). Next, separately for the shallow- and deep-cultivated complexes, we created management scenarios that considered incrementally greater proportions of the total grassland extent to be subject to management (in steps of ≈20%), providing ten scenarios overall. These resampled from either: i) 21 control plots (from 21 available) and 5 treatment subplots (from 80 shallow-cultivated and 80 deep-cultivated available) (19% of landscape managed); ii) 21 control plots and 15 treatment subplots (42%); iii) 17 control plots and 25 treatment subplots (59%); iv) 8 control plots and 34 treatment subplots (81%); and v) 0 control plots and 42 treatment subplots (100%), resampling each across 200 iterations. For each management scenario, in each iteration, treatment subplots were resampled independent of complex identity, but balanced across the four shallow- or deep-cultivated treatments (Fig. 6.2). Each management scenario iteration was subjected to rarefaction analysis (2,000 rarefactions: 200 iterations x 10 management scenarios). As total number of sampling units resampled differed between these scenarios, all scenarios were compared at a Base Sample Size (BSS) defined following convention as twice the smallest sample size (0% managed, 42 plots); (extrapolation beyond this range can lead to unreliable richness estimates, Chao *et al.* 2014), with 20% and 40% scenarios (that resampled 26 and 36 sampling units respectively) also extrapolated to the BSS; thus richness estimates were all based on a 42-ha hypothetical landscape. Finally, each resample iteration (from every management scenario) was compared to the control-only scenario, with richness estimates considered different (guaranteed at the 5% level, $p < 0.05$) when pairwise 95% CIs obtained by bootstrapping based on 200 replications were non-overlapping (Chao *et al.* 2014). Where 95% of the resampling iterations from any given management scenario held more species than the control-only landscape, we inferred an overall difference for that scenario. Note, this analysis is biased in favour of the control-only landscape, as some iterations resampling the 20% and 40% scenarios, and most iterations resampling the 60%, 80% and 100% scenarios, included multiple subplots from the same complex identity (limiting sampling to a more restricted geographical range, potentially under-sampling beta diversity).

6.3 Results

Sampling gave 28,846 plant observations from 150 non-priority and 12 priority species, and 132,251 sampled invertebrates (121,968 from pitfall traps and 10,283 from pan traps) from 708 non-priority and 170 priority species (see Table S.5.3 for the full species list and Table S.5.4 for the numbers per invertebrate group), including a new species to Britain (see thesis Appendix A). For spiders, ground beetles, rove beetles, other beetles, ants and plants, sample-based rarefaction approached the asymptote for each treatment (Fig. S.6.1), indicating sampling had effectively captured their composition. Although true bugs and true flies approached the asymptote for the shallow-cultivated treatments and controls, they were uncommon on, and therefore insufficiently sampled from, repeatedly-cultivated, first-time-cultivated and one-year-old fallowed (but not two-year-old fallowed) deep-cultivation. Bees and wasps were uncommon on the controls and the first-time deep-cultivation, but approached the asymptote across all other treatments.

For priority ants and true flies, the limited numbers of sampled species (4 priority ants and true flies), and for priority plants the limited number or observations (49), across the sampling units prohibited separate analysis of priority richness for these groups (Fig.

6.3). For NMDS ordination analyses, bees and wasps and true flies were excluded as, respectively, 40% and 89% of sampling units held fewer than ten individuals. Across remaining groups, most or all samples held ten or more individuals (see Fig. 6.4 for sample sizes per group) allowing reliable analysis of assemblage composition.

6.3.1 Spiders

For non-priority spiders, richness did not differ among the controls and any of the treatments but was greater on the two-year-old fallowed deep-cultivation than the repeatedly-cultivated treatments (whether shallow- or deep-cultivated) (Fig. 6.3). Richness was also greater on intermediate grassland than on calcareous or ancient-acid grassland (that were pooled). Neither treatment nor vegetation soil-vegetation strata influenced richness of priority spiders (Table S.6.2). Despite the limited richness response, species composition of spiders differed between treatments: samples from repeated- and first-time-cultivation were markedly distinct from controls (on the first NMDS axis, or both axes, respectively; Fig. 6.4), while those from repeated shallow- and deep-cultivation also tended to be distinct from each other (on NMDS axis 2). Composition of one-year-old fallows remained distinct from controls but two-year-old fallowed converged towards controls with overlap between fallowed deep- and shallow-cultivation (Fig. 6.4).

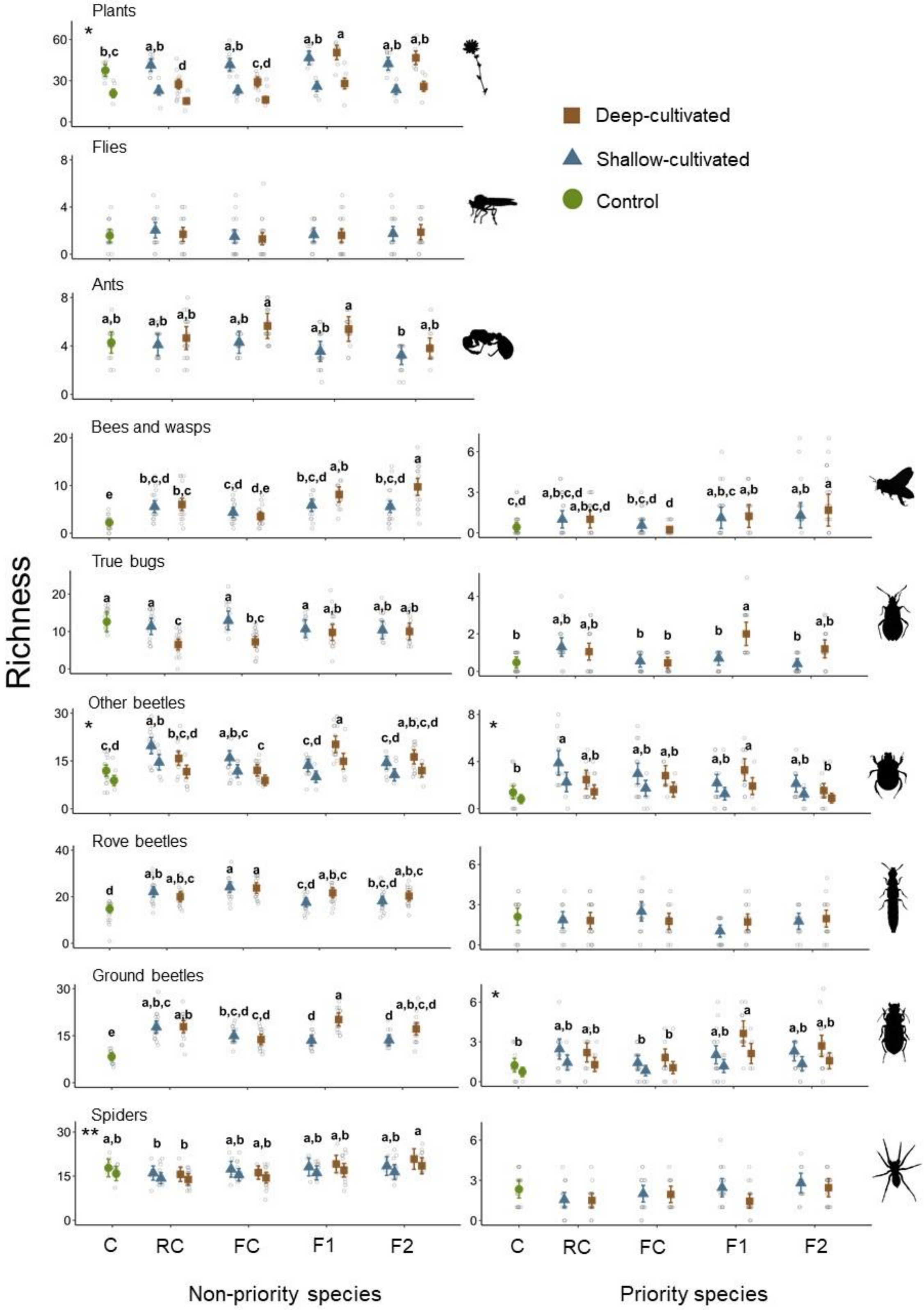
Richness
Plants
Flies
Ants
Bees and wasps
True bugs
Other beetles
Rove beetles
Ground beetles
Spiders
Deep-cultivated
Shallow-cultivated
Control
*
**
b,c
a,b
d
c,d
a
e
b,c,d
d,e
a,b,c,d
a,b,c
C
RC
FC
F1
F2
Non-priority species
Priority species

Figure 6.3. Richness of non-priority and priority (rare, scarce or threatened) species, for each of nine taxonomic groups, across recently-cultivated (RC), first-time-cultivated (FC), one-year-old fallow (F1), and two-year-old fallow (F2) treatments within shallow- and deep-cultivated complexes (denoted by triangle and square symbols respectively) and in untreated controls (C) (*n* = 181 and 144 sampling units for invertebrates and plants respectively). Treatments and controls were compared by Generalized Linear Mixed Models; where the fixed effect of soil-vegetation strata (two levels) was retained in models, calcareous and intermediate grassland (pooled) and ancient-acid grassland are reported separately (the former offset to the left, the latter to the right) (denoted by *); or intermediate grassland and calcareous and ancient-acid grassland (pooled) are reported separately (again the former offset to the left, the latter to the right) (denoted by **). Where soil-vegetation strata was excluded all grassland categories were combined. Symbols denote predicted richness, error bars 95% CIs, open circles individual data points, and superscripts indicate treatment categories (homogenous sub-sets, a – e) that did not differ significantly (Tukey pairwise comparisons *p* >0.05). Where no pairwise comparisons are reported the effect of treatment was not important (See Table S.6.2). For ants and true flies, limited numbers of priority species (four species per group) prohibited separate analysis.

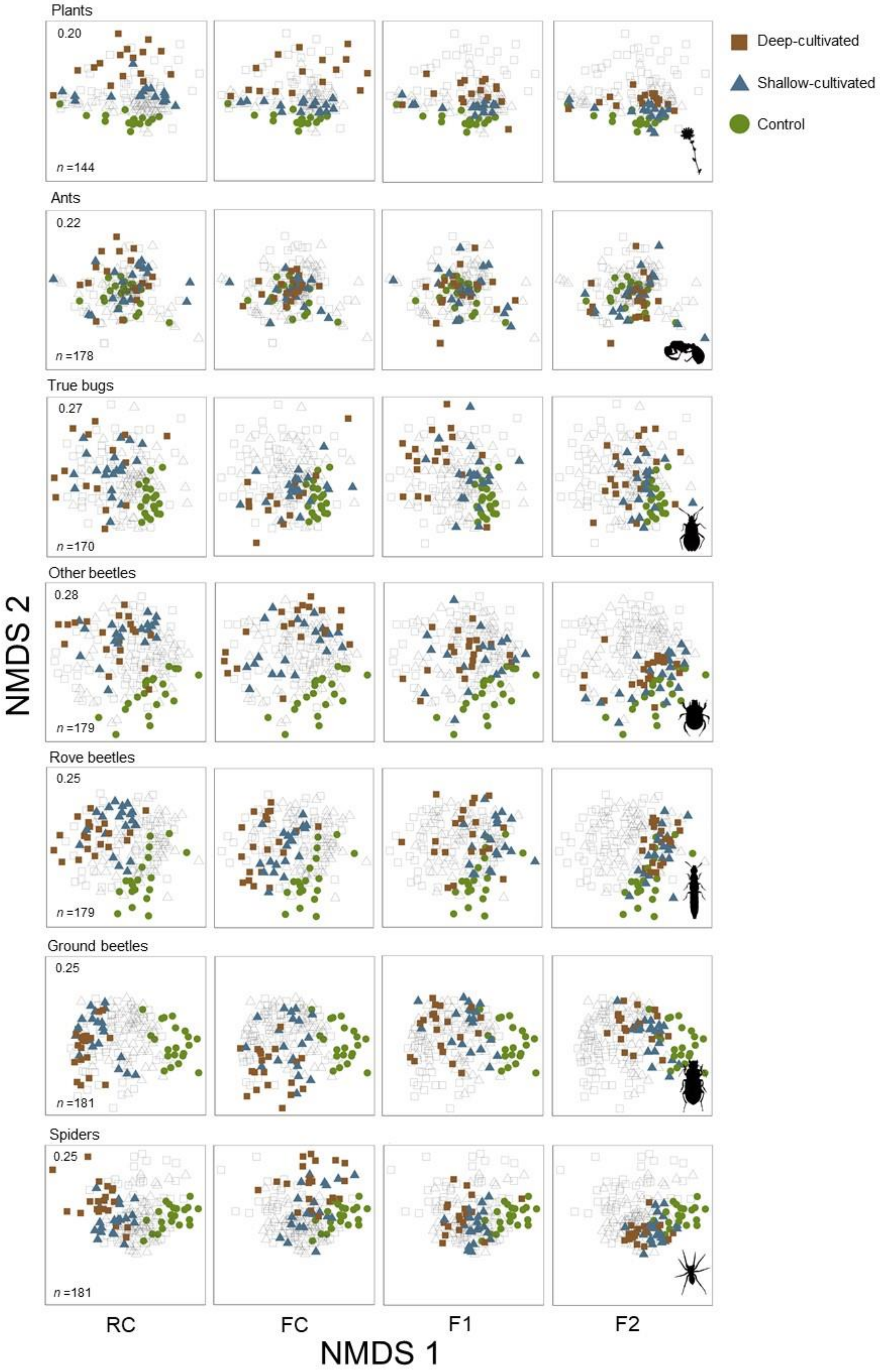
Plants
0.20
n =144
Deep-cultivated
Shallow-cultivated
Control
Ants
0.22
n =178
True bugs
0.27
n =170
Other beetles
0.28
n =179
Rove beetles
0.25
n =179
Ground beetles
0.25
n =181
Spiders
0.25
n =181
NMDS 2
RC
FC
F1
F2
NMDS 1

Figure 6.4. Species ordination by Non-metric Multidimensional Scaling (NMDS) for each of seven taxonomic groups (for bees and wasps and true flies, limited numbers of sampled individuals prohibited separate analysis) across recently-cultivated (RC), first-time-cultivated (FC), one-year-old fallow (F1), and two-year-old fallow (F2) treatments, within each of the shallow- and deep-cultivated complexes (see symbols), plus controls. For visual simplicity, results are separated by treatment category, but showing shallow- and deep-cultivated variants in the same panel (controls are shown in every panel for reference). Sample units with fewer than ten individuals were excluded from this analysis (samples size for each analysis are reported at the bottom left). Stress values for ordination of each group are shown on the leftmost panel.

6.3.2 Ground beetles

For non-priority ground beetles, richness was greater on every treatment compared to controls (soil-vegetation strata did not affect richness, Table S.6.2) (Fig. 6.3). Notably, one-year-old fallows of deep-cultivation held three times as many species than controls, and more species than either the first-time-cultivated, or fallowed (one- and two-year old), shallow-cultivations. For priority ground beetles, richness was greater on the one-year-old fallowed deep-cultivation than on either the controls or first-time-cultivation (both shallow- and deep-cultivated). Richness of priority ground beetles was also greater on calcareous or intermediate grassland (that were pooled) than on ancient-acid grassland, but no interaction between treatment and soil-vegetation strata was supported (Table S.6.2). The species composition of ground beetle assemblages differed markedly between repeated- or first-time-cultivation and controls (NMDS axis one, and both axes, respectively; Fig. 6.4), while composition of shallow- and deep-cultivation differed more for first-time-cultivation (on axis two). One-year-old fallows remained distinct from controls, but two-year-old fallows overlapped between shallow- and deep-cultivation treatments and again converged towards controls.

6.3.3 Rove beetles

For non-priority rove beetles, all treatments, aside from the shallow-cultivated fallow treatments, held more species than the controls (soil-vegetation strata was not important, Table S.6.2) (Fig. 6.3), while for priority rove beetles, neither treatment nor soil-vegetation strata influenced richness. The species composition of rove beetle assemblages on repeatedly- and first-time-cultivated treatments differed markedly from that of controls (NMDS axis one, Fig. 6.4); one-year-old fallows of deep-cultivations remained distinct while one-year-old fallows of shallow-cultivation and two-year-old fallows (of both the shallow- and deep-cultivation treatments) overlapped with controls.

6.3.4 Other beetles

For both non-priority and priority other beetles, richness was greater on the recently-cultivated shallow-cultivated treatment and the one-year-old deep-cultivated fallow treatment than the controls (the other treatments did not differ from controls), and on calcareous and intermediate grassland (that were pooled) than ancient-acid grassland, but no interaction between treatment and soil-vegetation strata was supported, Table S.6.2) (Fig. 6.3). Species composition again differed markedly between recently applied (repeated- and first-time) cultivation and controls, and became progressively similar to controls with fallowing (Fig. 6.4), but tended to overlap between shallow- and deep-cultivation versions of each treatment.

6.3.5 True bugs

For non-priority true bugs, richness did not differ among the controls and the shallow-cultivated treatments, but was lower on the repeatedly-deep-cultivated (compared to controls, all shallow-cultivated treatments and fallowed deep-cultivation) and first-time-deep-cultivated (compared to controls and three of the four shallow-cultivated treatments) treatments (soil-vegetation strata was not important, Table S.6.2) (Fig. 6.3). For priority true bugs, richness was greater on the one-year-old fallowed deep-cultivation than on either first-time-cultivation (whether shallow- or deep-cultivated), fallowed shallow-cultivation (soil-vegetation strata again was not important, Table S.6.2), or controls. Unlike other invertebrate groups, true bug composition differed most strongly to that of controls on repeatedly-cultivated treatments (both shallow- and deep-cultivated) and on one-year-old fallowed deep-cultivation (for both NMDS axis one and two, Fig. 6.4), with composition of first-time-cultivated treatments (both shallow- and deep-cultivated) also distinct from, but closer to, that of controls. The composition of fallowed shallow-cultivation and the two-year-old fallowed deep-cultivation treatments were similar to each other, and partially overlapped the controls.

6.3.6 Bees and wasps

For non-priority bees and wasps, richness was greater on every treatment, aside from first-time-cultivated deep-cultivated treatment, than the controls (Fig. 6.3). Notably, two-year-old fallowed deep-cultivation held more species than all shallow-cultivated and repeatedly- or first-time- deep-cultivation. For priority bees and wasps, richness was greater on the one-year-old fallowed deep-cultivation and two-year-old fallows (of both shallow- or deep-cultivation) than on the first-time-deep-cultivation or controls. Soil-vegetation strata did not influence non-priority or priority species richness.

6.3.7 Ants

For non-priority ants, richness on controls did not differ from any of the treatments (Fig. 6.3), but the first-time-cultivated and one-year-old fallowed deep-cultivation held more species than the two-year-old fallowed shallow-cultivation (soil-vegetation strata was not important, Table S.6.2). Species composition was similar on treatments and the controls (for both NMDS axis one and two, Fig. 6.4).

6.3.8 True flies

Neither treatment nor soil-vegetation strata influenced non-priority true fly richness (Fig. 6.3, Table S.6.2).

6.3.9 Plants

For non-priority plants, the repeatedly-deep-cultivated treatment held fewer species than controls, whilst one-year-old fallowed deep-cultivation held more species than controls (Fig. 6.3). The repeatedly-deep-cultivated treatment held fewer species than all other treatments, apart from first-time-deep-cultivation. Richness was also greater on calcareous and intermediate grassland (that were pooled) than on ancient-acid grassland, but no interaction between treatment and soil-vegetation strata was supported (Table S.6.2). Plant assemblage composition differed markedly between recently applied (repeated- and first-time-cultivation) treatments and controls, and between shallow- and deep-cultivation (NMDS axis two, Fig. 6.4), with the latter most distinct from controls. Fallows became progressively similar to controls with age.

6.3.10 Contrasting hypothetical landscapes with varying amounts of management

Compared to a hypothetical 42-ha control-only landscape, scenarios that considered treatments applied to 20% of the landscape increased the cumulative richness of non-priority invertebrates but only with deep-cultivation (Fig. 6.5). Priority invertebrates did not respond to either deep- or shallow-cultivation at this spatial scale of management. Treating 40% of the landscape increased the cumulative richness of non-priority invertebrates whether through deep- or shallow-cultivation, but only deep-cultivation increased the cumulative richness of priority invertebrates. Treating 60%, 80%, or 100% of the landscape increased the cumulative richness of non-priority and priority invertebrates with either deep- or shallow-cultivation. Notably, although mean non-priority and priority species cumulative richness (across resample iterations) apparently increased incrementally with each 20% threshold (from 20-100%, excluding the control-only landscape) with either deep- or shallow-cultivation, the confidence interval bounds across all management scenarios overlapped.

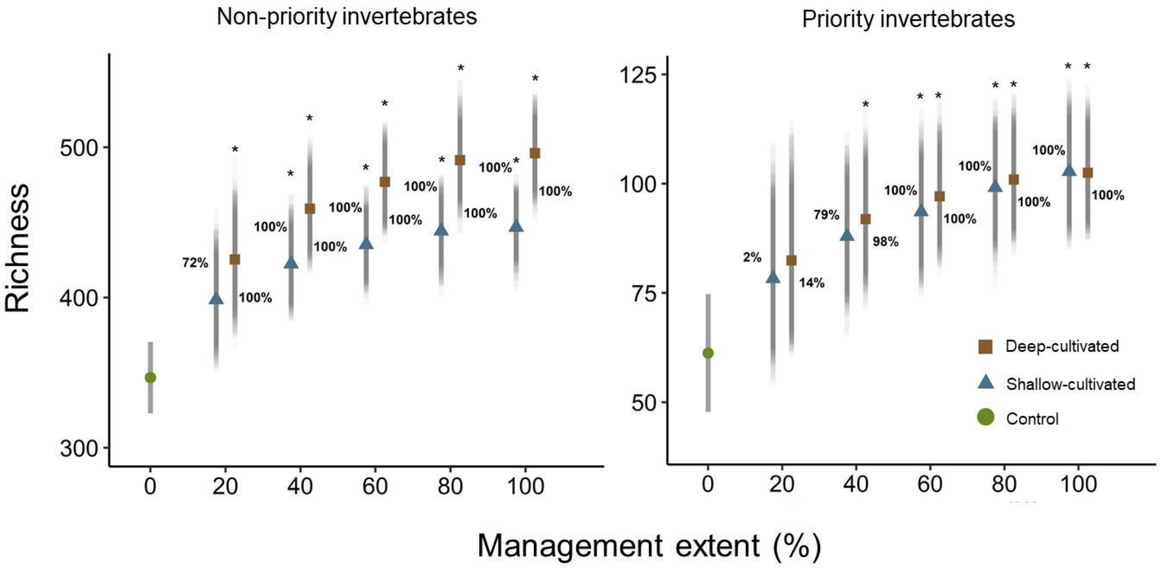

Figure 6.5. Cumulative richness of non-priority and priority invertebrates from hypothetical 42-ha landscapes, comparing a control-only landscape to management scenarios comprising different ratios of control plots to treatment subplots (expressed as the percentage of landscape managed; from 20% to 100%); separately for shallow- and deep-cultivated complexes. For the control-only landscape, the symbol represents observed richness and shading shows the 95% CI bounds, derived from sample-based rarefaction scaled to the number of samples and extrapolated up to Choa's Base Sample Size (all 21 control plots, extrapolated to 42, Chao *et al.* 2014). For each management scenario, the symbol represents the mean observed richness and shading shows the 95% CI bounds of 200 rarefaction iterations. For the 20% and 40% scenarios, samples were extrapolated to the Base Sample Size (BSS). For each management scenario the percentage of the 200 resample iterations where CI bounds do not span those of the control-only landscape is given; asterisks denote management scenarios where 95% of iterations exceed the control-only landscape.

