

RESEARCH ARTICLE

Plantation clear-fell patches benefit heathland arthropods

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Abstract

1. Plantation forests constitute a significant amount of the wooded area in many parts of the globe. However, the extent of biological provision conferred by plantation forest depends on regional conservation priorities and biogeographical context.
2. Here, we evaluate the arthropod biodiversity in a chronosequence of pine plantation (clear-felled, 1, 3, 5, 7, 9, 13, 21-years) in the largest lowland conifer forest in the UK. We compare the assemblage within 37 plantation stands and eight important open habitat remnants in a formerly heathland dominated region. We also assess the configuration and potential isolation of ephemeral open early growth stage habitat across a 60-year plantation rotation.
3. Carabid and spider assemblages changed throughout the sampled chronosequence. In the early growth stages (1–7 years) before canopy closure, arthropod assemblages contained many individuals and species associated with dry-open habitats, greater numbers of rare species than closed canopy plantation and had similar composition (non-metric multidimensional scaling) to heathland samples. Early growth stages and heathlands primarily differed in the additional presence of generalist species in the plantation. Species associated with woodland increased in abundance as the plantation aged, but remained far less numerous than dry-open or generalist species. The spatial distribution of young growth stages across the rotation cycle was significantly clustered in the early and late rotation phases.
4. Plantation landscapes often support high species richness but we highlight their value for vulnerable heathland biodiversity early in the rotation cycle. To increase plantation value regional conservation priorities should be supported with appropriate consideration of growth stage configuration across the full rotation.

KEYWORDS

arthropods, carabid, heathland, insect conservation, plantation forestry, spider

1 | INTRODUCTION

Plantation forestry is expanding globally and already contributes more than half of total forested land in some countries (FAO, 2016;

Forest Europe et al., 2011), while continued afforestation could increase this from 3% to 21% globally by 2100 (FAO, 2010). This is concerning due to inconsistent findings of biodiversity assessment between natural forest and plantations that are often associated with

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intensive crop production and use of non-native tree species (e.g., Calvino-Cancela, 2013; Calvino-Cancela et al., 2020; Finch, 2005; López-Bedoya et al., 2021; Paillet et al., 2010; Pedley et al., 2014; Peralta et al., 2018; Yu et al., 2006). Plantation forests have been likened to 'biological deserts' or 'green deserts', however, benefits to regional biota often depend on previous land use and management intensity (Bremer & Farley, 2010; Brockerhoff et al., 2008; Košulič et al., 2020; Stephens & Wagner, 2007; Suchomel et al., 2020). For example, where afforestation has been conducted on agricultural or degraded land, regional biodiversity value may be improved, conversely, where the previous land use was natural or semi-natural habitat, biodiversity value may be reduced (Brockerhoff et al., 2008). In the latter case, the impact to previous open habitats is severe with significant changes to hydrology, nutrients and light conditions after planting (Buytaert et al., 2007; Farley & Kelly, 2004). It is therefore important to understand how vulnerable biodiversity may be maintained alongside commercial operations and what management decisions may enhance biodiversity conservation in such contexts.

Where pre-plantation habitat was natural forest, studies have shown plantations lack specialist forest species (Fierro et al., 2017; Peralta et al., 2018). Peralta et al. (2018) showed that differences in community composition of plants, caterpillars and parasitoids between native *Nothofagaceae* forest and exotic pine plantation were largely the result of species turnover, suggesting that exotic pine plantations were not a suitable substitute for pre-plantation forest species. In areas where old growth forest biodiversity is the conservation priority then the plantation management focus may include continuous canopy cover, mixed species plantations, use of native timber species and proximity to natural forest (Brockerhoff et al., 2008). In these circumstances environmental structures such as deadwood, snags and well-developed understories may be critical for specialist species (Calladine et al., 2015; Finch, 2005; Humphrey et al., 2000; Košulič et al., 2021; Sweeney et al., 2010). These structures tend to be less abundant and developed under a clear-fell management regime (removal and restocking of even age stands) and especially in short rotation cycles. While several studies have measured the amount and type of deadwood found under clear-fell management and determined similar volumes between plantation and natural or semi-natural forest (Fierro et al., 2017; Sweeney et al., 2010), the condition and type of deadwood may differ with fewer large logs, more intact stumps and less late decay stages in plantations (Sweeney et al., 2010).

In contrast, in predominantly anthropogenic landscapes whose biodiversity interest is concentrated in open semi-natural habitats rather than old-growth forest, restoration of forest biota may not be an appropriate goal of plantation management. In western Europe, large areas of semi-natural heathland were afforested in the early 20th century. These areas, predominantly on nutrient-poor soil, were generally unproductive for traditional crops but suitable for slow-yielding timber production. The ecological and cultural value of heathland has since been recognised, including in EU and UK conservation policy (European Community, 1992), but remaining heathlands are highly fragmented, often degraded and their

associated biodiversity is threatened (Piessens et al., 2005; Rose et al., 2000). Paradoxically, plantation forestry may provide solutions that could alter the paradigm of biological desertification for these landscapes. Soils under plantations can be suitable for heathland restoration (Walker et al., 2004) as their nutrient status has not been artificially enriched like many arable soils and heathland seed banks remain viable throughout the rotation cycle (Pywell et al., 2002), although some characteristic plant species may be in low densities (Eycott et al., 2006b). While the removal and replacement of plantation with restored heathland may well support open habitat biodiversity, there is also potential to support these species within the plantation landscape without the loss of forest production. For example, permanent open areas within plantations, such as firebreaks and access tracks, can provide valuable habitat and dispersal conduits for heathland invertebrates (Bertoncelj & Dolman, 2013b; Greatorex-Davies et al., 1993; Pedley, Bertoncelj, et al., 2013; Pedley, Franco, et al., 2013). Where forestry management uses clear-fell rotation, there may also be opportunities for heathland species to colonise these young ephemeral open patches before canopy closure. Clear-fell rotation has been the dominant management type in the UK, although continuous forest cover has been promoted as a way of improving visitor and recreational experience (Mason, 2007, 2015). Clear-felling may also be a necessary solution when pathogen attack is prevalent, in particular, *Dothistroma* needle blight, which has caused significant reductions in timber production worldwide (Bulman et al., 2016). However, for these ephemeral open forest habitats to function effectively for heathland biota, such areas must not create isolated patches which could become population sinks.

To investigate the use of open habitat within the commercial forestry landscape, specifically clear-felled and restocked stands, we use two diverse groups of arthropods (carabid beetles and spiders) to survey biotic changes along a forestry chronosequence in the largest lowland pine plantation in the UK. Carabids and spiders are effective bioindicators and have been used successfully to monitor changes in forest biodiversity in temperate regions (Oxbrough et al., 2005; Pearce & Venier, 2006). Both taxa respond quickly to changes in environmental condition and have important roles in food webs while also being easily and rapidly surveyed with standard techniques (Maleque et al., 2009; Pedley et al., 2016; Rainio & Niemela, 2003; Standen, 2000). Due to the long history of surveying these groups in Europe, well-defined ecological and taxonomic information exists that can support the interpretation of biological assessments, such as habitat affinity and species rarity.

This study examined how arthropod assemblages change during the early growth stages of the clear-fell forestry cycle, particularly with a focus on open-habitat species that are regional conservation priorities in this former heathland region (Dolman et al., 2012). The potential contribution of young stands within the plantation cycle to the conservation of bio-regional open-habitat species was assessed relative to the assemblages supported in important open heathland habitats in close proximity to the forest. Specifically, we test the hypothesis that the species composition

of ground invertebrate assemblages in young second rotation plantations (up to 10 years after planting) will shift to become similar to that of heathland sites. Furthermore, although managed to achieve a steady-state/even harvest cycle (important to biodiversity and sustainability of local economies), the current forest landscape reflects a declining annual rate of young stand creation following the first rotation. We therefore appraise the isolation of the young-forest elements through the planned future forest rotation to a priori test whether open-habitat configuration will become less isolated as the next rotation progresses. Last, we discuss how the plantation configuration could be improved to support regional conservation agendas.

