Linking Landscape Structure to Demographic Processes in European Landbirds

A juvenile (left) and adult (right) treecreeper (*Certhia familiaris*). Birds handled under licence. © Chas Holt.

Sarah Elizabeth Binnie

Thesis submitted for the degree of Doctor of Philosophy

University of East Anglia

School of Biological Sciences

April 2026

Abstract

Human land-use change is considered the greatest threat to global biodiversity. Declines are increasingly being seen in common and widespread species, including many European landbirds. There is an urgent need to address these declines, and exploration of spatiotemporal variation in demography can serve as a vital tool for identifying and targeting appropriate conservation actions. In this thesis, I examine limitations of current approaches for studying demographic variation in birds, and specifically explore potential drivers of spatial variation in the productivity of European landbirds. In a review of the spatiotemporal structure of avian demographic research, I demonstrate that most studies have taken place over small spatial scales and annual timescales. While this captures local, short-term effects well, our ability to detect the impacts of changes operating over larger scales and longer timescales is limited. To address this, I use a long-term, continent-wide bird ringing dataset to show that spatial variation in the productivity of European landbirds is at least partly driven by landscape characteristics surrounding breeding sites. Sites within landscapes locally dominated by wetlands, and at larger-scales, low-intensity land uses are more frequently associated with higher productivity in both residents and migrants. This identifies landscape-scale conservation actions with potential benefits across the bird community. I then explore whether insect prey availability could be driving associations between productivity and landscape structure with a Pan-European citizen science study at bird ringing sites. This reveals a positive association between cross-community productivity and insect abundance at sites, highlighting the importance of conserving and enhancing insect populations for supporting landbird populations in Europe. Landscape features do not appear to be associated with insect abundance, suggesting investigation of site-level characteristics as an important avenue for future work. Overall, this thesis demonstrates the immense value of collaborative research projects and citizen science for exploring links between local-scale processes and large-scale patterns.

Access Condition and Agreement

Each deposit in UEA Digital Repository is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the Data Collections is not permitted, except that material may be duplicated by you for your research use or for educational purposes in electronic or print form. You must obtain permission from the copyright holder, usually the author, for any other use. Exceptions only apply where a deposit may be explicitly provided under a stated licence, such as a Creative Commons licence or Open Government licence.

Electronic or print copies may not be offered, whether for sale or otherwise to anyone, unless explicitly stated under a Creative Commons or Open Government license. Unauthorised reproduction, editing or reformatting for resale purposes is explicitly prohibited (except where approved by the copyright holder themselves) and UEA reserves the right to take immediate ‘take down’ action on behalf of the copyright and/or rights holder if this Access condition of the UEA Digital Repository is breached. Any material in this database has been supplied on the understanding that it is copyright material and that no quotation from the material may be published without proper acknowledgement.

Contents

Abstract 2

Contents 3

Acknowledgements 5

Chapter 1: Introduction 6

1.1. Biodiversity Loss in the Anthropocene 7

1.2. Demographic Processes 9

1.3. Landbirds in Europe 10

1.4. Thesis Aims and Structure 14

1.5. Pilot Study 15

References 18

Supplementary Material 26

Chapter 2: Spatial and Temporal Scales of Demographic Analyses in Birds: A Review 27

Abstract 28

2.1. Introduction 29

2.2. Methods 30

2.3. Results 35

2.4. Discussion 46

References 50

Supplementary Material 55

Chapter 3: Is Spatial Variation in the Productivity of European Passerines Associated with Landscape Structure? 99

Abstract 100

3.1. Introduction 101

3.2. Methods 103

3.3. Results 109

3.4. Discussion 117

References 121

Supplementary Material 127

Chapter 4: Productivity of European Landbirds is Positively Associated with Flying Insect Abundance at Breeding Sites 167

Abstract 168

4.1. Introduction 169

4.2. Methods 170

4.3. Results ... 176
4.4. Discussion ... 188
References ... 191
Supplementary Material ... 196
Appendix 4.1. ... 215
Chapter 5: General Conclusions ... 219
5.1. Synthesis of Results ... 220
5.2. Annual Variation in Insect Abundance ... 222
5.3. Implications for Conservation and Management ... 224
5.4. Conclusion ... 227
References ... 227

Acknowledgements

There are many people without whom this thesis would not have been possible. I would first like to thank all of the dedicated volunteer bird ringers across Europe who sacrifice their sleep to collect truly invaluable data as part of the EURING scheme. I hope the work presented in this thesis demonstrates just how worthwhile all your hard work is! I would especially like to thank all of the volunteers who took part in the sticky trapping project in 2024, and the EuroCES scheme organisers who were essential to setting it up. It was a mammoth effort for everyone involved!

I am incredibly grateful to my wonderful supervisory team, Simon Butler, Jenny Gill, Cat Morrison and Rob Robinson. Simon – thank you for your endlessly patient guidance and support throughout this whole process, and always encouraging the best from me; Jenny – thank you for your unwavering enthusiasm, you are truly an inspiration; Cat – thank you for always being a kind, listening ear and go to for all things stats; and Rob thank you for your thoughtful advice and encouragement throughout.

I would also like to thank the ARIES DTP for funding this PhD and the British Trust for Ornithology (and wider EURING scheme) for providing the datasets.

Thank you to my various 01.31 office mates over the past four years for the laughs and the knowledge sharing: Claire, Emily and Tom, with very welcome recent additions Mabel and Ruth. I have also really enjoyed being part of the wider BIO and ARIES communities during my PhD.

Special thanks to the amazing friends I have made: Lili, Karolina, Ellie, Phoebe, Becky, George, Marjorie, Beckie, Harry, Miriam, Guthrie, Vini and Campbell.

Beyond UEA I would like to thank my friends and family for their love and support, especially Mum, Dad, Andrew and my sister Rachel. And finally, thank you to Guy and Bruno the cat for always being there through the highs and lows.

Chapter 1: Introduction

An English aerial landscape, by Petr Kratochvi. CCO Public Domain.

1.1. Biodiversity Loss in the Anthropocene

Global biodiversity is in crisis, with over 1 million species of animals and plants currently threatened with extinction (Díaz et al., 2019; IPBES, 2019). In addition to species extinctions, of immediate concern are the pervasive declines of common and widespread species (Ceballos et al., 2017; Dirzo et al., 2014; Finn et al., 2023). These declines can have negative cascading impacts on ecosystem functioning and services (Gaston and Fuller, 2007), putting human wellbeing at risk (Cardinale et al., 2012; Díaz et al., 2006). Understanding and tackling the drivers of these declines is one of the greatest challenges facing humanity but will be essential for sustaining life on Earth as we know it.

Land-use change is the most severe threat to terrestrial biodiversity (Davison et al., 2021; Jaureguiberry et al., 2022; Sala et al., 2000). Human actions have directly altered at least 70% of land surface (Díaz et al., 2019), primarily for agriculture, forestry and urbanisation (IPBES, 2019). As landscapes are transformed by human activities, native vegetation is lost, land-use intensity in modified areas increases, and remnants of native vegetation are increasingly influenced by processes originating in modified areas (Fischer and Lindenmayer, 2007). There is a large body of evidence demonstrating reductions in species richness (Gibson et al., 2011; Gonçalves-Souza et al., 2025; Murphy and Romanuk, 2014; Newbold et al., 2015; Zingg et al., 2018) and changes in community composition (Dornelas et al., 2014; Newbold et al., 2018) directly as a result of landscape modification, with subsequent management intensification driving additional declines in abundance and species richness (Gerstner et al., 2014), especially in cropland (Beckmann et al., 2019).

Land-use change can drive population declines through the combined effects of habitat loss, fragmentation and degradation, which lower the capacity of the landscape to support individuals (Fischer and Lindenmayer, 2007; Heinrichs et al., 2016). Habitat loss is a reduction in habitat amount and has consistently been shown to have negative effects on populations of multiple taxa (Fahrig, 2003; Hallworth et al., 2021; Moreno and Teixido, 2025; Yan et al., 2025). Habitat fragmentation is the sub-division of habitat (while controlling for habitat amount), with increasingly fragmented landscapes having more, smaller habitat patches and a greater total length of habitat edge (Fahrig, 2017). The effects of fragmentation on biodiversity and species populations are variable and intensely disputed, partly resulting from the wide range of metrics used and their measurement at different scales, between which comparisons cannot reliably be made (Fahrig, 2017; Riva et al., 2024; but see Fletcher et al., 2023). Many studies have identified negative impacts at the smaller patch scale (Fletcher et al., 2018), for example reduced abundances of forest-core species close to habitat edges (Pfeifer et al., 2017). Meanwhile others find negligible or positive effects of fragmentation when measured at the landscape scale, such as increased species richness and abundance in response to greater landscape complementarity (Priyadarshana et al., 2024), whereby different required resources are more accessible to each other in more fragmented landscapes (Fahrig, 2017; Fahrig et al., 2019). Taken together, this means that further habitat loss should be avoided to address these negative impacts, but fragmented landscapes where this has already occurred can still be of conservation value.

Until recently, habitat degradation had received far less attention compared to habitat loss and fragmentation, but its effects on populations can be equally as important (Heinrichs et al., 2016; Mortelliti et al., 2010). Habitat degradation involves the gradual deterioration of the quality of a habitat, which can occur independently of, but often alongside, changes in habitat extent or continuity, for example due to grazing pressure (Barzan et al., 2021; Thompson et al., 2009) or selective logging (Ross et al., 2018). Habitat is, by definition, a species-specific concept, with quality determined by the provision of food, shelter, space and suitable climatic conditions (Fischer and Lindenmayer, 2007). Degradation therefore involves the diminishing ability of habitat to provide these key resources, and applies not only to remaining natural habitat patches, but also the wider non-native habitat surrounding these patches (the "matrix") (Zhao et al., 2025). Matrix habitat quality generally declines with increasing intensity of land-use, which involves the conversion of low-contrast matrix types, such as secondary forests or shade-grown low-intensive agriculture in forested regions, to high-contrast matrix types, such as intensive agriculture, built environments (Ramírez-Delgado et al., 2022), or surface mines (Deikumah et al., 2015). Species show varying trait-related responses to changing matrix quality, which can therefore mediate the effects of habitat loss and fragmentation on biodiversity metrics (Chetcuti et al., 2021; de Souza Leite et al., 2022; Ramírez-Delgado et al., 2022).

Habitat loss, fragmentation and degradation represent distinct phenomena in theory but, in real landscapes, they are difficult to separate because they are causally related and co-occur (Banks-Leite et al., 2020). This means that action to manage one of these components is likely to simultaneously address the other two (Banks-Leite et al., 2020). However, identifying appropriate management actions is challenging because the effects of habitat transformation are inherently species- and scale-dependent, as well as context-specific (Banks-Leite et al., 2020). Studies can obtain very different results if they are conducted at different spatial or temporal scales (Fletcher et al., 2023), in regions with different biogeographical history or at different parts of a species' range (Banks-Leite et al., 2022). For example, a study on Atlantic Forest bird species demonstrated that populations are more sensitive to deforestation when near the species' range edge (Orme et al., 2019). These complexities highlight the importance of measuring impacts of land-use change at scales relevant to the mechanisms which might be underlying observed patterns, while also considering macroecological context (Fletcher et al., 2023).

Climate change is a recent but rapidly intensifying threat to biodiversity (Jaureguiberry et al., 2022; Pereira et al., 2024). Its effects on species populations can interact with local changes in land-use, potentially leading to a greater overall impact on biodiversity change than either of these drivers operating in isolation (de Chazal and Rounsevell, 2009; Oliver and Morecroft, 2014; Williams et al., 2022; Zhao et al., 2019). For example, habitat loss and fragmentation has been shown to reduce population resilience to extreme climatic events like droughts (Ross et al., 2016), with smaller and more isolated habitat patches recording larger population declines under these conditions and slower rates of recovery (Oliver et al., 2013). In addition, more homogenous landscapes such as intensive agricultural land have less variable microclimates (Oliver et al., 2010), which could otherwise act as refuges for species facing unsuitable conditions under future climate scenarios (Suggitt et al., 2015). The impacts of climate change on species populations are often felt through changes to habitat suitability and quality (e.g. Kleijn et al., 2010; Zhao et al., 2019), and altered species interactions, rather than direct abiotic effects of temperature or precipitation, especially at higher trophic levels (Ockendon et al., 2014).

1.2. Demographic Processes

Large-scale biodiversity loss is underpinned by local population declines and extinction (Collen et al., 2011; Newbold et al., 2015). Ultimately this is driven by changes in demographic rates but studies examining the associations between environmental pressures and changes in species richness, occurrence or abundance are often limited to identifying correlations and not the mechanisms by which these pressures operate to drive population declines and extinctions (Selwood et al., 2015). Comparatively few studies have explored demographic responses to land-use change (Cosset et al., 2019; Davison et al., 2021; Gibson et al., 2011), but understanding the changes in reproductive output, survival and dispersal that underlie population declines is essential for identifying and addressing these threats (Anders and Marshall, 2005; Robinson et al., 2014; Selwood et al., 2015). For example, abundance or density patterns can mask underlying demographic processes associated with habitat quality (Cosset et al., 2019; Van Horne, 1983), such as ‘ecological traps’ where individuals occupy degraded habitat in which they cannot breed or face higher mortality rates (Hale and Swearer, 2016). Habitat quality is therefore best quantified by directly measuring demographic outcomes, rather than habitat attributes assumed to be a proxy of quality (Mortelliti et al., 2010).