6.4 Discussion

Through the largest land management experiment attempted in a European grassland, we quantified the consequences of ground disturbance interventions that varied in depth, frequency and grassland soil type or age, amassing records or observations of over 130,000 invertebrates and 28,000 plants. The effect of treatment on richness varied across taxonomic groups and with conservation status, with some groups responding more strongly to recently cultivated treatments within the shallow-cultivated complexes, and others responding more strongly to fallows within deep-cultivated complexes. Notably, the one-year-old fallowed deep-cultivation, but not the equivalent fallowed shallow-cultivation, was the only treatment which increased the richness of priority species across multiple taxa. Following both shallow- and deep-cultivation, for almost all taxonomic groups the composition of two-year old fallows was either similar to or converging towards the controls – suggesting treatments will require frequent reapplication. Based on a hypothetical 42-ha grassland block, we demonstrate that the deep-cultivated complexes need to take place across at least 40% of the landscape in order to optimise the cumulative richness of non-priority and priority invertebrates. In contrast, 40% shallow-cultivated complexes would optimise non-priority invertebrates, but 60% would be needed to optimise priority invertebrates.

6.4.1 Treatment efficacy varies according to taxa but not soil-vegetation strata

Across the nine taxonomic groups, the richness of non-priority species increased in at least one of the treatments for four and five of the groups in the shallow- and deep-cultivated treatments respectively (shallow: other, ground & rove beetles, bees and wasps; deep: identical to shallow with the addition of plants). In contrast, only the one-year-old fallowed deep-cultivation consistently increased richness among four of the six taxonomic groups for priority species. Deep cultivated, fallow treatments were probably most effective for priority species because, surprisingly, vegetation rapidly regenerated after shallow-cultivation (see Chapter 5) which quickly rendered this treatment unsuitable for large numbers of priority species (which require bare-open and recently disturbed habitats, Dolman *et al.* 2012). Although lighter methods of cultivation may provide suitable fallows in soils with much lower nutrient status than at our sites, accelerated succession owing to increased rates of atmospheric nutrient deposition across lowland grassland and heathland (Tipping *et al.* 2019; Ridding *et al.* 2020) may limit treatment longevity in most areas. Other establishment methods which retain bare ground for longer, such as topsoil removal, can remove soil nutrients (Härdtle *et al.* 2006) and provide fallows that support large numbers of priority species (Pedley *et al.* 2013).

The mosaic of soils from podsol to rendzina, and variation in grassland age within the study area supported assemblages that are characteristic of lowland heath, grass-heath and dry calcareous grassland (Rodwell 1991; Rodwell 1992). For most taxonomic groups, the soil-vegetation strata had no effect on richness; however, for other beetles, priority ground beetles, and non-priority plants, calcareous and intermediate grassland supported more species than ancient-acidic grassland; whilst for non-priority spiders, intermediate grassland supported more species than calcareous and ancient-acidic grassland. Given herbivorous invertebrates are positively associated with plant richness (Woodcock & Pywell 2010), the calcareous and intermediate grassland stratum probably supported a greater richness of beetles species because they also supported a wider range of plant species (see Fig. 6.3, also demonstrated by Eycott, Watkinson & Dolman 2006). It is unclear why intermediate grassland supported more non-priority spiders than the other categories. Regardless of these differences, even when species richness is low, species composition may be quite distinct between soil-vegetation strata. However, importantly, we found no evidence that response of richness to treatments differed between soil-vegetation strata for any taxonomic group, which suggests the effects of treatment were consistent across this wide range of grassland habitats.

6.4.2 Assemblage composition varies with treatment

Consistent with findings from early in this study (when all the treatments were homogenous plots lacking complexity, Hawkes *et al.* 2019b), assemblage composition varied with cultivation depth for most taxa (Fig. 6.4). Whilst this observation is unsurprising, given that shallow- and deep-cultivated complexes are known to support unique species (see Chapter 5), the assemblages within each treatment progressively converged towards controls with fallow age. Notably, for nearly all taxonomic groups, assemblage composition on the one- and two-year-old shallow-cultivated fallows tended to be more similar to the controls than their deep-cultivated equivalents, indicating that deep-cultivation is required to enhance beta diversity. This treatment-age shift in assemblage composition follows the observed increase in bare ground cover from the controls which were entirely vegetated, to the shallow-cultivated fallows which were almost entirely vegetated, to the partially vegetated deep-cultivated fallows and the recently cultivated treatments which had little or no vegetation (see Chapter 5). Studies from other dry-sand systems have reported similar shifts in ground beetle (Buchholz, Hannig & Schirmel 2013) and spider (Bonte, Baert & Maelfait 2002; Buchholz 2010) assemblages along similar structural gradients.

Our results suggest that the overall biodiversity benefit of cultivation (as demonstrated in Chapter 5) is attributable to the collective range of conditions provided by individual treatments. Whilst some treatments were particularly effective at increasing richness, this alone does not explain why most of the taxa responded strongly to the overall management complex (see Chapter 5). Instead, because each treatment was typically characterized by a distinct assemblage (with the exception of the two-year-old shallow-cultivation fallows; see Fig. 6.4), we believe that a combination of recently cultivated and fallowed areas are needed to cater for the widest range of species.

6.4.3 Increasing the proportionate extent of management enhances biodiversity

Whilst our richness and assemblage composition analyses point towards the need for a range of management interventions to cater for the widest suite of priority and non-priority species associated with grassland communities, until now there has been no explicit test of the extent and combination of treatment complexes required to optimise cumulative species richness at the landscape-scale. Previous experiments have compared ground disturbance treatments of varying size (e.g. Cameron & Leather 2011); however, as far as we are aware, ours is the first to evaluate how much of a semi-natural landscape should be subject to dramatic management intervention.

Based on a 42-ha hypothetical landscape, we showed that deep-cultivation across at least 20% or 40% of the landscape is necessary to optimise the cumulative richness of non-priority and priority invertebrates, respectively. For shallow-cultivated complexes, this proportion increased to 40% or 60% for non-priority and priority invertebrates, respectively. For both deep- and shallow-cultivation, increasing the proportionate amount of management beyond 40% or 60% (respectively) did not increase the cumulative richness further for non-priority or priority invertebrates – which suggests that these thresholds are optimal. Given priority species are typically more localised and range restricted in the wider landscape than non-priority species (Lin, James & Dolman 2007), it is unsurprising that more management was needed to enhance their richness. Since assemblage composition in deep cultivated treatments varied more from one another and the controls than their shallow-cultivated equivalents, we suspect that this explains why less management, in terms of proportionate extent, was needed to enhance cumulative richness with deep-cultivation. This novel analytical way of using resampling and rarefaction to evaluate potential outcomes of contrasting landscape-scale management scenarios could be extended to other semi-natural systems through similar well-replicated experiments.

6.5 Conservation implications

Within dry-grasslands and lowland heaths characterized by closed swards and limited bare ground, we recommend implementing physical ground-disturbance complexes to ensure a continuity of recently-cultivated and fallowed grassland. Although some treatments within these complexes may be more effective than others (as per our findings), providing the full complement of treatments will cater for the widest range of species. However, the two-year-old shallow-cultivated fallows, for which composition merged towards that of the untreated control grasslands for most evaluated taxa, could be omitted from this design. Further work is needed to establish the consequence of managing treatment complexes over successive rotations.

In terms of how much management is needed to increase cumulative richness, per c.40-ha of closed grassland, the scale we could justifiably examine in our hypothetical landscape analyses, treatment complexes should be implemented across at least 16-ha or 40% of the area. Although shallow-cultivated complexes were less effective at this threshold, they support different assemblages (Fig. 6.4) and unique species (see Chapter 5); thus a combination of deep- and shallow-cultivation is probably optimal. Where bare-open habitats are already present, for example through heavy ground disturbance is created by European rabbits *Oryctolagus cuniculus*, this threshold may be less, given these areas already support assemblages characteristic of dry-open disturbed habitats (Burggraaf-van Nierop & van der Meijden 1984). Importantly, since the effect of each treatment was consistent across soil-vegetation strata, regardless of taxa or priority status, these guidelines are relevant to a range of lowland dry grassland systems, including lowland heath and calcareous grassland.

Treating 80% or 100% of the landscape did not reduce the cumulative richness of non-priority and priority species relative to the 40% and 60% thresholds (Fig. 6.5), probably because the loss of non-intervention associated species was compensated by the gain of additional species brought about through the treatment. However, such a strategy would undoubtably disbenefit those species that are unique to the controls (see Chapter 5). Additionally, although our assessment was extensive in terms of its taxonomic coverage, responses may vary among some other, unassessed, taxa such as fungi, bryophytes or lichens. Therefore, to maximise the benefit of treatment without impacting species potentially associated with the status quo, we recommend treating between 40 - 60%. Practitioners seeking to adopt these guidelines should first ensure that the planned interventions avoid areas with potentially sensitive assemblages (e.g. species with a known intolerance of ground disturbance) or archaeological remains (Robertson & Hawkes 2017); in these instances, treatment may need to be avoided all together.

Across Europe, argi-environment schemes (AES) are one of the main policy initiatives for delivering biodiversity objectives for semi-natural habitats, indeed this experiment was implemented using through one of these schemes (Higher-Level Stewardship). AES options within established grasslands usually maintain the status quo (at least in terms of their botanical assemblage), but they rarely led to an enhanced response (Critchley, Burke & Stevens 2004). Based on our experiment, we recommend the inclusion of a bespoke ground disturbance option into future schemes, which covers the cost of creating and managing complex physical disturbance interventions, to facilitate the wide-spread adoption of this management at the scales necessary to optimise cumulative richness and opportunities for biodiversity gain.

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References

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2017). Linear mixed-effects models using 'Eigen' and S4. *R package Version 1.1-1.5*. Available at: https://cran.r-project.org/web/packages/lme4/ (accessed May 2018).

Bonte, D., Baert, L. & Maelfait, J.-P. (2002). Spider assemblage structure and stability in a hetrogeneous coastal dune system (Belgium). *The Journal of Arachnology,* 30(2), 331-343, 313.

Buchholz, S. (2010). Ground spider assemblages as indicators for habitat structure in inland sand ecosystems. *Biodiversity and Conservation,* 19(9), 2565-2595.

Buchholz, S., Hannig, K. & Schirmel, J. (2013). Losing uniqueness – shifts in carabid species composition during dry grassland and heathland succession. *Animal Conservation,* 16(6), 661-670.

Burggraaf-van Nierop, Y.D. & van der Meijden, E. (1984). The influence of rabbit scrapes on dune vegetation. *Biological Conservation,* 30(2), 133-146.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York.

Cameron, K.H. & Leather, S.R. (2011). Heathland management effects on carabid beetle communities: the relationship between bare ground patch size and carabid biodiversity. *Journal of Insect Conservation,* 16(4), 523-535.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. & Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs,* 84(1), 45-67.

Clarke, K.R. & Warwick, R.M. (2001). *Change in marine communities: an approach to statistical analysis and interpretation,* 2nd edn edn. Plymouth Marine Laboratory, Plymouth.

Critchley, C.N.R., Burke, M.J.W. & Stevens, D.P. (2004). Conservation of lowland semi-natural grasslands in the UK: a review of botanical monitoring results from agri-environment schemes. *Biological Conservation,* 115(2), 263-278.

Dicks, L.V., Baude, M., Roberts, S.P.M., Philips, J., Green, M. & Carvell, C. (2015). How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge. *Ecological Entomology,* 40(S1), 22-35.

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology,* 49, 986-997.

Dolman, P.M. & Sutherland, W.J. (1994). The use of soil disturbance in the management of Breckland grass heaths for nature conservation. *Journal of Environmental Management,* 41(2), 123-140.

Eycott, A.E., Watkinson, A.R. & Dolman, P.M. (2006). Ecological patterns of plant diversity in a plantation forest managed by clearfelling. *Journal of Applied Ecology,* 43(6), 1160-1171.

Fitter, A.H. (1982). Influence of soil heterogeneity on the coexistence of grassland species. *Journal of Ecology,* 70(1), 139-148.

Fuller, R.J., Williamson, T., Barnes, G. & Dolman, P.M. (2017). Human activities and biodiversity opportunities in pre-industrial cultural landscapes: relevance to conservation. *Journal of Applied Ecology,* 54(2), 459-469.

Goodenough, A.E. & Sharp, M.H. (2016). Managing calcareous grassland for the declining Duke of Burgundy *Hamearis lucina* butterfly: effects of grazing management on Primula host plants. *Journal of Insect Conservation,* 20(6), 1087-1098.

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.-S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006). Global distribution and conservation of rare and threatened vertebrates. *Nature,* 444(7115), 93-96.

Härdtle, W., Niemeyer, M., Niemeyer, T., Assmann, T. & Fottner, S. (2006). Can management compensate for atmospheric nutrient deposition in heathland ecosystems? *Journal of Applied Ecology,* 43(4), 759-769.

Hawkes, R.W., Smart, J., Brown, A., Jones, H. & Dolman, P.M. (2019a). Experimental evidence that ground-disturbance benefits Woodlark *Lullula arborea*. *Ibis,* 161, 447-452.

Hawkes, R.W., Smart, J., Brown, A., Jones, H., Lane, S., Wells, D. & Dolman, P.M. (2019b). Multi-taxa consequences of management for an avian umbrella species. *Biological Conservation,* 236, 192-201.

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal,* 50(3), 346-363.

Hsieh, T., C, Ma, K., H & Chao, A. (2018). Interpolation and extrapolation for species diversity. http://chao.stat.nthu.edu.tw/blog/software-download (accessed July 2018).

Hülber, K., Moser, D., Sauberer, N., Maas, B., Staudinger, M., Grass, V., Wrbka, T. & Willner, W. (2017). Plant species richness decreased in semi-natural grasslands in the Biosphere Reserve Wienerwald, Austria, over the past two decades, despite agri-environmental measures. *Agriculture, Ecosystems & Environment,* 243, 10-18.

Lin, Y.-C., James, R. & Dolman, P.M. (2007). Conservation of heathland ground beetles (Coleoptera, Carabidae): the value of lowland coniferous plantations. *Biodiversity and Conservation,* 16(5), 1337.

Manning, P., Gossner, M.M., Bossdorf, O., Allan, E., Zhang, Y.-Y., Prati, D., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Hölzel, N., Jung, K., Klaus, V.H., Klein, A.M., Kleinebecker, T., Krauss, J., Lange, M., Müller, J., Pašalić, E., Socher, S.A., Tschapka, M., Türke, M., Weiner, C., Werner, M., Gockel, S., Hemp, A., Renner, S.C., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Weisser, W.W. & Fischer, M. (2015). Grassland management intensification weakens the associations among the diversities of multiple plant and animal taxa. *Ecology,* 96(6), 1492-1501.

Marks, K.M.D., James, R., Laurence, B.R. & Sutherland, W.J. (1992). The effects of conservation management of reed beds. I. The invertebrates. *Journal of Applied Ecology,* 29(2), 265-276.

Merckx, T., Feber, R.E., Hoare, D.J., Parsons, M.S., Kelly, C.J., Bourn, N.A.D. & Macdonald, D.W. (2012). Conserving threatened Lepidoptera: Towards an effective woodland management policy in landscapes under intense human land-use. *Biological Conservation,* 149(1), 32-39.

Mikoláš, M., Svitok, M., Tejkal, M., Leitão, P.J., Morrissey, R.C., Svoboda, M., Seedre, M. & Fontaine, J.B. (2015). Evaluating forest management intensity on an umbrella species: Capercaillie persistence in central Europe. *Forest Ecology and Management,* 354, 26-34.

Oksanen, J., Blanchet, F., G, Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., R, O'Hara, R., B, Simpson, G., L, Solymos, P., Henry, M., Stevens, H., Szoecs, E. & Wagner, H. (2018). Community ecology package version 2.5-2. https://cran.r-project.org/web/packages/vegan/vegan.pdf (accessed July 2018).

Pedley, S.M., Franco, A.M.A., Pankhurst, T. & Dolman, P.M. (2013). Physical disturbance enhances ecological networks for heathland biota: A multiple taxa experiment. *Biological Conservation,* 160, 173-182.

Perkins, A.J., Maggs, H.E., Watson, A. & Wilson, J.D. (2011). Adaptive management and targeting of agri-environment schemes does benefit biodiversity: a case study of the corn bunting *Emberiza calandra*. *Journal of Applied Ecology,* 48(3), 514-522.

Power, S.A., Ashmore, M.R. & Cousins, D.A. (1998). Impacts and fate of experimentally enhanced nitrogen deposition on a British lowland heath. *Environmental Pollution,* 102(1, Supplement 1), 27-34.

Pywell, R.F., Bullock, J.M., Tallowin, J.B., Walker, K.J., Warman, E.A. & Masters, G. (2007). Enhancing diversity of species-poor grasslands: An experimental assessment of multiple constraints. *Journal of Applied Ecology,* 44(1), 81-94.

R Core Team (2015). R: a language and environment for statistical computing. Version 3.2.2. R Foundation for Statistical Computing, Vienna.

Ratcliffe, D. (1977). *A Nature Conservation Review: Volume 1: The Selection of Biological Sites of National Importance to Nature Conservation in Britain*. Cambridge University Press, New York.

Ridding, L.E., Bullock, J.M., Pescott, O.L., Hawes, P., Walls, R., Pereira, M.G., Thacker, S.A., Keenan, P.O., Dragosits, U. & Pywell, R.F. (2020). Long-term change in calcareous grassland vegetation and drivers over three time periods between 1970 and 2016. *Plant Ecology*.

Robertson, D. & Hawkes, R.W. (2017). Nature conservation, ground disturbance and protecting archaeological remains on Brecks heaths. *The Journal of Breckland Studies,* 1, 68-79.

Rodwell, J.S. (1991). *British Plant Communities. Volume 2: Mires and Heaths*. Cambridge University Press, Cambridge.

Rodwell, J.S. (1992). *British Plant Communities. Volume 3: Grasslands and Montane Vegetation*. Cambridge University Press, Cambridge.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S. & Weisser, W.W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature,* 574, 671-674.

Tipping, E., Davies, J.A.C., Henrys, P.A., Jarvis, S.G., Rowe, E.C., Smart, S.M., Le Duc, M.G., Marrs, R.H. & Pakeman, R.J. (2019). Measured estimates of semi-natural terrestrial NPP in Great Britain: comparison with modelled values, and dependence on atmospheric nitrogen deposition. *Biogeochemistry,* 144(2), 215-227.

Wells, T.C.E., Sheail, J., Ball, D.F. & Ward, L.K. (1976). Ecological studies on the Porton ranges: Relationships between vegetation, soils and land-use History. *Journal of Ecology,* 64(2), 589-626.

Westgate, M.J., Barton, P.S., Lane, P.W. & Lindenmayer, D.B. (2014). Global meta-analysis reveals low consistency of biodiversity congruence relationships. *Nature Communications,* 5(1), 3899.

Wilson, J.D., Evans, A.D. & Grice, P.V. (2010). Bird conservation and agriculture: a pivotal moment? *Ibis,* 152(1), 176-179.

Woodcock, B.A. & Pywell, R.F. (2010). Effects of vegetation structure and floristic diversity on detritivore, herbivore and predatory invertebrates within calcareous grasslands. *Biodiversity and Conservation,* 19(1), 81-95.

Wright, H.L., Lake, I.R. & Dolman, P.M. (2012). Agriculture—a key element for conservation in the developing world. *Conservation Letters,* 5(1), 11-19.