2 | MATERIALS AND METHODS

2.1 | Study site and design

Thetford Forest is a commercial plantation in eastern England occupying 185 km² (0°40' E, 52°27' N); planted in the early 20th century it is the largest lowland conifer forest in the UK, with 80% comprising Corsican (*Pinus nigra*) and Scots (*P. sylvestris*) pine (Appendix A). The forest is managed by clear-felling (typically at 60–80 years) and replanting of even-aged stands (mean area 9.0 ha ± 8.6 SD). Clear-felled areas are cleared of coarse woody debris before ploughing of planting lines that exposes bare mineral sub-soil. Replanting then takes place the following winter. Tree canopy cover and height increase with age, open conditions are retained for up to 10 years with full canopy closure at approximately 20 years (Hemami et al., 2005).

Forest trackways, used for management access and fire breaks, subdivide the plantation stands (total length 1290 km, average width mean 13.7 m ± 5.8 SD). Trackways provide a considerable amount of open habitat within the forested landscape and may provide important resources for arthropod communities (Wolstenholme & Pedley, 2021). A substantial proportion of the regionally important heathland associated carabid and spider fauna have been recorded from open habitat within the forestry landscape (Lin et al., 2007; Pedley, Bertoncelj, et al., 2013; Pedley, Franco, et al., 2013).

Arthropods were sampled in each of 37 second rotation forest stands (Appendix A), to characterise a chronosequence across the initial open stages of the plantation cycle, comprising: five replicates each of clear-felled but unplanted stands (year 0, mean 5.7 ha ± 1.5 SD), 1 year old (year 1; mean 11.1 ha ± 2.7 SD), 3 year old (year 3; mean 6.9 ha ± 3.5) and 5 year old (year 5; mean 11.4 ha ± 5.4 SD); four replicates each of 7 year old stands (year 7; mean 7.2 ha ± 3.4 SD), 9 year old (year 9; mean 12.4 ha ± 4.2 SD) and 13 year old (year 13; mean 8.4 ha ± 2.4 SD); and five replicate 21 year old sites (year 21; mean 9.8 ha ± 3.4 SD). We use descriptions of plantation growth stages defined in Hemami et al. (2005); restocked (0–4 years after planting), pre-thicket (5–10 years), thicket (11–20 years), pole (21–30 years) and pre-felling (>30 years).

Eight reference sites, comprising remnant patches of heathland considered important for regionally vulnerable invertebrate and plant species, were also sampled at the same time and in the same manner as plantation sites. Reference sites (mean area 106 ha ± 130 SD) were all either adjacent to, or within 2.5 km of the northern, western and south-eastern margins of the forest (mean = 0.72 km ± 1.11 SD) and included one National Nature Reserve and six Sites of Special Scientific Interest, of which five were also Special Areas of Conservation. Heathland habitats, along with marginal agricultural sites, represent the dominant pre-plantation habitat in this region.

2.2 | Sampling

Carabid and spider communities were sampled by pitfall trapping, with two sampling transects established in each of the 37 sampled forestry stands and eight heathland sites. Transects were located at the centre of forestry stands (i.e., typically 100–150 m from the edge) and at least 100 m from the edge of reference sites, to reduce possible edge impacts and spill-over from adjacent areas. As the area of stands was consistent across the plantation cycle any edge effects are unlikely to affect comparisons across the rotation. In 2009, arthropod assemblages were sampled in each transect on two occasions representing the peak period of carabid and spider abundance and activity, May and June. In each period, six pitfall traps (each 7.5 cm deep, 6.5 cm diameter, filled with 50 mL of 70% ethylene glycol), set 15 m apart along each transect, were opened for seven consecutive days. Transects within a site (stand or heathland) were separated by 50 m to ensure independence. Traps in each transect were pooled and data from the two sampling months were combined giving one composite sample per transect (i.e., two composite samples per stand or heathland). We acknowledge that this sampling scheme may have missed species that are active later in the season (Lövei & Sunderland, 1996) but due to logistical reasons were unable to increase the sampling season. While the standardised pitfall trap sampling allows comparison of ground-active arthropod composition between study sites (Luff, 1975; Luff & Eyre, 1988), it may not be comparable to studies conducted over longer periods due to differences in activity periods between species (Topping & Sunderland, 1992). Hereafter, we use 'abundance' to refer to the pitfall catch activity-abundance indexes of our sampled arthropod communities. We show sampling efficiency within our analysis to highlight the completeness of our sampling scheme.

Identification of carabids followed Luff (2007) and spiders followed Roberts (1987, 1996); juvenile and sub-adult spiders were not identified due to the lack of developed reproductive structures. Species were classified according to habitat descriptions for spiders in Harvey et al. (2002) and Roberts (1996), and for carabids Luff (1998, 2007). Habitat associations comprised: 'dry-open' species associated with dry calcareous or acidic grassland, dry lowland heathland, sand dunes, sand or gravel pits; shaded woodland habitats (hereafter 'woodland'); 'generalist' species of multiple or any mesic habitat.

Information on rare, threatened or designated species (i.e., Near Threatened, Nationally Rare, Nationally Scarce, Section 41 priority species) were obtained from the online Pantheon database (Webb et al., 2017; <https://pantheon.brc.ac.uk>).

2.3 | Analysis

The unit of replication used for analysis was individual transects (pooled pitfall traps over two sampling months). All analyses were conducted using R v3.6.1 statistics software (R Development Core Team, 2019). Sampling efficiency was compared between plantation stands and reference heathland by sample-size based rarefaction using the iNext package (Hsieh et al., 2016). To identify characteristic carabids and spiders for each habitat type (plantation stand age, and heathland), indicator species analysis was implemented by calculating indicator values (Dufrene & Legendre, 1997) using the function `multipatt` in the R package `indicspecies` (De Cáceres et al., 2010), which uses permutation (999) to test the significance of the indicator-habitat relationships. We used a threshold of $p < 0.01$ to increase the chance of identifying strong indicators. Assemblage composition was examined separately for carabids and spiders using non-metric multidimensional scaling (NMDS) performed on a matrix of Bray–Curtis dissimilarities of abundance data (square root transformed and Wisconsin double standardisation) using the `vegan` package (Oksanen et al., 2018). Centroids for each plantation age and for the reference heathland were plotted to visualise differences, and differences in species compositions between habitat types were analysed statistically by multivariate implementation of generalised linear models (using likelihood-ratio-tests) in the `mvabund` package (Wang et al., 2012).

Species richness and abundance of carabids and spiders was compared using generalised linear mixed models with a random component for site (specific forestry stand or heathland site) specified within the model. The appropriate error term (Poisson, negative binomial or normal) was selected by comparing patterns of residuals and by assessing model dispersion. We implemented the models in R using the `glmer` and `glmmabmb` functions from the packages `lme4` (Bates et al., 2015) and `glmmADMB`. Differences among habitat means were examined by Tukey pairwise comparisons using the `glht` function in the `multcomp` package (Hothorn et al., 2008).

Isolation of open-habitat young-growth patches, both within the current forest landscape and that predicted from planned rotational felling and restocking management, was compared between landscapes periods, at 10-year intervals across one rotation of 60 years. For each period, the distribution of early growth habitats (defined as forest stands that contain substantial proportions of open-dry habitat arthropod abundance and richness, and with the most similar community composition to reference heathland), was extracted using Quantum GIS (QGIS Development Team, 2009) from GIS datasets provided by the Forestry Commission, England (2016, 2017). Isolation was quantified by the proximity

index using `FRAGSTATS` (McGarigal et al., 2012) that considers the size and distance of neighbouring habitats of the same type; those having larger values comprising a less isolated arrangement of patches (Gustafson & Parker, 1992). Log-transformed mean patch isolation was compared between periods by non-parametric Kruskal-Wallis rank tests in R.

3 | RESULTS

Identification of pitfall trapped invertebrates recorded 3899 carabids from 72 species and 12,402 spiders from 141 species. The trapping regime effectively represented carabids and spiders with species rarefaction curves approaching asymptotes (Appendix B). The most abundant carabids recorded were *Harpalus rufipalpis* ($n=827$) and *Pterostichus madidus* ($n=437$); however, these were only represented in the heathland samples by five individuals and one individual respectively. In heathland, the dominant carabid species recorded was *Amara aenea* ($n=248$). The most abundant spiders recorded, by an order of magnitude, were the Lycosids *Pardosa monticola* ($n=3159$) and *Pardosa pullata* ($n=2852$). *P. monticola* was the dominant species in heathland samples ($n=1933$), whereas *P. pullata* was the most dominant species within forest stands ($n=2819$). Within closed canopy forest (21-year-old stands) the Linyphid *Agyreta subtilis* ($n=110$) and the Lycosidae *Pirata hygrophilus* ($n=91$) were most abundant; *P. monticola* was not recorded in closed canopy forest and only a single individual of *P. pullata* was recorded.