A synthesis by Selwood et al., (2015) demonstrated that anthropogenic changes in landscape condition are often associated with reduced reproductive output and immigration rates, and increased mortality and emigration rates. For example, lower food availability and accessibility in fragmented landscapes and degraded habitat have been shown to reduce reproductive output and survival rates across multiple taxa, including birds (Hinam and Clair, 2008; Luck, 2003; Ruiz-Gutiérrez et al., 2008), mammals (Butler et al., 2021; Mbora et al., 2009) and insects (Maurer et al., 2020). In addition, edge effects in fragmented landscapes can increase predation risk, which has been well-documented in the form of increased nest predation and brood parasitism rates, and therefore reduced nest success, closer to habitat edges in forest bird species (Akresh et al., 2024; Lampila et al., 2005). Mutualistic species interactions can also be disrupted by landscape modification, including plant-pollinator systems, leading to reduced fruit production in wild plants (Cunningham, 2000; Eeraerts et al., 2017). Regarding dispersal, reduced pairing success has frequently been reported in fragmented landscapes due to lower immigration rates of females to more isolated or poorer quality patches (Burke and Nol, 1998; Lampila et al., 2005; Morrison et al., 2016b; Winiarski et al., 2017). Dispersal may also be disrupted in modified landscapes where mortality risk is increased for individuals crossing matrix habitats, for example due to increased predation rates (Rodríguez et al., 2001).

Despite these general patterns, there is considerable between-species variation and context-dependence in demographic responses to land-use change (Cosset et al., 2019). Changes to vital rates might not occur where matrix habitat can still provide adequate resources, for example in generalist species (Walkup et al., 2017) or in low-intensity land uses (Siriwardena et al., 2000). In addition, where predator populations are negatively affected, this reduces top-down control and may balance out any direct negative impacts on vital rates (Cosset et al., 2019). Due to this variability in demographic responses, general conservation guidance across species, or even different populations of the same species, is not recommended (Burgess et al., 2020; Zhao et al., 2023). This highlights the importance of examining how vital rates vary spatially and temporally in order to understand the environmental drivers of population change (Green, 1999; Frederiksen et al., 2014; Piironen et al., 2025) and effectively target conservation actions (Burgess et al., 2020).

1.3. Landbirds in Europe

Demographic data need to be collected over sufficiently large spatial and temporal scales to fully capture the range of conditions influencing population trends, but this is challenging due to the resource-heavy nature of demographic research. Birds have frequently been the subject of demographic studies (Robinson et al., 2014), including over long time-periods and large scales through the contribution of citizen science and collaborative research (Robinson et al., 2009). They also serve as important indicators for ecological communities due to their sensitivity to changes at lower trophic levels (Fraixedas et al., 2020). Avian population dynamics therefore provide an excellent context to explore the role of demographic processes in driving population-scale responses to land-use change, and form the main focus of this thesis going forwards. I make particular reference to landbirds in Europe, but species from other realms and regions are also considered.

European breeding bird numbers have declined by nearly 20% since 1980, with more common species declining faster than less abundant species (Burns et al., 2021; Inger et al., 2015). Especially strong declines have occurred in landbird species associated with agricultural or grassland systems (Bowler et al., 2019; Burns et al., 2021), which are largely driven by the increasing intensification of farming practices (Donald et al., 2006; Rigal et al., 2023). Various demographic mechanisms have been attributed to these declines, including reduced overwinter survival due to loss of seed resources (Peach et al., 1999), reduced reproductive output due to nesting habitat loss (Newton, 2004a), mechanistic destruction or livestock trampling of nests (Donald et al., 2002), reduced insect food for nestlings after insecticide applications (Britschgi et al., 2006) and increased nest predation (Brickle et al., 2000) in agro-intensive landscapes.

Severe declines have also been recorded in species associated with long-distance migration between breeding areas in the Palaearctic region and non-breeding grounds in sub-Saharan Africa (Burns et al., 2021; Vickery et al., 2023). A considerable body of research has demonstrated that these species are declining significantly faster than short-distance migrants and residents which remain within Europe (Howard et al., 2020; Sanderson et al., 2006; Thaxter et al., 2010; Vickery et al., 2023, 2014). Long-distance migrants are exposed to a wide range of environmental conditions and anthropogenic threats due to their use of multiple areas throughout the annual cycle, making it challenging to identify the causes of population declines and appropriate conservation actions (Newton, 2004b; Runge et al., 2014). Since the 1980s, species over-wintering in the humid tropics of sub-Saharan Africa have exhibited consistent declines, whilst those wintering within the more northerly arid-zone have shown partial recovery in numbers (Morrison et al., 2021; Vickery et al., 2014, 2023). These divergent trends have focused attention on anthropogenic pressures acting on non-breeding grounds, with many studies examining the association between drivers such as drought (Norman and Peach, 2013; Ockendon et al., 2014), hunting (Lormée et al., 2020) or land-use change (Adams et al., 2014), and population trends and demographic rates recorded on European breeding grounds. However, there is considerable uncertainty around the non-breeding season distribution of migrant populations (Beresford et al., 2019), and weak migratory connectivity is typical of many species (Finch et al., 2017), and so studies haven't been able to detect any consistent patterns (Vickery et al., 2023). This makes it very challenging to identify direct conservation actions in non-breeding grounds and stopover sites.

In comparison, there are several lines of evidence demonstrating the importance of changing conditions at European breeding grounds for migrant populations and demography (Burgess et al., 2025; Vickery et al., 2023). Regional within-species variation in population trends has been identified in both long-distance migrants and residents breeding in the UK, and this variation in the quality of breeding conditions is likely interacting with non-breeding conditions to exacerbate or buffer population changes (Morrison et al., 2013). Similar regional variation was detected in productivity but not survival rates of several long-distance migrants, which further demonstrates the importance of breeding conditions (Morrison et al., 2016a). This also highlights the possibility of measuring demographic variation to identify situations where low rates could be improved through conservation action (Morrison et al., 2022).

Europe-wide analysis of long-term breeding abundance data from the Pan-European Common Bird Monitoring Scheme (PECBMS) revealed positive covariation in site-level population trends of residents and migrants (Figure 1.1a-b; Morrison et al., 2021). Demographic data from the European Constant Effort Sites (Euro-CES) scheme showed that this strong positive covariation is mirrored for site-level productivity but not survival rates (Figure 1.1c-f; Morrison et al., 2021). In addition, spatiotemporal analysis found that productivity varies more between sites than between years, such that sites tend to have consistently high or low productivity, while survival tends to show more annual variation across sites (Figure 1.2; Morrison et al., 2022). This indicates that local breeding conditions are likely to be key drivers of local population trends, through impacts on productivity, and targeting conservation actions on breeding grounds could be a feasible means of delivering population recovery in both migrants and residents (Morrison et al., 2021, 2022). However, the conditions associated with high and low productivity sites and potential conservation actions are yet to be identified.

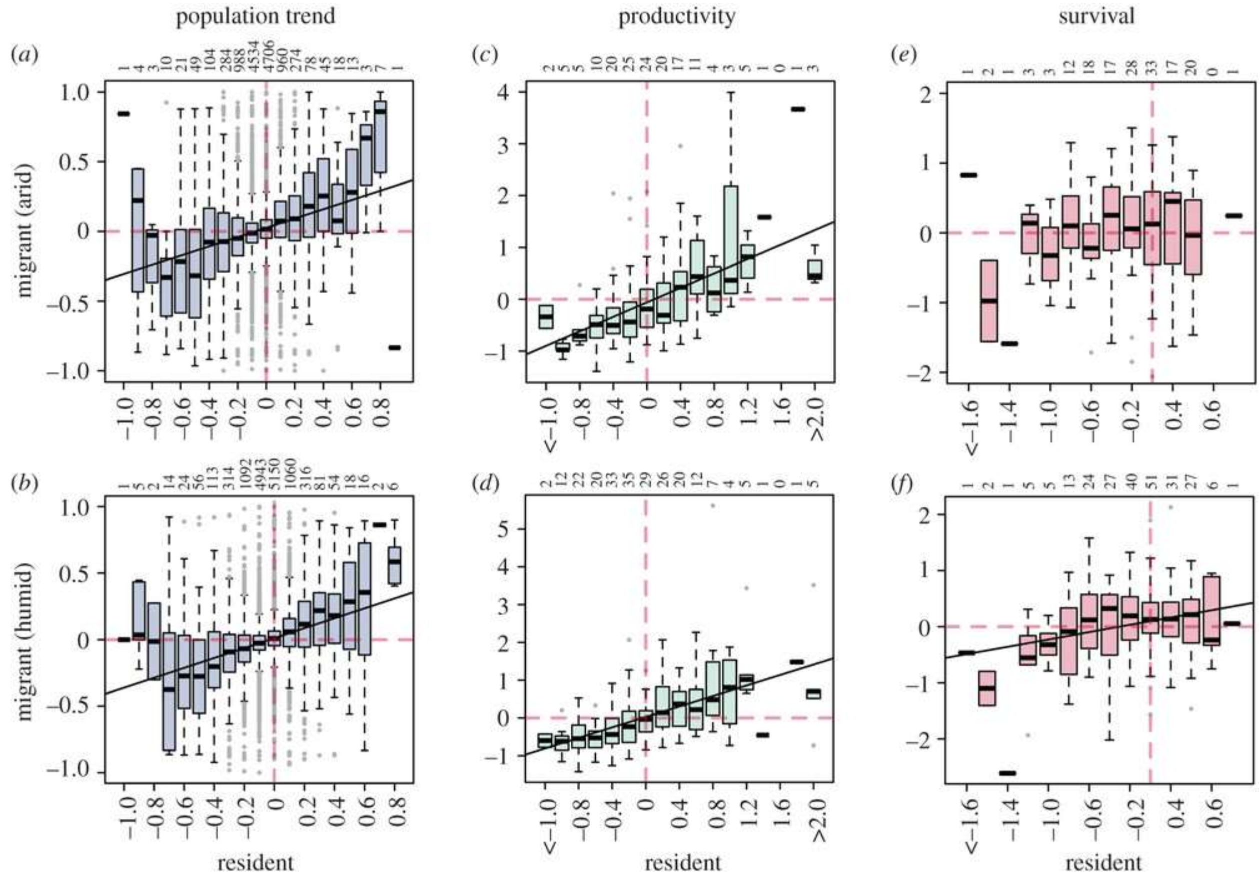


Figure 1.1. Covariation between resident bird species and their co-occurring arid-zone (*a,c,e*) and humid-zone (*b,d,f*) migrant species in mean site-level (*a,b*) population trends (*a:* 12 103 sites; *b* 13 267 sites), (*c,d*) standardised mean site-level productivity (*c:* 156 sites; *d*: 247 sites), and (*e,f*) standardised mean site-level annual survival rates (*e:* 156 sites; *f*: 247 sites). Lines of best fit are shown for significant associations and numbers indicate the number of sites. Horizontal bars indicate medians, boxes indicate interquartile range, whiskers indicate minimum and maximum values and circles indicate values 1.5 times higher or lower than 1st and 3rd interquartile, respectively. Reproduced from Morrison et al., 2021 (Figure 2).

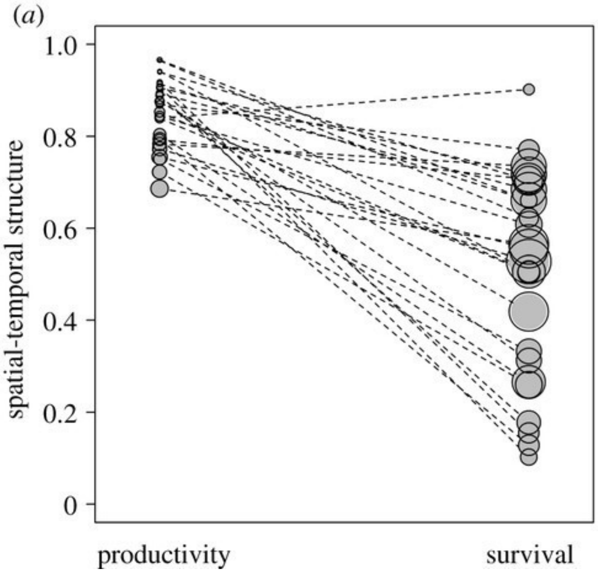


Figure 1.2. Differences between productivity (juveniles per adult) and survival (annual adult rates) in their spatio-temporal structure (0 = wholly annual, 1 = wholly spatial). Dashed lines join each species' estimates. Point size varies relative to the standard deviation of each estimate (smallest = 0.03, largest = 0.36). Adapted from Morrison et al., 2022 (Figure 2).