Chapter 6

Supplementary material

Figure S.6.1. Treatment and control rarefactions

Table S.6.1. Sampling across soil-vegetation strata

Table S.6.2. Candidate richness models

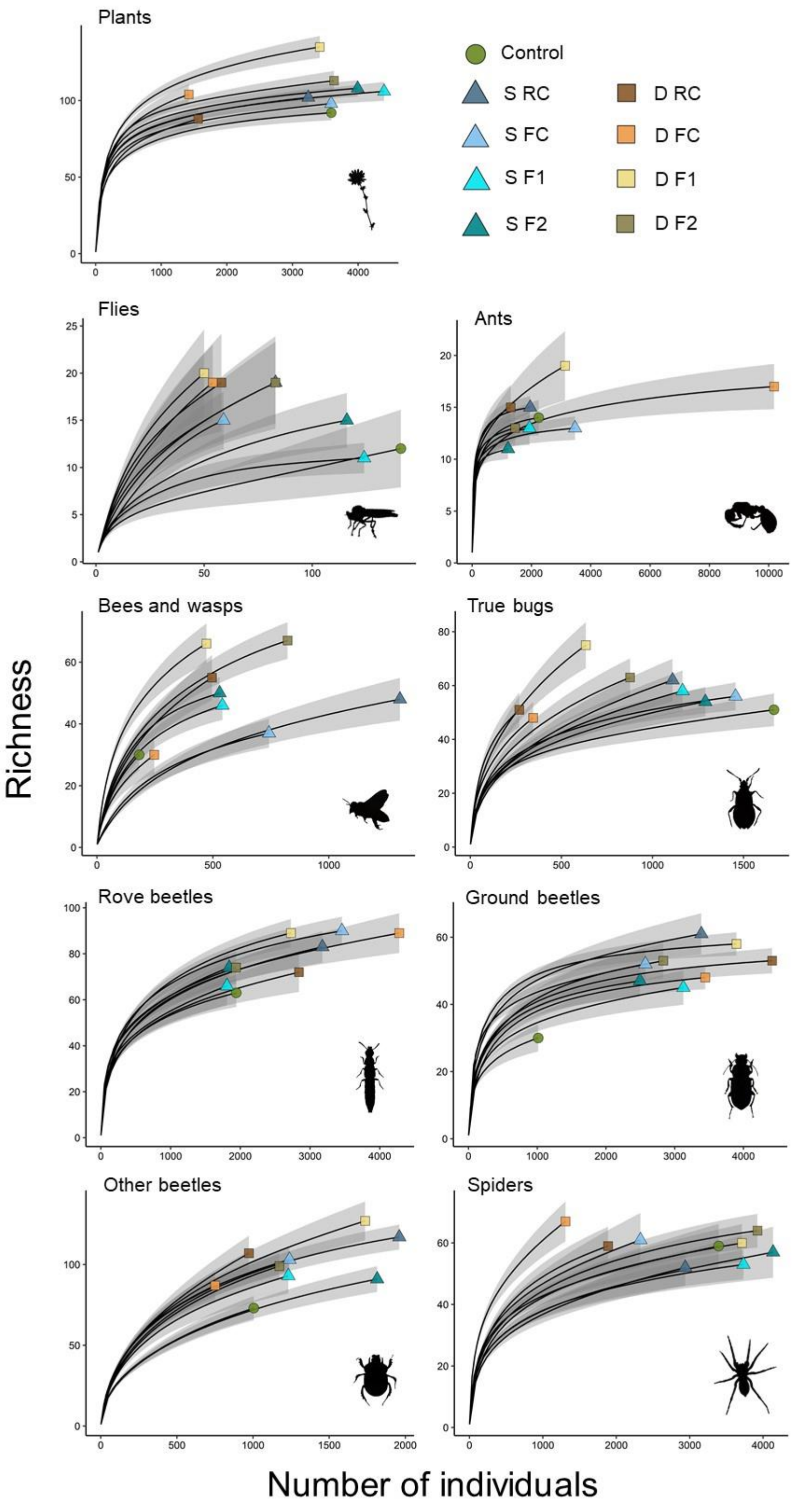

Figure S.6.1. Sample-based rarefaction (number of species encountered for the number of individuals captured) of nine taxonomic groups (pooling non-priority and priority species), shown separately for repeatedly-cultivated (RC), first-time cultivated (FC), one-year fallow (FL1), and two-year fallow (FL2) treatments, within shallow-cultivated (SC) and deep-cultivated (DC) complexes (providing eight treatments, *n* = 160, 20 per treatment), and control plots (*n* = 21). Shading denotes 95% CI bounds.

Table S.6.1. Sampling across vegetation strata, showing category definitions and the number of replicate deep-cultivated, shallow-cultivated, and control sampling units per strata (deep- and shallow-cultivated plots comprised four treatments: repeat-cultivatation, first-time-cultivation, one-year fallow and two-year fallow). For each indicator plant species, Ellenberg indicator scores for soil pH association (ranging from 1 to 9, with 1 = extremely acidic, 5 = mildly acidic, 9 = alkaline, Hill, Preston & Roy 2004) are given in parentheses. See Chapter 5 supplementary material for the biolography.

Vegetation strata	**Definition** [a]	**Number of sampling units**		
		Deep-cultivated	Shallow-cultivated	Control plots
Calcareous grassland	Grassland of any age (Sheail 1979) located on well-drained brown calcareous sands or rendzinas (soil association codes: 0521 and 0343f, respectively, NSRI 2014); or young, semi-improved, grassland (arable between 1904-1932, ≤110 years old) located on acidic brown sands (soil association code: 0554b), but with evidence of historic soil amelioration through 'marling' from presence of both acidiphilous (*Calluna vulgaris* (2), *Rumex acetosella* (4), *Galium saxatile* (3), *Teucrium scorodonia* (4)); and calcareous (*Thymus* spp. (6 - 8), *Pilosella officinarum* (7), *Galium verum* (6)) vascular plant indicators	44	40	11
Intermediate grassland	Mostly intermediate-aged grassland (arable at 1846 but reverted by 1904, 111-167 years old, 11 of the 14 plots), but some ancient grassland (no cultivation since 1845, ≥168 years old, 3 of 14 plots), located on acidic brown sands, with evidence of historic soil amelioration through 'marling'	16	20	5
Ancient-acid grassland	Mostly ancient grassland (12 plots) located on acidic brown sands, with no evidence of historic marling and calcareous indicator plants infrequent. Three additional plots were also included in this category on the basis of characteristic plant assemblages (confirmed through indicator plant and soil surveys; Marsden 2017) despite being mapped as rendzinas (two plots ≥131 years old) or as deep permeable peaty sands affected by groundwater (soil association code 0861b; one plot ≥131 years old)	20	20	5

[a] Grass-heath ages were based on the Tithe Survey of 1846, the Ordnance Surveys of 1883 and 1904 and the Land Utilization Survey of 1932; for STANTA these were previously overlain and collated by Sheail (1979), the same data sources were used to classify grassland age on Brettenham and Bridgham Heaths (see Hawkes *et al.* 2019)

Table S.6.2. Candidate models relating the richness of non-priority and priority species from eight invertebrate taxa and for plants to treatment (nine levels), soil-vegetation strata (three levels), and a treatment*strata interaction. For each candidate model the degrees of freedom (*df*), Akaike's information criterion with small-sample bias adjustment (AIC$_c$), and the difference in AICc value compared to the most parsimonious model (ΔAIC$_c$) are shown. (s) denotes the selected model for each analysis. Bold type denotes cases where the fixed effect of treatment (in the selected model) was important (i.e. the model deteriorate upon variable removal, ΔAICc >2)

Candidate model	*df*	AIC$_c$	ΔAIC$_c$
Spiders (non-priority species)			
Treatment + strata (s)	168	964.4	0.0
Treatment	170	967.1	2.7
Treatment + strata + treatment*strata	152	994.7	30.3
Spiders (priority species)			
Treatment (s)	170	577.1	0.0
Treatment + strata	168	580.2	3.1
Treatment + strata + treatment*strata	152	610.9	32.9
Ground beetles (non-priority species)			
Treatment (s)	170	948.4	0.0
Treatment + strata	168	952.8	4.4
Treatment + strata + treatment*strata	152	981.2	32.8
Ground beetles (priority species)			
Treatment + strata (s)	168	599.3	0.0
Treatment	170	606.5	7.2
Treatment + strata + treatment*strata	152	627.8	28.4
Rove beetles (non-priority species)			
Treatment (s)	170	1075.1	0.0
Treatment + strata	168	1075.6	0.5
Treatment + strata + treatment*strata	152	1094.8	19.8
Rove beetles (priority species)			
Treatment (s)	170	581.6	0.0
Treatment + strata	168	583.6	2.0
Treatment + strata + treatment*strata	152	616.2	34.6
Other beetles (non-priority species)			
Treatment + strata (s)	168	1025.6	0.0
Treatment	170	1036.9	11.3
Treatment + strata + treatment*strata	152	1051.1	25.5
Other beetles (priority species)			
Treatment + strata (s)	168	633.7	0.0
Treatment	170	641.5	7.9
Treatment + strata + treatment*strata	152	661.2	27.6

Candidate model	*df*	AIC_c	ΔAIC_c
True bugs (non-priority species)			
Treatment + strata	167	967.3	0.0
Treatment (s)	169	969.2	1.9
Treatment + strata + treatment*strata	151	999.1	31.8
True bugs (priority species)			
Treatment (s)	169	420.7	0.0
Treatment + strata	167	422.3	1.7
Treatment + strata + treatment*strata	151	451.5	30.9
Bees and wasps (non-priority species)			
Treatment (s)	169	878.5	0.0
Treatment + strata	167	881.1	2.7
Treatment + strata + treatment*strata	151	913.0	34.5
Bees and wasps (priority species)			
Treatment (s)	169	552.8	0.0
Treatment + strata	167	553.0	0.2
Treatment + strata + treatment*strata	151	569.3	16.5
Ants (non-priority species)			
Treatment (s)	170	683.4	0.0
Treatment + strata	168	686.2	2.8
Treatment + strata + treatment*strata	152	722.4	39.1
True flies (non-priority species)			
Treatment (s)	170	606.1	0.0
Treatment + strata	168	607.3	1.2
Treatment + strata + treatment*strata	152	625.4	19.3
Plants (non-priority)			
Treatment + strata (s)	169	987.6	0.0
Treatment + strata + treatment*strata	153	1014.0	26.4
Treatment	171	1034.6	47.1

Chapter 7

Discussion

Semi-natural habitats are amongst the most important areas for biodiversity conservation in western Europe (see Chapter 1), but species continue to disappear from them (Hülber *et al.* 2017; Seibold *et al.* 2019). Conservation interventions in semi-natural habitats have often been simplistic and homogenous (Fuller, Williamson, Barnes & Dolman 2017) and as a result have failed to meet the resource needs of diverse taxonomic groups, including very large numbers of priority species (Dolman, Panter & Mossman 2012). This thesis provides a detailed account of the largest land management experiment ever attempted in a European grassland and demonstrates that 'enhanced' interventions, inspired by land-use history (Fuller *et al.* 2017) and informed by a bio-regional analysis of ecological requirements of priority species (Dolman *et al.* 2012), benefits both focal species of conservation concern and wider biodiversity. To facilitate the widespread adoption of our approach to management, we recommend developing a bespoke agri-environment scheme option which enables landowners to adopt complex physical-disturbance interventions across closed-sward semi-natural grassland and lowland heathland sites.

7.1 Well replicated multi-taxa experiments

Thanks to the strengths of this study, I have been able to make several important, robust, evidence-based recommendations about the way grasslands and other semi-natural sites are managed (see section 7.3). First, with 21 non-intervention controls, 40 complexes, and 26 homogenous plots (considered in Chapters 3 & 4 only), this experiment was exceptionally well-replicated. Next, the treatment and control plots were large (each 2 – 4 ha), substantially reducing edge effects such as invertebrate spill over from the surrounding matrix (e.g. compared to the narrow 150 x 5 m treatment plots examined by Pedley, Franco, Pankhurst & Dolman 2013). Last, and arguably the most import component of the experiment, a large number of taxonomic groups were considered, not just a few focal species or taxa. This is particularly important because species richness correlations between different taxonomic groups are often weak (Vessby, Söderström, Glimskär & Svensson 2002) and vary with management intensity (Manning *et al.* 2015). This thesis corroborates these studies, further emphasising the importance of assessing outcomes across multiple groups; for example, whilst some groups showed a marked increase in richness in response to the treatment complexes (e.g. non-priority rove beetles) others showed no response (e.g. non-priority spiders) (Chapter 5). In addition, responses also varied within taxa according to priority status, with a stronger response among the priority species for most groups. This may be attributable to their habitat association; specifically, for those groups which showed a stronger response amongst the priorities, those species associated with ‘short sward’ or ‘short sward and bare ground’ (the intended recipients) comprised a greater proportion of the total for priority species than for non-priority species (Chapter 5). I am reluctant to suggest that any of the sampled taxa could have been omitted from the analysis, as each helped the interpretation of the overall treatment effect.

Although the sampling program was exceptionally comprehensive, some of the taxonomic groups could have been sampled more intensively; for example, bees and wasps, are often sampled several times throughout the year (Wood, Holland & Goulson 2015) but were only sampled once in this study (during July and August) owing to resource constraints. Aerial invertebrates (e.g. the true flies and bees and wasp, as well as day flying Lepidoptera) could have been further sampled through malaise trapping (Drake, Lott, Alexander & Webb 2007), but this would not have been compatible with the sites grazing regime. Night flying Lepidoptera could have been surveyed using light traps, but this method would have drawn in individuals associated with areas far beyond the treated plots. Irrespective of these limitations, malaise trap or light trap sampling would have required a large curtailment to the sampling program in other ways (e.g. a reduced number of treatment replicates). It is important that the relative trade-offs between sampling intensity (in terms the groups considered, number of trapping/sampling rounds, and trapping methods) and treatment replication (i.e. more treatments replicates will provide more reliable inference) are considered from the onset of any multi-taxa study.

7.2 Evaluation of analytical methods

Chapter 3 used Generalised Linear Mixed Models (GLMM) to examine the effect of treatment, soil-vegetation strata, year and landscape co-variates on Woodlark abundance, whilst controlling for repeat sampling of the same treatment/control locations by including ‘plot identity’ as a random effect. Consistent with ecological studies that consider many predictors (e.g. Pearce-Higgins, Grant, Robinson & Haysom 2007; Gilroy, Anderson, Grice, Vickery & Sutherland 2010), I used multi-model inference to estimate model-averaged coefficients across competing models. This approach worked particularly well because several competing models (with equal support) would have been omitted if inference was based entirely on the most parsimonious model (Burnham & Anderson 2002).

Chapter 4 used a different form of regression - Generalized Estimating Equations (GEE) - to model resource selection functions for breeding and post-breeding Stone-curlews from highly autocorrelated GPS data. GEEs are suited to the type of analysis because they replace the assumption of independence with a defined correlation structure (Koper & Manseau 2009), which in this case assumes correlations between locations decreases progressively with time. GLMMs would have provided a credible alternative to GEEs, with locations grouped by individuals to control for non-independence (e.g. following Morato *et al.* 2018). However, with the software I had available (‘R’), I was unable to model empirical (Huber–White sandwich) standard errors for GLMMs, which are robust to both among- and within-animal correlations, in the same way that I could for GEEs. It would be useful if this option could be added to existing GLMM packages in ‘R’ (e.g. 'lme4', Bates, Maechler, Bolker & Walker 2017) for use in future resource selection studies.

Another analytical challenge of the fourth chapter was the way ‘random location’ were selected. Resource selection studies often select random locations across each tracked individuals’ home range (e.g. van Eeden, Whitfield, Botha & Amar 2017; Morato *et al.* 2018; Pollander *et al.* 2019), but for a central place forager like Stone-curlew (see Chapter 4 and Green, Tyler & Bowden 2000) this approach would have oversampled less accessible distant locations. To overcome this problem, I paired each used location with four random locations positioned the same distance from the nest-site (breeding period) or day-roost (post-breeding period), but in randomly selected directions. Thus, the modelled sample represented used and unused sites equally available to each individual for the same travel investment. Whilst I believe that this approach is conceptually and analytically sound, generating these points through a manual set of processes was particularly time consuming. An ‘R’ function or GIS module which implements this random selection approach automatically would serve as a useful tool for other resource selection studies that focus on central place foragers.

For Chapters 2 and 6 I used Non-metric Multidimensional Scaling (NMDS, based on a Bray-Curtis dissimilarity matrix) to explore whether the treatments and controls supported distinct assemblages, separately for each taxonomic group. Whilst this approach was successful in describing relative assemblage composition, this does not establish whether these assemblages significantly differ. To overcome this problem, I used a Kruskal–Wallis test in Chapter 2 to examine whether ordination scores differed between treatments and controls (three categories); however, a better approach would be to rerun this analysis as a constrained ordination to explicitly test the effects of treatment and soil-vegetation strata on species composition. Unlike unconstrained ordination (such as Correspondence Analysis, Detrended Correspondence Analysis and NMDS), which provide a descriptive account of species composition differences, constrained ordination uses an ANOVA/regression approach, which enables the user to examine the effects of different environmental variables on species composition (ter Braak & Šmilauer 2015). Options would include Canonical Correspondence Analysis (that rotates the species ordination to maximise the relation to a set of orthogonal environmental axes that are a linear combination of environmental variables), or the more recent manyglm approach available in the package 'mvabundn' that allows testing of a priori hypotheses concerning the multi-variate species-environment relation (Wang, Naumann, Wright & Warton 2012). Such approaches would be especially informative for Chapter 6, where the fixed effect of treatment considered nine levels (instead of the three levels considered in Chapter 2) and the effect of soil-vegetation strata may be important for some groups (e.g. plants, See Chapter 6).

Last, to determine how much enhanced management is needed to optimise overall cumulative richness at the landscape-scale, Chapter 6 compared hypothetical management scenarios, compromising varying amounts (in terms of proportions of overall grassland extent) of shallow or deep-cultivated complexes, to a control-only landscape. This was achieved using resampling to explore different combinations of treatment and control plots ranging from 0% management (all control plots) to 100% management (all treated plots) (hereafter, 'management scenario'), and then rarefaction to explore the consequence of each resampling iteration (for each management scenario) on species richness. Rarefactions were suited to this form of analysis because they control for uneven sampling (in this case, the number of sampling units considered for each management scenario, as well as differing numbers of individuals per sample) (Chao *et al.* 2014). A radically different way to address this question would be to trial these different management scenarios in reality (i.e. considering multiple replicate grassland sites, each of similar size, cultivated to different extents and in different ways while controlling for grassland type and structure); however, this would require an entirely new experiment. Moreover, I strongly suspect that such a trial would simply confirm what the rarefactions show.

7.3 Conservation recommendations

7.3.1 Conservation surrogates

Previous tests of conservation surrogacy typically examine whether the overall richness or abundance of other species is higher where the species is present (e.g. Suter, Graf & Hess 2002), or whether they occupy similar habitats (e.g. Maslo *et al.* 2016). Whilst this approach is well suited to protected area conservation, it does not establish the consequences for other biota of management for the surrogate – the appropriate appraisal within semi-natural landscapes. The second Chapter provides an exceptionally rare test of the consequence for multi-taxa biodiversity, of management for a surrogate species. Here, we demonstrated that conservation interventions for Eurasian Stone-curlew *Burhinus oedicnemus* benefit several other invertebrate groups. Crucially, this chapter also showed that the landscapes diversified by this management support a greater cumulative species richness of priority invertebrates than a control-only counterfactual.

This second chapter clearly demonstrates the value of land management interventions targeted towards Stone-curlew, confirming the species status as a conservation surrogate; but what are the implications for other candidate surrogates in other systems? We selected our surrogate because a systematic bioregional process (that classified species with shared autecological requirements, Dolman *et al.* 2012) suggested many priority species should benefit from the same management interventions that provide suitable Stone-curlew breeding habitat. Our experiment subsequently confirmed that the richness of those species that we *a priori* predicted to benefit from the management increased as expected. This experience suggests that bioregional analyses not only provide a suitable tool for selecting possible surrogates, but the predictions derived from such assessments are valid without confirmation from costly and time-consuming experiments. Where surrogates can be identified, this strengthens the case for their conservation.

7.3.2 Stone-curlew

The UK's Stone-curlew population declined for much of the 20th Century, but has been subject to an intensive conservation programme and has partly recovered (Evans & Green 2007). Despite this success, the species is reliant upon brood protection interventions on arable farmland to sustain the population (Johnston 2009). In the UK (Johnston 2009) and elsewhere in Europe (Gaget, Fay, Augiron, Villers & Bretagnolle 2019), reducing the reliance of Stone-curlew conservation on these costly and resource-intensive rescue interventions, by increasing the proportion of breeding attempts on semi-natural grassland, is considered a high priority. Previous research has demonstrated that grassland habitats are only suitable for breeding Stone-curlew where they contain short swards and bare ground created and sustained by grazing (Green & Griffiths 1994), but this habitat has become increasingly scarce as a result of reduced livestock densities, the loss or decline of rabbits (Panter, Mossman & Dolman 2013) and accelerated vegetation growth attributable to increased rates of nutrient deposition (Tipping *et al.* 2019; Ridding *et al.* 2020).

The second chapter confirmed that recent cultivations provided suitable Stone-curlew nesting habitat (evidenced by vegetation structure as a proxy for suitability), but it remained unclear whether the treatments also provided important foraging areas for this cryptic nocturnal species – that could potentially be used to support breeding productivity by other pairs nesting elsewhere in the landscape. By using GPS tracking data from five adult birds, the fourth chapter showed that Stone-curlew were two (by night) to three (by day) times more likely to select the treated areas over the surrounding closed sward grassland for foraging during the breeding period, and approximately fifteen times more likely to do so post-breeding. Other farmland habitats, including sugar beet and maize, manure heaps and pig fields, were also important. Locating this management close to the arable edge will facilitate access to these other important foraging habitats.

Whilst Chapters 2 and 4 demonstrated that the management created suitable Stone-curlew breeding habitat (for nesting and foraging), over the three-year experiment exhaustive searchers across the treatment plots revealed only 4, 6 and 2 breeding pairs (all on plots) in each of 2015, 2016, and 2017. This is far below the combined potential of the three sites, which could support up to 240 pairs of breeding Stone-curlew if all grassland habitat was suitable for nesting (<2cm, based on the maximum observed breeding densities on grassland, Green *et al.* 2000) or 66 pairs if all the treated plots were occupied (one pair per plot); though the true suitable extent is probably considerably less owing to military disturbance (Taylor, Green & Perrins 2007) and other factors (e.g. nearby buildings, Clarke, Liley, Sharp & Green 2013). This limited response is not surprising, given that range shifts in long-lived birds like Stone-curlew are driven by natal dispersal, especially in females (which show weaker natal philopatry than males, Gunnarsson, Sutherland, Alves, Potts & Gill 2012; Trochet *et al.* 2016). My own observations corroborate this paradigm (albeit in a very limited and untested way) as all colonising pairs were either first-time breeders or established adults from nearby arable fields. However, during the experiment, we know that productivity was low in the wider population (i.e. below the required 0.61 fledged chicks per pair to maintain a table population), which presumably limited recruitment opportunities. Over time, as the population starts to increase, conspecific attraction cues (which are stronger at sites with more individuals) could gradually increase recruitment rates onto treated plots (Danchin, Giraldeau, Valone & Wagner 2004; Morrison, Robinson, Clark & Gill 2016).

It is also possible that a sustained period of high breeding productivity, across the wider landscape, would facilitate recruitment across treated semi-natural grassland. This could be achieved through a combination of nest and brood protection measures, including arable interventions (which have been reduced in recent years), predator control, and anti-predator fencing (as demonstarted for other waders, Rickenbach *et al.* 2011; Malpas *et al.* 2013). Experience elsewhere suggests that this is possible, perhaps most notably based on the restoration of a large block of grassland in Eastern England (Minsmere) and its subsequent (but gradual) accumulation of breeding birds over the following decade (Kemp pers. comm). Nevertheless, these measures would require a significant investment in time and money.