Of the 72 carabid species, eight were solely recorded from heathland, of which seven were associated with dry-open habitats with four having national designations (NS, NR, NT): *Harpalus pumilus*, *Masoreus wetterhallii*, *Amara consularis* and *Amara lucida*. Of the 141 spider species, nine were solely recorded from heathland, of which five were associated with dry-open habitats and nationally designated (NS): *Lepthyphantes insignis*, *Typhochrestus digitatus*, *Walckenaeria monoceros*, *Sitticus saltator* and *Ozyptila scabricula*. See Appendix C for full species list, recorded abundance, habitat associations and designation status. Indicator analysis identified 14 species preferentially associated with heathland (ten dry-open species, three generalists and one woodland species, Table 1). In early 0–7-year-old stands, 22 indicator species were identified (nine dry-open species, ten generalist species and three woodland species). Indicator species preferentially associated with older plantation stages did not include any dry-open species, but instead comprised generalist or woodland species (nine-year-old stands: six generalist and two woodland indicator species; 13-year-old stands: four generalists and one woodland indicator species; 21-year-old stands: four generalists and eight woodland indicator species).

3.1 | Assemblage composition

Significant differences in species composition were found between heathland and different forest growth stages in both carabid and

TABLE 1 Carabid and spider indicator species results.

Site type	Taxon	Species	Dry-open	Generalist	Woodland	Test statistic	p-value
Heathland	Carabid	<i>Amara aenea</i>	*			0.889	0.001
Heathland	Carabid	<i>Harpalus anxius</i>	*			0.837	0.001
Heathland	Carabid	<i>Harpalus pumilus</i>	*			0.612	0.002
Heathland	Carabid	<i>Masoreus wetterhallii</i>	*			0.612	0.002
Heathland	Carabid	<i>Amara tibialis</i>	*			0.572	0.005
Heathland	Spider	<i>Steatoda phalerata</i>	*			0.745	0.001
Heathland	Spider	<i>Hypsosinga albovittata</i>	*			0.740	0.001
Heathland	Spider	<i>Pardosa monticola</i>	*			0.692	0.001
Heathland	Spider	<i>Steatoda albomaculata</i>	*			0.591	0.004
Heathland	Spider	<i>Zelotes electus</i>	*			0.549	0.005
Heathland	Spider	<i>Hahnina nava</i>		*		0.806	0.001
Heathland	Spider	<i>Xysticus cristatus</i>		*		0.616	0.001
Heathland	Spider	<i>Xysticus kochi</i>		*		0.606	0.001
Heathland	Carabid	<i>Syntomus truncatellus</i>			*	0.642	0.001
0 year	Spider	<i>Pardosa prativaga</i>		*		0.945	0.001
0 year	Spider	<i>Erigone atra</i>		*		0.706	0.001
0 year	Spider	<i>Pardosa saltans</i>			*	0.655	0.001
0 year	Spider	<i>Dicymbium tibiale</i>			*	0.548	0.006
1 year	Carabid	<i>Harpalus rufipes</i>	*			0.653	0.001
1 year	Spider	<i>Xerolycosa nemoralis</i>	*			0.855	0.001
1 year	Carabid	<i>Cicindela campestris</i>		*		0.694	0.001
1 year	Spider	<i>Agelena labyrinthica</i>		*		0.769	0.001
1 year	Spider	<i>Pardosa palustris</i>		*		0.616	0.006
3 year	Carabid	<i>Harpalus rufipalpis</i>	*			0.708	0.001
3 year	Carabid	<i>Amara convexior</i>	*			0.513	0.002
3 year	Carabid	<i>Amara equestris</i>	*			0.480	0.009
3 year	Spider	<i>Haplodrassus signifer</i>	*			0.598	0.001
3 year	Spider	<i>Trachyzelotes pedestris</i>	*			0.560	0.001
3 year	Spider	<i>Alopecosa barbipes</i>	*			0.547	0.001
3 year	Spider	<i>Drassyllus pusillus</i>	*			0.506	0.004
3 year	Carabid	<i>Amara lunicollis</i>		*		0.562	0.002
3 year	Carabid	<i>Poecilus versicolor</i>		*		0.545	0.010
3 year	Spider	<i>Drassodes pubescens</i>		*		0.545	0.001
3 year	Carabid	<i>Carabus problematicus</i>			*	0.570	0.001
7 year	Spider	<i>Phrurolithus festivus</i>		*		0.640	0.001
7 year	Spider	<i>Alopecosa pulverulenta</i>		*		0.529	0.005
9 year	Spider	<i>Bathyphantes parvulus</i>		*		0.646	0.001
9 year	Spider	<i>Pocadicnemis juncea</i>		*		0.635	0.001
9 year	Spider	<i>Episinus angulatus</i>		*		0.624	0.001
9 year	Spider	<i>Walckenaeria atrotibialis</i>		*		0.584	0.001
9 year	Spider	<i>Centromerus sylvaticus</i>		*		0.518	0.007
9 year	Spider	<i>Pardosa pullata</i>		*		0.491	0.005
9 year	Carabid	<i>Pterostichus madidus</i>			*	0.607	0.007
9 year	Spider	<i>Leptyphantes menzei</i>			*	0.603	0.001
13 year	Spider	<i>Meioneta saxatilis</i>		*		0.662	0.001

(Continues)

TABLE 1 (Continued)

Site type	Taxon	Species	Dry-open	Generalist	Woodland	Test statistic	p-value
13 year	Spider	<i>Zora spinimana</i>		*		0.611	0.001
13 year	Spider	<i>Saariosta abnormis</i>		*		0.527	0.006
13 year	Spider	<i>Robertus lividus</i>		*		0.507	0.006
13 year	Spider	<i>Pirata hygrophilus</i>			*	0.593	0.001
21 year	Carabid	<i>Carabus nemoralis</i>		*		0.623	0.001
21 year	Spider	<i>Agyneta conigera</i>		*		0.978	0.001
21 year	Spider	<i>Micrargus herbigradus</i>		*		0.635	0.001
21 year	Spider	<i>Diplostyla concolor</i>		*		0.514	0.007
21 year	Carabid	<i>Notiophilus biguttatus</i>			*	0.568	0.008
21 year	Spider	<i>Agyneta subtilis</i>			*	0.895	0.001
21 year	Spider	<i>Lepthyphantes flavipes</i>			*	0.775	0.001
21 year	Spider	<i>Lepthyphantes alacris</i>			*	0.707	0.001
21 year	Spider	<i>Metellina merianae</i>			*	0.707	0.001
21 year	Spider	<i>Clubiona comta</i>			*	0.632	0.001
21 year	Spider	<i>Agyneta ramosa</i>			*	0.560	0.001
21 year	Spider	<i>Porrhomma pallidum</i>			*	0.548	0.007

Note: For each species identified as an indicator the sampled habitat, test statistic, p-value and habitat association (dry-open, generalist, woodland) is given.