As described above, land-use is likely to be a key determinant of productivity because it affects the availability of resources required by landbirds to successfully raise young. This includes nesting habitat with shelter from predators and adverse weather, and food for nestlings, fledglings and breeding adults. The type of land cover, the management intensity and the configuration of landscape features all have the potential to impact the availability of these resources. For example, nest success can vary with small-scale habitat characteristics, such as sward height (e.g. Pärt, 2001a, 2001b) or tree composition and maturity within territories (e.g. Arriero et al., 2006; Glądalski et al., 2019), which in turn can be determined by the intensity of grassland or forest management. These factors can also drive variation in insect prey availability between sites, which is likely to be important for productivity because the vast majority of landbirds (excluding birds of prey) feed on insects during the breeding season (Cramp, 2006), and insectivory is strongly associated with long-distance migration (Jiguet et al., 2007). Insect abundance and biomass have been shown to vary with landscape composition, being greater in semi-natural landscapes compared to urban environments (Seress et al., 2018) and agricultural landscapes (Garrett et al., 2022). In addition, the availability of high-quality aquatic insect prey is positively associated with productivity (Twining et al., 2018) and is driven by the prevalence of water features in the landscape (Berzins et al., 2022). The potential role of these factors in driving productivity rates warrants further exploration.

1.4. Thesis Aims and Structure

The overarching aim of this thesis is to better understand spatial variation in the productivity of breeding landbirds in Europe, and consider implications for their conservation. In **Chapter 2**, I present a review of the spatiotemporal structure of demographic research in a representative sample of the ornithological literature. The objective was to examine the limitations of current approaches for exploring spatiotemporal variation in demography and consider their implications for our understanding of its potential drivers. This review highlights that most studies of variation in productivity have been limited in spatial scale and have focused on single species or habitats.

To address these limitations, in Chapters 3 and 4 I report analyses of productivity data collected by the EuroCES scheme, which is a large network of constant-effort bird ringing sites across 13 countries in Europe, where standardised mist-netting is carried out every breeding season. This dataset presents a rare opportunity to examine the effects of large-scale drivers on local demographic processes across multiple species and at a continental scale. Specifically, in **Chapter 3**, I use EuroCES data to examine whether features of the landscape surrounding sites drive spatial variation in productivity. I consider whether productivity is associated with landscape composition and configuration, measured at three spatial scales around sites, and also examine whether responses differ between species with different migratory strategies.

In **Chapter 4**, I explore whether insect prey availability could be a mechanism driving associations between landscape structure and bird productivity. My methodology for this chapter was based on a pilot study I conducted at 12 sites in central England in 2023 (see below), which found that sites with high bird productivity had greater flying insect abundance than sites with low productivity. In 2024, I expanded this sampling to a Pan-European scale, recruiting citizen scientists at 176 Constant Effort Sites across 10 countries to measure flying insect abundance across the breeding season. I subsequently examined whether insect abundance maps onto spatial variation in site-level productivity, and whether these patterns vary with the landscape variables identified as important in Chapter 3.

Finally, in **Chapter 5**, the General Conclusions, I synthesise the results presented in each chapter of this thesis and consider the broader implications of this research and potential future directions.

All chapters are written as standalone pieces of work with separate figures, reference lists and supporting materials presented at the end of each chapter.

1.5. Pilot Study

In 2023, I carried out a pilot study in the UK to investigate differences in local conditions between breeding sites identified as consistently "good" or "poor", across years and species. Field data was collected on invertebrate abundance and vegetation structure at 12 sites from the BTO's Constant Effort Sites (CES) ringing scheme. To identify CESs with consistently high or low bird productivity, active sites were ranked from best to worst for 22 passerine species individually (Table S1.1.), using average productivity values calculated across sampling years falling between 1998 and 2019 at each site. A mean rank across species was then calculated for each site, and six top-ranking ('good') sites from the upper quantile and six low-ranking ('poor') sites from the lower quantile were selected within central England for fieldwork (Fig. 1.3a.). This was restricted to sites classified as scrub-dominated, with woodland and reedbed sites excluded to maximise comparability between sites.

Each site was visited on two separate occasions in 2023: once during the nesting period in June ("early"), and once during the post-fledging period in July/August ("late"). Visits to the different sites were made as close together as possible on days with warm, dry weather. To measure the relative abundance of flying or foliage-dwelling invertebrates, 6 yellow sticky traps were deployed throughout the mist net rides for approximately 8 hours (~08:00 – 16:00), placed in the same locations on both visits (Figure 1.3b.). Invertebrates >1mm caught on the traps were subsequently identified to Order and counted in three size classes (1 - 2 mm, 3 – 5 mm, > 5 mm). The total invertebrate count in all size classes for each trap was modelled as the response variable in a generalised linear mixed model with a negative binomial error structure to account for overdispersion ('lme4' package (Bates et al., 2015), R 4.4.1. (R Core Team, 2024)). Fixed effects consisted of the site quality, as defined by productivity (factor, levels: good or poor), and the visit period (factor, levels: early, late), as well as their interaction, and site ID was fitted as a random intercept.

The total invertebrate count per sticky trap was significantly greater on the good-quality sites than the poor-quality sites (Figure 1.4.), with the average count per trap twice as high on good-quality sites (mean and 95% CIs (*n*): good sites = 41.7, 29.5 – 58.8 (72); poor sites = 20.1, 14.1 – 28.8 (60)). In addition, the invertebrate counts recorded in the early visit period were significantly greater than those recorded in the late visit period (mean and 95% CIs (*n*): early visit = 33.8, 25.6 – 44.6 (60); late visit = 24.8, 19.0 – 32.3 (72); Figure 1.3.). The majority of invertebrates caught were within the 1 – 2 mm and 3 – 5 mm size classes, and these two size-classes demonstrated very similar patterns. (Invertebrates > 5 mm were too few to compare between sites and visits).

Figure 1.3: a) Map of the selected pilot study sites, consisting of six "good" quality sites with relatively high average productivity, and six "poor" quality sites with relatively low average productivity. **b)** Image of one of the yellow sticky traps deployed at study sites.

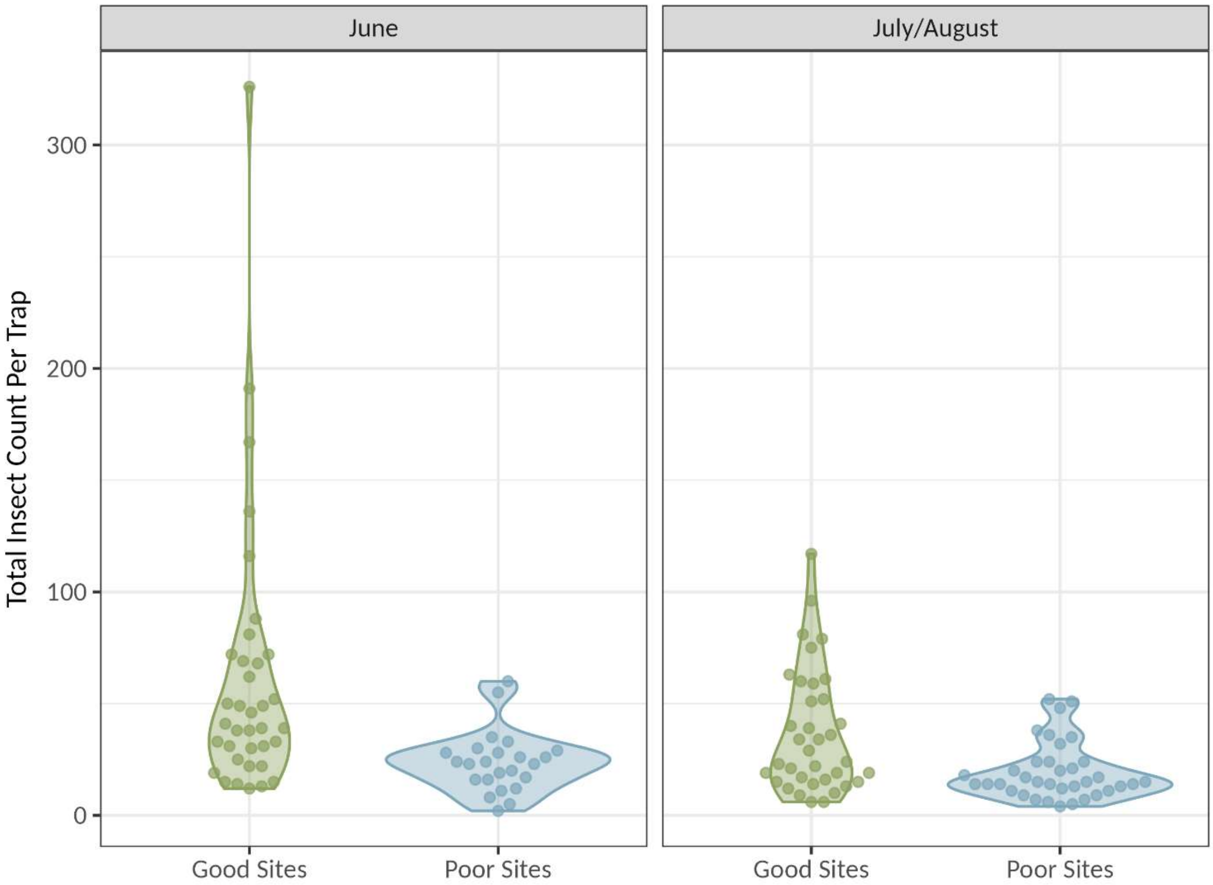


Figure 1.4: Total invertebrate count on each sticky trap deployed at six good- and six poor-quality breeding sites during early (June) and late (July/August) visit periods in 2023 (*n* traps = 132).

Table 1.1: Model outputs from a generalised linear mixed model testing the effects of breeding site quality ("Good", "Poor") visit period ("Early", "Late"), and their interaction on the total invertebrate count recorded on sticky traps during a pilot study in 2023. Outputs are given on the log scale. Total *n* = 132. Site (*n* = 12) was fitted as a random effect.

Fixed effects	Estimate	Standard Error	Z value	p value
Intercept (Good, Early)	3.96	0.19	20.62	<0.001
Poor	-0.96	0.29	-3.33	**<0.001**
Late	-0.46	0.14	-3.39	**<0.001**
Poor : Late	0.39	0.22	1.80	0.07

This study revealed that sticky trap sampling is a suitable method for measuring spatial and temporal variation in invertebrate abundance and that this variation maps onto spatial variation in bird productivity. This warranted further exploration and so in 2024, I expanded this sampling to a European scale with the help of volunteer bird ringers at European Constant Effort Sites. Some modifications were made to the methodology to increase the temporal resolution of the sampling and simplify the procedures for volunteers (see Chapter 4 methods for more details). Additional data on ground-invertebrate abundance using pitfall traps and vegetation structure was collected during the pilot study, but did not show any patterns with bird productivity and so was not taken forward.

This study was conducted with approval from the University of East Anglia Research Ethics Committee (ETH2223-2236).

References

Adams, W.M., Small, R.D.S., Vickery, J.A., 2014. The impact of land use change on migrant birds in the Sahel. Biodiversity 15, 101–108. https://doi.org/10.1080/14888386.2014.931822

Akresh, M.E., McInvale, S.L., King, D.I., 2024. A meta-analysis of edge effects on nesting success in forest and shrubland birds of eastern North America. Journal of Field Ornithology 95. https://doi.org/10.5751/JFO-00481-950212

Anders, A.D., Marshall, M.R., 2005. Increasing the Accuracy of Productivity and Survival Estimates in Assessing Landbird Population Status. Conservation Biology 19, 66–74. https://doi.org/10.1111/j.1523-1739.2005.00543.x

Arriero, E., Sanz, J.J., Romero-Pujante, M., 2006. Habitat structure in Mediterranean deciduous oak forests in relation to reproductive success in the Blue Tit Parus caeruleus. Bird Study. https://doi.org/10.1080/00063650609461411

Banks-Leite, C., Betts, M.G., Ewers, R.M., Orme, C.D.L., Pigot, A.L., 2022. The macroecology of landscape ecology. Trends in Ecology & Evolution 37, 480–487. https://doi.org/10.1016/j.tree.2022.01.005

Banks-Leite, C., Ewers, R.M., Folkard-Tapp, H., Fraser, A., 2020. Countering the effects of habitat loss, fragmentation, and degradation through habitat restoration. One Earth 3, 672–676. https://doi.org/10.1016/j.oneear.2020.11.016

Barzan, F.R., Bellis, L.M., Dardanelli, S., 2021. Livestock grazing constrains bird abundance and species richness: A global meta-analysis. Basic and Applied Ecology 56, 289–298. https://doi.org/10.1016/j.baae.2021.08.007

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Beckmann, M., Gerstner, K., Akin-Fajiye, M., Ceaușu, S., Kambach, S., Kinlock, N.L., Phillips, H.R.P., Verhagen, W., Gurevitch, J., Klotz, S., Newbold, T., Verburg, P.H., Winter, M., Seppelt, R., 2019. Conventional land-use intensification reduces species richness and increases production: A global meta-analysis. Global Change Biology 25, 1941–1956. https://doi.org/10.1111/gcb.14606

Beresford, A.E., Sanderson, F.J., Donald, P.F., Burfield, I.J., Butler, A., Vickery, J.A., Buchanan, G.M., 2019. Phenology and climate change in Africa and the decline of Afro-Palearctic migratory bird populations. Remote Sensing in Ecology and Conservation 5, 55–69. https://doi.org/10.1002/rse2.89