Encouraging more breeding Stone Curlew onto treated areas would not be successful if this nesting habitat was in fact an ecological trap; for example, if it was a focal point for greater levels of nest predator activity than other breeding habitats, resulting in low breeding productivity and recruitment failure. If such a trap is operating, it is crucial that this is established and the underlying causes mitigated to ensure that future recruits do face a period of sustained low productivity (thus worsening the conservation prospects for the species). However, the low number of breeding Stone-curlew during this experiment prohibited meaningful examination of their breeding productivity on treated plots. Therefore, we (myself and Natalia Zielonka) instead examined the breeding ecology of a more widespread and locally abundant ground-nesting wader - the Eurasian Curlew *Numenius arquata* (hereafter 'Curlew'). Curlew daily nest survival rates differed markedly between STANTA (0.16 ± 0.06 SE) and Brettenham Heath (0.70 ± 0.18), consistent with greater intensity of predator control on the latter site (see thesis Appendix B, or Zielonka, Hawkes, Jones, Burnside & Dolman 2020). Across both sites these rates were similar on treated and untreated grassland, suggesting that the plots themselves do not affect nest survival. Nest camera footage and temperature sensors confirmed that Red Fox *Vulpes vulpes* were the main culprit. Whilst caution must be advised when transferring inference from one species to another, this research suggests that anti-predator measures need to part of any strategy to enhance breeding Stone-curlew populations on semi-natural grassland, regardless of their nest site choice; certainly on this site, but also further afield.

To summarise, the evidence gathered by this thesis suggests that a national Stone-curlew conservation strategy cannot rely on physical-disturbing grassland habitats alone, at least in the short- to medium-term. This is because treated areas are more likely to colonised gradually by young recruits and not established site-faithful breeders. As breeding populations start to accumulate across these areas, additional measures, such as predator control, are likely to be a necessary component of successful strategy. Furthermore, a detailed demographic study (Johnston 2009), shows that a large proportion of the population would need to accumulate on this habitat before nest interventions on arable farmland could cease. Nevertheless, for the reasons discussed in the subsequent sub-sections, it is crucial that these interventions are adopted across other grassland sites to ensure that their management is optimised for other taxa.

7.3.3 Woodlark

Though the British Woodlark population underwent a partial recovery between the mid-1980s and mid-2000s (Conway *et al.* 2009), there have been considerable losses since in some areas and the species here is Threatened, classified as IUCN Vulnerable in a GB context (Stanbury *et al.* 2017). These losses may relate to the loss of important bare and sparsely-vegetated foraging sites on lowland heathland, with which most British territories are associated (Conway *et al.* 2009). However, it is not clear whether treatments that open-up closed swards will necessarily promote population recovery. Chapter 3 demonstrated that Woodlark abundance increased over the three-year experiment and was higher on plots closer to woodland, regardless of establishment method (shallow- versus deep-cultivation) or complexity (homogenous versus complex plots). This confirms the value of physical-ground disturbance interventions in providing suitable breeding habitat (previously observed by Bowden 1990; Mallord, Dolman, Brown & Sutherland 2007b), and - contrary to our *a priori* prediction - showed that treatment complexity does not appear to matter for this species. This may be because recent cultivations in a matrix of fallows (the complex plots) offered little by way of additional resource to recent-cultivations in a matrix of grassland (the homogenous plots).

To enhance Woodlark populations, I recommend implementing mechanical ground disturbance interventions close to woodland (<50 m) in otherwise lightly grazed calcareous grassland and lowland heathland sites (the former habitat once beingstronghold for the species). However, in many instances, grassland sites are considerably smaller than STANTA, Bridgham Heath and Brettenham Heath, which may prohibit the use of large 2 – 4 ha treatment plots. Instead, where space is limited, smaller plots over an equivalent area (e.g. 4 x 0.5 ha plots, or 2 x 1 ha plots) could be created, but sizes smaller than this may be ineffectual (in commercial clear-fell forests the minimum suitable patch size is c.2 ha, Wright 2007). Regardless of how bare ground is established, regular intervention is needed to maintain these areas as bare and open (once a year with cultivation, Chapter 4; perhaps more infrequently with more severe methods such as top-soil removal, Pedley *et al.* 2013).

Last, consistent with my recommendations for Stone-curlew, further work is needed to establish the consequence of these interventions on Woodlark productivity. Although the treated areas are unlikely to provide suitable nesting habitat (given their preference for concealed vegetated areas, Mallord, Dolman, Brown & Sutherland 2007a) they will nest immediately adjacent to the plots (e.g. < 1 m) (pers. obs.). It would be useful to know whether productivity is higher for those pairs that choose to nest closer to the treated areas, though such a study would require a large sample of nests spanning several years (e.g. Mallord *et al.* 2007b).

7.3.4 Wider biodiversity

To establish the multi-taxa consequence of the treatments, we (I, in collaboration with a team of taxonomic experts) sampled more than 130,000 individual invertebrates of 878 species and made over 28,000 observations of 167 vascular plant species during the third year of the experiment (2017). The analysis of these data demonstrated that the complexes (both shallow- and deep-cultivated) increased the overall richness of non-priority species, doubled the richness of priority species, and held more unique priority species than the undisturbed grassland controls (Chapter 5). Building on the knowledge gained in the fifth chapter, the sixth chapter explored the impact of the treatment complexes in more detail. Within the complexes, the one-year-old fallowed deep-cultivation (but not the shallow-cultivated equivalent) was the only treatment which increased priority species richness across multiple taxa. However, the analysis of assemblage composition showed that nearly every treatment supported a distinct assemblage of species within most individual taxonomic groups – which suggests the full treatment complex design will support the widest suite of species by ensuring a continuity of fallowed and recently disturbed areas.

As discussed in Chapter five, the considerable wider biodiversity value of the treatment complexes is most likely attributable to the range of conditions within each plot; ranging from recent cultivations with extensive bare ground, which support the warmer conditions required by many regional priority species (Dolman *et al.* 2012); to regenerating fallows, which provide important resources for herbivores and granivores (Woodcock & Pywell 2010). Juxtaposition of cultivation sub-treatments (fallows, fresh- and repeated-cultivation) within complexes may have further increased richness through complementarity of sub-treatments for species dependent on contrasting micro-habitats.

Despite the overall wider biodiversity benefit of the treatment complexes (in terms of richness), and the strong response shown across many taxa, some groups responded less well than I anticipated. As discussed in section 7.2, for some invertebrate groups (such as priority bees and wasps) greater sampling intensity may have revealed a treatment effect. Probably the biggest surprise was the apparently rather limited response of priority plants (which responded positively to the deep-cultivated complexes, but the effect size was small; Chapter 5), given large numbers require ground disturbance and bare-open habitats (Dolman *et al.* 2012), and respond particularly well to severe forms of physical-disturbance (Pedley *et al.* 2013). It is possible that this result is a consequence of the location of the study site toward the north-eastern part of the bio-region, that is geographically marginal for priority species, particularly for priority vascular plants (Fig. 7.1). However, despite the sites location in the landscape, it is important to note that priority species (overall, across all taxa) doubled in response to treatment, which suggests that implementing the same treatments in high biodiversity hotspots would result in an even larger response.

It is beyond the scope of this thesis to establish why priority species with some taxonomic groups responded more strongly to treatments than others (see Chapter 5). For priority invertebrates, some may have already persisted within (or near to) the study area before the treatment plots were implemented (albeit at a lower density); allowing these species to rapidly colonise the newly established treated areas. Those invertebrate groups which responded particularly well may contain a large number of species that are able to easily disperse (though the exact traits which facilitate dispersal vary between taxa, Pedley & Dolman 2014). For priority plants, although some survive long periods in the seed bank (Eycott, Watkinson & Dolman 2006) the study area has long been recognised as floristically depauperate for many Breckland priorities (Bull 2011); which probably prohibited a large instant response to treatment. Some plants are particularly well suited to dispersal (a very large proportion of the regional biota are dispersed by red deer, Eycott, Hemami, Watkinson & Dolman 2007) and may colonise in future years should favourable conditions persist; whilst others are poor dispersers (Wells, Sheail, Ball & Ward 1976) and may never colonise unless facilitated by some other means. One option would be to translocate these species from existing populations to the treated plots; but this form of intervention is subject to strict international guidelines (IUCN/SSC 2013).

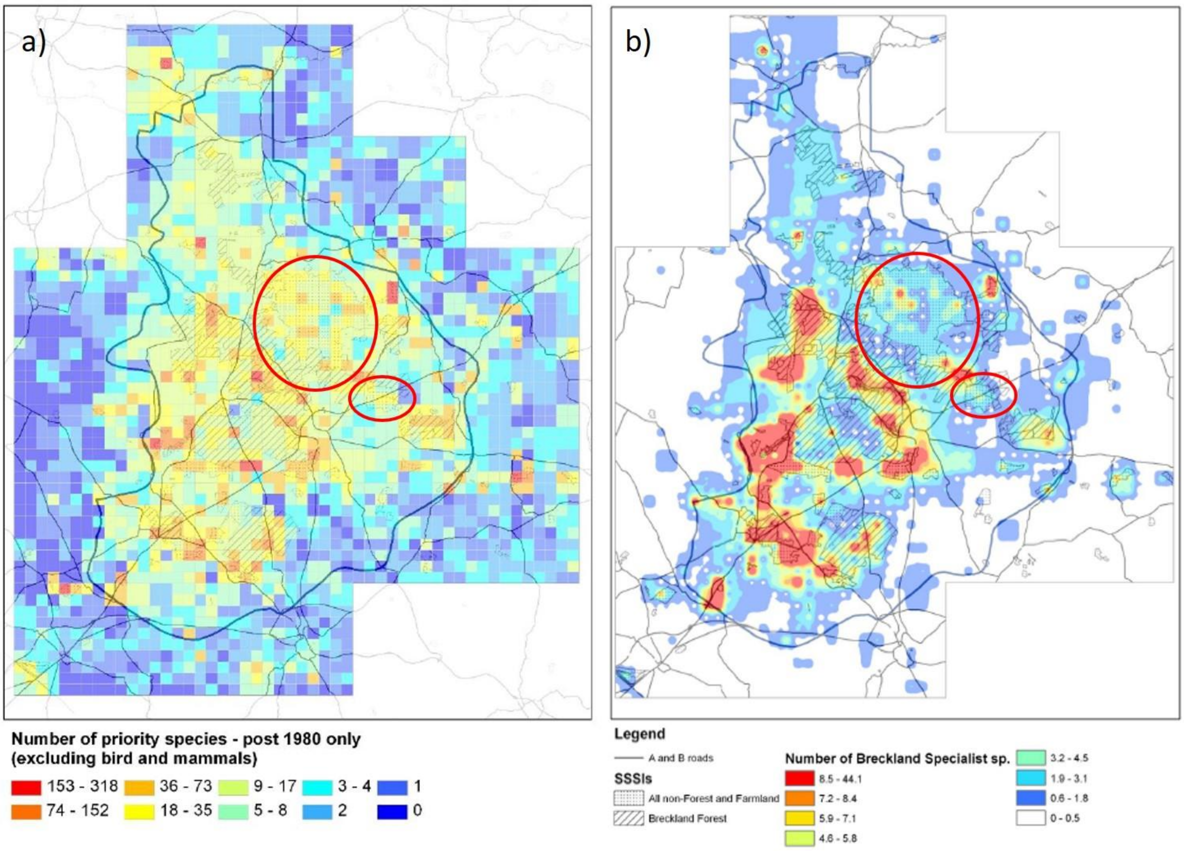

Figure 7.1. Number of (a) priority (rare, scarce and threatened) and (b) Breckland specialist (for the selection criteria, see Dolman, Panter & Mossman 2010) non-vertebrate species recorded during and subsequent to 1980 in each of the 1 km squares within Breckland. Note, the data in (b) is plotted as inverse distance weighted, where the value of each point is influenced by its neighbours, with the weight of that influence inversely weighted with distance. The red circles indicate the part of the landscape where our land management experiment took place (the Stanford Training Area, Brettenham Heath and Bridgham Heath). These figures are reproduced from Dolman *et al.* (2010)

7.3.5 Implications for different grassland habitats

To ensure the findings of this thesis are relevant to a range of grassland habitats, the treatment and control plots were distributed across a range of soil-vegetation strata. The mosaic of soils (from podsol to rendzina) and variation in grassland age across the study area formed the basis of these strata classifications, which were broadly characteristic (in terms of their vegetation community) of lowland heath (classified as ancient-acid grassland), mesophotic intermediate grassland, and calcareous grassland (Rodwell 1991; Rodwell 1992). Chapter six demonstrates that whilst the richness of taxonomic groups was higher in some strata, the effect of treatment is always consistent across grassland habitats. Based on this evidence, conservation practitioners seeking to adopt complex physical-ground disturbance interventions across lowland dry grasslands and heathlands can ignore fine-scale classifications in vegetation communities (e.g. NVC classifications of CG7, U1, SD8, H1, see Rodwell 1991; Rodwell 1992) – implementing this management in any lowland dry grassland ecosystem will benefit biodiversity.

It is also worth emphasising that the implications of this thesis are not limited to lowland dry grasslands and heathlands habitats alone. Other habitats which support characteristic dry-sand assemblages such as coastal dunes (Howe, Litt & Pye 2012) and brown field sites (Eyre, Luff & Woodward 2003), among many others, may benefit from similar forms of management.

7.3.6 Treatment extent

To optimise the cumulative richness of non-priority and priority invertebrates at a landscape-scale, the treatment complexes need to take place across 40% (deep-cultivated) or 60% (shallow-cultivated) of the landscape (Chapter 6). Given both shallow- and deep-cultivated treatments support unique species (Chapter 5), I recommended implementing a combination of both (i.e. half of each to achieve 40 - 60%).

This recommendation represents a radical change to way many large areas of semi-natural grassland are currently managed, which too often comprises extensive livestock grazing coupled with limited and sporadic scrub control. Nevertheless, conservation practitioners seeking to adopt these recommendations should first assess whether the planned intervention areas are likely to cause any harm to existing assemblages (e.g. priority plant species that may be intolerant of the intervention, or reptile hibernacula habitats) and important archeology (Robertson & Hawkes 2017). In these instances, management should be targeted in such a way that it avoids these sensitive areas.

As an urgent follow-on to this study, it would be extremely valuable to identify all the major UK sites where these recommendations could and should be applied. For example, areas like Salisbury Plain and Porton Down in Wessex, the Breckland sites of Lakenheath Warren, Deadman's Graves and Cavenham Heath; and heathland blocks across Surrey, the New Forest in Hampshire, and much of the Poole basin heaths, would be excellent candidate areas to implement these or similar recommendations. On large sites (e.g. > 100 ha) the treatments could be applied across 40 – 60% of the area as patchwork (e.g. spreading the 4 ha treatment complexes across the whole site). On smaller sites (< 100 ha) instead of implementing 2 ha plots to create 4 ha complexes, which could destroy range-restricted populations, it may be more appropriate to implement the treatments as long, partially-overlapping, strips (e.g. each c.5 m wide, buffered by undisturbed habitat) that are built up over a period of years to create the same range of treatments as the complexes. Regardless of the sites size, this patchwork approach is considerably more favorable than the alternative of treating large contiguous blocks whilst leaving equally large blocks untreated – which would reduce opportunities for species that require habitat juxtaposition, and may harm populations with patchy distributions (e.g. as a consequence of limited areas of suitable niche, soil differences, or land-use history).

Notwithstanding the issue of sensitive communities and archeology, some proponents of the status quo may be reluctant to see vast proportions subject to an enhanced management regime. Whilst I am confident in the reliability and generality of the research findings (for the reasons previously discussed), practitioners may wish to trial the 40 – 60% treated area recommendation across a few replicate grassland blocks with subsequent monitoring to validate response. Nevertheless, whilst their may be a temptation to be cautious about taking such radical management intervention, many priority species continue to decline (even in surviving grassland remnants, Seibold *et al.*

2019) and are Threatened (Hayhow *et al.* 2019). A key threat to these species is neglect through inappropriate, poorly-informed, interventions (Dolman *et al.* 2012), or the right inventions implemented across a limited area (as demonstrated by Chapter 6). Urgent and divisive action is therefore necessary to enhance the conversation prospects of vast numbers of priority species.

7.3.7 Alternative ways of implementing enhanced management

In terms of how enhanced management is implemented, this thesis considered two widely available and cost-effective cultivation methods – shallow-cultivations created with a rotatory rotavator, and deep-cultivations created with an agricultural plough. Whilst we cannot appraise the relative efficacy of other alternative but as-yet unassessed methods, this section explores other potential ways enhanced management could be implemented within this system.

First, more severe methods of establishment, such as turf stripping or sod cutting, are particularly effective at reducing nutrients (Härdtle, Niemeyer, Niemeyer, Assmann & Fottner 2006) and support large numbers of priority species (Pedley *et al.* 2013). It is possible that these methods, which retain bare habitats longer than cultivations (Pedley *et al.* 2013), may allow a longer return time before re-treatment is needed. In addition, if these methods were to result in a large biodiversity benefit, less management in terms of proportionate extent may be needed. However, turf stripping and sod cutting can be prohibitive due to the transport costs associated with removing the arisings. To remove this cost, the arisings could be scraped into piles or into linear banks and left *in situ* (as undertaken by Forestry Commission England in creating a 278 km open-habitat connectivity network across Thetford Forest, Armour-Chelu, Brookes & Nichols 2012), but the resulting nutrient-rich top-soil mounds are likely to harbor an abundance of undesirable plants (e.g. *Urtica urens*) and could block visibility and predator vigilance for ground nesting species such as Stone Curlew, reducing the likelihood of recruiting these to treated plots.

Next, intensive grazing by high density European rabbit *Oryctolagus cuniculus* populations creates and maintains bare-open microhabitats (Bealey, Green, Robson, Taylor & Winspear 1999) which supports characteristic priority assemblages (Burggraaf-van Nierop & van der Meijden 1984). Spatial and temporal variability in rabbit densities across a site historically created similar patterns of habitat heterogeneity as those observed within the treatment complexes (Farrow 1925). However, rabbit populations have suffered long-term declines across many grassland sites (e.g. Norfolk Wildlife Trust unpublished data; Panter *et al.* 2013) and the wider landscape (Harris *et al.* 2019), potentially attributable to at least two pandemic diseases (myxomatosis and viral hemorrhagic disease) and high rates of predation by re-established generalist predators (e.g. Red Fox and Buzzard *Buteo buteo)*. Little is known about how rabbit populations can be successfully restored (at least outside the Mediterranean); thus mechanical interventions, such as those trialed in this thesis, provide a predictable and proven way of implementing enhanced management.

Last, some elements of more natural processes, advocated by proponents of rewilding, could create structural complex and dynamic habitats. For example large herbivorous, but especially wild boar *Sus scrofa* create and can maintain these conditions, with resulting benefits for some species and taxa (Sandom, Hughes & Macdonald 2013; De Schaetzen, Van Langevelde & WallisDeVries 2018; Van Klink & WallisDeVries 2018). However, simply restoring natural process without any regard for how early successional habitats and structural complexity is maintained will not cater for the needs of many priority species associated with grassland habitats (Dolman *et al.* 2012). Future multi-taxa studies could compare rewilding initiatives that incorporate ways of maintaining structural complex habitats to the treatment complexes trialed in this thesis.

7.4 Future research

Beyond some the ideas that I have alluded to throughout this discussion, there are several important priorities for future research. It is unclear whether the efficacy of the treatment complexes produced in this study is diminished or enhanced by successive rotations (i.e. retreated the same complex over a subsequent three-year period). In addition, expanding on the ideas raised in the previous section (7.3.7), it is unclear whether less management is necessary within systems where bare-open micro habitats are already present, due to low-nutrient status mineral soils (in contrast to the relatively high organic content of soils over much of the study site considered in this thesis) or localised, but not extensive, rabbit grazing. This is probably true, but empirical guidance on how much management is needed in these circumstances would be useful.

Another important area for future research is to establish whether there is a reliable way of using biodiversity proxies to evaluate the multi-taxa consequence of management interventions. I have already discussed why the notion of proxies such as indicator species are problematic with this type of study, but it might be possible to strengthen cross-taxa associations if species are *a priori* classified based on their autecological requirements (i.e. using the same classification approach as the biodiversity audit, Dolman *et al.* 2012). For example, in the context of this thesis, the presence of a few distinctive bare-ground associated proxies may co-occur alongside large numbers of other bare-ground associated priority species. This would provide a powerful monitoring tool if this could be demonstrated. Another promising and upcoming technique is DNA metabarcoding (Ji *et al.* 2013); however, whilst this approach generates reliable alpha and beta biodiversity information (e.g. species richness among taxa), it does not consistently identify all specimens to species level (e.g. Barsoum, Bruce, Forster, Ji & Yu 2019). As a result, the current capacity for metabarcoding to make accurate inferences about priority species responses is still limited (where species identity is needed).

7.5 Informing enhanced management without experiments

Despite the clear value of multi-taxa experiments as a way of evaluating the efficacy of enhanced management interventions, they are exceptionally resource intensive and reliant upon taxonomic expertise. To put this into perspective, the invertebrate and plant dataset used in the fifth and sixth chapters took approximately 3,638 person hours to generate (570 deploying the traps; 528 sampling vascular plants; 540 processing invertebrate material; and six taxonomic experts spending a collective 2,000 hours identifying invertebrates). In many instances this amount of effort and resource would be prohibitive; so how can we inform land management interventions in other systems without experiments?

As an alternative, where biodiversity is well-characterised and autecological knowledge is strong, this thesis demonstrates that bioregional systematic analysis of autecological requirements across the full suite of priority species, can reliably inform enhanced management interventions (Chapter 5). The Biodiversity Audit approach (for details, see Dolman *et al.* 2012) provides a particularly effective way of achieving this (see Chapter 5), but requires a bespoke region-specific desk-based study and expert engagement. Instead, where regional biodiversity data are readily available (i.e. as a regional species list) and resources are limited, Pantheon (an online database for UK invertebrates, Webb *et al.* 2018) will instantly summarise the habitat associations of the entire species-pool; however, unlike biodiversity audits, it does not recommend interventions. To resolve this problem, Pantheon could incorporate an online module which advises bespoke management actions based on input species list and site-specific information.