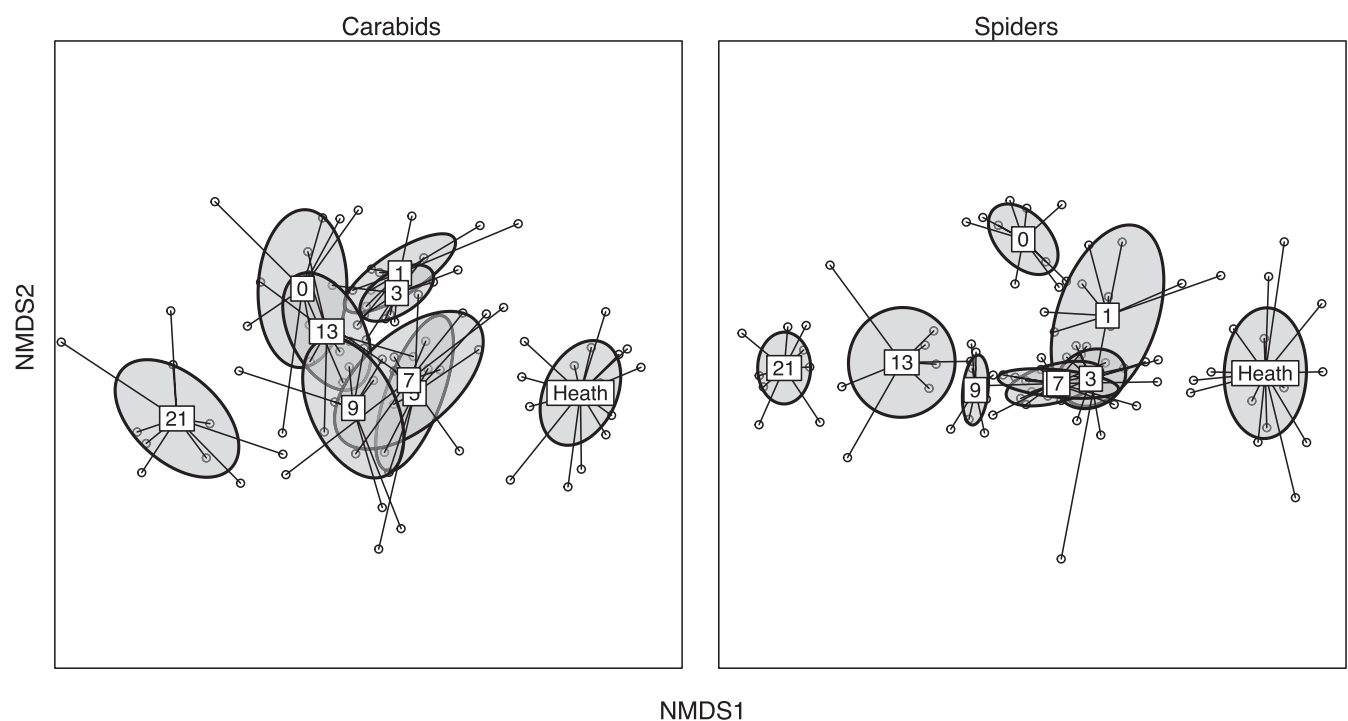


FIGURE 1 Non-metric multi-dimensional scaling (NMDS) of carabid and spider assemblages collected by pitfall trapping (stress=0.20, 0.15 respectively). Open circles represent sampled transects. Shaded ellipses represent 95% confidence intervals of habitat centroids. Heath=Heathland patches, 0=cleared unplanted, 1=one year old, 3=three year old, 5=five year old, 7=seven year old, 9=nine year old, 13=thirteen year old and 21=twenty one year old plantation stands.

spider assemblages (Deviance=6279, $p < 0.001$; Deviance=16,476, $p < 0.001$; Figure 1). Carabid and spider assemblages in closed canopy 21-year-old stands differed significantly ($p < 0.001$) from all other sampled chronosequence plots and from heathland reference

sites; likewise, all plantation assemblages were significantly different to heathland reference assemblages ($p < 0.001$, Appendix D gives full results for multivariate generalised linear models testing the composition differences between site types). For both arthropod groups,

heathland and 21-year-old stands, each contained distinct assemblages and no overlap in NMDS space with 0–13-year-old chronosequence plots. One- to seven-year-old chronosequence ages were closest in ordination space to heathland samples along axis one of NMDS plots for both carabids and spiders (Figure 1).

3.2 | Richness

Total abundance and total species richness patterns were similar for carabids and spiders (Figure 2, see Appendix E for statistical output of generalised linear mixed models) with peaks in the 1-year-old stands, and significantly fewer individuals and species in the oldest stands sampled. Young stages of the forest cycle supported greater carabid abundance and richness, and greater spider richness, than heathland plots; however, spider abundance did not differ between heathland plots and 1–13-year-old stands (Figure 2).

For dry-open habitat species, patterns of richness and abundance were very similar between carabids and spiders (Figures 3

and 4; Appendix E). Dry-open habitat species were most abundant in 1–7-year-old stands, which had similar richness and abundance of dry-open species to heathland sites (Figures 3 and 4), and were least abundant in clear-felled (year 0) and 9-, 13- and 21-year-old stands.

For generalist species, abundance was low in heathlands for both taxa but peaked in 3- and 5-year-old stands for carabids and 5-, 7- and 9-year-old stands for spiders (Figure 3). Species richness of generalist carabids is relatively consistent throughout the growth stages sampled, except for the later closed canopy stage where richness of generalists is reduced, although only significantly so for spiders (Figure 4).

For woodland species, patterns of richness contrasted those for generalists, with peaks at both the very early and very late stages of the sampled chronosequence (Figure 4). Abundance of woodland species was more mixed than patterns shown for species richness; however, low levels of abundance appear to be consistent throughout the sampled chronosequence for both taxa (Figure 3). For spiders, the abundance of woodland species mirrored

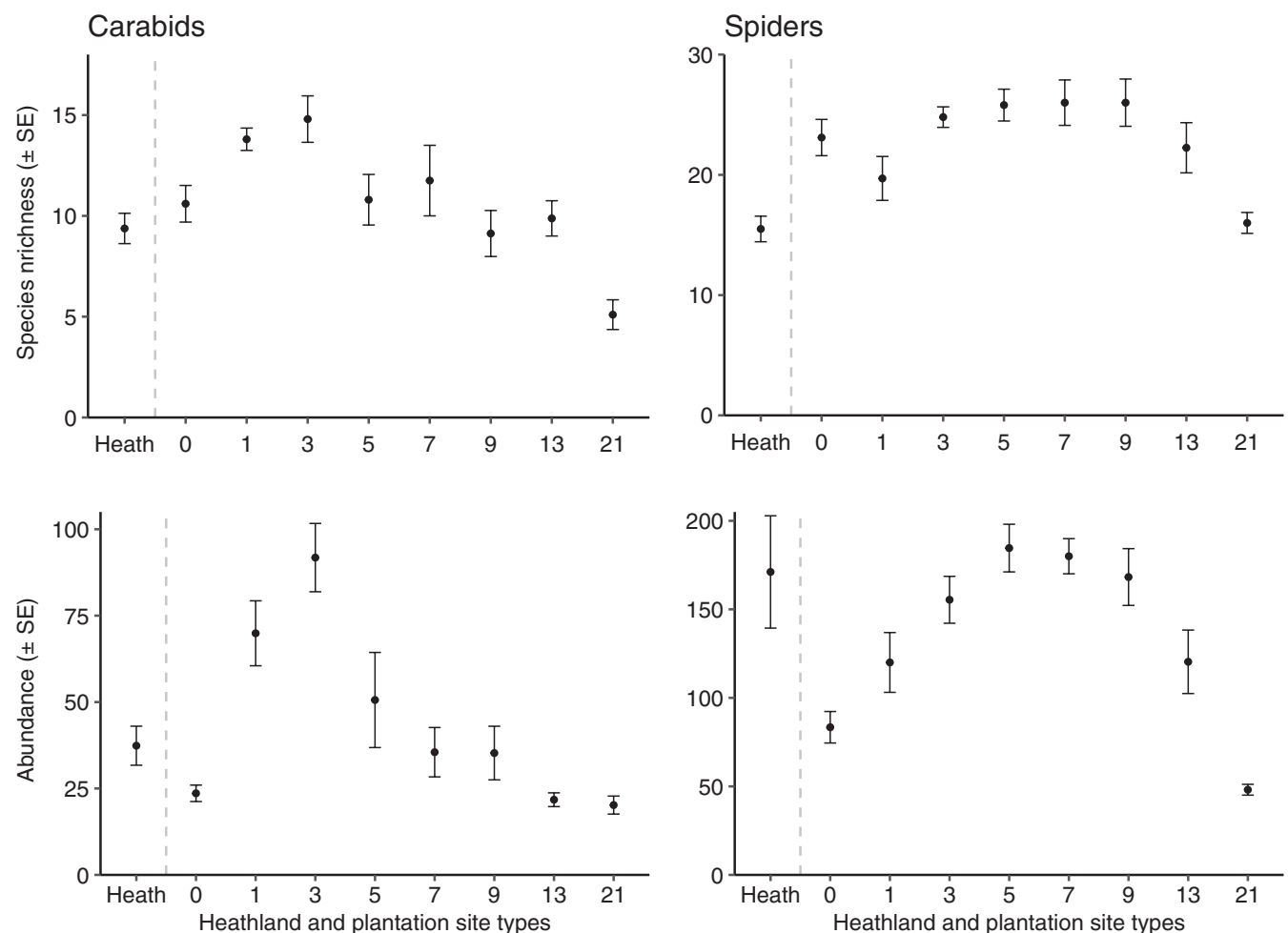


FIGURE 2 Mean abundance and richness \pm SE of carabids and spiders collected using pitfall trapping in each habitat type (heath or plantation age class). The dotted line separates heathland reference samples from the sampled forestry chronosequence. Heath=Heathland patches, 0=cleared unplanted, 1=one year old, 3=three year old, 5=five year old, 7=seven year old, 9=nine year old, 13=thirteen year old and 21=twenty one year old plantation stands.