Berzins, L.L., Morrissey, C.A., Howerter, D.W., Clark, R.G., 2022. Conserving wetlands in agroecosystems can sustain aerial insectivore productivity and survival. Can. J. Zool. 100, 617–629. https://doi.org/10.1139/cjz-2021-0204

Bowler, D.E., Heldbjerg, H., Fox, A.D., Jong, M. de, Böhning-Gaese, K., 2019. Long-term declines of European insectivorous bird populations and potential causes. Conservation Biology 33, 1120–1130. https://doi.org/10.1111/cobi.13307

Brickle, N.W., Harper, D.G.C., Aebischer, N.J., Cockayne, S.H., 2000. Effects of agricultural intensification on the breeding success of corn buntings Miliaria calandra. Journal of Applied Ecology 37, 742–755. https://doi.org/10.1046/j.1365-2664.2000.00542.x

Britschgi, A., Spaar, R., Arlettaz, R., 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. Biological Conservation 130, 193–205. https://doi.org/10.1016/j.biocon.2005.12.013

Burgess, M.D., Eaton, M.A., Gregory, R.D., 2020. A review of spatial patterns across species ranges to aid the targeting of conservation interventions. Biological Conservation 251, 108755. https://doi.org/10.1016/j.biocon.2020.108755

Burgess, M.D., Sheehan, D.K., White, P.J.C., Anderson, G.Q.A., Fisher, G., Grice, P.V., Peach, W.J., Norris, K., 2025. Inadequate reproductive success is a potential cause of Spotted Flycatcher (Muscicapa striata) population decline in England. Ibis n/a. https://doi.org/10.1111/ibi.13460

Burke, D.M., Nol, E., 1998. Influence of Food Abundance, Nest-Site Habitat, and Forest Fragmentation on Breeding Ovenbirds. Auk 115, 96–104. https://doi.org/10.2307/4089115

Burns, F., Eaton, M.A., Burfield, I.J., Klvaňová, A., Šilarová, E., Staneva, A., Gregory, R.D., 2021. Abundance decline in the avifauna of the European Union reveals cross-continental similarities in biodiversity change. Ecology and Evolution n/a. https://doi.org/10.1002/ece3.8282

Butler, A.R., Bly, K.L.S., Harris, H., Inman, R.M., Moehrenschlager, A., Schwalm, D., Jachowski, D.S., 2021. Life on the edge: habitat fragmentation limits expansion of a restored carnivore. Animal Conservation 24, 108–119. https://doi.org/10.1111/acv.12607

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148

Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences 114, E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Chetcuti, J., Kunin, W.E., Bullock, J.M., 2021. Matrix composition mediates effects of habitat fragmentation: a modelling study. Landscape Ecol 36, 1631–1646. https://doi.org/10.1007/s10980-021-01243-5

Collen, B., McRae, L., Deinet, S., De Palma, A., Carranza, T., Cooper, N., Loh, J., Baillie, J.E.M., 2011. Predicting how populations decline to extinction. Phil. Trans. R. Soc. B 366, 2577–2586. https://doi.org/10.1098/rstb.2011.0015

Cosset, C.C.P., Gilroy, J.J., Edwards, D.P., 2019. Impacts of tropical forest disturbance on species vital rates. Conservation Biology 33, 66–75. https://doi.org/10.1111/cobi.13182

Cramp, S., 2006. The birds of the western Palearctic interactive. Oxford University Press and BirdGuides, Oxford, U.K.

Cunningham, S.A., 2000. Depressed pollination in habitat fragments causes low fruit set. Proceedings of the Royal Society of London. Series B: Biological Sciences 267, 1149–1152. https://doi.org/10.1098/rspb.2000.1121

Davison, C.W., Rahbek, C., Morueta-Holme, N., 2021. Land-use change and biodiversity: Challenges for assembling evidence on the greatest threat to nature. Global Change Biology 27, 5414–5429. https://doi.org/10.1111/gcb.15846

de Chazal, J., Rounsevell, M.D.A., 2009. Land-use and climate change within assessments of biodiversity change: A review. Global Environmental Change, Traditional Peoples and Climate Change 19, 306–315. https://doi.org/10.1016/j.gloenvcha.2008.09.007

de Souza Leite, M., Boesing, A.L., Metzger, J.P., Prado, P.I., 2022. Matrix quality determines the strength of habitat loss filtering on bird communities at the landscape scale. Journal of Applied Ecology 59, 2790–2802. https://doi.org/10.1111/1365-2664.14275

Deikumah, J.P., McAlpine, C.A., Maron, M., 2015. Matrix Intensification Affects Body and Physiological Condition of Tropical Forest-Dependent Passerines. PLOS ONE 10, e0128521. https://doi.org/10.1371/journal.pone.0128521

Díaz, S., Fargione, J., Iii, F.S.C., Tilman, D., 2006. Biodiversity Loss Threatens Human Well-Being. PLOS Biology 4, e277. https://doi.org/10.1371/journal.pbio.0040277

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R.R., Shin, Y.-J., Visseren-Hamakers, I., Willis, K.J., Zayas, C.N., 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science 366, eaax3100. https://doi.org/10.1126/science.aax3100

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401–406. https://doi.org/10.1126/science.1251817

Donald, P.F., Evans, A.D., Muirhead, L.B., Buckingham, D.L., Kirby, W.B., Schmitt, S.I.A., 2002. Survival rates, causes of failure and productivity of Skylark Alauda arvensis nests on lowland farmland. Ibis 144, 652–664. https://doi.org/10.1046/j.1474-919X.2002.00101.x

Donald, P.F., Sanderson, F.J., Burfield, I.J., van Bommel, F.P.J., 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems & Environment 116, 189–196. https://doi.org/10.1016/j.agee.2006.02.007

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., Magurran, A.E., 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. Science 344, 296–299. https://doi.org/10.1126/science.1248484

Eeraerts, M., Meeus, I., Van Den Berge, S., Smagghe, G., 2017. Landscapes with high intensive fruit cultivation reduce wild pollinator services to sweet cherry. Agriculture, Ecosystems & Environment 239, 342–348. https://doi.org/10.1016/j.agee.2017.01.031

Fahrig, L., 2017. Ecological Responses to Habitat Fragmentation Per Se. Annu. Rev. Ecol. Evol. Syst. 48, 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fahrig, L., 2003. Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology, Evolution, and Systematics 34, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J., Eigenbrod, F., Ford, A.T., Harrison, S.P., Jaeger, J.A.G., Koper, N., Martin, A.E., Martin, J.-L., Metzger, J.P., Morrison, P., Rhodes, J.R., Saunders, D.A., Simberloff, D., Smith, A.C., Tischendorf, L., Vellend, M., Watling, J.I., 2019. Is habitat fragmentation bad for biodiversity? Biological Conservation 230, 179–186. https://doi.org/10.1016/j.biocon.2018.12.026

Finch, T., Butler, S.J., Franco, A.M.A., Cresswell, W., 2017. Low migratory connectivity is common in long-distance migrant birds. Journal of Animal Ecology 86, 662–673. https://doi.org/10.1111/1365-2656.12635

Finn, C., Grattarola, F., Pincheira-Donoso, D., 2023. More losers than winners: investigating Anthropocene defaunation through the diversity of population trends. Biological Reviews 98, 1732–1748. https://doi.org/10.1111/brv.12974

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16, 265–280. https://doi.org/10.1111/j.1466-8238.2007.00287.x

Fletcher, R.J., Betts, M.G., Damschen, E.I., Hefley, T.J., Hightower, J., Smith, T.A.H., Fortin, M.-J., Haddad, N.M., 2023. Addressing the problem of scale that emerges with habitat fragmentation. Global Ecology and Biogeography 32, 828–841. https://doi.org/10.1111/geb.13658

Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., Holt, R.D., Gonzalez, A., Pardini, R., Damschen, E.I., Melo, F.P.L., Ries, L., Prevedello, J.A., Tscharntke, T., Laurance, W.F., Lovejoy, T., Haddad, N.M., 2018. Is habitat fragmentation good for biodiversity? Biological Conservation 226, 9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Fraixedas, S., Lindén, A., Piha, M., Cabeza, M., Gregory, R., Lehikoinen, A., 2020. A state-of-the-art review on birds as indicators of biodiversity: Advances, challenges, and future directions. Ecological Indicators 118, 106728. https://doi.org/10.1016/j.ecolind.2020.106728

Frederiksen, M., Lebreton, J.-D., Pradel, R., Choquet, R., Gimenez, O., 2014. REVIEW: Identifying links between vital rates and environment: a toolbox for the applied ecologist. Journal of Applied Ecology 51, 71–81. https://doi.org/10.1111/1365-2664.12172

Garrett, D.R., Pelletier, F., Garant, D., Bélisle, M., 2022. Combined influence of food availability and agricultural intensification on a declining aerial insectivore. Ecological Monographs 92, e1518. https://doi.org/10.1002/ecm.1518

Gaston, K.J., Fuller, R.A., 2007. Biodiversity and extinction: losing the common and the widespread. Progress in Physical Geography: Earth and Environment 31, 213–225. https://doi.org/10.1177/0309133307076488

Gerstner, K., Dormann, C.F., Stein, A., Manceur, A.M., Seppelt, R., 2014. Effects of land use on plant diversity – A global meta-analysis. Journal of Applied Ecology 51, 1690–1700. https://doi.org/10.1111/1365-2664.12329

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381. https://doi.org/10.1038/nature10425

Glądalski, M., Cyżewska, I., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J., Wawrzyniak, J., Bańbura, J., 2019. Influence of habitat composition on nestling body condition and breeding success in European Pied Flycatchers (Ficedula hypoleuca). Avian Biology Research 12, 67–72. https://doi.org/10.1177/1758155919834466

Gonçalves-Souza, T., Chase, J.M., Haddad, N.M., Vancine, M.H., Didham, R.K., Melo, F.L.P., Aizen, M.A., Bernard, E., Chiarello, A.G., Faria, D., Gibb, H., de Lima, M.G., Magnago, L.F.S., Mariano-Neto, E., Nogueira, A.A., Nemésio, A., Passamani, M., Pinho, B.X., Rocha-Santos, L., Rodrigues, R.C., Safar, N.V.H., Santos, B.A., Soto-Werschitz, A., Tabarelli, M., Uehara-Prado, M., Vasconcelos, H.L., Vieira, S., Sanders, N.J., 2025. Species turnover does not rescue biodiversity in fragmented landscapes. Nature 640, 702–706. https://doi.org/10.1038/s41586-025-08688-7

Green, R.E., 1999. Applications of large-scale studies of demographic rates to bird conservation. Bird Study 46, S279–S288. https://doi.org/10.1080/00063659909477255

Hale, R., Swearer, S.E., 2016. Ecological traps: current evidence and future directions. Proc. R. Soc. B. 283, 20152647. https://doi.org/10.1098/rspb.2015.2647

Hallworth, M.T., Bayne, E.M., McKinnon, E.A., Love, O.P., Tremblay, A., Drolet, B., Ibarzabal, J., Van Wilgenburg, S.L., Marra, P.P., 2021. Habitat loss on the breeding grounds is a major contributor to population declines in a long-distance migratory songbird. Proceedings of The Royal Society B: Biological Sciences 288, 20203164–20203164. https://doi.org/10.1098/rspb.2020.3164

Heinrichs, J.A., Bender, D.J., Schumaker, N.H., 2016. Habitat degradation and loss as key drivers of regional population extinction. Ecological Modelling 335, 64–73. https://doi.org/10.1016/j.ecolmodel.2016.05.009

Hinam, H.L., Clair, C.C.St., 2008. High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of Northern saw-whet owls. Biological Conservation 141, 524–535. https://doi.org/10.1016/j.biocon.2007.11.011

Howard, C., Stephens, P.A., Pearce-Higgins, J.W., Gregory, R.D., Butchart, S.H.M., Willis, S.G., 2020. Disentangling the relative roles of climate and land cover change in driving the long-term population trends of European migratory birds. Diversity and Distributions 26, 1442–1455. https://doi.org/10.1111/ddi.13144

Inger, R., Gregory, R., Duffy, J.P., Stott, I., Voříšek, P., Gaston, K.J., 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. Ecology Letters 18, 28–36. https://doi.org/10.1111/ele.12387

IPBES, 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES, Bonn, Germany.