References

Armour-Chelu, N., Brookes, R. & Nichols, B. (2012). Open habitats implementation plan for the Forestry Commission Thetford Public Forest Estate 2012. FC, Santon Downham.

Barsoum, N., Bruce, C., Forster, J., Ji, Y.-Q. & Yu, D.W. (2019). The devil is in the detail: Metabarcoding of arthropods provides a sensitive measure of biodiversity response to forest stand composition compared with surrogate measures of biodiversity. *Ecological Indicators,* 101, 313-323.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2017). Linear mixed-effects models using 'Eigen' and S4. *R package Version 1.1-1.5*. Available at: https://cran.r-project.org/web/packages/lme4/ (accessed May 2018).

Bealey, C.E., Green, R.E., Robson, R., Taylor, C.R. & Winspear, R. (1999). Factors affecting the numbers and breeding success of Stone Curlews *Burhinus oedicnemus* at Porton Down, Wiltshire. *Bird Study,* 46(2), 145-156.

Bowden, C. (1990). Selection of foraging habitats by Woodlarks (*Lullula arborea*) nesting in pine plantations. *Journal of Applied Ecology,* 27, 410.

Bull, A. (2011). *A flora of STANTA*. Catton Print, Norwich.

Burggraaf-van Nierop, Y.D. & van der Meijden, E. (1984). The influence of rabbit scrapes on dune vegetation. *Biological Conservation,* 30(2), 133-146.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. & Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs,* 84(1), 45-67.

Clarke, R.T., Liley, D., Sharp, J.M. & Green, R.E. (2013). Building development and roads: implications for the distribution of Stone curlews across the Brecks. *PLOS ONE,* 8(8), e72984.

Conway, G., Wotton, S., Henderson, I., Eaton, M., Drewitt, A. & Spencer, J. (2009). The status of breeding Woodlarks *Lullula arborea* in Britain in 2006. *Bird Study,* 56(3), 310-325.

Danchin, É., Giraldeau, L.-A., Valone, T.J. & Wagner, R.H. (2004). Public information: From nosy neighbors to cultural evolution. *Science,* 305(5683), 487.

De Schaetzen, F., Van Langevelde, F. & WallisDeVries, M.F. (2018). The influence of wild boar (*Sus scrofa*) on microhabitat quality for the endangered butterfly *Pyrgus malvae* in the Netherlands. *Journal of Insect Conservation,* 22(1), 51-59.

Dolman, P.M., Panter, C. & Mossman, H.L. (2010). *Securing biodiversity in Breckland: guidance for conservation and research. First report of the Breckland biodiversity audit*. University of East Anglia, Norwich.

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology,* 49, 986-997.

Drake, C.M., Lott, D.A., Alexander, K.N.A. & Webb, J. (2007). Surveying terrestrial and freshwater invertebrates for conservation evaluation. Natural England Research Report NERR005.

Evans, A.D. & Green, R.E. (2007). An example of a two-tiered agri-environment scheme designed to deliver effectively the ecological requirements of both localised and widespread bird species in England. *Journal of Ornithology,* 148(2), 279-286.

Eycott, A.E., Hemami, M.R., Watkinson, A.R. & Dolman (2007). Deer and lagomorphs as dispersers of vascular plants in a forest mosaic. *Oecologia,* (154), 107-118.

Eycott, A.E., Watkinson, A.R. & Dolman, P.M. (2006). The soil seedbank of a lowland conifer forest: The impacts of clear-fell management and implications for heathland restoration. *Forest Ecology and Management,* 237(1), 280-289.

Eyre, M.D., Luff, M.L. & Woodward, J.C. (2003). Beetles (Coleoptera) on brownfield sites in England: An important conservation resource? *Journal of Insect Conservation,* 7(4), 223-231.

Farrow, E.P. (1925). *Plant life on East Anglian heaths. Being observational and experimental studies of the vegetation of Breckland*. Cambridge University Press, Cambridge.

Fuller, R.J., Williamson, T., Barnes, G. & Dolman, P.M. (2017). Human activities and biodiversity opportunities in pre-industrial cultural landscapes: relevance to conservation. *Journal of Applied Ecology,* 54(2), 459-469.

Gaget, E., Fay, R., Augiron, S., Villers, A. & Bretagnolle, V. (2019). Long-term decline despite conservation efforts questions Eurasian Stone-curlew population viability in intensive farmlands. *Ibis,* 0(ja).

Gilroy, J.J., Anderson, G.Q.A., Grice, P.V., Vickery, J.A. & Sutherland, W.J. (2010). Mid-season shifts in the habitat associations of Yellow Wagtails *Motacilla flava* breeding in arable farmland. *Ibis,* 152(1), 90-104.

Green, R.E. & Griffiths, G.H. (1994). Use of preferred nesting habitat by stone curlews *Burhinus oedicnemus* in relation to vegetation structure. *Journal of Zoology,* 233(3), 457-471.

Green, R.E., Tyler, G.A. & Bowden, C.G.R. (2000). Habitat selection, ranging behaviour and diet of the stone curlew (*Burhinus oedicnemus*) in southern England. *Journal of Zoology,* 250(2), 161-183.

Gunnarsson, T.G., Sutherland, W.J., Alves, J.A., Potts, P.M. & Gill, J.A. (2012). Rapid changes in phenotype distribution during range expansion in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences,* 279(1727), 411-416.

Härdtle, W., Niemeyer, M., Niemeyer, T., Assmann, T. & Fottner, S. (2006). Can management compensate for atmospheric nutrient deposition in heathland ecosystems? *Journal of Applied Ecology,* 43(4), 759-769.

Harris, S.J., Massimino, D., Eaton, M.A., Gillings, S., Noble, D.G., Balmer, D.E., Pearce-Higgins, J.W. & Woodcock, P. (2019). The Breeding Bird Survey 2018. BTO Research Report 717. British Trust for Ornithology, Thetford.

Hayhow, D.B., Eaton, M.A., Stanbury, A.J., Burns, F., Kirby, W.B., Bailey, N., Beckmann, B., Bedford, J., Boersch-Supan, P.H., Coomber, F., Dennis, E.B., Dolman, S.J., Dunn, E., Hall, J., Harrower, C., Hatfield, J.H., Hawley, J., Haysom, K., Hughes, J., Johns, D.G., Mathews, F., McQuatters-Gollop, A., Noble, D.G., Outhwaite, C.L., Pearce-Higgins, J.W., Pescott, O.L., Powney, G.D. & Symes, N. (2019). The State of Nature 2019. The State of Nature partnership.

Howe, M., Litt, E. & Pye, K. (2012). Rejuvenating Welsh dunes. *British Wildlife,* 24, 85-94.

Hülber, K., Moser, D., Sauberer, N., Maas, B., Staudinger, M., Grass, V., Wrbka, T. & Willner, W. (2017). Plant species richness decreased in semi-natural grasslands in the Biosphere Reserve Wienerwald, Austria, over the past two decades, despite agri-environmental measures. *Agriculture, Ecosystems & Environment,* 243, 10-18.

IUCN/SSC (2013). Guidelines for reintroductions and other conservation translocations. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission, viiii + 57 pp.

Ji, Y., Ashton, L., Pedley, S.M., Edwards, D.P., Tang, Y., Nakamura, A., Kitching, R., Dolman, P.M., Woodcock, P., Edwards, F.A., Larsen, T.H., Hsu, W.W., Benedick, S., Hamer, K.C., Wilcove, D.S., Bruce, C., Wang, X., Levi, T., Lott, M., Emerson, B.C. & Yu, D.W. (2013). Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding. *Ecology Letters,* 16(10), 1245-1257.

Johnston, A. (2009). Demographic analsis of the impact of conservation action on Stone-curlew populations. PhD Thesis, University of Cambridge

Koper, N. & Manseau, M. (2009). Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. *Journal of Applied Ecology,* 46(3), 590-599.

Mallord, J.W., Dolman, P.M., Brown, A. & Sutherland, W.J. (2007a). Nest-site characteristics of Woodlarks *Lullula arborea* breeding on heathlands in southern England: are there consequences for nest survival and productivity? *Bird Study,* 54(3), 307-314.

Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. (2007b). Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology,* 44(1), 185-195.

Malpas, L.R., Kennerley, R.J., Hirons, G.J.M., Sheldon, R.D., Ausden, M., Gilbert, J.C. & Smart, J. (2013). The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland. *Journal for Nature Conservation,* 21(1), 37-47.

Manning, P., Gossner, M.M., Bossdorf, O., Allan, E., Zhang, Y.-Y., Prati, D., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Hölzel, N., Jung, K., Klaus, V.H., Klein, A.M., Kleinebecker, T., Krauss, J., Lange, M., Müller, J., Pašalić, E., Socher, S.A., Tschapka, M., Türke, M., Weiner, C., Werner, M., Gockel, S., Hemp, A., Renner, S.C., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Weisser, W.W. & Fischer, M. (2015). Grassland management intensification weakens the associations among the diversities of multiple plant and animal taxa. *Ecology,* 96(6), 1492-1501.

Maslo, B., Leu, K., Faillace, C., Weston, M.A., Pover, T. & Schlacher, T.A. (2016). Selecting umbrella species for conservation: a test of habitat models and niche overlap for beach-nesting birds. *Biological Conservation,* 203, 233-242.

Morato, R.G., Connette, G.M., Stabach, J.A., De Paula, R.C., Ferraz, K.M.P.M., Kantek, D.L.Z., Miyazaki, S.S., Pereira, T.D.C., Silva, L.C., Paviolo, A., De Angelo, C., Di Bitetti, M.S., Cruz, P., Lima, F., Cullen, L., Sana, D.A., Ramalho, E.E., Carvalho, M.M., da Silva, M.X., Moraes, M.D.F., Vogliotti, A., May, J.A., Haberfeld, M., Rampim, L., Sartorello, L., Araujo, G.R., Wittemyer, G., Ribeiro, M.C. & Leimgruber, P. (2018). Resource selection in an apex predator and variation in response to local landscape characteristics. *Biological Conservation,* 228, 233-240.

Morrison, C.A., Robinson, R.A., Clark, J.A. & Gill, J.A. (2016). Causes and consequences of spatial variation in sex ratios in a declining bird species. *Journal of Animal Ecology,* 85(5), 1298-1306.

Panter, C.J., Mossman, H.L. & Dolman, P.M. (2013). *Stanford Training Area (STANTA) biodiversity audit to support grass heath management*. University of East Anglia, Norwich.

Pearce-Higgins, J.W., Grant, M.C., Robinson, M.C. & Haysom, S.L. (2007). The role of forest maturation in causing the decline of Black Grouse *Tetrao tetrix*. *Ibis,* 149(1), 143-155.

Pedley, S.M. & Dolman, P.M. (2014). Multi-taxa trait and functional responses to physical disturbance. *Journal of Animal Ecology,* 83(6), 1542-1552.

Pedley, S.M., Franco, A.M.A., Pankhurst, T. & Dolman, P.M. (2013). Physical disturbance enhances ecological networks for heathland biota: A multiple taxa experiment. *Biological Conservation,* 160, 173-182.

Pollander, K.M., Little, A.R., Hinton, J.W., Byrne, M.E., Balkcom, G.D. & Chamberlain, M.J. (2019). Seasonal habitat selection and movements by mottled ducks. *The Journal of Wildlife Management,* 83(2), 478-486.

Rickenbach, O., GrÜEbler, M.U., Schaub, M., Koller, A., Naef-Daenzer, B. & Schifferli, L.U.C. (2011). Exclusion of ground predators improves Northern Lapwing *Vanellus vanellus* chick survival. *Ibis,* 153(3), 531-542.

Ridding, L.E., Bullock, J.M., Pescott, O.L., Hawes, P., Walls, R., Pereira, M.G., Thacker, S.A., Keenan, P.O., Dragosits, U. & Pywell, R.F. (2020). Long-term change in calcareous grassland vegetation and drivers over three time periods between 1970 and 2016. *Plant Ecology*.

Robertson, D. & Hawkes, R.W. (2017). Nature conservation, ground disturbance and protecting archaeological remains on Brecks heaths. *The Journal of Breckland Studies,* 1, 68-79.

Rodwell, J.S. (1991). *British Plant Communities. Volume 2: Mires and Heaths*. Cambridge University Press, Cambridge.

Rodwell, J.S. (1992). *British Plant Communities. Volume 3: Grasslands and Montane Vegetation*. Cambridge University Press, Cambridge.

Sandom, C.J., Hughes, J. & Macdonald, D.W. (2013). Rewilding the Scottish Highlands: Do Wild Boar, *Sus scrofa*, use a suitable foraging strategy to be effective ecosystem engineers? *Restoration Ecology,* 21(3), 336-343.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S. & Weisser, W.W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature,* 574, 671-674.

Stanbury, A., Brown, A., Eaton, M., Aebischer, N., Gillings, S., Hearn, R., Noble, D., Stroud, D. & Gregory, R. (2017). The risk of extinction for birds in Great Britain. *British Birds,* 110, 502-517.

Suter, W., Graf, R.F. & Hess, R. (2002). Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conservation Biology,* 16, 778–788.

Taylor, E.C., Green, R.E. & Perrins, J. (2007). Stone-curlews *Burhinus oedicnemus* and recreational disturbance: developing a management tool for access. *Ibis,* 149(s1), 37-44.

ter Braak, C.J.F. & Šmilauer, P. (2015). Topics in constrained and unconstrained ordination. *Plant Ecology,* 216(5), 683-696.

Tipping, E., Davies, J.A.C., Henrys, P.A., Jarvis, S.G., Rowe, E.C., Smart, S.M., Le Duc, M.G., Marrs, R.H. & Pakeman, R.J. (2019). Measured estimates of semi-natural terrestrial NPP in Great Britain: comparison with modelled values, and dependence on atmospheric nitrogen deposition. *Biogeochemistry,* 144(2), 215-227.

Trochet, A., Courtois, E.A., Stevens, V.M., Baguette, M., Chaine, A., Schmeller, D.S., Clobert, J. & Wiens, J.J. (2016). Evolution of sex-biased dispersal. *The Quarterly Review of Biology,* 91(3), 297-320.

van Eeden, R., Whitfield, D.P., Botha, A. & Amar, A. (2017). Ranging behaviour and habitat preferences of the Martial Eagle: Implications for the conservation of a declining apex predator. *PLOS ONE,* 12(3), e0173956.

Van Klink, R. & WallisDeVries, M.F. (2018). Risks and opportunities of trophic rewilding for arthropod communities. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 373(1761).

Vessby, K., Söderström, B., Glimskär, A. & Svensson, B. (2002). Species-richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology,* 16(2), 430-439.

Wang, Y., Naumann, U., Wright, S.T. & Warton, D.I. (2012). mvabund– an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution,* 3(3), 471-474.

Webb, J., Heaver, D., Lott, D., Dean, H.J., van Breda, J., Curson, J., Harvey, M.C., Gurney, M., Roy, D.B., van Breda, A., Drake, M., Alexander, K.N.A. & Foster, G. (2018). Pantheon - database version 3.7.6. Available at: http://www.brc.ac.uk/pantheon/ (accessed on 17/12/2018).

Wells, T.C.E., Sheail, J., Ball, D.F. & Ward, L.K. (1976). Ecological studies on the Porton ranges: Relationships between vegetation, soils and land-use History. *Journal of Ecology,* 64(2), 589-626.

Wood, T.J., Holland, J.M. & Goulson, D. (2015). Pollinator-friendly management does not increase the diversity of farmland bees and wasps. *Biological Conservation,* 187, 120-126.

Woodcock, B.A. & Pywell, R.F. (2010). Effects of vegetation structure and floristic diversity on detritivore, herbivore and predatory invertebrates within calcareous grasslands. *Biodiversity and Conservation,* 19(1), 81-95.

Wright, L. (2007). Demography and productivity of woodlark (*Lullula arborea*) in Breckland. PhD thesis, University of East Anglia

Zielonka, N.B., Hawkes, R.W., Jones, H., Burnside, R.J. & Dolman, P.M. (2020). Placement, survival and predator identity of Eurasian Curlew Numenius arquata nests on lowland grass-heath. *Bird Study*, 1-13.

Appendix A

Arocephalus languidus (Hemiptera: Cicadellidae) - A Leafhopper new to Britain

Robert W. Hawkes[a], Steve A. Lane[b], Colin Lucas[c], Jennifer Smart[d,e], Andy Brown[f], & Paul M. Dolman[a]

[a]School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ

[b]5, Lancaster Way, East Winch, King's Lynn, Norfolk, PE32 1NY

[c]49 Mill Road, Beccles, Suffolk, NR34 9UT

[d]RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL

[e]School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ

[f]Natural England, Suite D Unex House Bourges Boulevard, Peterborough, PE1 1NG

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1. Abstract

The leafhopper *Arocephalus languidus* (Florf) is reported here as a species new to Britain on the basis of three specimens found on the Stanford Training Area in Breckland, West Norfolk (VC28). The specimens, which were all male, were collected from a composite of six pitfall traps, between 19th and 26th September 2017, on a first-time shallow-cultivated Breckland grass-heath, as part of a wider study to assess the multi-taxa consequences of landscape-scale experimental management. The species is known from Iceland and many other European countries including France, Belgium and Germany. The location and circumstances of capture suggest that this species is an overlooked native rather than an introduction or recent colonist.

1. Introduction

The first specimens of the cicadellid *Arocephalus languidus* (Flor) for Britain were collected as part of an extensively monitored and replicated landscape-scale management experiment across the largest remaining extent of grass-heath in the UK, the Stanford Military Training Area (STANTA) (0°76'E, 52°51'N, 3,500 ha) in Breckland, eastern England.

Breckland is a biogeographical region characterised by a semi-continental climate, sandy, nutrient-poor soils and a history of grazing with episodic cultivation (Dolman & Sutherland 1992). Within remaining grass-heaths, bare-open ground supports a large number of range-restricted, rare and/or threatened species, some in numbers of international significance (Dolman & Sutherland 1992; Dolman, Panter & Mossman 2012; Pedley, Franco, Pankhurst & Dolman 2013). However, these internationally important sites have deteriorated over the last few decades due to the loss of the dynamic processes that historically created the conditions required by many of these species (e.g. rabbit grazing, turf removal, and episodes of arable cultivation) (Fuller, Williamson, Barnes & Dolman 2017).

The experiment, conducted between 2015 and 2017, was investigating the efficiency of physical ground disturbance as a conservation measure to increase the biodiversity value of lightly-grazed and undisturbed grass-heath (66 treatment and 40 control plots; totalling 248ha), across different combinations of underlying soil type (deep sands *vs* rendzina soils) and grass-heath ages. Subsequent multi-taxa monitoring focused on birds, plants and invertebrates (Araneae, Coleoptera, Hemiptera, and aculeate Hymenoptera).

All three *A. languidus* were pitfall-trapped at TL8890 from a single 1ha subplot between the 19th and 26th September 2017. No specimens were caught during two prior trapping rounds (late May/early June, and late July/early August). The subplot (Fig. A.1) had been cultivated for the first time seven months prior, with a rotary rotovator, and was located in grassland that was arable land less than 86 years ago (Sheail 1979) on deep moderately acidic sands (although previously ‘marled’ by addition of chalk material when arable). The locality was on a slight south-facing slope, 150 m away from an 8ha Scots pine *Pinus sylvestris* plantation. In April 2017, vascular plants were recorded from 16 evenly spaced 1m^2 quadrats in the subplot. Fourteen species of grass were found, four of which were present in at least half of the quadrats (*Festuca rubra, Holcus lanatus,* *Koeleria macrantha* and *Phleum pratense agg.*) (Table A.1). Sixteen other species of Hemipitera were recorded from the subplot by pitfall trapping during the same year (Table A.2).

The specimens were collected by Robert Hawkes and identified by Steve Lane with a second opinion given by Colin Lucas (Norfolk County recorder for Auchenorrhyncha). Dr Alan Stewart of the UK Auchenorrhyncha Recording Scheme subsequently confirmed this as the first record for Britain.

Figure A.1. The first-time shallow-cultivated subplot where *Arocephalus languidus* was collected in September 2017. Photograph taken in February 2017. Photo: Robert Hawkes.

Table A.1. Frequency of occurrence of vascular plant species from 16 quadrats in the *Arocephalus languidus* subplot in April 2017.

Species	**Frequency**	**Species**	**Frequency**
Agrostis capillaris	3	*Koeleria macrantha*	9
Anthoxanthum odoratum	7	*Leontodon autumnalis*	1
Arabis hirsuta	2	*Lolium perenne*	5
Arenaria serpyllifolia	7	*Lotus corniculatus*	7
Bromus hordeaceus	6	*Luzula campestris*	6
Capsella bursa-pastoris	5	*Medicago lupulina*	2
Cerastium fontanum	2	*Phleum pratense agg*	14
Cerastium glomeratum	12	*Pilosella officinarum*	16
Cirsium arvense	3	*Plantago lanceolata*	16
Convolvulus arvensis	2	*Poa pratensis*	5
Conyza canadensis	1	*Reseda lutea*	7
Dactylis glomerata	7	*Rumex acetosella*	8
Erodium cicutarium	1	*Sonchus oleraceaus*	1
Erophila verna	1	*Stellaria graminea*	1
Festuca ovina	7	*Taraxacum officinale agg*	15
Festuca rubra	10	*Thymus pulegioides*	6
Galium saxatile	2	*Trifolium repens*	14
Galium verum	7	*Urtica dioica*	3
Geranium molle	13	*Veronica arvensis*	1
Glechoma hederacea	1	*Veronica chamaedrys*	7
Helictotrichon pubescens	2	*Vicia lathyroides*	1
Holcus lanatus	12	*Vicia sativa*	1

Table A.2. Hemiptera recorded in the *Arocephalus languidus* subplot from a composite of six pitfall-traps deployed on three occasions (30th May to 6th June, 26th July to 2nd August, and 19th to 26th September 2017; totalling 126 trap days). Abundance refers to the number of individual specimens of each species across all trapping rounds.