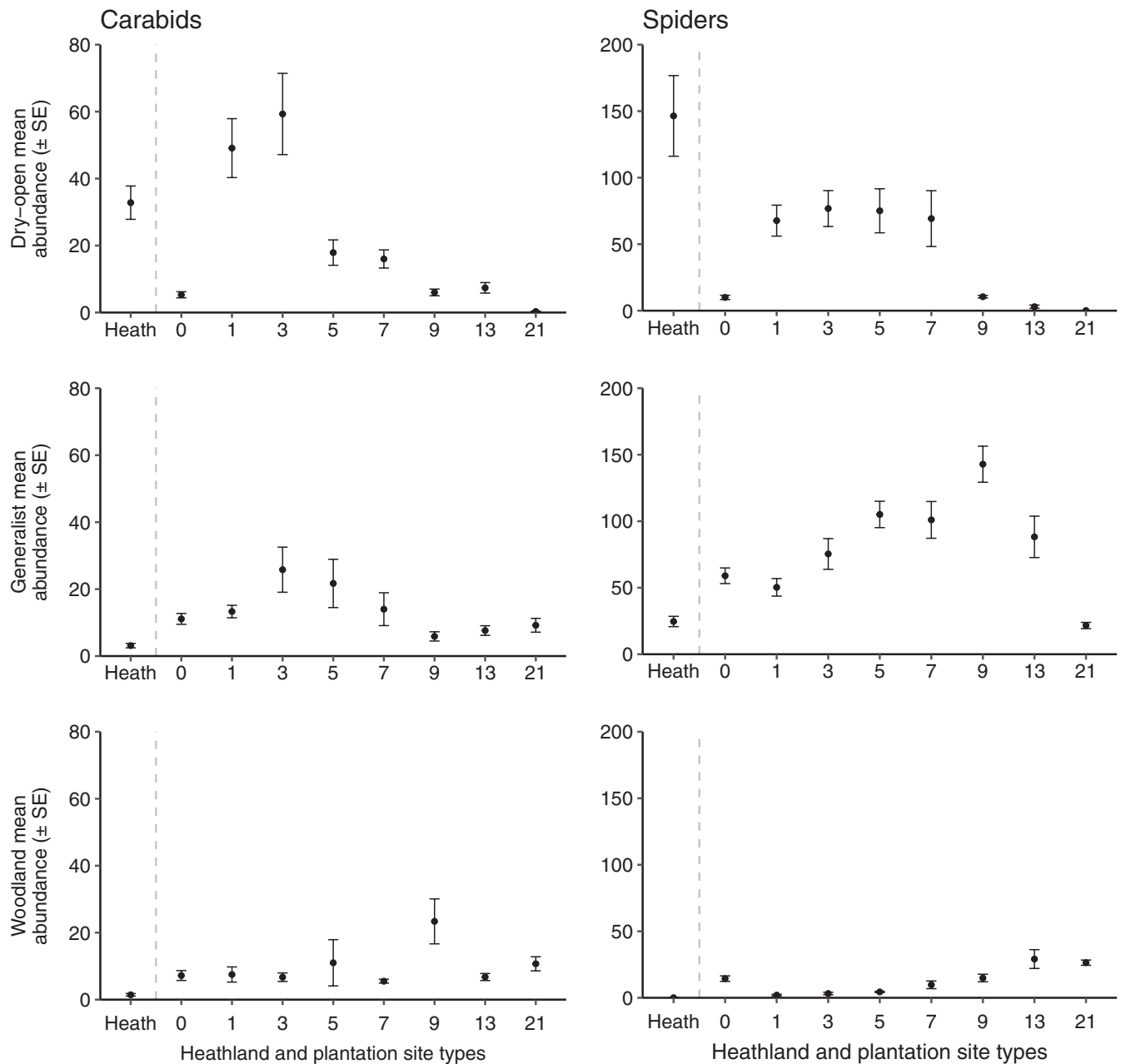


FIGURE 3 Mean abundance \pm SE of carabids and spiders collected using pitfall trapping in each habitat type, shown separately for: dry-open habitat, generalist and woodland associated species. The dotted line separates heathland reference samples from the sampled forestry chronosequence. Heath = Heathland patches, 0 = cleared unplanted, 1 = one year old, 3 = three year old, 5 = five year old, 7 = seven year old, 9 = nine year old, 13 = thirteen year old and 21 = twenty one year old plantation stands.

the pattern shown for species richness, with peaks at the year zero stage and then again at the 13-year-old and closed canopy 21-year-old stages.

3.3 | Threatened species

A total of 259 threatened carabids and 784 threatened spiders representing 15 and 20 species respectively were recorded, which included three woodland and 12 dry-open carabid species, and three woodland and 14 dry-open spider species (Appendix C). For

carabids, heathlands contained the greatest abundance of threatened species but this was not significantly different to the 1- and 3-year-old stands (Figure 5; Appendix E). The abundance of threatened spiders was greatest in 1-year old stands and this was significantly greater than the abundances recorded in heathlands. Within the plantation stands, the greatest threatened species abundance and richness were found early in the chronosequence, particularly in 1- and 3-year-old stands (Figure 5). Richness of threatened species was not significantly different between heathlands and 1-, 3-, 5- and 7-year-old stands for both carabids and spiders. The closed canopy phase of the plantation chronosequence supported fewest