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, L., Golden, A.S., Guerra, C.A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., Purvis, A., 2022. The direct drivers of recent global anthropogenic biodiversity loss. Science Advances 8, eabm9982. https://doi.org/10.1126/sciadv.abm9982

Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S.E., Couvet, D., 2007. Climate envelope, life history traits and the resilience of birds facing global change. Global Change Biology 13, 1672–1684. https://doi.org/10.1111/j.1365-2486.2007.01386.x

Kleijn, D., Schekkerman, H., Dimmers, W.J., Van Kats, R.J.M., Melman, D., Teunissen, W.A., 2010. Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits Limosa l. limosa in the Netherlands. Ibis 152, 475–486. https://doi.org/10.1111/j.1474-919X.2010.01025.x

Lampila, P., Mönkkönen, M., Desrochers, A., 2005. Demographic Responses by Birds to Forest Fragmentation. Conservation Biology 19, 1537–1546. https://doi.org/10.1111/j.1523-1739.2005.00201.x

Lormée, H., Barbraud, C., Peach, W., Carboneras, C., Lebreton, J.D., Moreno-Zarate, L., Bacon, L., Eraud, C., 2020. Assessing the sustainability of harvest of the European Turtle-dove along the European western flyway. Bird Conservation International 30, 506–521. https://doi.org/10.1017/S0959270919000479

Luck, G.W., 2003. Differences in the reproductive success and survival of the rufous treecreeper (*Climacteris rufa*) between a fragmented and unfragmented landscape. Biological Conservation 109, 1–14. https://doi.org/10.1016/S0006-3207(02)00085-X

Maurer, C., Bosco, L., Klaus, E., Cushman, S.A., Arlettaz, R., Jacot, A., 2020. Habitat amount mediates the effect of fragmentation on a pollinator's reproductive performance, but not on its foraging behaviour. Oecologia 193, 523–534. https://doi.org/10.1007/s00442-020-04658-0

Mbora, D.N.M., Wieczkowski, J., Munene, E., 2009. Links between habitat degradation, and social group size, ranging, fecundity, and parasite prevalence in the Tana River mangabey (Cercocebus galeritus). American Journal of Physical Anthropology 140, 562–571. https://doi.org/10.1002/ajpa.21113

Moreno, M.H.T., Teixido, A.L., 2025. Disentangling the effects of habitat loss and fragmentation on a highly diverse European wildlife. Journal of Animal Ecology 94, 1133–1145. https://doi.org/10.1111/1365-2656.70041

Morrison, C.A., Butler, S.J., Clark, J.A., Arizaga, J., Baltà, O., Cepák, J., Nebot, A.L., Piha, M., Thorup, K., Wenninger, T., Robinson, R.A., Gill, J.A., 2022. Demographic variation in space and time: implications for conservation targeting. Royal Society Open Science 9, 211671. https://doi.org/10.1098/rsos.211671

Morrison, C.A., Butler, S.J., Robinson, R.A., Clark, J.A., Arizaga, J., Aunins, A., Baltà, O., Cepák, J., Chodkiewicz, T., Escandell, V., Foppen, R.P.B., Gregory, R.D., Husby, M., Jiguet, F., Kålås, J.A., Lehikoinen, A., Lindström, Å., Moshøj, C.M., Nagy, K., Nebot, A.L., Piha, M., Reif, J., Sattler, T., Škorpilová, J., Szép, T., Teufelbauer, N., Thorup, K., van Turnhout, C., Wenninger, T., Gill, J.A., 2021. Covariation in population trends and demography reveals targets for conservation action. Proceedings of the Royal Society B: Biological Sciences 288, 20202955. https://doi.org/10.1098/rspb.2020.2955

Morrison, C.A., Robinson, R.A., Butler, S.J., Clark, J.A., Gill, J.A., 2016a. Demographic drivers of decline and recovery in an Afro-Palaearctic migratory bird population. Proc. R. Soc. B. 283, 20161387. https://doi.org/10.1098/rspb.2016.1387

Morrison, C.A., Robinson, R.A., Clark, J.A., Gill, J.A., 2016b. Causes and consequences of spatial variation in sex ratios in a declining bird species. Journal of Animal Ecology 85, 1298–1306. https://doi.org/10.1111/1365-2656.12556

Morrison, C.A., Robinson, R.A., Clark, J.A., Risely, K., Gill, J.A., 2013. Recent population declines in Afro-Palaearctic migratory birds: the influence of breeding and non-breeding seasons. Diversity and Distributions 19, 1051–1058. https://doi.org/10.1111/ddi.12084

Mortelliti, A., Amori, G., Boitani, L., 2010. The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. Oecologia 163, 535–547. https://doi.org/10.1007/s00442-010-1623-3

Murphy, G.E.P., Romanuk, T.N., 2014. A meta-analysis of declines in local species richness from human disturbances. Ecology and Evolution 4, 91–103. https://doi.org/10.1002/ece3.909

Newbold, T., Hudson, L.N., Contu, S., Hill, S.L.L., Beck, J., Liu, Y., Meyer, C., Phillips, H.R.P., Scharlemann, J.P.W., Purvis, A., 2018. Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. PLOS Biology 16, e2006841. https://doi.org/10.1371/journal.pbio.2006841

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324

Newton, I., 2004a. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146, 579–600. https://doi.org/10.1111/j.1474-919X.2004.00375.x

Newton, I., 2004b. Population limitation in migrants. Ibis 146, 197–226. https://doi.org/10.1111/j.1474-919X.2004.00293.x

Norman, D., Peach, W.J., 2013. Density-dependent survival and recruitment in a long-distance Palaearctic migrant, the Sand Martin Riparia riparia. Ibis 155, 284–296. https://doi.org/10.1111/ibi.12036

Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E.A., Amano, T., Bertram, E., Bradbury, R.B., Bradley, C., Butchart, S.H.M., Doswald, N., Foden, W., Gill, D.J.C., Green, R.E., Sutherland, W.J., Tanner, E.V.J., Pearce-Higgins, J.W., 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. Global Change Biology 20, 2221–2229. https://doi.org/10.1111/gcb.12559

Oliver, T., Roy, D.B., Hill, J.K., Brereton, T., Thomas, C.D., 2010. Heterogeneous landscapes promote population stability. Ecology Letters 13, 473–484. https://doi.org/10.1111/j.1461-0248.2010.01441.x

Oliver, T.H., Brereton, T., Roy, D.B., 2013. Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. Ecography 36, 579–586. https://doi.org/10.1111/j.1600-0587.2012.07665.x

Oliver, T.H., Morecroft, M.D., 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. WIREs Climate Change 5, 317–335. https://doi.org/10.1002/wcc.271

Orme, C.D.L., Mayor, S., dos Anjos, L., Develey, P.F., Hatfield, J.H., Morante-Filho, J.C., Tylianakis, J.M., Uezu, A., Banks-Leite, C., 2019. Distance to range edge determines sensitivity to deforestation. Nat Ecol Evol 3, 886–891. https://doi.org/10.1038/s41559-019-0889-z

Pärt, T., 2001a. The effects of territory quality on age-dependent reproductive performance in the northern wheatear, Oenanthe oenanthe. Animal Behaviour 62, 379–388. https://doi.org/10.1006/anbe.2001.1754

Pärt, T., 2001b. Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. Proceedings of The Royal Society B: Biological Sciences 268, 2267–2271. https://doi.org/10.1098/rspb.2001.1803

Peach, W.J., Siriwardena, G.M., Gregory, R.D., 1999. Long-term changes in over-winter survival rates explain the decline of reed buntings Emberiza schoeniclus in Britain. Journal of Applied Ecology 36, 798–811. https://doi.org/10.1046/j.1365-2664.1999.00445.x

Pereira, H.M., Martins, I.S., Rosa, I.M.D., Kim, H., Leadley, P., Popp, A., van Vuuren, D.P., Hurtt, G., Quoss, L., Arneth, A., Baisero, D., Bakkenes, M., Chaplin-Kramer, R., Chini, L., Di Marco, M., Ferrier, S., Fujimori, S., Guerra, C.A., Harfoot, M., Harwood, T.D., Hasegawa, T., Haverd, V., Havlík, P., Hellweg, S., Hilbers, J.P., Hill, S.L.L., Hirata, A., Hoskins, A.J., Humpenöder, F., Janse, J.H., Jetz, W., Johnson, J.A., Krause, A., Leclère, D., Matsui, T., Meijer, J.R., Merow, C., Obersteiner, M., Ohashi, H., De Palma, A., Poulter, B., Purvis, A., Quesada, B., Rondinini, C., Schipper, A.M., Settele, J., Sharp, R., Stehfest, E., Strassburg, B.B.N., Takahashi, K., Talluto, L., Thuiller, W., Titeux, N., Visconti, P., Ware, C., Wolf, F., Alkemade, R., 2024. Global trends and scenarios for terrestrial biodiversity and ecosystem services from 1900 to 2050. Science 384, 458–465. https://doi.org/10.1126/science.adn3441

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., D'Cruze, N., Faria, D., Hadley, A., Harris, S.M., Klingbeil, B.T., Kormann, U., Lens, L., Medina-Rangel, G.F., Morante-Filho, J.C., Olivier, P., Peters, S.L., Pidgeon, A., Ribeiro, D.B., Scherber, C., Schneider-Maunoury, L., Struebig, M., Urbina-Cardona, N., Watling, J.I., Willig, M.R., Wood, E.M., Ewers, R.M., 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551, 187–191. https://doi.org/10.1038/nature24457

Piironen, A., Knetter, J.M., Spragens, K.A., Dooley, J.L., Patil, V., Reed, E.T., Ross, M., Gibson, D., Behney, A.C., Petrie, M.J., Sanders, T.A., Weegman, M.D., 2025. Environmental drivers of productivity explain population patterns of an Arctic-nesting bird across a half-century. Ecological Applications 35, e70067. https://doi.org/10.1002/eap.70067

Priyadarshana, T.S., Martin, E.A., Sirami, C., Woodcock, B.A., Goodale, E., Martínez-Núñez, C., Lee, M.-B., Pagani-Núñez, E., Raderschall, C.A., Brotons, L., Rege, A., Ouin, A., Tscharntke, T., Slade, E.M., 2024. Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: A global review and meta-analysis. Ecology Letters 27, e14412. https://doi.org/10.1111/ele.14412

R Core Team, 2024. R: A Language and Environment for Statistical Computing.

Ramírez-Delgado, J.P., Di Marco, M., Watson, J.E.M., Johnson, C.J., Rondinini, C., Corredor Llano, X., Arias, M., Venter, O., 2022. Matrix condition mediates the effects of habitat fragmentation on species extinction risk. Nat Commun 13, 595. https://doi.org/10.1038/s41467-022-28270-3

Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkő, Z., Brotons, L., Chodkiewicz, T., Chylarecki, P., de Carli, E., del Moral, J.C., Domşa, C., Escandell, V., Fontaine, B., Foppen, R., Gregory, R., Harris, S., Herrando, S., Husby, M., Ieronymidou, C., Jiguet, F., Kennedy, J., Klvaňová, A., Kmecl, P., Kuczyński, L., Kurlavičius, P., Kålås, J.A., Lehikoinen, A., Lindström, Å., Lorrillière, R., Moshøj, C., Nellis, R., Noble, D., Eskildsen, D.P., Paquet, J.-Y., Pélissié, M., Pladevall, C., Portolou, D., Reif, J., Schmid, H., Seaman, B., Szabo, Z.D., Szép, T., Florenzano, G.T., Teufelbauer, N., Trautmann, S., van Turnhout, C., Vermouzek, Z., Vikstrøm, T., Voříšek, P., Weiserbs, A., Devictor, V., 2023. Farmland practices are driving bird population decline across Europe. Proceedings of the National Academy of Sciences 120, e2216573120. https://doi.org/10.1073/pnas.2216573120

Riva, F., Koper, N., Fahrig, L., 2024. Overcoming confusion and stigma in habitat fragmentation research. Biological Reviews 99, 1411–1424. https://doi.org/10.1111/brv.13073

Robinson, R.A., Julliard, R., Saracco, J.F., 2009. Constant effort: Studying avian population processes using standardised ringing. Ringing & Migration 24, 199–204. https://doi.org/10.1080/03078698.2009.9674392

Robinson, R.A., Morrison, C.A., Baillie, S.R., 2014. Integrating demographic data: towards a framework for monitoring wildlife populations at large spatial scales. Methods in Ecology and Evolution 5, 1361–1372. https://doi.org/10.1111/2041-210X.12204

Rodríguez, A., Andrén, H., Jansson, G., 2001. Habitat-mediated predation risk and decision making of small birds at forest edges. Oikos 95, 383–396. https://doi.org/10.1034/j.1600-0706.2001.950303.x

Ross, B.E., Haukos, D.A., Hagen, C.A., Pitman, J.C., 2016. Landscape composition creates a threshold influencing Lesser Prairie-Chicken population resilience to extreme drought. Global Ecology and Conservation 6, 179–188. https://doi.org/10.1016/j.gecco.2016.03.003

Ross, S.R.P.-J., Garcia, F.H., Fischer, G., Peters, M.K., 2018. Selective logging intensity in an East African rain forest predicts reductions in ant diversity. Biotropica 50, 768–778. https://doi.org/10.1111/btp.12569

Ruiz-Gutiérrez, V., Gavin, T.A., Dhondt, A.A., 2008. Habitat Fragmentation Lowers Survival of a Tropical Forest Bird. Ecological Applications 18, 838–846. https://doi.org/10.1890/07-1090.1

Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G., Fuller, R.A., 2014. Conserving mobile species. Frontiers in Ecology and the Environment 12, 395–402.