Species	**Abundance**
Acalypta parvula (Fallén)	2
Agramma laetum (Fallén)	1
Anoscopus albifrons (Linnaeus)	2
Aphrodes makarovi complex	1
Arocephalus languidus (Flor)	3
Chlamydatus pullus (Reuter)	2
Conostethus roseus (Fallén)	2
Deltocephalus pulicaris (Fallén)	2
Doratura stylata (Boheman)	1
Graphocraerus ventralis (Fallén)	1
Kalama tricornis (Schrank)	1
Kosswigianella exigua (Boheman)	1
Orius niger (Wolff)	1
Psammotettix cephalotes (Herrich-Schäffer)	2
Psammotettix nodosus (Ribaut)	5
Recilia coronifera (Marshall)	1
Turrutus socialis (Flor)	21

2. Description

The following description is taken from Biedermann and Niedringhaus (2009) and our own personal observations. Superficially, the appearance is of a more-or-less uniformly dull yellow-green *Arocephalus* (Fig. A.2), very similar to the only other representative from Britain from the genus; *Arocephalus punctum* (Flor), which was also recorded from this experiment in 2017. However, it differs from that species in lacking the characteristic black spot towards the apex of the wing and also in the absence of any dark streaks on the vertex. All three of the Stanford Training Area (STANTA) specimens exhibit diffuse dark edging to the apical cells, a characteristic that can be shared by *A. punctum.*

The most obvious difference between the two taxa is in the form of the aedeagus (Fig. A.2). In *A. languidus* the base of the structure forms a broad roughly triangular 'back-plate' which is similar to that found in *Psammotettix* males. The aedeagus shaft is thin and near its apex, there is a short, centrally-positioned longitudinal slit resembling the thread-hole of a needle. Two distinct long and down-curved appendages are situated at the apex, each approximately one-third the length of the shaft. Also diagnostic are the form of the male genital valve and sub-genital plates which have rounded apices. The right style from above is slightly both narrowed and curved at its apex.

In *A*. *punctum,* by contrast, the basal back-plate is a narrow, laterally indented structure, whilst the appendages, of which there are two sets, are appreciably shorter (approximately one-fifth the length of the shaft) and the longer sub-apical set is barely-curved in an upward direction. The male genital valve and sub-genital plates are pointed and truncated respectively and the apex of the right style from above is nearly straight.

The female of *A*. *languidus* has a blunt and indistinct projection centrally at the apex of the seventh abdominal sternite. In *A*. *punctum,* by comparison, the apical edge of the sternite is slightly concave.

Biedermann and Niedringhaus (2009) state that *A*. *languidus* is smaller than *A*. *punctum* and give a size range for males of 2.2 - 2.6 mm and for females of 2.4 - 2.9 mm. Corresponding ranges for *A*. *punctum* are given as 2.4 - 3.1 mm and 2.4 - 3.2 mm respectively. Two of the three STANTA specimens exceed 2.6 mm in length (3.0mm and 2.9mm); the third measured 2.5 mm. The specimens had been preserved in dilute methylated sprit for approximately six months and it is possible that some abdominal distension had occurred to effect an increase in length. Equally possible explanations for the length discrepancy between the STANTA specimens and the literature may be that the British population has a greater size range than the mainland European populations or that the STANTA specimens are merely at the upper end of a size range that is currently inadequately represented by mainland European sampling to date.

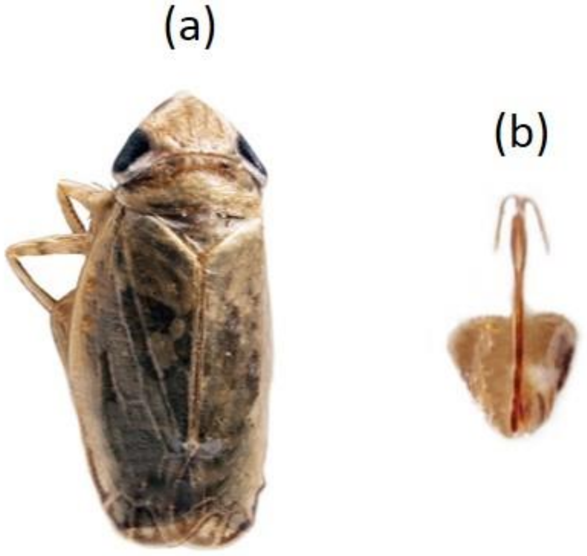

Figure A.2. Image of (a) one of the *Arocephalus languidus* specimens, and (b) aedeagus. Photo: Annabelle Horton.

3. Distribution and ecology

The species is known from Iceland and many other European countries including France, Belgium and Germany (Ossiannilsson 1983). Biedermann and Niedringhaus (2009) state that the species is found 'in dry grasslands, also open forests; on grasses (*Sesleria, Stipa, Koeleria*)', whilst Nickel (2003) states that the species is found 'in moderately dry to dry, sunny to moderately shady sites on basic as well as acidic, gravelly to loamy substrates, usually in various types of xerothermic grassland (also with stands of pine or oak) as well as in pastures and meadows of the subalpine and alpine belt'. Nickel (2003) also states that the host plants are *Sesleria albicans*, *Stipa* spp, and probably *Koeleria glauca*. The association of *A. languidus* with xerothermic grasslands is consistent with its occurrence within Breckland, that supports numerous other xerothermic plant and invertebrate species with a continental or Mediterranean distribution (Dolman, Panter & Mossman 2010). It is possible that *Koeleria macrantha*, which was present on the same STANTA subplot from which *A. languidus* was recorded (Table. 1), is the host plant here, though further research is required to establish this.

4. Discussion

A. languidus may have an established but overlooked population in Britain, given three specimens were found together on an inland site which has been closed to the public since the 1940's. However, it is noteworthy that it has only occurred in one of 181 sampling units, 18 of which were within a 1km radius of the location where the specimens were caught (two of which were managed the same way). It is quite likely that the species has been overlooked elsewhere on the site, particularly as pitfall trapping alone is not regarding as the preferred method for Auchenorrhyncha sampling (Drake, Lott, Alexander & Webb 2007). Given the specimens were from a first-time shallow-cultivated plot this management may be beneficial for the species, though we intend to undertake further surveys employing a wider suite of sampling methods in an effort to locate additional individuals and establish the true extent of the population and its ecology at STANTA, and potentially other grass-heaths in this region. This in turn will help to inform subsequent conservation action.

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References

Biedermann, R. & Niedringhaus, R. (2009). *The plant and leafhoppers of Germany – identification key to all species*. Wissenschaftlich Akademischer Buchvertrieb – Frűnd, Scheeßel, Germany.

Dolman, P.M., Panter, C. & Mossman, H.L. (2010). *Securing biodiversity in Breckland: guidance for conservation and research. First report of the Breckland biodiversity audit*. University of East Anglia, Norwich.

Dolman, P.M., Panter, C.J. & Mossman, H.L. (2012). The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *Journal of Applied Ecology,* 49, 986-997.

Dolman, P.M. & Sutherland, W.J. (1992). The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology,* 29(2), 402-413.

Drake, C.M., Lott, D.A., Alexander, K.N.A. & Webb, J. (2007). Surveying terrestrial and freshwater invertebrates for conservation evaluation. Natural England Research Report NERR005.

Fuller, R.J., Williamson, T., Barnes, G. & Dolman, P.M. (2017). Human activities and biodiversity opportunities in pre-industrial cultural landscapes: relevance to conservation. *Journal of Applied Ecology,* 54(2), 459-469.

Nickel, H. (2003). *The leafhoppers and planthoppers of Germany (Hemiptera, Auchenorrhyncha): patterns and strategies in a highly diverse group of phytophagous insects.* . Pensoft series faunistica No 28. Pensoft Publishers, Sofia-Moscow wt Goecke & Evers, Keltern.

Ossiannilsson, F. (1983). *The Auchenorrhyncha (Homoptera) of Fennoscandia and Denmark. Part 3: The family Cicadellidae: Deltocephalinae, catalogue, literature and index*. Fauna Entomologica Scandinavica. Copenhagen. Vol. 7. Pt. 3.

Pedley, S.M., Franco, A.M.A., Pankhurst, T. & Dolman, P.M. (2013). Physical disturbance enhances ecological networks for heathland biota: A multiple taxa experiment. *Biological Conservation,* 160, 173-182.

Sheail, J. (1979). Documentary evidence of the changes in the use, management and appreciation of the grass-heaths of Breckland. *Journal of Biogeography,* 6(3), 277-292

Appendix B

Placement, survival and predator identity of Eurasian Curlew *Numenius arquata* nests on lowland grass-heath

Natalia B. Zielonka[a], Robert W. Hawkes[b], Helen Jones[c], Robert J. Burnside[b], Paul M. Dolman[b]

[a]School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK
[b]School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK
[c]RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

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Note, this published paper in furtherance of a previous University of East Anglia dissertation thesis submitted by Natalia Zielonka in August 2018 as part of the Applied Ecology and Conservation MSc course. The contributions of each author are detailed on page 10 of the present thesis.

Photo credit:
Natalia Zielonka

Abstract

Capsule: Within the UKs largest lowland Eurasian Curlew *Numenius arquata* population, Curlew preferentially nested on physically-disturbed (treated) than undisturbed (control) grassland, and low nest survival rates were primarily attributable to Red Fox *Vulpes vulpes.*

Aims: To inform conservation interventions for Curlew within semi-natural lowland dry-grassland landscapes.

Methods: Across a 3,700 ha lowland dry-grassland landscape, over two years, effects of ground-disturbance management on Curlew nest placement (n=41) were examined using GLMs controlling for vegetation strata; effects of site and management on nest survival (n=44) were examined controlling for lay date and year. Nest predator identity was investigated using temperature sensors (n=28) and nest cameras (n=10).

Results: Curlews were five times more likely to nest on physically-disturbed than undisturbed grassland. Nest survival (overall mean 0.24 ± 0.07, SE) was not influenced by year or ground-disturbance but declined with lay date and differed markedly between the two sites, consistent with predator control. Predation accounted for 29/32 of failed nests and was predominantly at night (17/23 cases where timing was known, $p<0.001$), consistent with mammalian predators. Cameras indicated Foxes to be the main predator (4/5 cases). Overall breeding productivity was 0.16 ± 0.01 (SE) chicks per nesting attempt.

Conclusion: Curlew suffered from unsustainably high rates of nest predation primarily attributable to Foxes. A combination of perimeter fencing and lethal predator control appeared to improve nest success at one site. Ground-disturbance treatment could encourage nesting attempts in areas managed to minimise predator density.

Keywords: Nest predation, nest survival, Red Fox, *Vulpes vulpes*, wader, ground-disturbance management

1. Introduction

Global wader (shorebird) populations are declining (Butchart *et al.*, 2010), primarily due to habitat loss and degradation through agricultural intensification and climate change (Pearce-Higgins *et al.*, 2017, Franks *et al.*, 2017). Almost half of European wader populations for which trends are known are either IUCN Threatened or declining (Stroud *et al.,* 2006) and in the UK, 16 of 20 breeding wader species are classified nationally as IUCN Threatened (Stanbury *et al.,* 2017). One such species is the Eurasian Curlew *Numenius arquata* (hereafter 'Curlew'), which has been recently classified nationally as Threatened. As a result of the species' global conservation status (IUCN Near Threatened; BirdLife International 2017), the international significance of the UK breeding population (~68,000 breeding pairs, accounting for over a quarter of the global breeding population; Musgrove *et al.* 2013, Hayhow *et al.*, 2017), and its long-term decline (65% between 1970-2015; Hayhow *et al.*, 2017), Curlew are considered to be the UK's highest bird conservation priority (Brown *et al.*, 2015). Although the number of Curlew in the UK uplands (including moorland: upland heath, bog and unenclosed grassland; and enclosed upland grassland) is not known with precision, these hold the majority of the population, where considerable research has focused on their breeding ecology and conservation (Douglas *et al.,* 2017; Johnstone *et al.,* 2017). Although lowland Curlew are less studied, their loss would reduce the species' breeding range, increasing the dependence on vulnerable upland populations (Baldock *et al.*, 2017).

The main driver of UK Curlew decline is low breeding productivity, attributable to predation and reduced quality of breeding habitats (Franks *et al.*, 2017; Hayhow *et al.*, 2017). Research from the uplands has informed habitat provision (e.g. controlled cutting of moorland to provide a mosaic of vegetation heights and creation of pools, Fisher & Walker 2015) and demonstrated that legal predator control (of Red Fox *Vulpes vulpes,* hereafter 'Fox', Carrion Crow *Corvus corone*, hereafter 'Crow', Stoat *Mustela erminea* and Weasel *M. nivalis*) can increase Curlew breeding success and abundance (Fletcher *et al.*, 2010; Ludwig *et al.*, 2019); however, lethal control does not work in all cases (e.g. Bodey *et al.,* 2011, Bolton *et al.* 2007b). In lowland regions of the UK, recent monitoring (Smart, 2017; Curlew Call, 2017) has confirmed low breeding productivity with a mean across studies (weighted by square-root of sample sizes) of 0.23 ± 0.13 SD fledged chicks nesting attempt^{-1} year^{-1} (Table S1), considerably less than the 0.48 - 0.62 pair^{-1} year^{-1}

required for population stability (Grant *et al.*, 1999). Previous research into the predator assemblage and efficacy of anti-predator solutions (e.g. lethal control and anti-predator fencing, Bolton *et al.,* 2007b; Malpas *et al.,* 2013) in lowland habitats, which has focused on other wader species, particularly Northern Lapwing *Vanellus vanellus* (hereafter 'Lapwing')*,* Common Redshank *Tringa totanus* and Common Snipe *Gallinago gallinago*, has demonstrated that nocturnal mammalian predators are the main cause of nest failure (MacDonald & Bolton 2008, Teunissen *et al.,* 2008). However, these findings may not be applicable to lowland Curlew due to differences in nest exposure (Curlew nests are less concealed compared to Common Redshank or Snipe), adult size, social aggregation and habitat preferences (Bolton *et al.,* 2007b). This, along with the vulnerability of Curlew breeding populations, emphasises the need for a study into nest predation (Leyrer *et al.,* 2018).

Most lowland Curlew breed on dry grasslands and heathland (Table S1, Johnstone *et al.,* 2017) where conservation management can radically alter habitat structure. Within these habitats, physical ground-disturbance is increasingly advocated as a land management intervention for other rare, scarce and threatened species, such as Stone-Curlew *Burhinus oedicnemus* and Woodlark *Lullula arborea* (Fuller *et al.*, 2017; Hawkes *et al.*, 2019b); however, it is not known whether this influences Curlew nest placement or breeding success. Understanding whether Curlew nests on disturbed grassland are easily visible to corvid nest predators, or conversely, whether placement of disturbed-plots can be used to manipulate nest placement into areas protected from mammalian predators, would better inform such management on sites with breeding Curlew.

To inform conservation interventions for Curlew, we studied nest placement, nest survival and nest-predator identity within the UK's largest lowland Curlew population (Breckland, Eastern England, Balmer *et al.,* 2013; holding at least 100 breeding pairs but likely more, H. Ewing pers. comm.), across two extensive grass-heath sites (total c. 3,700 ha) that differed in predator density and management. Across both sites, vegetation structure was diversified prior to this study with ground-disturbance plots as part of a wider multi-taxa experiment (see Hawkes *et al.*, 2019a,b), which may influence Curlew nest site selection and productivity. We *a priori* predicted that: (1) Curlew would select undisturbed grassland over disturbed grassland as nesting habitat (given that Curlew prefer rougher habitats with longer swards for nesting: Baines 1988;

Ewing *et al.,* 2018), (2) nest survival would be higher on the site with lower predator density and decrease through the season (informed by Franks *et al.* 2017 and MacDonald & Bolton 2008), and (3) predation events would be attributable to nocturnal mammalian predators (as with other lowland wader species, MacDonald & Bolton 2008).

2. Methods

2.1 Study site

The study was carried out in 2017 and 2018 in Breckland across the Stanford Military Training Area (hereafter 'STANTA', 52.50ºN, 0.71ºE) and Brettenham Heath NNR (0°83'E, 52°43'N). Both sites contain extensive areas of dry grassland and grass-heath (hereafter 'grassland', STANTA 3,500 ha; Brettenham Heath, 200 ha) surrounded by arable farmland and woodland (Fig. B.1). Generalist predator control on STANTA was focussed around pheasant release pens (approximately 130 Foxes were removed annually; 0.03 ha^{-1} $year^{-1}$) but was lacking across remaining parts of STANTA and most of the surrounding arable and woodland. In contrast, Brettenham Heath was subject to continuous predator control across the whole site (10-20 Foxes were removed annually; 0.05-0.1 ha^{-1} $year^{-1}$) with similar levels of intensive control across the surrounding arable farmland (but not woodland). Brettenham Heath is also enclosed by a two-meter high deer fence with a single electric strand set half meter above the ground. Although we lacked the time and resource to compare generalist predator densities between the two sites, we saw at least one Fox during each of seven of the 75 fieldwork days on STANTA, compared to none during 23 fieldwork days on Brettenham Heath (though this ratio did not differ significantly, Fisher Exact test, p=0.194). Both sites are sheep-grazed (approximately one ewe ha^{-1}) with regular scrub and bracken *Pteridium aquilinum* control (see Appendix S1 for additional site management details). STANTA is subject to regular vehicle and soldier movements.

We used the Centre for Ecology and Hydrology Land Cover Map 2015 (LCM2015, Rowland *et al.,* 2017) to identify areas of grassland and dwarf shrub heath across both study sites (hereafter collectively 'grassland', Fig. B.1). Grassland was then categorised based on underlying soil type (NSRI, 2014) and age since last cultivation (Sheail, 1979) to give two vegetation strata which differed in structure and vascular plant composition; 'calcareous/young' and 'older acidic' grassland. Calcareous/young grassland was characterised by shorter swards (4.15 cm, 3.77 - 4.58 95% CI; Hawkes *et al.,* 2019b), comprising a mixture of calcicolous and acidiphilous plant species developed on rendzina or following arable abandonment (73-113 years ago), whilst older acidic grassland (at least 114 years since arable cultivation) was characterised by taller swards (5.14 cm, 4.66 - 5.67 95% CI) mainly comprising acidiphilous plant species (see Appendix S1 for details).

Across both sites, 64 experimental ground-disturbance plots (32 deep-cultivated and 32 shallow-cultivated; see Hawkes *et al*., 2019a for details) were established in early 2015 and subsequently disturbed annually to create: (i) 25 2 ha 'homogenous' plots (13 deep- and 12 shallow-cultivated, repeated annually in the same location), and (ii) 39 4 ha 'complex-mosaic' plots (19 deep- and 20 shallow-cultivated) cultivating half-overlapping and half freshly-disturbed sections building up a mosaic of 1 ha subplots varying in fallow age and disturbance frequency. Potential for unexploded ordnance excluded ground-disturbance plots in the central 'impact area' of STANTA (1,180 ha), restricting treatment plots to Brettenham Heath and outer areas of STANTA (Fig. B.1). In analyses, ground-disturbance treatments were combined as a single 'disturbed grassland' category, with aggregate area of 206 ha in both years of study, comprising ~5.6% of the available grassland extent (~8.2% of available grassland outside the impact area). We did not attempt to model relative preference for deep- or shallow-cultivation, homogenous or complex-mosaic owing to limited statistical power and also as different treatments were not available in each Curlew home range.

Tests of wader nest placement and nest survival frequently consider landscape context (Bertholdt *et al.*, 2017; Laidlaw *et al.,* 2015), however this is problematic in this study. Although woodland may harbour mammalian predators, Foxes also den in rabbit warrens, bracken, scrub and hedgerows, so that distance to woodland is not a reliable proxy for their activity. Woodland may offer perches but Crows also perched on individual trees that were scattered throughout the entire landscape. Arable farmland may also be a source of predators (Roos *et al.,* 2019) and cause disturbances that affect the distribution of nests. However, exploratory modelling showed no effects on nest placement or survival of either distance to woodland or arable farmland; these variables were therefore omitted from subsequent analysis to avoid over-fit models.

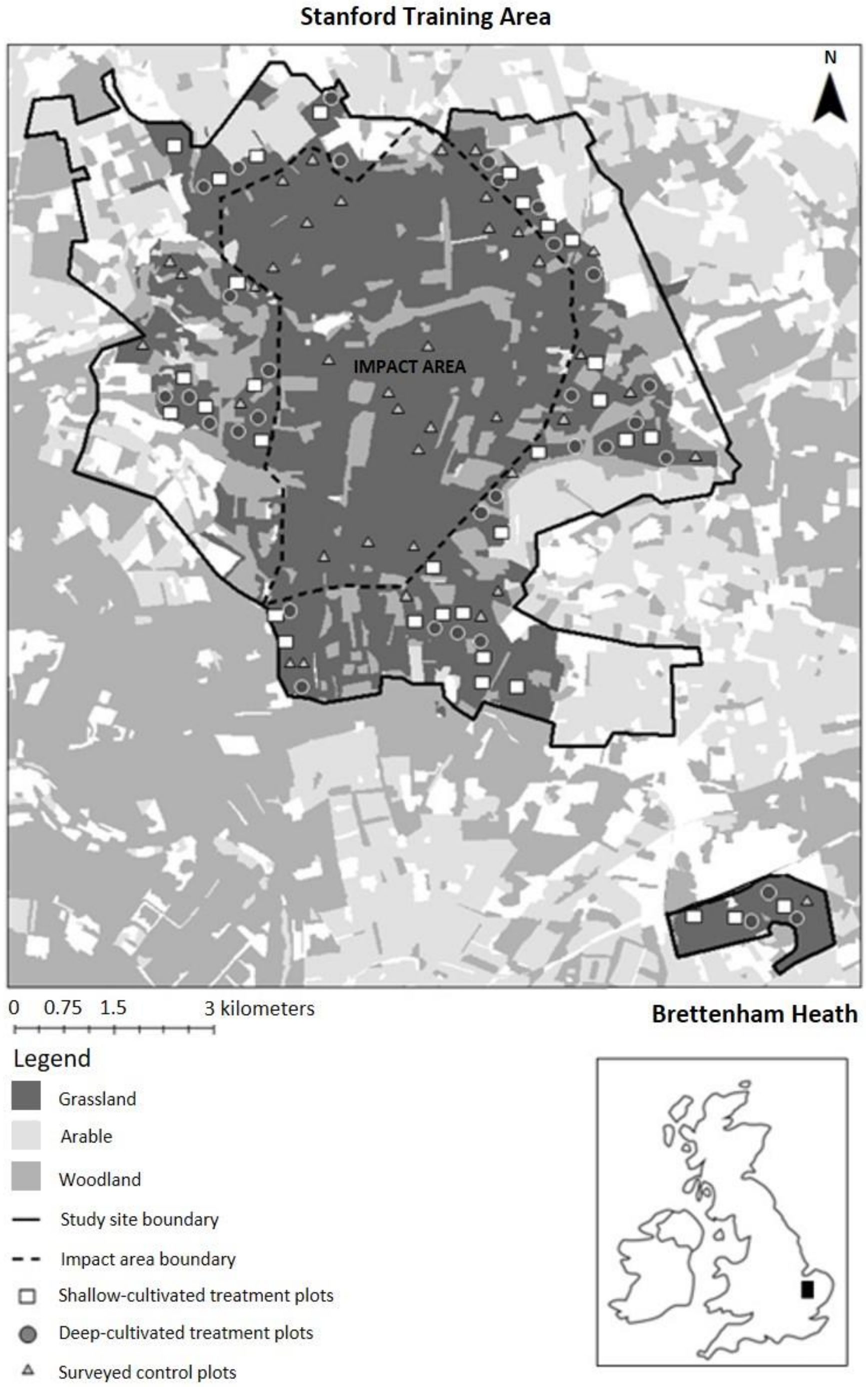

Figure B.1. Surveyed grassland (dark grey, c. 3,700 ha) across the study sites (Stanford Training Area and Brettenham Heath). Symbols (not to scale) show the location of experimental ground-disturbance plots (totalling 206 ha) and grassland controls. The dashed line shows the boundary of the Stanford Training Area 'impact area' (within which ground-disturbance was precluded). Arable farmland and woodland are also shown.