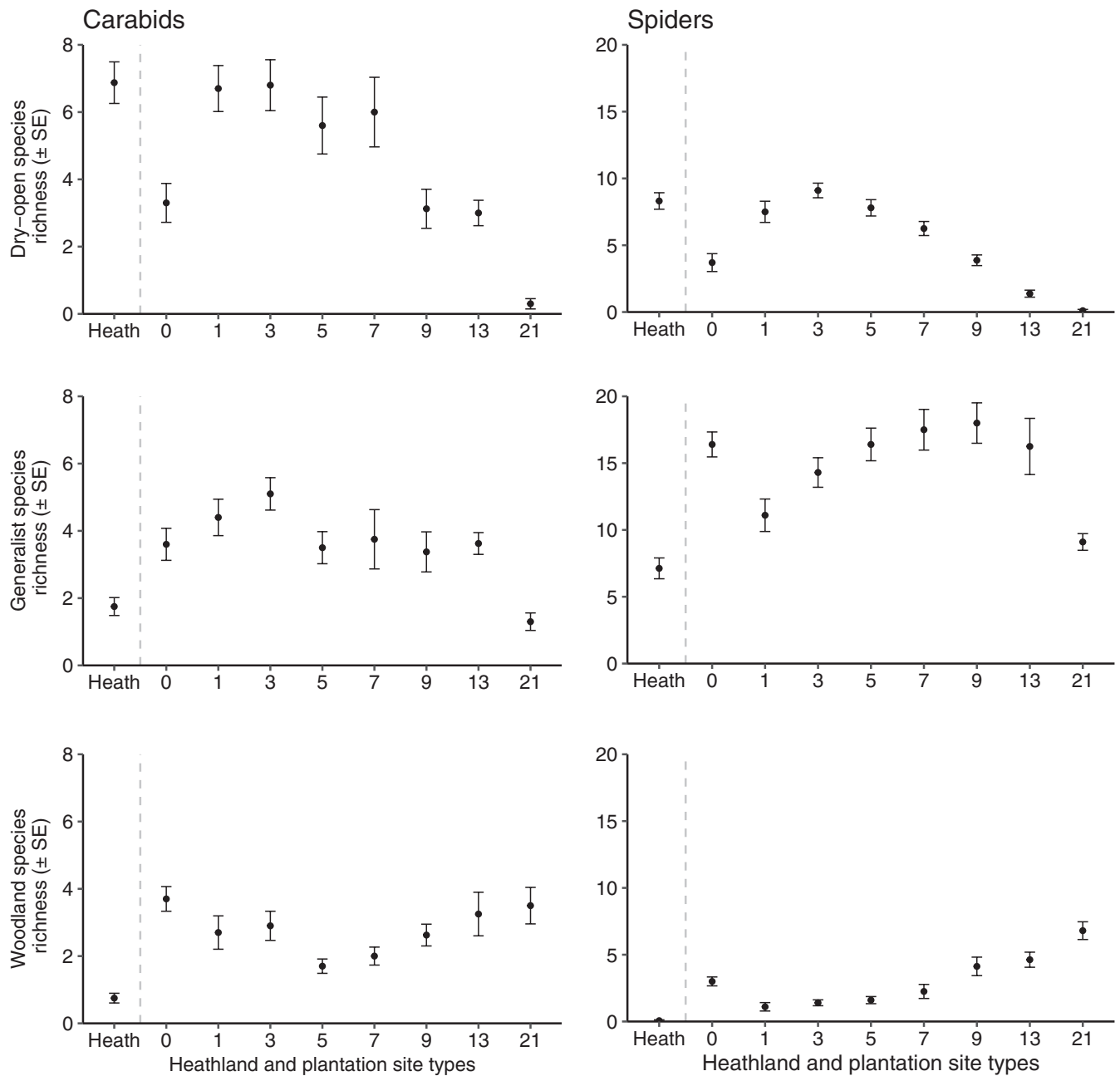


FIGURE 4 Mean species richness ± SE of carabids and spiders collected using pitfall trapping in each habitat type, shown separately for: dry-open habitat, generalist, and woodland associated species. The dotted line separates heathland reference samples from the sampled forestry chronosequence. Heath=Heathland patches, 0=cleared unplanted, 1=one year old, 3=three year old, 5=five year old, 7=seven year old, 9=nine year old, 13=thirteen year old and 21=twenty one year old plantation stands.

threatened species, with just three woodland associated spiders, and four woodland associated and one dry-open associated carabid (Appendix C).

3.4 | Landscape analysis

For spatial analysis, we defined early growth habitats (i.e., those suitable for open-habitat associated species) as forest stands aged between 1 and 7 years old, based on assemblage composition and

the richness and abundance patterns of dry-open habitat associated arthropods. Spatial aggregation and isolation of early growth habitats is predicted to change significantly over the 60-year plantation cycle (Figure 6), as the patch proximity index differed significantly between time intervals (Kruskal-Wallis $\chi^2=48.5$, $df=6$, $p<0.05$; Figure 7). In the current design plan for future forest management, isolation of these habitats should be steadily improved over the first 40 years before declining toward the end of the cycle (Figures 6 and 7). The proposed felling plan for the forest will result in the creation of young growth habitats in close proximity but within the 60-year

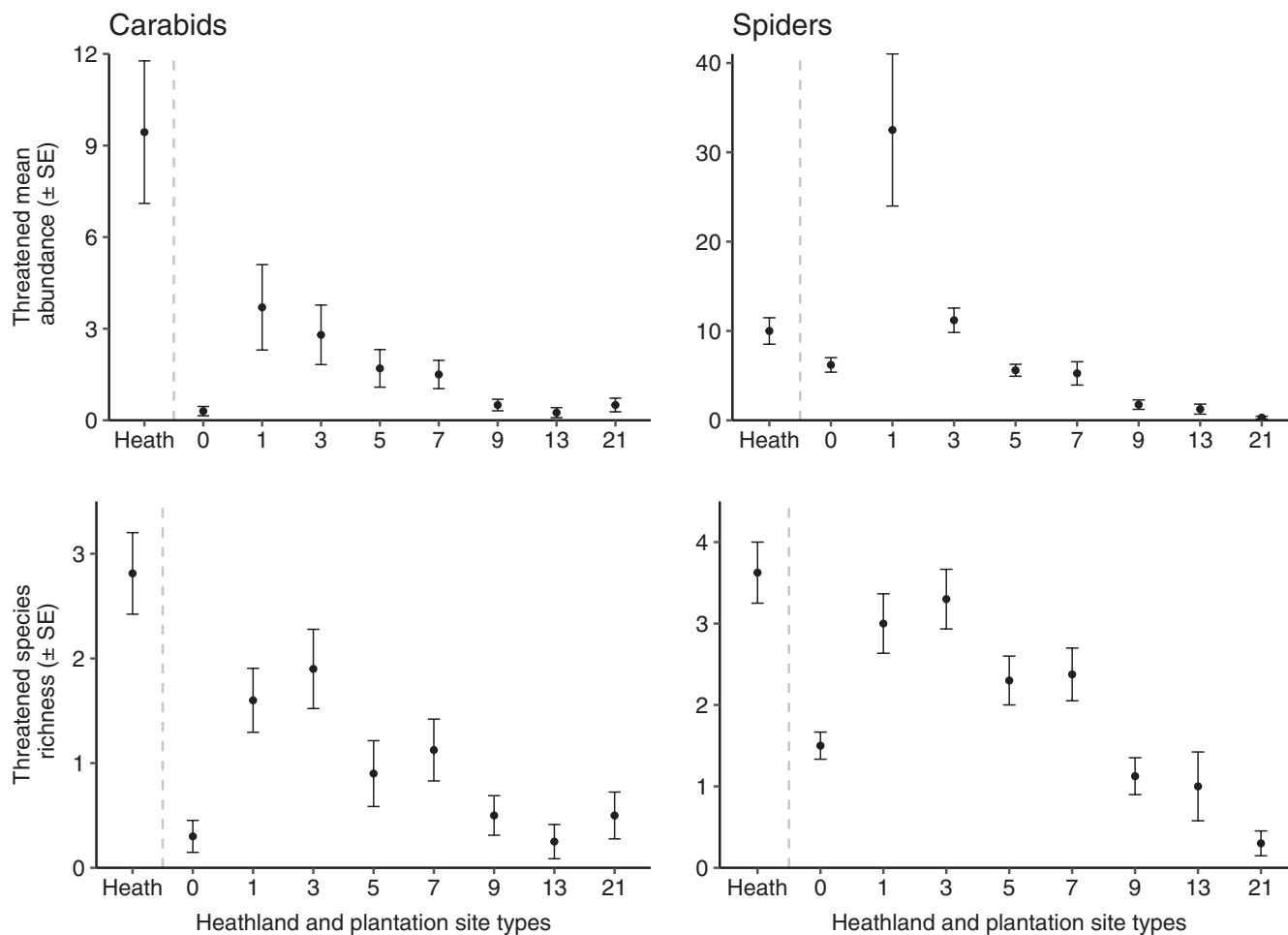


FIGURE 5 Mean abundance and species richness \pm SE of threatened carabids and spiders sampled from each habitat type. The dotted line separates heathland reference samples from the sampled forestry chronosequence. Heath=Heathland patches, 0=cleared unplanted, 1=one year old, 3=three year old, 5=five year old, 7=seven year old, 9=nine year old, 13=thirteen year old and 21=twenty one year old plantation stands.

rotation period, there will be increased isolation and fragmentation at the beginning and end of the rotation.

4 | DISCUSSION

Clear-fell harvesting had a major impact on the ground-active arthropod assemblages inhabiting plantation forest stands and species composition significantly changed throughout the sampled chronosequence. Although different to reference heathland communities, the assemblages in young ephemeral stands (1–7 years after planting) contained many individuals of species associated with dry-open habitats, such as heathland areas of regional conservation concern. These young stands supported a substantial number of threatened species from both sampled arthropod taxa, as well as many indicator species associated with dry-open habitats. The distribution of young ephemeral stands (1–7 years) throughout the planned forestry rotation highlights greater patch isolation at the start and end of the cycle, which could provide periods of less favourable connectivity for dispersal-limited arthropods associated with dry-open habitats.