Sala, O.E., Stuart Chapin, F., III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global Biodiversity Scenarios for the Year 2100. Science 287, 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J., van Bommel, F.P.J., 2006. Long-term population declines in Afro-Palearctic migrant birds. Biological Conservation 131, 93–105. https://doi.org/10.1016/j.biocon.2006.02.008

Selwood, K.E., McGeoch, M.A., Mac Nally, R., 2015. The effects of climate change and land-use change on demographic rates and population viability. Biol Rev Camb Philos Soc 90, 837–853. https://doi.org/10.1111/brv.12136

Seress, G., Hammer, T., Bókony, V., Vincze, E., Preiszner, B., Pipoly, I., Sinkovics, C., Evans, K.L., Liker, A., 2018. Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. Ecological Applications 28, 1143–1156. https://doi.org/10.1002/eap.1730

Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P., Wilson, J.D., Gates, S., 2000. The demography of lowland farmland birds, in: Ecology and Conservation of Lowland Farmland Birds. British Ornithologists' Union, Tring, pp. 117–133.

Suggitt, A.J., Wilson, R.J., August, T.A., Fox, R., Isaac, N.J.B., Macgregor, N.A., Morecroft, M.D., Maclean, I.M.D., 2015. Microclimate affects landscape level persistence in the British Lepidoptera. J Insect Conserv 19, 237–253. https://doi.org/10.1007/s10841-014-9749-y

Thaxter, C.B., Joys, A.C., Gregory, R.D., Baillie, S.R., Noble, D.G., 2010. Hypotheses to explain patterns of population change among breeding bird species in England. Biological Conservation 143, 2006–2019. https://doi.org/10.1016/j.biocon.2010.05.004

Thompson, M., Vlok, J., Rouget, M., Hoffman, M.T., Balmford, A., Cowling, R.M., 2009. Mapping Grazing-Induced Degradation in a Semi-Arid Environment: A Rapid and Cost Effective Approach for Assessment and Monitoring. Environmental Management 43, 585–596. https://doi.org/10.1007/s00267-008-9228-x

Twining, C.W., Shipley, J.R., Winkler, D.W., 2018. Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. Ecology Letters 21, 1812–1820. https://doi.org/10.1111/ele.13156

Van Horne, B., 1983. Density as a Misleading Indicator of Habitat Quality. The Journal of Wildlife Management 47, 893–901. https://doi.org/10.2307/3808148

Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J., Gregory, R.D., 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156, 1–22. https://doi.org/10.1111/ibi.12118

Vickery, J.A., Mallord, J.W., Adams, W.M., Beresford, A.E., Both, C., Cresswell, W., Diop, N., Ewing, S.R., Gregory, R.D., Morrison, C.A., Sanderson, F.J., Thorup, K., Van Wijk, R.E., Hewson, C.M., 2023. The conservation of Afro-Palaearctic migrants: What we are learning and what we need to know? Ibis n/a. https://doi.org/10.1111/ibi.13171

Walkup, D.K., Leavitt, D.J., Fitzgerald, L.A., 2017. Effects of habitat fragmentation on population structure of dune-dwelling lizards. Ecosphere 8, e01729. https://doi.org/10.1002/ecs2.1729

Williams, J.J., Freeman, R., Spooner, F., Newbold, T., 2022. Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. Global Change Biology 28, 797–815. https://doi.org/10.1111/gcb.15978

Winiarski, J.M., Moorman, C.E., Carpenter, J.P., Hess, G.R., 2017. Reproductive consequences of habitat fragmentation for a declining resident bird of the longleaf pine ecosystem. Ecosphere 8, e01898. https://doi.org/10.1002/ecs2.1898

Yan, Y., Qi, Z., Zhang, Q., 2025. Cross-scale effects of habitat fragmentation on local biodiversity and ecosystem multifunctionality in a fragmented grassland landscape. Journal of Ecology 113, 1573–1584. https://doi.org/10.1111/1365-2745.70045

Zhao, J., Yu, L., Newbold, T., Chen, X., 2025. Trends in habitat quality and habitat degradation in terrestrial protected areas. Conservation Biology 39, e14348. https://doi.org/10.1111/cobi.14348

Zhao, Q., Arnold, T.W., Devries, J.H., Howerter, D.W., Clark, R.G., Weegman, M.D., 2019. Land-use change increases climatic vulnerability of migratory birds: Insights from integrated population modelling. Journal of Animal Ecology 88, 1625–1637. https://doi.org/10.1111/1365-2656.13043

Zhao, Q., Devries, J.H., Clark, R.G., Weegman, M.D., 2023. Causes and consequences of demography in continent-scale, full-annual-cycle population dynamics under global change. Global Ecology and Conservation 43, e02461. https://doi.org/10.1016/j.gecco.2023.e02461

Zingg, S., Grenz, J., Humbert, J.-Y., 2018. Landscape-scale effects of land use intensity on birds and butterflies. Agriculture, Ecosystems & Environment 267, 119–128. https://doi.org/10.1016/j.agee.2018.08.014

Chapter 1 Supplementary Material

Table S1.1: List of bird species for which average productivity across years was calculated at Constant Effort Sites for the UK pilot study.

English name	Scientific name
Eurasian Blackbird	*Turdus merula*
Eurasian Blackcap	*Sylvia atricapilla*
Blue Tit	*Cyanistes caeruleus*
Eurasian Bullfinch	*Pyrrhula pyrrhula*
Cetti's Warbler	*Cettia cetti*
Chaffinch	*Fringilla coelebs*
Common Chiffchaff	*Phylloscopus collybita*
Dunnock	*Prunella modularis*
Garden Warbler	*Sylvia borin*
European Goldfinch	*Cardeulis carduelis*
Great Tit	*Parus major*
European Greenfinch	*Chloris chloris*
Lesser Whitethroat	*Curruca curruca*
Long-tailed Tit	*Aegithalos caudatus*
Reed Bunting	*Emberiza schoeniclus*
Eurasian Reed Warbler	*Acrocephalus scirpaceus*
European Robin	*Erithacus rubecula*
Sedge Warbler	*Acrocephalus schoenobaenus*
Song Thrush	*Turdus philomelos*
Greater Whitethroat	*Curruca communis*
Willow Warbler	*Phylloscopus trochilus*
Wren	*Troglodytes troglodytes*

Chapter 2: Spatial and Temporal Scales of Demographic Analyses in Birds: A Review

CCO Public Domain.

Abstract

Demographic variation in bird populations can be measured over different spatial and temporal scales, which may influence the environmental processes captured. Productivity and survival rates may vary in the scales at which they are typically measured, potentially resulting in an incomplete understanding of their drivers. To explore this issue, we collated and reviewed published studies of spatiotemporal variation in productivity and survival rates of birds, and compared the spatial (from <1 km^2 to >10,000 km^2) and temporal (from sub-annual to decadal) scales at which each rate has been characterised. We found that similar percentages of studies measuring productivity have explored spatial (53%) and temporal (47%) variation, while the majority of studies measuring survival have explored temporal variation (62%). Smaller spatial scales were more frequently examined than larger scales, and productivity studies were significantly less likely to examine larger spatial scales compared to survival studies. Among temporal analyses, annual variation was the most well-studied scale for both productivity and survival, and survival studies were significantly less likely to measure variation at sub-annual timescales compared to productivity studies. Most studies measuring spatiotemporal variation in productivity and survival of bird populations have taken place over relatively small ($\leq$ 10 km^2) spatial scales, and over annual timescales. The local-scale focus of these studies may limit opportunities to identify environmental drivers operating over larger spatial scales and longer timescales. Given this spatiotemporal structure of demographic research, it will be important to understand the extent to which local-scale studies can capture large-scale changes.

2.1. Introduction

Almost half of the world's bird species are undergoing population declines, with one in eight threatened with extinction (Lees et al., 2022). To identify and address the causes of these declines, it is essential to understand the demographic processes (i.e. productivity, survival and dispersal) that underlie them (Anders and Marshall, 2005; Robinson et al., 2014; Selwood et al., 2015). Examining spatiotemporal variation in these vital rates can help characterise the environmental drivers of population change (Green, 1999; Frederiksen et al., 2014), and even identify situations where low rates could potentially be improved through conservation actions (Burgess et al., 2020; Morrison et al., 2016, 2022).

The spatial and temporal scales over which demographic rates are measured may influence understanding of their drivers. For example, studies measuring small-scale spatial variation might capture effects of local conditions, such as habitat structure (e.g. Ruth and Skagen, 2018), but may be less able to detect the contributions of conditions varying over larger spatial scales, such as landscape composition (Arrondo et al., 2020) or climate (Eglington et al., 2015). In addition, small-scale focal studies can provide detailed insights into the mechanisms behind change (e.g. Paquet et al., 2019), but often take place in areas where populations are abundant to ensure sufficient sample sizes, and therefore may not fully capture the range of conditions influencing population trends (Gunnarsson et al., 2005). Meanwhile, larger-scale studies tend to be correlative, but can capture a broader range of conditions, for instance allowing range-wide processes to be explored (DeMay and Walters, 2019). Similarly, studies explore temporal variation in demography over varying timescales, including seasonal, annual or decadal time periods, and these are likely to capture different processes and drivers (e.g. Folk et al., 2007). Studies measuring short-term variation may be better able to examine mechanisms, while longer-term studies may cover a more complete range of conditions.

The scales at which temporal and spatial variation in demography are typically captured may vary with the rate being measured, as well as the metrics used to describe these rates. For example, productivity can be measured at the nest-level (e.g. clutch size, hatching success), individual-level (e.g. numbers of fledged offspring), and/or population-level (e.g. proportions of juveniles) (Etterson et al., 2011), while survival can be measured over differing life stages (e.g. juveniles, immatures, adults). If different rates and metrics tend to be measured at different spatial and/or temporal scales, the resulting biases may limit our understanding of the drivers of population change.

No single scale can characterise all demographic processes (Gurevitch et al., 2016) and so data covering a broad range of spatial and temporal scales are needed for all key demographic metrics. There is a large body of research measuring demographic variation across a wide range of scales in bird species, including small focal studies (e.g. Delgado et al., 2021) and large citizen science projects (e.g. Robinson, 2023). Here, we assess the spatial and temporal scales at which variation in demographic rates of birds has been studied in a representative sample of the ornithological literature, in order to explore (1) the frequency with which productivity and survival are measured spatially and/or temporally, and the (2) spatial and (3) temporal scales over which different metrics of productivity and survival are most commonly measured.

2.2. Methods

Literature Search

We searched for studies measuring at least one productivity, survival or recruitment metric (Table 2.1) in at least one (wild) bird species, with replication over space (spatial variation) and/or over time (temporal variation). We did not consider studies measuring only dispersal rates due to the already broad scope of the review. We performed a systematic search for published studies using the Web of Science (Core Collection: SCI-EXPANDED, CPCI-S and ESCI editions) and Scopus online databases on 5th April 2022. The search string consisted of terminology relating to three concept groups: Taxa (i.e. birds), Demography and Variation, as well as a series of exclusion terms (Table S2.1). The search string was developed iteratively by conducting trial searches and checking for a series of key references within search results, as well as looking for large numbers of non-relevant papers belonging to a particular topic to inform exclusion terms. The final searches returned 2790 results from Web of Science and 2992 results from Scopus.

Inclusion and Exclusion Criteria

For studies to be included, they had to meet three main criteria. First, studies had to focus on a wild bird species; studies on captive birds were excluded. Second, they had to measure at least one productivity or survival metric of interest (Table 2.1). Third, studies had to measure spatial and/or temporal variation in these metrics. No restrictions were applied to the year of publication or the language of the paper. However, it should be noted that because our search terms were in English, our search was confined to studies with an English title and/or abstract, which therefore excludes some literature in other languages and may induce some geographical bias. We excluded meta-analyses and simulation studies using data from elsewhere to avoid duplication of data already included from primary research papers.

Screening Process

We followed the de-duplication process described by Bramer et al., (2016) to achieve a final list of 3339 references for screening (2785 from Web of Science, 554 additional records from Scopus). Due to time constraints, half of these studies were randomly selected for subsequent screening. Titles and abstracts were screened by one person (SEB) using a decision tree (Figure S2.1), and either excluded if the inclusion criteria were not met or taken forward for full-text review. This process is detailed in a PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) flowchart (O'Dea et al., 2021) provided in the Supplementary Material (Figure S2.2). Of the 1670 papers screened, 859 were included for data extraction (51%) and 811 were excluded (49%).

Table 2.1: Names, definitions and units of the metrics of bird productivity and survival that were considered within this review.

Demographic Rate	Metric Type	Definitions	Units
Productivity	**Nest**	Clutch or Brood size	Number of eggs or chicks in breeding attempt
		Hatching success	% eggs hatching; % nests hatching at least 1 chick
		Fledging success	Number of fledglings in breeding attempt; % eggs or chicks fledging; chick survival rate
		Nest success	% nests producing at least 1 fledgling (or hatchling in precocial species)
		Daily nest survival rate	Egg stage, nestling stage, or overall
	Individual	Number of successful clutches or broods per breeding season	
		Annual reproductive success	Probability of individual, pair or territory producing at least 1 fledgling in breeding season; total number of fledglings across breeding attempts in single season
		Lifetime reproductive success	Total number of fledglings across all breeding attempts recorded for an individual or pair
	Population	Ratio of juveniles to adults (on breeding sites)	
		Total count of juveniles (on breeding sites)	
Survival	**Adult**	Known individuals defined as of breeding age in the paper	
	Juvenile	Known individuals defined as juvenile or immature in the paper	
	Post-fledging	Known individuals during period immediately following fledging when likely to be at least partially dependent on parents	
	Recruitment	Known individuals from fledging until recruitment into breeding populations	
		Per capita rate of new individuals recruiting into breeding populations	

Data Extraction

All data were collated by one author (SEB). We first recorded the demographic rate (productivity or survival), and the type of metric measured. Productivity metrics of interest were grouped into three main types: nest-level, individual-level or population-level (Table 2.1). Studies measuring survival rates had to use known individuals and we excluded those estimating survival using territory occupancy or counts of individuals. For survival rates, we recorded whether these related to the adult, juvenile or post-fledging periods, or to rates of recruitment into breeding populations (Table 2.1). Individual studies could measure multiple types of demographic data, and we recorded each one separately.