2.2 Nest searching and monitoring

Our approach to locating Curlew territories differed between 2017 and 2018. In 2017, territory-searches focused initially on the 64 ground-disturbance plots, plus 38 4 ha untreated grassland control plots (Hawkes *et al.,* 2019a; see Fig. B.1), with at least three 40-minute visits to each plot between 14 March and 26 June (days between visits: mean 27 ± 7 SD) during still, dry mornings (Beaufort wind force <4) between dawn and 11:00. Additional opportunistic searches were made in 2017 on any grassland areas where Curlew were detected. We are confident that detectability of territories was comprehensive on both Brettenham Heath and outer areas of STANTA. As unexploded ordinance precluded ground-disturbance treatments from the STANTA 'impact area' (Fig. B.1) and furthermore, in 2017 searches in this area were largely restricted to 20 control plots and were not comprehensive; impact area nests were excluded from analyses of nest placement relative to random points (see below). In contrast, in 2018 we conducted systematic searches for Curlew territories across the entire grassland extent (including the impact area), conducted by one observer walking linear transects spaced 250 m apart (following Brown and Shepherd, 1993) repeated three times between 1 April and 8 June (days between visits: 18 ± 6 SD), between dawn and dusk. In both years, the location and behaviour of any detected Curlew was recorded.

In both years, nests were located between mid-April and late June, visiting any area where Curlew had been seen and looking for adults sitting on, or walking back to, the nest. To determine the date and timing of nest failure, temperature sensors were placed under nests (iButtons thermocrons, Maxim Integrated Products Ltd, CA, USA; set to record the temperature every 10 minutes, following Berg, 1992). Nests were remotely checked every three-to-seven days to confirm adults were still incubating, and the scrape was visited once a week to record any predation events (e.g. partial clutch predation). To avoid leaving tracks that could lead predators to nests, observers adopted a different meandering path during subsequent nest visits. It is also important to note that, particularly at STANTA, our activity was superimposed on ubiquitous tracks and scent trails from frequent ground troop and shepherd movements, further reducing the likelihood that Foxes would follow our tracks. From three days before the predicted hatch date (calculated from egg measurements at STANTA only in 2018, following Grant, 1996) nests were remotely monitored daily to accurately determine their fate.

Nest outcome was inferred from visits and temperature sensor data. Successfully hatched nests were characterised by the presence of small shell fragments within the nest cup and the presence of chicks or alarming adults in the area. Nest failure was assumed if nests were found empty before the predicted hatching date and if no adult birds or chicks were seen around the nest site. Failure was attributed to predation if the nest contained shell remains or no eggs (larger predators, particularly Foxes, remove intact eggs, Guilherme *et al.,* 2018) and a sharp permanent decline in temperature (when temperature sensor data were available). Destroyed nests were identified by obvious signs of sheep trampling or freshly cut grass. When temperature sensor data were not available, due to the sensor being removed from the nest (5/28 cases), failure date was calculated as the mid-point between the final two visits (Johnson, 1979). After hatching, the nest site was visited every three-to-five days to observe adults and chicks from a vehicle at a distance, continuing until the chicks fledged (determined by observing chicks flying or their survival to 35 days post-hatching), or the breeding attempt had failed.

Laying date of the first egg (hereafter 'lay date') was estimated in one of three ways. For successful nests with known hatch date, or when expected hatch date of a failed nest was available from egg measurement, lay date was back-estimated allowing for a 29-day incubation (Berg, 1992) and n x 1.5-day laying period (where n = number of eggs in the clutch). When the nest was found during-laying (with clutch size incrementing by the second nest visit), lay date was estimated allowing 1.5 days per egg present at the find date. In remaining cases (n = 16, 33%), when the nest was found after incubation commenced, eggs were not measured and the clutch failed prior to hatching, the lay date was estimated as the mid-point of the earliest and latest possible lay dates, based on find and failure dates (following Mallord *et al.*, 2007; Koshkin *et al.,* 2016).

Where available, temperature sensor data informed classification of diurnal (after sunrise, before sunset), crepuscular (between dawn and sunrise, and between sunset and dusk) and nocturnal (between dusk and dawn) predation events, with nocturnal and crepuscular events attributable to mammalian predators (most likely Fox or Badger *Meles meles*, but potentially also European Hedgehog *Erinaceus europaeus*, as found by Jackson 2001) and diurnal events unattributable (MacDonald & Bolton, 2008). To further validate predator identity, in 2018 infra-red nest cameras were placed at 10 nests on STANTA (as 2017 monitoring indicated a higher incidence of nest predation at STANTA than at Brettenham Heath) following Bolton *et al.* (2007a). The camera (~3.6mm lens, ~30x20x20mm camera head including the hood and infrared array) was placed about a meter from the nest and c. 15 cm above the ground within vegetation (to help concealment), with the battery (between 180x76x167mm and 269x174x225mm) and recording unit buried seven-to-ten meters away to reduce disturbance, trampling or scent in the vicinity of the nest (that could potentially attract a predator) whilst changing batteries. Cameras triggered by movement were set to save five consecutive images within two seconds, with one image before triggering (the device continuously records and temporarily stores frames, but only saves these frames if triggered), and four after, with a five-second pause before it could be triggered again.

2.3 Data analysis

To examine nest placement in relation to ground-disturbance treatments and vegetation strata, we compared characteristics of nest locations to those of random points sampled in ArcGIS 10.3 (ESRI, 2014; 'used-available' design), using Generalised Linear Models (GLMs) with binomial error and log-link, conducted in R (R Core Team 2017). We excluded nests within the STANTA central 'impact area', thereby restricting analyses to areas with both disturbed and undisturbed grassland available (Fig. B.1), and that were comprehensively surveyed in both years. Analyses were conducted separately at the 'study-area' scale, considering the entire grassland area, and the 'home-range' scale, considering grassland with a 164 m radius of each nest site (the distance within which >85% of breeding adults or broods were observed foraging; threshold follows Odum & Kuenzler 1955, see Appendix S2). At both scales, we sampled three times as many random points as nests. At the study-area scale, the placement of control points was restricted to outside the STANTA impact area, and GLMs examined fixed effects of treatment (two levels: disturbed vs. undisturbed grassland) and vegetation strata (two levels: calcareous/young grassland vs older acidic grassland). We did not examine the effects of site on nest placement as the two study sites both contained experimental ground-disturbance plots and were comparable in terms of vegetation structure (Hawkes *et al.,* 2019b). For the home-range scale, we sampled three random points within a 164 m radius (of each nest) and GLMs examined fixed effects of treatment (two levels) but not vegetation strata, as most (38/41) home ranges contained only a single stratum.

To examine factors influencing daily nest survival, GLMs were performed with the number of binomial trials of each nest determined by the number of 'nest days' it was active and monitored, incorporating fixed effects of year (two levels), treatment (two levels), vegetation strata (two levels), site (two levels, reflecting differing predator control effort across sites) and lay date (following Dinsmore *et al.,* 2002), using the RMark 2.2.5 package (Dinsmore & Dinsmore, 2007). Analysis considered all monitored nests as independent observations, as: (i) lack of treatment plots within the impact area affects settlement options but does not bias failure relative to nest-site characteristics; (ii) failure was assumed to be largely caused by stochastic factors independent of parental quality, and (iii) within each year most nests were from different pairs (90% in 2017; 92% in 2018) with few re-nesting attempts. The mean probability of nest success (hatching at least one egg) per nesting attempt was calculated from the product of daily clutch survival rates across the 29-day incubation period. Breeding productivity was quantified as the number of fledglings per nesting attempt, including any re-nesting attempt, as independent observations; it was not possible to estimate productivity per pair per year as adults were unmarked and we could not reliably allocate re-nests to individual pairs. For analysis of nest placement and nest survival, candidate model sets comprising all possible variable combinations were examined using the 'lme4' package. The model with the lowest value of Akaike Information Criterion adjusted for small sample size (AICc) was accepted as 'best' if the difference (ΔAICc) relative to all other candidate models was >2. When multiple models were within two AICc units of the 'best' model, multimodal inference was conducted to estimate model-averaged coefficients across these competing models (following Burnham & Anderson, 2002), using the MuMIn package (Barton, 2019). Candidate variables were considered to be supported where their 95% CI did not span zero (following Burnham & Anderson, 2002; Boughey *et al.,* 2011). Where the fixed effect of treatment was supported in nest placement models, we quantified the probability of selection of disturbed grassland relative to undisturbed grassland (model intercept) using odds ratios derived from the model coefficients. For each analysis, spatial autocorrelation of residuals (from the best or averaged model, as appropriate) was examined, calculating Moran's I in the 'Ape' package (Paradis *et al.*, 2004).

For nests where the timing of nest predation failure was known (through temperature logger or nest camera data) we examined whether predation events were more likely during the night (nocturnal and crepuscular) or day, relating the ratio of observed night/day predation events to the numbers of night/day hours summed across all monitored nest-days (as day length varies through the season), using a 2x2 Fisher Exact test.

Finally, considering all predated nests for which the date and time of failure were known, we used a Fishers Exact test to determine whether nest predation was more likely during the 24 hours following a direct monitoring visit (2x2 Fishers Exact: the number of predation events in relation to the number of nights within 24 hours of a disturbance event, against the numbers of predation events in relation to the number of other nights monitored).

3. Results

3.1 Nest placement

Across the two years of study 46 Curlew nests were located (2017, 20 including two re-nests; 2018, 26 including two re-nests). Of these, 41 were outside the impact area (2017, 17 nests; 2018, 24 nests), with 20 (49%) on disturbed grassland (17 on shallow-cultivated and three on deep-cultivated treatments) and 21 (51%) on undisturbed grassland.

For models of nest placement, at the study-area scale multi-model inference was undertaken across two candidate models within <2 AICc units (Table S2) and at the home-range scale the best-supported model was >2 AICc relative to all other models. At both spatial scales, Curlew were five- to six-times more likely to select disturbed than undisturbed grassland as nesting habitat (Fig. B.2; study-area scale, odds ratio = 5.16, 95% CI: 2.0 – 13.3; home-range scale, odds ratio = 6.3, 95% CI: 2.8 – 14.6). No effect of vegetation strata was found in the study-area scale averaged model (vegetation strata was not considered in the home-range scale analysis). Modelled residuals from nest placement analyses were not spatially autocorrelated.

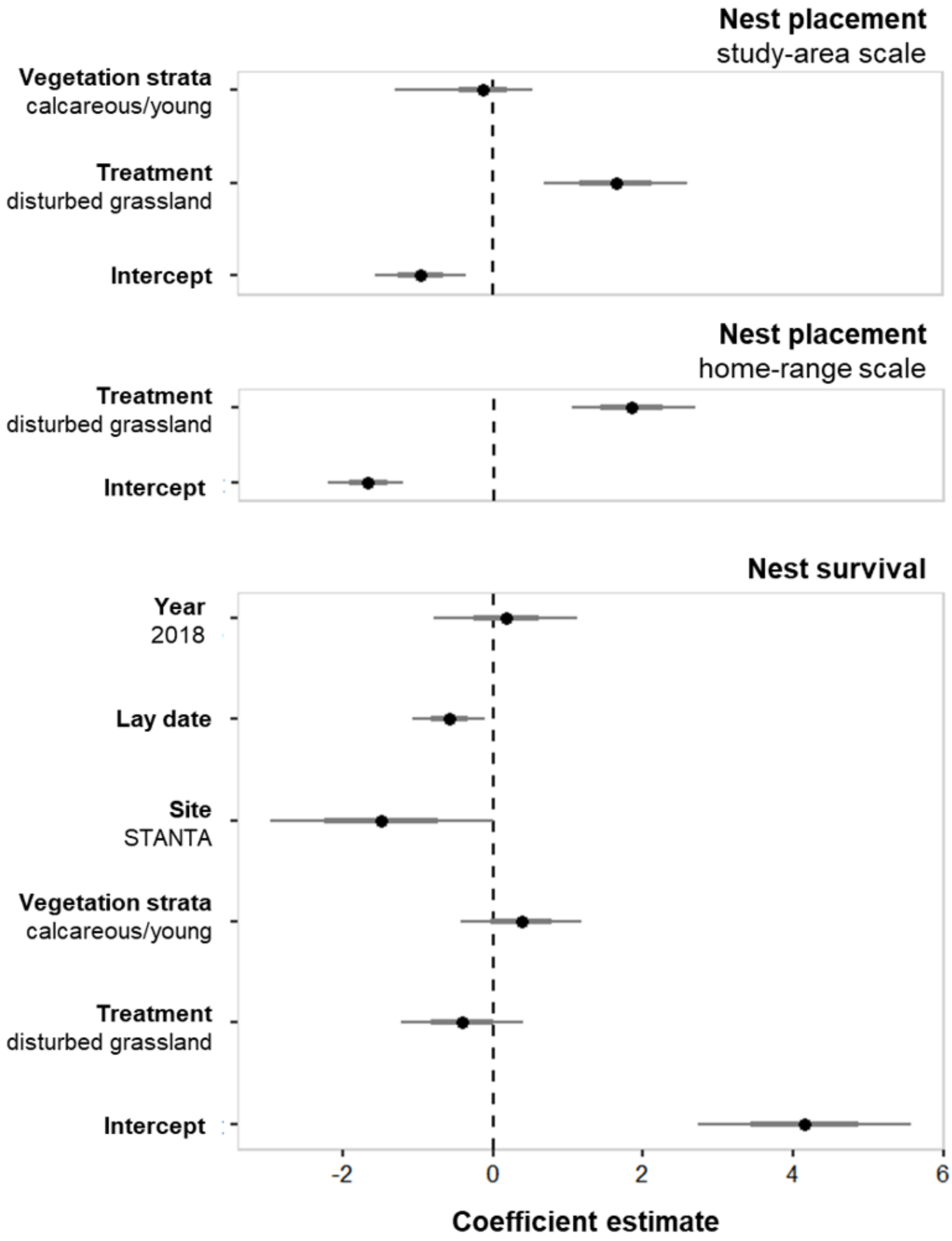

Figure B.2. Coefficient estimates from models relating Eurasian Curlew *Numenius arquata*: i) nest placement at the study-area and home-range scale to treatment (two levels, reference level undisturbed grassland) and vegetation strata (study-area scale model only: two levels, reference level older acidic grassland); and ii) nest survival to treatment, vegetation strata, year (two levels, reference level 2017), site (two levels, reference level Brettenham Heath) and lay date (continuous), showing model coefficients (black dot), standard error (thick grey line) and 95% CI (thin grey line). Variables were deemed to be supported when their 95% CIs did not span zero (dashed line).

3.2 Nest survival

Excluding two nests with zero observation days (found at or after failure or hatching), 44 nests were monitored (for 557 nest-days) of which 32 failed (Brettenham Heath: 3 of 11, STANTA 29 of 33), with 29 predated (Brettenham Heath: 3, STANTA: 26), one trampled by livestock (STANTA), one destroyed by grass cutting (STANTA) and one deserted (a single-egg re-nest late in the season at STANTA). Mean overall nest survival probability from start of incubation to hatching was 0.24 ± 0.07 SE (Brettenham Heath: 0.70 ± 0.18 SE, STANTA: 0.16 ± 0.06). Overall breeding productivity was 0.16 ± 0.01 SE fledged chicks per nesting attempt.

For analysis of daily nest survival rate, multi-model inference was undertaken across four candidate models within <2 AICc units (Table S2). The effects of lay date and site were supported; daily nest survival rate decreased through the nesting season and was greater at Brettenham Heath than at STANTA (Fig. B.2, Fig. B.3). No support was found for effects of treatment, vegetation strata or year (Fig. B.2). Residuals of the averaged-model were not spatially autocorrelated.

3.3 Timing of nest failure and predator identity

Of the ten 2018 nests with nest cameras: three survived to hatching; four were predated by Fox (one diurnal and three nocturnal; Fig. B.4, Digital material 1); one was predated by an unknown predator (following camera malfunction); one was predated by a Sheep *Ovis aries* (two out of four eggs remained but incubation was not resumed and the clutch was classified as failed; Digital material 2) and a single-egg late-season re-nesting attempt was abandoned three days after camera deployment (with failure therefore not directly attributable to the installation). For all four confirmed fox-predation events, the scrapes were undisturbed, and no shell fragments remained. In one predated nest without a camera, large shell fragments were found with teeth marks, which suggested a further predation event attributable to a Fox (following Green *et al.,* 1987). Cameras also recorded an unsuccessful predation attempt by a Crow, fended off by the incubating Curlew (Digital material 3), and two instances of Crows scavenging abandoned clutches; one 29 hours after the partial-predation by a sheep (that had already resulted in complete clutch failure), the second five hours after the late-season desertion of a re-nesting attempt. There was no effect of nest cameras on daily nest survival rate (see Appendix S3).

The timing of failure was known for 23 predated nests (28/29 predated nests were fitted with temperature loggers but five were removed from the nest by the bird) of which 17 events were during the night (13 nocturnal, four crepuscular) and six during the day (Fig. B.4). Relative to the ratio of night/day hours monitored (pooled across each nest-day monitored, ratio 0.50) predation more often occurred at night (night/day ratio, 2.83) than expected by chance (Fisher Exact test, p<0.001). Nest predation did not occur more frequently during the 24 hours following a disturbance event caused by monitoring (three predation events <24 hours after a disturbance event, n=52, 20 predation events >24 hours after disturbance, n=164; Fisher Exact test, p=0.303).

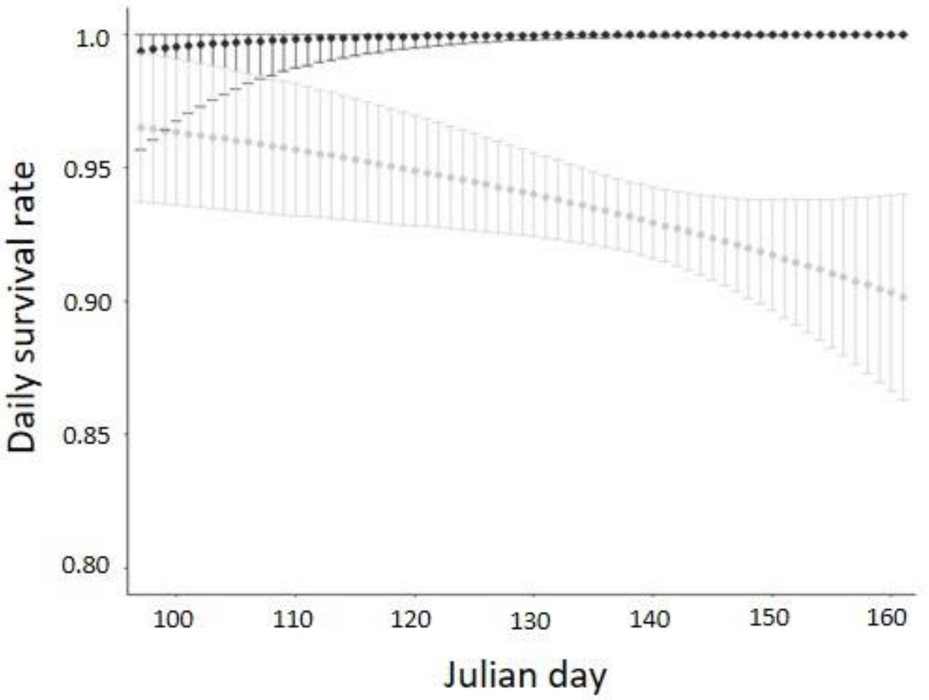

Figure B.3. Estimated variation in the daily nest survival probability for Eurasian Curlew *Numenius arquata* within the Stanford Training Area (black) and Brettenham Heath (grey) in 2017 and 2018. Estimates are based on multi-model inference (Table S2, see Fig. B.2 for included variable). Vertical bars show SE.