4.1 | Composition of arthropod communities

The sampled plantation chronosequence supported greater species richness than open heathland. This finding largely agrees with other plantation systems in temperate regions, that have found higher species richness than surrounding open habitat, and also higher than adjacent natural woodland, largely due to open-habitat species colonising clear-felled sites (Butterfield et al., 1995; Fahy & Gormally, 1998; Mullen et al., 2008; Niemela et al., 1993; Oxbrough et al., 2005). Our findings of increased richness directly after clear-felling, followed by a brief dominance of open-habitat species, are consistent with carabids (Magura et al., 2015; Mullen et al., 2008; Niemela et al., 1993), staphylinids (Pohl et al., 2007) and spiders (Oxbrough et al., 2005, 2010) in developing plantations. However, this pattern is not universal, as Pawson et al. (2009) found no difference in carabid richness across stand ages in exotic pine plantations in New Zealand. Oxbrough et al. (2010) suggests that, after canopy closure spider composition changed little in maturing plantation forest in Ireland and suggested that canopy cover and ground layer homogeneity were the main drivers of arthropod composition. Carabid

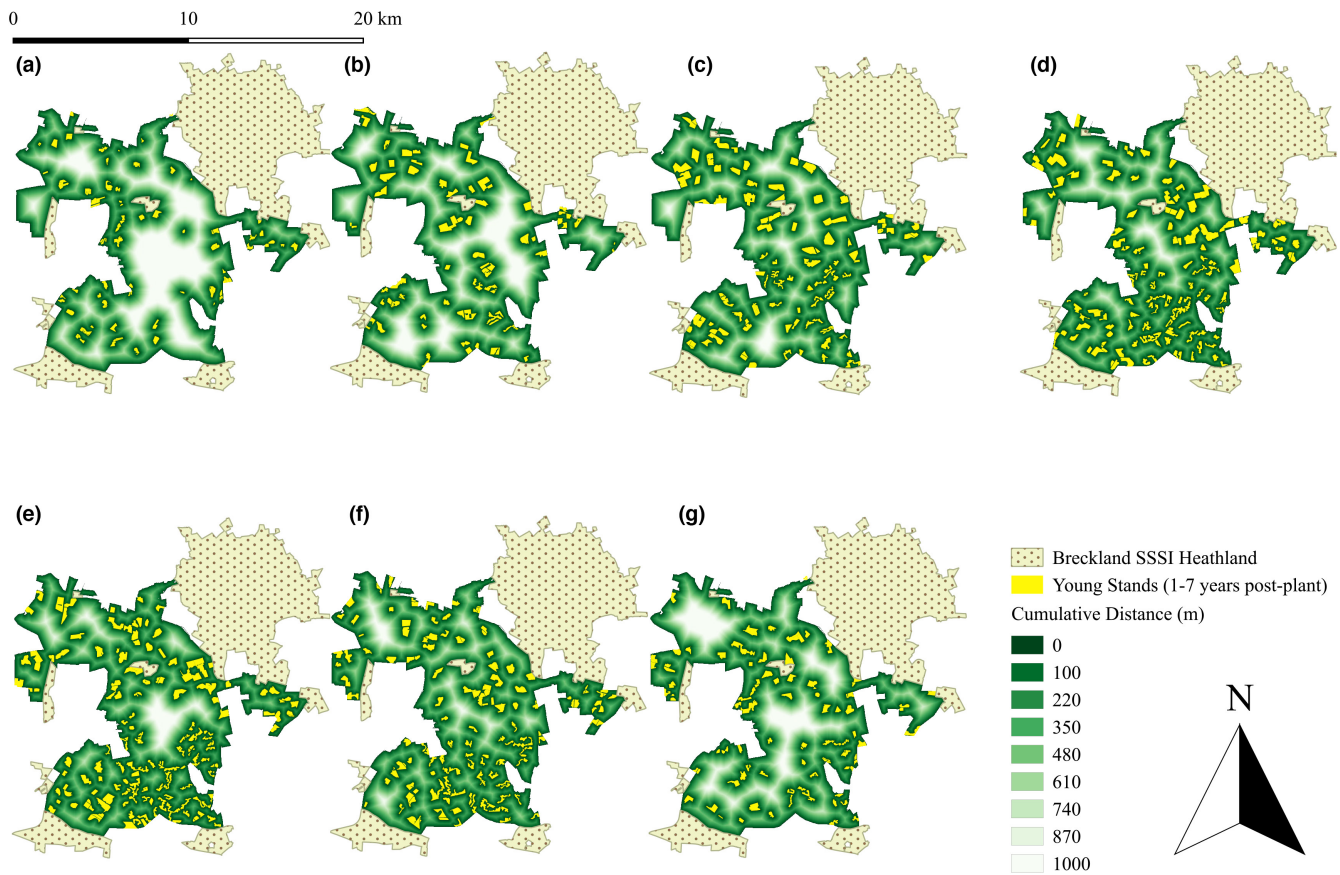
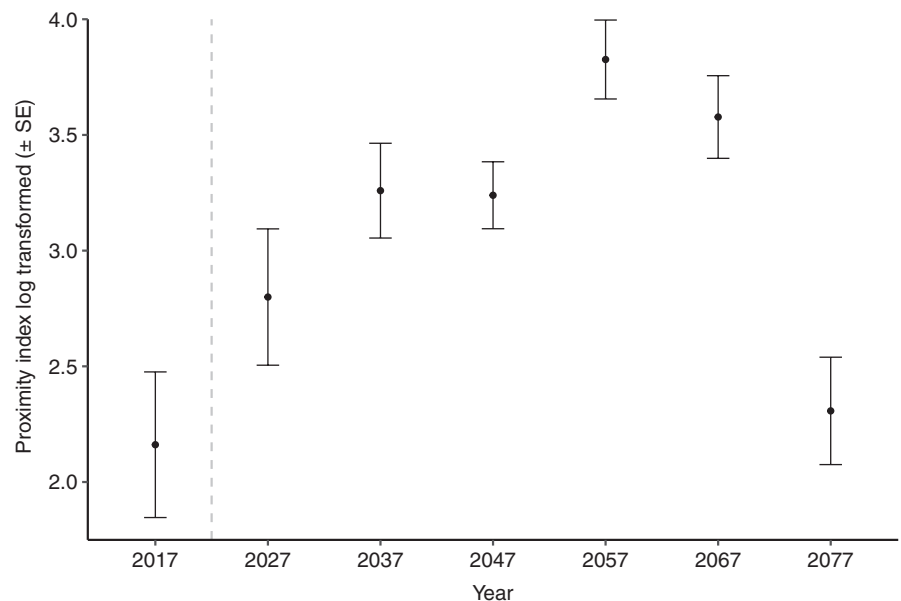


FIGURE 6 The core area of Thetford Forest showing the current and planned spatial patterns of early growth stages (1–7-year-old stands) for the years: (a) 2017, (b) 2027, (c) 2037, (d) 2047, (e) 2057, (f) 2067, (g) 2077. Cumulative distance refers to the distance between patches within the landscape.

FIGURE 7 Mean \pm SE of the log transformed proximity index (measure of patch isolation) at 10-year intervals over a 60-year forest rotation in Thetford Forest, UK.



and spider composition in stands older than 21 years in our study system may still have been in flux and additional woodland species may still accumulate as the stands mature further, but open habitat species are unlikely to re-colonise until the mature crop is felled.

The majority of open habitat species recorded in remnants of heathland habitat (that predominated pre-plantation) were also found within the largely exotic pine plantations in the current study. Of the 213 species recorded in the current study, very few (just eight

carabids and nine spiders), were not recorded within the plantation forest. However, of these 17 species not found in the plantations, eight were designated as nationally scarce and may be highly restricted, either due to specific resource requirements or to dispersal limitations. It should also be noted that open heathland in the region only persists in small remnant patches and has sustained significant environmental pressures over the last century (Dolman et al., 2010; Dolman & Sutherland, 1992) which may have reduced the species pool of specialist heathland species at the scale of individual heathland sites, but potentially also at the bioregional scale, similar to forest carabids in parts of New Zealand which appear to have 'collapsed assemblages' likely due to habitat loss and introduced mammalian predators (Lövei & Cartellieri, 2000; Pawson et al., 2009).