We then recorded whether the study measured spatial and/or temporal variation in each demographic metric, and all spatial or temporal scales at which this variation was measured (i.e. the scales at which the demographic data were pooled for analysis) (Table 2.2, Figure S2.3). Spatial scales were measured in orders of magnitude, ranging from <1 km^2 to >10,000 km^2. We differentiate spatial "scale" from the spatial "extent" of the demographic data, which we define as the total geographic area over which the data was collected. This was recorded for each study in one of four categories: "local" (single, small study site <1 km^2), "regional" (multiple study sites up to country level), "continental" (multiple states or countries) and "global" (multiple continents).

This information was extracted from the data analysis section of the methods (e.g. which predictors were fitted in models) and/or reported in the results (e.g. comparing averages between study sites, or years). If this information was not provided, we traced back through references or citing papers on the same study system to determine the appropriate scales wherever possible. For 7% of studies measuring spatial variation, we were not able to determine the scale at which this was measured (either from the paper itself or referenced papers). These studies were included within analyses of studies measuring spatial versus temporal variation but excluded from subsequent analyses of specific scales (see below). Amongst studies where we could determine the spatial scale(s), 71% specifically described this information, 21% provided enough information in the paper for this to be approximated, and for the remaining 8% the information was extracted from referenced or citing papers. We were able to determine the appropriate temporal scale(s) for all studies measuring temporal variation.

Table 2.2: The categories of spatial and temporal scales over which variation in demographic rates were measured in the reviewed studies, with associated descriptive terminology.

Spatial Scales	< 1 km^2	*nesting site, territory, patch*
	1 – 10 km^2	*study site*
	11 – 100 km^2	*study area*
	101 – 1000 km^2	*landscape*
	1001 – 10,000 km^2	*region*
	> 10,000 km^2	*country*
Temporal Scales	Sub-annual	*within-season (weeks) or seasonal (months)*
	Annual	*one year to the next*
	Decadal	*multiple years*

Statistical Analysis

1. Spatial vs Temporal Variation

We modelled the probability that a study measured spatial (0) or temporal (1) variation as a function of the demographic rate or metric type, study year and the interaction between these terms to determine if this probability has changed over time. We used a binomial generalised linear model (GLM) with the R package 'lme4' (Bates et al., 2025). Each data point consisted of a spatial or temporal analysis of a type of demographic data by a reviewed study. Studies could contribute multiple data points (e.g. analysis of both spatial and temporal variation, or multiple demographic data types), so study ID was fitted as a random effect, but this was estimated as zero ("a singular fit") and was subsequently removed. We ran three models:

1.1. spatial (0) or temporal (1) ~ demographic rate (productivity, survival) * year

1.2. spatial (0) or temporal (1) ~ productivity metric type (nest, individual, population)
** year (if statistically significant effect in 1.1.)*

1.3. spatial (0) or temporal (1) ~ survival metric type (adult, juvenile, post-fledging, recruitment)
** year (if statistically significant effect in 1.1.)*

2. Spatial Scales of Demographic Metrics

We then analysed the probability that different demographic rates or metric types were explored over increasing spatial scales. The response variable was the spatial scale(s) over which data reported in each study were analysed (Table 2.2), with demographic rate, study year and the interaction between these terms as predictors to determine if the scales at which each rate has been studied have changed over time. Scale was modelled as an ordinal factor (from <1 km^2 to >10,000 km^2) using a cumulative link mixed model (CLMM) with the 'ordinal' R package (Christensen, 2023). Each data point consisted of an analysis conducted at a particular spatial scale on one of the demographic data types (Table 2.1). As above, studies could contribute multiple data points (e.g. analysis at multiple spatial scales, or of multiple demographic data types), and so a random effect of study ID was fitted. This model structure was then replicated for studies measuring productivity and for studies measuring survival, with either productivity metric type or survival metric type replacing demographic rate. Study year was only fitted as a predictor in these models if it had a significant effect in the initial demographic rate model.

3. Temporal Scales of Demographic Metrics

We similarly modelled the probability that different demographic rates or metric types were examined over increasing temporal scales. The response variable was the temporal scale(s) over which data reported in each study were analysed (Table 2.2), with demographic rate, study year and the interaction between these terms as predictors. Each data point consisted of an analysis conducted at a particular temporal scale on a demographic data type. As before, scale was modelled as an ordinal response variable (from sub-annual to decadal) in a cumulative link model. The model with a random effect of study ID did not converge and so this random effect was subsequently removed. This model structure was again repeated with productivity metric or survival metric replacing demographic rate as predictors, and if significant in the initial model, study year and its interaction with metric.

Likelihood ratio tests (LRTs) were conducted on all models to examine the statistical significance of fixed effects. Marginal means were calculated using the 'emmeans' package (Lenth et al., 2024). All analyses were conducted in R version 4.4.1. (R Core Team 2024).

2.3. Results

Of the 859 studies included in the review, 721 measured variation in productivity metrics and 243 measured variation in survival metrics. Most productivity studies measured nest-level metrics, followed by individual-level metrics and population-level metrics (Table 2.3). Meanwhile, the most studied survival metric was adult survival, followed by juvenile survival and recruitment rates, with post-fledging survival measured in the fewest studies (Table 2.3).

Table 2.3: The number and percentage of reviewed studies measuring spatial and/or temporal variation in productivity and survival rates, and in differing metrics of each rate. Studies measuring more than one metric appear in more than one column and/or row.

Metric	Total	Metric	Total
Productivity	721	Survival	243
Nest	618 (86%)	Adult	190 (78%)
Individual	144 (20%)	Juvenile	83 (34%)
Population	54 (7%)	Post-fledging	28 (12%)

The spatial extent of demographic data collected by studies was most often regional, followed by local, with a small number of studies measuring data at the continental or global scales (Figure 2.1). These patterns were similar for studies measuring productivity and survival metrics.

The majority of studies from which data were collated were conducted in North America (44% studies) and Europe (37% studies), with the remaining regions combined being the focus of only 19% of studies (Table 2.4). 89% of the sampled studies collected data at temperate latitudes compared to just 7% each in polar and tropical biomes. Overall, 379 species from 32 bird orders were represented within our sample of studies (Tables S2.2 & S2.3). Of these, spatiotemporal variation in productivity rates were studied in 332 species and survival rates in 158 species (top 10 in Table S2.4).

Table 2.4: The number and percentage of reviewed studies located within each region and biome. Some studies span more than one region or biome so appear in more than one row.

Region	Number of studies	Percentage of studies	Biome	Number of studies	Percentage of studies
Africa	43	5.0	Polar	60	7.0
Asia	29	3.0	Temperate	764	89.0
Europe	321	37.0	Tropical	58	7.0
North America	380	44.0			
Oceania	31	4.0			
South America	28	3.0			
Southern Ocean	34	4.0			

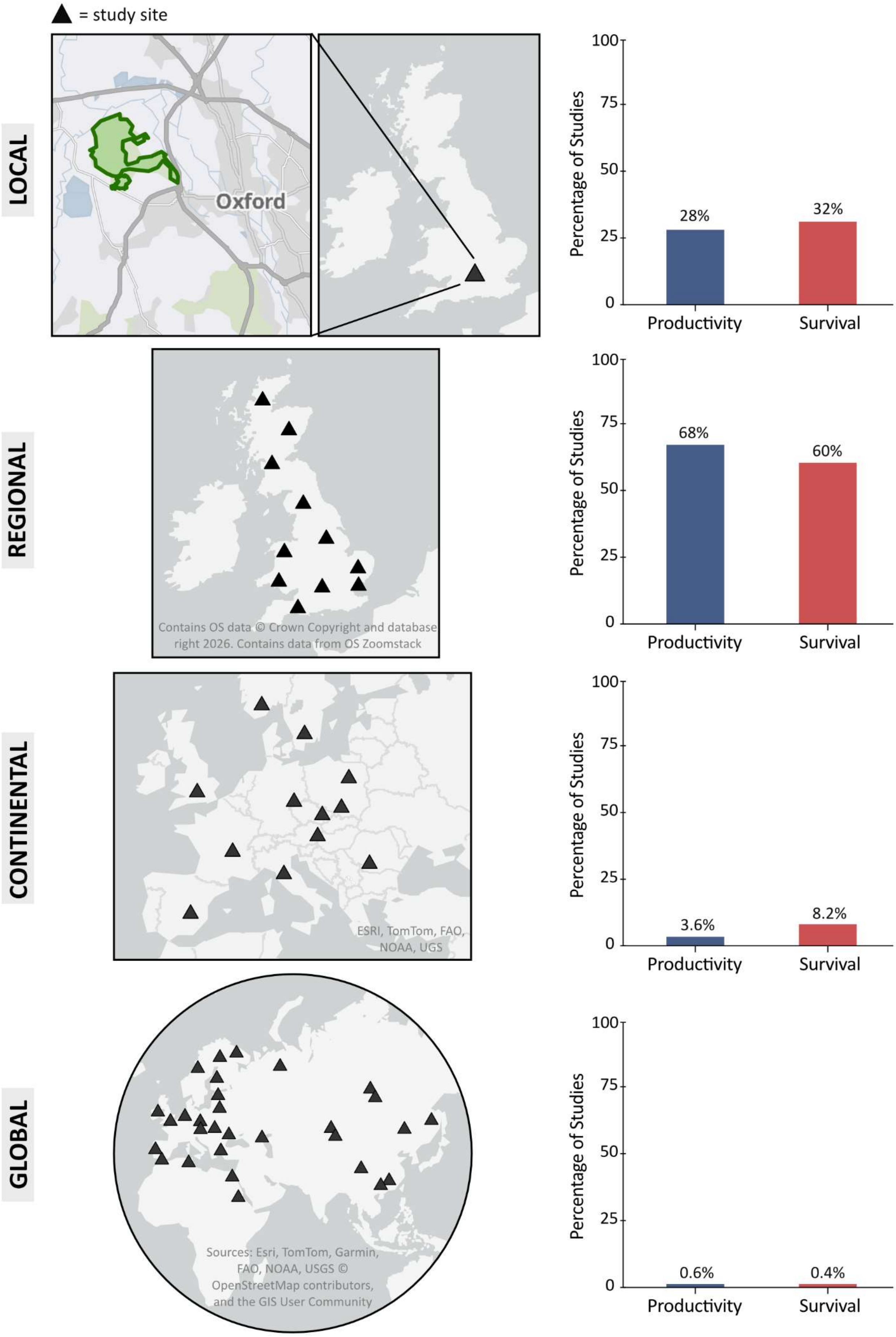


Figure 2.1: The four spatial extent categories used to group reviewed studies, representing the total geographic area over which demographic data was collected by each study. Maps exemplify the spread of sites at which a study within each category might collect data. Bar charts represent the percentage of studies exploring variation in productivity and in survival for each of the spatial extent categories.

Spatial vs Temporal Variation

Studies measuring variation in survival rates were significantly more likely to examine temporal variation than those measuring variation in productivity, which were in turn more likely to examine spatial variation than survival rate studies (LRT deviance = -8.99, $p < 0.01$; Table S2.5). 53% of the recorded analyses of productivity rates explored temporal variation, while 47% measured spatial variation (Table 2.5). In contrast, 62% of survival rate analyses examined temporal variation and 38% examined spatial variation.

Table 2.5: The total number of analyses within reviewed studies reporting variation in productivity and survival and the probability, standard error and 95% Confidence Intervals that this variation was a) temporal and b) spatial, estimated from a binomial generalised linear model using the *emmeans* package. Number datapoints = 1453.

a) Temporal	Number of Analyses	Probability	Standard Error	95% Confidence Intervals
Productivity	590	0.53	0.02	0.50 – 0.56
Survival	213	0.62	0.03	0.57 – 0.67
b) Spatial	Number of Analyses	Probability	Standard Error	95% Confidence Intervals
Productivity	521	0.47	0.02	0.44 – 0.50
Survival	129	0.38	0.03	0.33 – 0.43

We also found significant differences in the probability that spatial or temporal variation was measured across different productivity metrics (LRT deviance = -8.57, $p = 0.02$). Studies of population-level productivity were more likely to measure temporal variation than nest-level studies, for which spatial variation was more commonly measured than in population-level studies (Table S2.6). Approximately 50% of the recorded analyses of nest- and individual-level metrics explored temporal variation and 50% reported spatial variation, whereas temporal variation was measured in 70% of population-level analyses (Table 2.6).