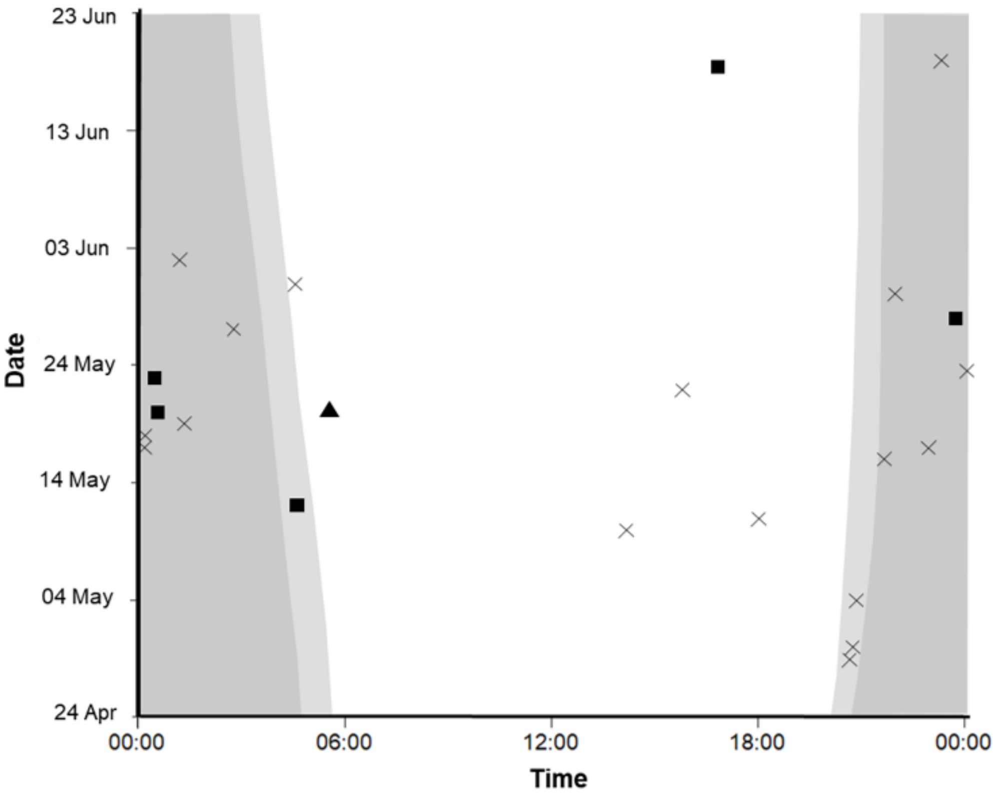

Figure B.4. Date and time of 23 Eurasian Curlew *Numenius arquata* nest predation events across two years of study. Light shading indicates crepuscular (between dawn and sunrise, and between sunset and dusk) and darker shading indicates nocturnal (between dusk and dawn) periods. Symbols indicate predation events: crosses denote cases where the predator identity was not known, squares denote predation by Red Fox *Vulpes vulpes*, and a triangle predation by a Sheep *Ovis aries*.

4. Discussion

Through a two-year study on one of the UK's largest remaining semi-natural grassland sites, we have demonstrated that breeding Curlew selectively placed nests on physically-disturbed grassland (deep-cultivated by ploughing, or shallow-cultivated by rotovation) over undisturbed grassland. Overall breeding productivity was low due to high rates of nest predation, primarily attributed to Foxes. While nest survival was not influenced by ground-disturbance treatment, it decreased with lay date and was substantially lower at STANTA than at Brettenham Heath; probably due to differences in Fox activity between these two sites (though this was not directly measured). As far as we are aware, this is the first study to simultaneously investigate Curlew nest placement, survival and predator identity within a lowland system.

4.1 Nest placement

Contrary to our predictions, Curlew were five- to six-times more likely to select nest-sites on physically-disturbed than undisturbed grassland, with 48.7% of nests located on disturbed grassland across both years, which only occupied ~8.2% of the grassland area. Curlew are long-lived and site-faithful (Currie *et al.*, 2001); as ground-disturbance was first applied two years prior to this study, treated plots may have been created within already-established breeding territories, rather than influencing territory settlement. However, analysis of nest placement relative to random locations within home-ranges showed nests were more frequently placed on disturbed than undisturbed grassland relative to availability.

Disturbed grassland is characteristically bare and short compared to uncultivated grassland (Dolman & Sutherland, 1994; Hawkes *et al.,* 2019b). Curlew may have placed nests on this habitat because it allows greater vigilance (to facilitate and evade predator detection, Amat & Masero, 2004) and a greater abundance of some important prey (confirmed experimentally by Hawkes *et al.,* 2019b) than the surrounding grassland. Although we did not examine whether ground-disturbance detail matters (to avoid overparameterizing the models), most nests were on shallow-cultivated plots (n = 17, 41.5%), with few on deep-cultivated plots (n = 3, 7.3%). It is possible that the likelihood of attracting nest placement is greater on shallow-cultivated grassland, though further work is needed to establish this.

4.2 Nest survival

Nest survival was low and re-nesting following failure appeared infrequent. Annual productivity was lower than found in other lowland UK Curlew populations (Call of the Curlew 2017, Table S1), and is likely to be substantially below that required to maintain a stable population. Consistent with other passerine and non-passerine species (Gunnarsson *et al.,* 2006), daily nest survival rate decreased during the breeding season (by 39% from start to end). For Lapwing and Common Redshank, this is related to predator phenology, particularly as Foxes become more active once their cubs require more prey (Kentie *et al.*, 2015; Mason *et al.*, 2017). Seasonal declines in nest survival may also be attributable to decreasing visibility of predators as vegetation grows taller (Whittingham & Evans, 2004; MacDonald & Bolton, 2008). Importantly, nest survival was not influenced by ground-disturbance, which suggests that this management intervention (which positively influenced nest placement) did not increase nest exposure to predators.

4.3 Predator identity

Predation accounted for most nest failures in this study, similar to predation rates reported in other Curlew (Grant *et al.,* 1999) and wader populations (MacDonald & Bolton, 2008). Timing of nest predation was disproportionately higher during the night (nocturnal or crepuscular), consistent with mammalian rather than avian predators. Although predator identity was confirmed by camera for only five nest predation events, Foxes where responsible for all three nocturnal and one of two diurnal events, with the other confirmed diurnal nest predator a Sheep. In all cases but one, where predator identity was not certain, scrapes were undisturbed and had no shell remains, consistent with confirmed Fox predation events in this and other studies (e.g. Koshkin *et al*., 2016). We found no evidence of activity by other predators; for example, nests predated by Badgers are usually characterised by trampled vegetation and disturbed nest scrapes (Draycott *et al.*, 2008). It is notable that, although Crows were not scared off by cameras and were recorded at nests, they were not found to be predators of Curlew nests and in one instance the sitting adult successfully defended the clutch against a Crow (see Digital material 3); this is unlike other smaller wader species where Crows are frequent nest predators (Teunissen *et al.*, 2008; Ausden *et al.*, 2009). The combined evidence of cameras and timing of predation therefore implicated Fox as the primary nest predator of Curlew in this landscape, consistent with studies that have identified Fox as the major predator of lowland nests of other wader species in the UK (Teunissen *et al.*, 2008; Ausden *et al.*, 2009).

Monitoring protocols were designed to minimise disturbance to the nest site, but in any nest monitoring study there remains a concern as to whether the study has itself affected the fate of nests. However, we found no difference in nest survival rate within the 24 hour periods immediately following direct nest visits, or between nest days with and without nest cameras, consistent with other studies that found no effect of nest cameras on survival of ground-nesting Lapwing (Bolton *et al*., 2007a) or Asian Houbara

Chlamydotis macqueenii (Koshkin *et al*., 2016). We are therefore confident that reported outcomes were not affected by the study protocols.

In agreement with our *a priori* predictions, nest survival was lower at STANTA than Brettenham Heath. Although this is a quasi-anecdotal contrast between only two sites, it is consistent with greater predator control effort and lower apparent Fox densities at Brettenham Heath. In the UK uplands, predator control can reduce generalist predator abundance and increase Curlew breeding success (Fletcher *et al.*, 2010). However, predator control may be more effective at high initial predator densities (Bolton *et al.,* 2007b), and its effectiveness may be compounded by meso-predator release (Bodey *et al.,* 2011) and replacement of culled individuals by inward dispersal from surrounding habitat. Supplementing lethal control with predator-exclusion fencing along a site boundary reduces the need for shooting (important for ethical reasons) and their combination could reduce Fox activity within the fences towards zero (P. Merrick, pers. comm.). Site-fencing reduces Fox predation of Lapwing clutches (Malpas *et al.,* 2013) and chicks (Rickenback *et al.,* 2011) and in our study, Brettenham Heath, which was both fenced and subject to lethal Fox control, had a breeding productivity well above that considered necessary for replacement (Grant *et al.,* 1999). We recommend further experimental evaluation of whether combined fencing and lethal Fox control consistently increases Curlew productivity in lowland contexts.

5. Conservation implications

The impact of land management interventions (e.g. rotational moorland burning) on Curlew abundance has previously been studied in upland habitats (Douglas *et al.,* 2014, Littlewood *et al.*, 2019). Here, for the first time, we have shown that physical ground-disturbance, which is advocated as a conservation measure within lowland dry grassland and grass-heath for many rare, scarce and threatened species (Fuller *et al.,* 2017; Hawkes *et al.,* 2019a,b), also provides suitable Curlew nesting habitat, with no reduction in nest survival. Implementing ground-disturbance, particularly through shallow-cultivating, in areas with few or no mammalian nest predators (e.g. inside anti-predator fenced sites with effective Fox control) could provide a useful management tool for attracting breeding Curlew to safer areas.

Here, nest predation was unsustainably high, and Foxes were the main predator. Given low breeding productivity is an issue across all UK lowland Curlew populations

(Table S1), experimental tests which examine the efficacy of different anti-predator options (whether lethal or not) as a way of improving breeding success (not just clutch survival) are urgently needed.

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Supporting information

Supporting information can be found with the online version of the article: https://doi.org/10.1080/00063657.2020.1725421

References

Amat, J. & Maserom J. (2004). Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour,* 67, 293-300.

Ausden, M., Bolton, M., Butcher, N., Hoccom, D.G., Smart, J. & Williams, G. (2009). Predation of breeding waders on lowland wet grassland – is it a problem? *British Wildlife*, 21(1), 29–38.

Baines, D. (1988). The effects of improvement of upland, marginal grasslands on the distribution and density of breeding wadering birds (Charadriiformes) in northern England. *Biological Conservation*, 45, 221-236.

Baldock, D., Buckwell, A., Hart, K. & Maréchal, A. (2017). EU referendum and implications for UK agriculture and the environment. Available at: https://www.brexitenvironment.co.uk/policy-briefs/#expertrev (Accessed 1 November 2018)

Balmer, D., Gillings, S., Caffrey, B., Swann, B., Downie, I. & Fuller, R. (2013). Bird Atlas 2007-11: The breeding and wintering birds of Britain and Ireland. British Trust for Ornithology, Thetford.

Barton, K. (2019). Multi-model inference. Available at: https://cran.r-project.org/web/packages/MuMIn/ (Accessed 2 July 2018).

Berg, Å. (1992). Habitat selection by breeding Curlews *Numenius arquata* on mosaic farmland. *Ibis,* 134, 355–360.

Bertholdt, N.P., Gill, J.A., Laidlaw, R.A. & Smart, J. (2017). Landscape effects on nest site selection and nest success of northern Lapwing *Vanellus vanellus* in lowland wet grasslands. *Bird Study,* 64, 30–36.

BirdLife International. (2017). *Numenius arquata*. The IUCN Red List of Threatened Species 2017. Available at: http://datazone.birdlife.org/species/factsheet/eurasian-Curlew-numenius-arquata (Accessed 30 June 2018).

Bodey, T., McDonald, R., Sheldon, R. & Bearhop, S. (2011). Absence of effects of predator control on nesting success of Northern Lapwings *Vanellus vanellus*: Implications for conservation. *Ibis,* 153, 543-555.

Bolton, M., Butcher, N., Sharpe, F., Stevens, D. & Fisher, G. (2007a). Remote monitoring of nests using digital camera technology. *Journal of Field Ornithology*, 78, 213–220.

Bolton, M., Tyler, G., Smith, K.E.N. & Bamford, R.O.Y. (2007b). The impact of predator control on Lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *Journal of Applied Ecology*, 44, 534–544

Boughey, K.L., Lake, I.R., Haysom, K.A. & Dolman, P.M. (2011). Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. *Biological Conservation*. 144, 2300–2310.

Brown, A.F. & Shepherd, K.B. (1993). A method for censusing upland breeding waders. *Bird Study,* 40, 189–195.

Brown, D.J., Wilson, J.D., Douglas, D.J.T., Thompson, P.S., Foster, S., McCulloch, N., et al. (2015). The Eurasian Curlew – the most pressing bird conservation priority in the UK? *British Birds,* 108, 660–668.

Burnham, K.P. & Anderson, D.R. (2002). Model Selection and Multimodal Inference: A practical information-theoretic approach, second. Springer, New York.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., et al. (2010). Global biodiversity: Indicators of recent declines. *Science*, 328, 1164-1168.

Call of the Curlew. 2017. Curlew Forum Newsletter 3, 31 August 2017. Available at: http://www.Curlewcall.org/category/newsletters/ (Accessed 3 July 2018).

Currie, D., Valkama, J., Berg, Å.K.E., Boschert, M., Norrdahl, K.A.I., Hanninen, M., et al. (2001). Sex roles, parental effort and offspring desertion in the monogamous eurasian Curlew *Numenius arquata*. *Ibis,* 143, 642–650.

Dinsmore, S.J. & Dinsmore, J.J. (2007). Modeling avian nest survival in program MARK. *Studies in Avian Biology*. 34, 73–83.

Dinsmore, S.J., White, G.C. & Knopf, F.L. (2002). Advanced techniques for modeling avian nest survival. *Ecology,* 83, 3476–3488.

Dolman, P.M. & Sutherland, W.J. (1994). The use of soil disturbance in the management of Breckland grass heaths for nature conservation. *Journal of Environmental Management*, 41, 123-140.

Douglas, D.J.T., Bellamy, P.E., Stephen, L.S., Pearce-Higgins, J.W., Wilson, J.D. & Grant, M.C. (2014). Upland land use predicts population decline in a globally near-threatened wader*. Journal of Applied Ecology*, 51, 194-203.

Douglas, D.J.T., Beresford, A., Selvidge, J., Garnett, S., Buchanan, G.M., Gullett, P., et al. (2017). Changes in upland bird abundances show associations with moorland management. *Bird Study,* 64, 242–254.

Draycott, R.A.H., Hoodless, A.N., Woodburn, M.I.A. & Sage, R.B. (2008). Nest predation of common pheasants *Phasianus colchicus*. *Ibis,* 150, 37–44.

ESRI. (2014). ArcGIS Release 10.3. Redlands, CA.

Ewing, S.R., Scragg, E.S., Butcher, N., & Douglas, D.J.T. (2018). GPS tracking reveals temporal patterns in breeding season habitat use and activity of a globally Near Threatened wader, the *Eurasian Curlew*. *Wader Study,* 124, 206-214

Fisher, G. & Walker, M. (2015). Habitat restoration for Curlew *Numenius arquata* at the Lake Vyrnwy reserve, Wales. *Conservation Evidence,* 12, 48–52.

Fletcher, K., Aebischer, N.J., Baines, D., Foster, R. & Hoodless, A.N. (2010). Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology*, 47, 263–272.

Franks, S.E., Douglas, D.J.T., Gillings, S. & Pearce-Higgins, J.W. (2017). Environmental correlates of breeding abundance and population change of eurasian Curlew *Numenius arquata* in Britain. *Bird Study,* 64, 393–409.

Fuller, R.J., Williamson, T., Barnes, G. & Dolman, P.M. (2017). Human activites and biodiversity opportunities in pre-industrial cultural landscapes: Relevance to conservation. *Journal of Applied Ecology*, 54, 459-469.

Grant, M.C. (1996). Predicting the hatching dates of Curlew *Numenius arquata* clutches. *Wader Study Group Bull*, 80, 53–54.

Grant, M.C., Orsman, C., Easton, J., Lodge, C., Smith, M., Thompson, G., et al. (1999). Breeding success and causes of breeding failure of Curlew *Numenius arquata* in Northern Ireland. *Journal of Applied Ecology*, 36, 59–74.

Green, R.E., Hawell, J. & Johnson, T.H. (1987). Identification of predators of wader eggs from egg remains. *Bird Study*, 34, 87–91.

Guilherme, J.L., Burnside, R.J., Collar, N.J. & Dolman, P.M. (2018). Consistent nest-site selection across habitats increases fitness of Asian Houbara. *Auk*, 135, 192-205.

Gunnarsson, T.G., Gill, J.A., Atkinson, P.W., Gélinaud, G., Potts, P.M., Croger, R.E., et al. (2006). Population-scale drivers of individual arrival times in migratory birds. *Journal of Animal Ecology*, 75, 1119–1127.

Hawkes, R.W., Smart, J., Brown, A., Jones, H. & Dolman, P.M. (2019a). Experimental evidence that ground-disturbance benefits woodlark. *Ibis*, 161, 447–452.

Hawkes, R.W., Smart, J., Brown, A., Jones, H., Lane, S., Wells, D. & Dolman, P.M. (2019b). Multi-taxa consequences of management for an avian umbrella species. *Biological Conservation*, 236, 192–201.

Hayhow, D.B., Ausden, M., Bradbury, R.B., Burnell, D., Copeland, A.I., Crick, H.Q.P., et al. (2017). The State of the UK's birds 2017. RSPB, BTO, WWT, DAERA, JNCC, NE and NRW, Sandy, Bedfordshire.

Jackson, D.B. (2001). Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland. *Journal of Applied Ecology,* 38, 802-812.

Johnson, D.H. (1979). Estimating nest success: The Mayfield method and an alternative. *The Auk*, 96, 651–661.

Johnstone, I., Elliot, D., Mellenchip, C. & Peach, W.J. (2017). Correlates of distribution and nesting success in a Welsh upland eurasian Curlew *Numenius arquata* population. *Bird Study,* 64, 535–544.

Kentie, R., Both, C., Hooijmeijer, J.C.E.W. & Piersma, T. (2015). Management of modern agricultural landscapes increases nest predation rates in black-tailed godwits *Limosa limosa*. *Ibis,* 157, 614–625.

Koshkin, M., Burnside, R.J., Packman, C.E., Collar, N.J. & Dolman, P.M. (2016). Effects of habitat and livestock on nest productivity of the Asian houbara *Chlamydotis macqueenii* in Bukhara Province, Uzbekistan. *European Journal of Wildlife Research*, 62, 447–459.

Laidlaw, R.A., Smart, J., Smart, M.A. & Gill, J.A. (2015). The influence of landscape features on nest predation rates of grassland-breeding waders. *Ibis*, 157, 700–712.

Leyrer, J., Brown, D., Gerritsen, G., Hotker, H. & Ottvall, R. (2018). International multi-species action plan for the conservation of breeding waders in wet grassland habitats in Europe (2018-2028). Report of action A13 under the framework of Project LIFE EuroSAP (LIFE 14 PRE/UK/002). NABU, RSPB, VBN and SOF.

Littlewood, N.A., Mason, T.H.E., Hughes, M., Jaques, R., Whittingham, M.J. & Willis, S.G. (2019). The influence of different aspects of grouse moorland management on nontarget bird assemblages. *Ecology and Evolution*, 9, 11089-11101.

Ludwig, S.C., Roos, S. & Baines, D. (2019). Responses of breeding waders to restoration of grouse management on a moor in South-West Scotland. *Journal of Ornithology*, 160, 787-797.

MacDonald, M.A. & Bolton, M. (2008). Predation on wader nests in Europe. *Ibis*, 150, 54–73.

Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. (2007). Nest site characteristics of woodlarks Lullula arborea breeding on heathlands in southern England: are there consequences for nest survival and productivity? *Bird Study 54*, 307-314 .

Malpas, L.R., Kennerley, R.J., Hirons, G.J.M., Sheldon, R.D., Ausden, M., Gilbert, J.C., et al. (2013). The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland. *Journal of Nature Conservation*, 21, 37–47.

Mason, L.R., Smart, J. & Drewitt, A.L. (2017). Tracking day and night provides insights into the relative importance of different wader chick predators. *Ibis*, 160, 71–88.

Massey, K., Cosgrove, P., Massey, F., Jackson, D. & Chapman, M. (2016). Habitat characteristics of breeding eurasian whimbrel *Numenius phaeopus* on Mainland Shetland, Scotland, UK. *Bird Study*, 63, 500–508.

Musgrove, A., Aebischer, N., Eaton, M., Hearn, R., Newson, S., Noble, D., Parsons, M., Risely, K. & Stroud, D. (2013). Population estimates of birds in Great Britain and the Uniterd Kingdom. *British Birds*, 106, 64-100.

NSRI. (2014). National soil map of England and Wales - NATMAP, 1:250,000 scale. Cranfield University, Bedfordshire. Available at http://www.landis.org.uk (Accessed July 2014).

Odum, E.P. & Kuenzler, E.J. (1955). Measurement of territory and home range size in birds. *Auk*, 72, 128-137.

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics,* 20, 289–290.

Pearce-Higgins, J.W., Brown, D.J., Douglas, D.J.T., Alves, J.A., Bellio, M., Bocher, P., et al. (2017). A global threats overview for Numeniini populations: synthesising expert knowledge for a group of declining migratory birds. *Bird Conservation International*, 27, 6–34.

R Core, T. (2017). R Core Team. R: a language and environment for statistical computing. Version 3.2.2. R Foundation for Statistical Computing, Vienna (2015)

Rickenbach, O., Grüebler, M.U., Schaub, M., Koller, A., Naef-Daenzer, B. & Schifferli, L.U.C. (2011). Exclusion of ground predators improves northern Lapwing *Vanellus vanellus* chick survival. *Ibis,* 153, 531–542.

Rowland, C.S., Morton, R.D., Carrasco, L., McShane, G., O'Neil, A.W. & Wood, C.M. (2017). Land Cover Map 2015 (25m raster, GB). NERC Environmental Information Data Centre.

Sheail, J. (1979). Documentary evidence of the changes in the use, management and appreciation of the grass-heaths of Breckland. *Journal of Biogeography*, 6, 277–292.

Smart, M. 2017. Curlews in the Severn and Avon Vales. Report on a breeding survey in 2016: suggestions on future action. Southern Curlew Conference, WWT, Slimbridge, 02.02.2017. Available at: http://www.Curlewcall.org/wpcontent/uploads/2017/07/Curlews-in-the-Severn-and-Avon-Vales-REV-3.pdf (Accessed 16 November 2018)

Stanbury, A., Brown, A., Eaton, M., Aebischer, N.J., Gillings, S., Hearn, R., et al. (2017). The risk of extinction for birds in Great Britain. *British Birds,* 110, 502-517.

Stroud, D.A., Baker, A., Blanco, D.E., Davidson, N.C., Delany, S., Ganter, B., et al. (2006). The conservation and population status of the world's waders at the turn of the millennium. Waterbirds around the world. Eds. G.C. Boere, C.A. Galbraith & D.A. Stroud. The Stationery Office, Edinburgh, UK. pp. 643-648.

Teunissen, W., Schekkerman, H., Willems, F. & Majoor, F. (2008). Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and black-tailed godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis*, 150, 74–85.

Whittingham, M.J. & Evans, K.L. (2004). The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis,* 146, 210–220.