Generalist species tend to dominate in fragmented, disturbed and changing habitat (Marvier et al., 2004). Generalist arthropods are well known to benefit from the plantation cycle (Fuller et al., 2008; Maeto & Sato, 2004; Niemela et al., 1993; Peralta et al., 2018) as their habitat niches likely overlap with multiple rotation stages (restock, thicket, mature), compared to habitat specialists which may only appear through a narrow range of environment conditions (Clavel et al., 2011). Both Mullen et al. (2008) and Jukes et al. (2001) have shown that forest-associated carabids increase in numbers over the plantation cycle in both Ireland and the UK respectively, but that generalists dominate across all stages of the rotation. Maeto and Sato (2004) also found generalist ant species dominate secondary growth native forests and conifer plantations in Japan, whereas old growth forests were dominated by forest specialists. They also noted that open habitat specialists were only recorded in secondary and plantation forests. Our study shows how regionally important open habitat specialists dominated in the very early stages of the plantation (1–7 years), slightly before generalist species dominance which then appears to persist longer into the plantation cycle and after canopy closure. For both arthropod taxa, species composition of 1-, 3-, 5- and 7-year-old stands was more similar to that of the heathland sites than later plantation stages. The main difference in arthropod assemblage composition between heathland and these young plantations, was the inclusion of habitat generalists in the plantations, not a lack of open habitat specialists from the forest landscape.

Restricted numbers of woodland associated species manage to persist through the felling process and have been recorded in clear-fell sites in North America (Niemela et al., 1993), Ireland (Mullen et al., 2008) and in the current study. At this unplanted stage a thick cover of organic litter (from conifer needles and bracken) and woody debris remained following felling operations and this may provide cover for persistent woodland species. Although the abundance of woodland species remained low throughout our sampled chronosequence, species richness was relatively high in the cleared and unplanted stage compared to other stages. Furthermore, woodland species richness showed an increasing trend as the plantation developed through our chronosequence, even though the focus of the sampling regime was heavily concentrated toward the early stages of the rotation. Studies that have sampled older rotation stages tend

to suggest that plantations are not able to support many of the most specialised, or rarest forest species, and assemblages differ significantly to those of natural woodlands (Fierro et al., 2017; Finch, 2005; Fuller et al., 2008; Niemela et al., 1993). While many factors such as vegetation structure, understorey diversity, well developed organic soil layers, light levels, and moisture will contribute to differences in diversity and composition of the faunal biodiversity, deadwood has been suggested as a particularly important aspect for many arthropods. Michaels and Bornemissza (1999) suggest that saproxylic species may do particularly poorly under clear-fell management. Of the 19 rare or threatened species recorded in our study only three have known associations with woodland habitats, and none of the 16 woodland associated carabids recorded are known to be saproxylic.

4.2 | Conservation of regional specialists

In human-modified landscapes lacking natural habitat, biological conservation needs pragmatic solutions to maintain and enhance remnant biodiversity. Forestry landscapes may provide such solutions if conservation minded management options are implemented throughout rotation cycles. Regional conservation priorities and biogeographical context must be accounted for in such management decisions (Eycott et al., 2006a; Pawson et al., 2011). In regions where extensive afforestation has converted open natural or semi-natural habitat (e.g., heathland, moorland, coastal dunes), effective use of open space including clear-fells, young restocks and access trackways is critical (Eycott et al., 2006a; Greatorex-Davies et al., 1994; Noordijk et al., 2011; Pedley, Bertoncelj, et al., 2013). We show that throughout a 60-year rotation cycle, both the landscape composition and configuration of early growth habitat (1–7-year-old stands) will change significantly; early growth habitats were more clustered (and thus more isolated) in the landscape in the very initial and late stages of the rotation. Management options should look to encourage a greater mosaic of age structures throughout the rotation cycle to reduce dispersal distances between patches, and improve the permeability of habitat networks, including management of trackways and permanent open space in the forestry landscape (Pedley, Franco, et al., 2013; Wolstenholme & Pedley, 2021). Analogous to the paradigm of increased habitat heterogeneity to support farmland biodiversity (Benton et al., 2003), here we advocate the expansion of forestry heterogeneity, consisting of an increased mosaic of ephemeral young restocks and permanent open space across the forestry rotation to support vulnerable pre-plantation biodiversity.

We show that the majority of heathland carabids and spiders colonised the clear-felled and replanted stands, but sympathetic management of early successional structures in rides and trackways may accelerate spillover from these linear features and facilitate dispersal of more restricted species, similar to field edges in agriculture settings (Rand et al., 2006; Tscharrntke et al., 2005). Previous research has shown the benefit of targeted management on these linear features, such as widening to reduce shade and physical disturbance to create early successional vegetation structures

that support specialist biodiversity (Bertoncelj & Dolman, 2013a; Pedley, Franco, et al., 2013). The next steps should concentrate on the most effective distribution of features to encourage dispersal and colonisation from permanent open space into ephemeral open habitats created by clear-fell operations. Wolstenholme and Pedley (2021) have shown how linear features can be modelled within a plantation landscape; future landscape planning should also incorporate ephemeral features. The goal should be to facilitate the permeability of the forestry landscape by open habitat specialists by enhancing the quality and spatial connectivity of open space across full rotation cycles. While the functional composition of biota will differ in other forestry systems, where a conservation goal is to increase their value to open-habitat arthropod species and assemblages associated with pre-plantation habitats, then similar considerations of spatial heterogeneity, connectivity, and dispersal will apply.

5 | CONCLUSIONS

We recorded high overall species richness across the combined plantation growth stages, but our focus on the early phases of the rotation highlights how fleeting the opportunity is for open habitat specialists in a former heathland region. Clear-fell management provided habitat colonised by the majority of heathland carabids and spiders, and differences in assemblage composition to reference heathland samples was largely due to the additional presence of generalist species in forestry sites. However, it should be noted that a number of specialist species were restricted solely to heathland samples. With remnant heathland surviving in small, isolated, and often degraded patches across western Europe (Gimingham, 1972; Piessens et al., 2005; Webb, 2009), young growth stages in plantation landscapes may provide alternative habitat for heathland arthropods and support this vulnerable biodiversity. The results of this study suggest that a heterogenous mosaic of young growth stages would maximise the biodiversity potential of the plantation landscape.

AUTHOR CONTRIBUTIONS

Scott M. Pedley and Paul M. Dolman conceived the ideas and designed methodology. Scott M. Pedley collected the data. Scott M. Pedley and Paul Wolstenholme analysed the data. Scott M. Pedley and Paul M. Dolman led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available on Figshare: <https://doi.org/10.6084/m9.figshare.24064737.v1> (Pedley et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix A. Map of study sites showing arthropod sampling locations within the plantation chronosequence and heathland reference sites. Also shown are the heathland nature reserves in the study area to illustrate their proximity to forested areas.

Appendix B. Rarefaction curves for the carabid and spider communities sampled in plantation stands and heathland reference sites. The vertical dotted black line indicates the sample size of the least abundant habitat to represents a comparison point. Shaded areas are 95% confidence intervals. In each plot extrapolation extends to the number of individuals of the habitat element with the greatest sampled abundance. Analyses were conducted in the iNext package in R (Hsieh et al., 2016).

Appendix C. Species identified in heathland reference sites and chronosequence plantation plots (0–21-year-old stands) together with their abundance in each habitat type, species status in the UK (NR, Nationally Rare; NS, Nationally Scarce; NT, Near Threatened; S41, Section 41 priority species) and habitat association. Species in bold are those solely recorded in heathland sites.

Appendix D. Results of Multivariate Generalised Linear Models (using Poisson likelihood-ratio-tests in the mvabund package) comparing community composition of carabids and spiders in (a) 21-year-old plantation stands to other planting ages and heathland reference sites, and (b) heathland reference sites to plantation stands.

Appendix E. Results of generalised linear mixed models (χ^2 and p -value) comparing abundance and species richness of dry-open, generalist, woodland and threatened species among the chronosequence plantation plots (0–21 years old stands) and heathland reference sites. Tukey pairwise comparisons were used to define homogenous sub-sets (a–f ranked highest to lowest); means that share a superscript do not differ significantly ($p > 0.05$).

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