Table 2.6: The total number of analyses within reviewed studies reporting variation in nest-level, individual-level and population-level productivity metrics and the probability, standard error and 95% Confidence Intervals that this variation was a) temporal and b) spatial, estimated from a binomial generalised linear model, using the *emmeans* package. Number of datapoints = 1240.

a) Temporal	Number of Analyses	Probability	Standard Error	95% Confidence Intervals
Nest	502	0.52	0.02	0.49 – 0.55
Individual	112	0.56	0.04	0.49 – 0.63
Population	50	0.69	0.05	0.57 – 0.78
b) Spatial	Number of Analyses	Probability	Standard Error	95% Confidence Intervals
Nest	466	0.48	0.02	0.45 – 0.51
Individual	87	0.44	0.04	0.37 – 0.51
Population	23	0.32	0.05	0.22 – 0.43

Similarly, the probability that spatial or temporal variation was measured differed between survival rate metrics (LRT deviance = -9.50, $p = 0.02$). Analyses of variation in adult survival, juvenile survival and recruitment rates were more likely to examine temporal than spatial variation, whereas analyses of post-fledging survival showed an approximately equal split between spatial and temporal variation (Table 2.7). Therefore, studies measuring variation in post-fledging survival were significantly less likely to examine temporal variation and more likely to examine spatial variation compared to the other metrics (Table S2.7).

Table 2.7: The total number of analyses within reviewed studies reporting variation in adult, juvenile and post-fledging survival and recruitment rates and the probability, standard error and 95% Confidence Intervals that this variation was a) temporal and b) spatial, estimated from a binomial generalised linear model, using the *emmeans* package. Number datapoints = 463.

a) Temporal	Number of Analyses	Probability	Standard Error	95% Confidence Intervals
Adult	170	0.63	0.03	0.58 - 0.69
Juvenile	74	0.69	0.04	0.59 - 0.77
Post-fledging	21	0.47	0.07	0.33 - 0.61
Recruitment	32	0.76	0.07	0.61 - 0.87
b) Spatial	Number of Analyses	Probability	Standard Error	95% Confidence Intervals
Adult	98	0.37	0.03	0.31 - 0.43
Juvenile	34	0.32	0.04	0.23 - 0.43
Post-fledging	24	0.53	0.07	0.39 - 0.67
Recruitment	10	0.24	0.07	0.13 - 0.39

Scales of Spatial Variation

Studies measuring spatial variation in productivity or survival more frequently examined smaller spatial scales than larger scales (Figure 2.2), but survival studies were significantly more likely to measure variation at larger spatial scales compared to productivity studies (LR statistic = 9.27, $p < 0.01$; Table 2.8a, Table S2.8). There was no significant effect of study year on the scales studied (LR statistic = 0.64, $p = 0.43$).

The spatial scales examined by studies differed between the productivity metrics measured (LR statistic = 11.25, $p < 0.01$). Analyses of nest-level metrics were significantly less likely to examine variation across larger spatial scales compared to analyses of population-level metrics (Table 2.8b, Table S2.9). Meanwhile, analyses of individual-level metrics did not differ from nest-level metrics in the scales over which variation was examined and were marginally less likely to examine larger scales compared to population-level metrics (Table 2.8b, Table S2.9). Therefore, studies measuring nest-level productivity metrics most frequently examined smaller spatial scales, followed by those measuring individual-level metrics, while population-level studies had greater representation of intermediate and larger scales compared to these other metrics (Figure 2.3).

In contrast, the spatial scales examined did not significantly differ between the survival metrics (LR statistic = 4.34, *p* = 0.23). The only difference found was that analyses of juvenile survival were marginally more likely to examine larger spatial scales than analyses of post-fledging survival (Table 2.8c, Table S2.10, Figure 2.4). There were no studies in our sample measuring variation in recruitment at the largest spatial scales (> 11-100 km^2; Figure 2.4). Similarly, there was very low representation of the large spatial scales beyond 11-100km^2 in studies measuring post-fledging survival (Figure 2.4).

Table 2.8: Mean log-odds that reviewed studies measured demographic variation at increasing spatial scales, estimated from cumulative link mixed models with spatial scale as the ordinal response variable (from <1 km^2 to >10,000 km^2), and a) demographic rate, b) productivity metric and c) survival metric as fixed effects, using the *emmeans* package. “LCL” = Lower Confidence Level, “UCL” = Upper Confidence Level.

a)	Demographic Rate	Mean Log-odds	Standard Error	95% LCL	95% UCL
	Productivity	-1.87	0.12	-2.10	-1.64
	Survival	-1.39	0.16	-1.69	-1.08
b)	Productivity Metric				
	Nest	-2.00	0.13	-2.26	-1.75
	Individual	-1.68	0.21	-2.10	-1.27
	Population	-0.94	0.34	-1.60	-0.28
c)	Survival Metric				
	Adult	-1.93	0.36	-2.63	-1.23
	Juvenile	-1.55	0.46	-2.45	-0.66
	Post-fledging	-2.70	0.58	-3.84	-1.56
	Recruitment	-2.47	0.78	-3.99	-0.94

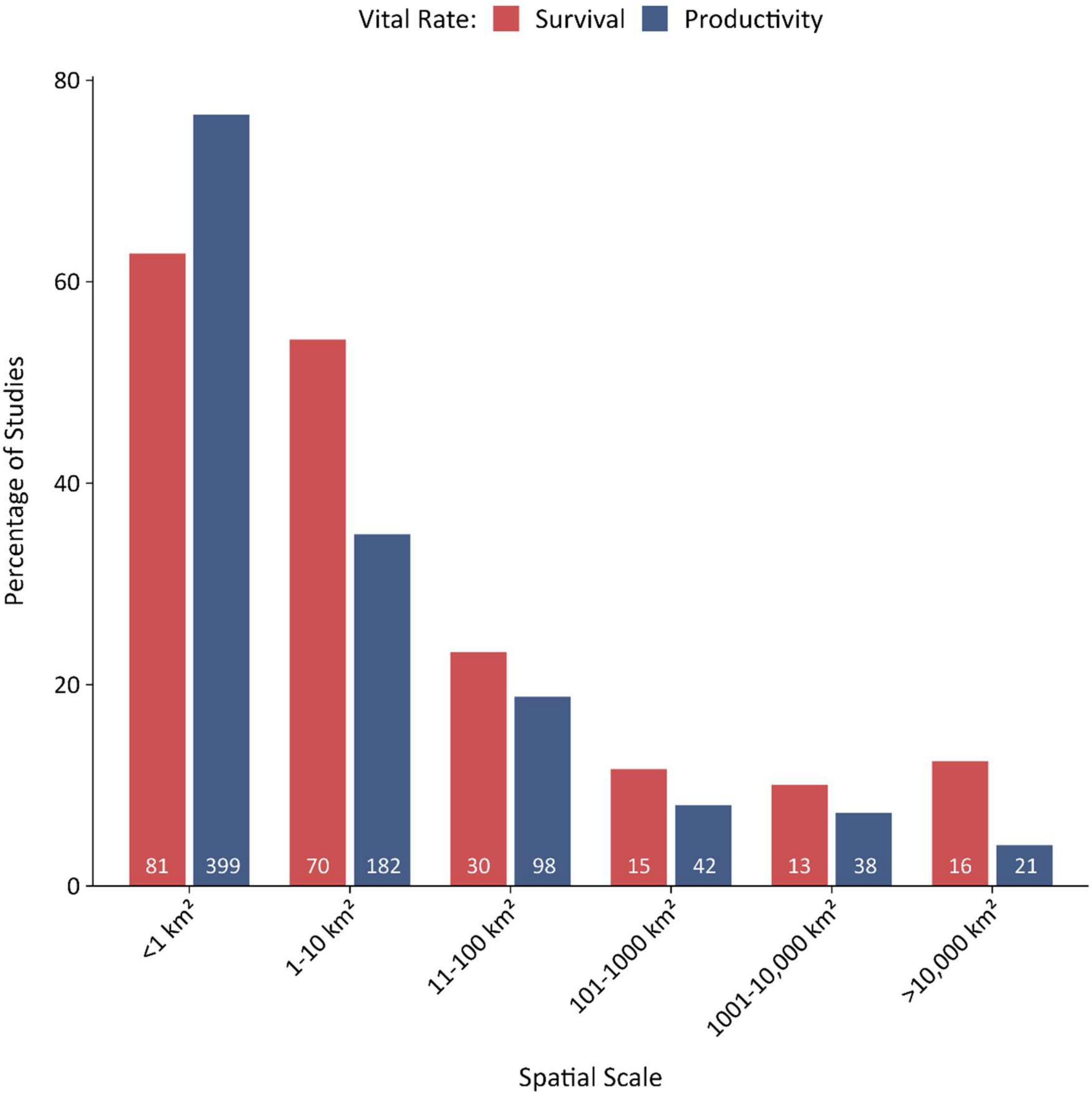


Figure 2.2: The percentage of reviewed studies measuring spatial variation in productivity (blue) or survival (red) at differing spatial scales. The number of studies is given at the base of each bar. As studies can measure variation at multiple scales, the summed percentages are greater than 100.

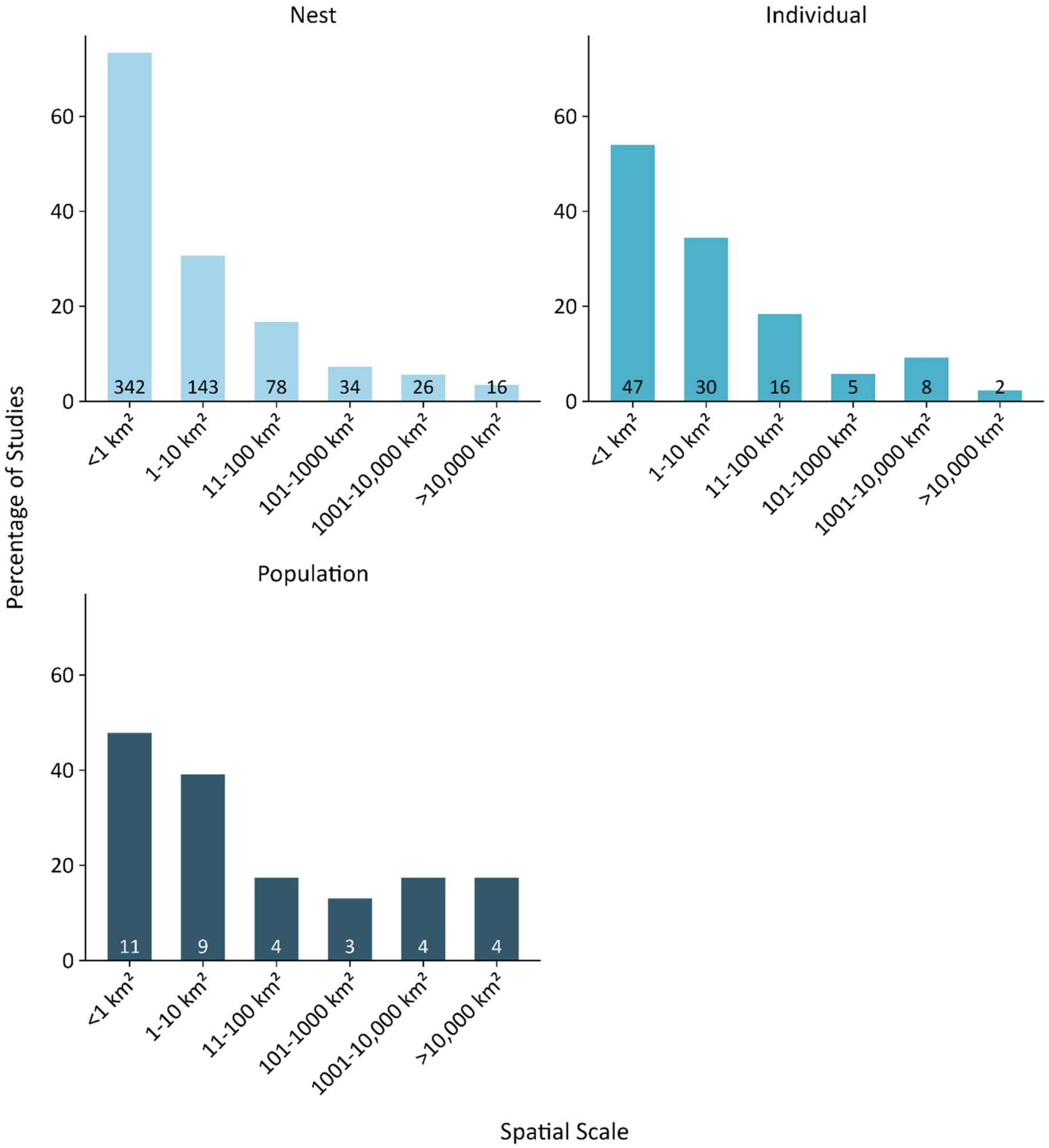


Figure 2.3: The percentage of reviewed studies measuring spatial variation in nest, individual or population-level productivity metrics at different spatial scales. The number of studies is given at the base of each bar. Many studies measure variation at multiple scales and so the summed percentages are greater than 1.

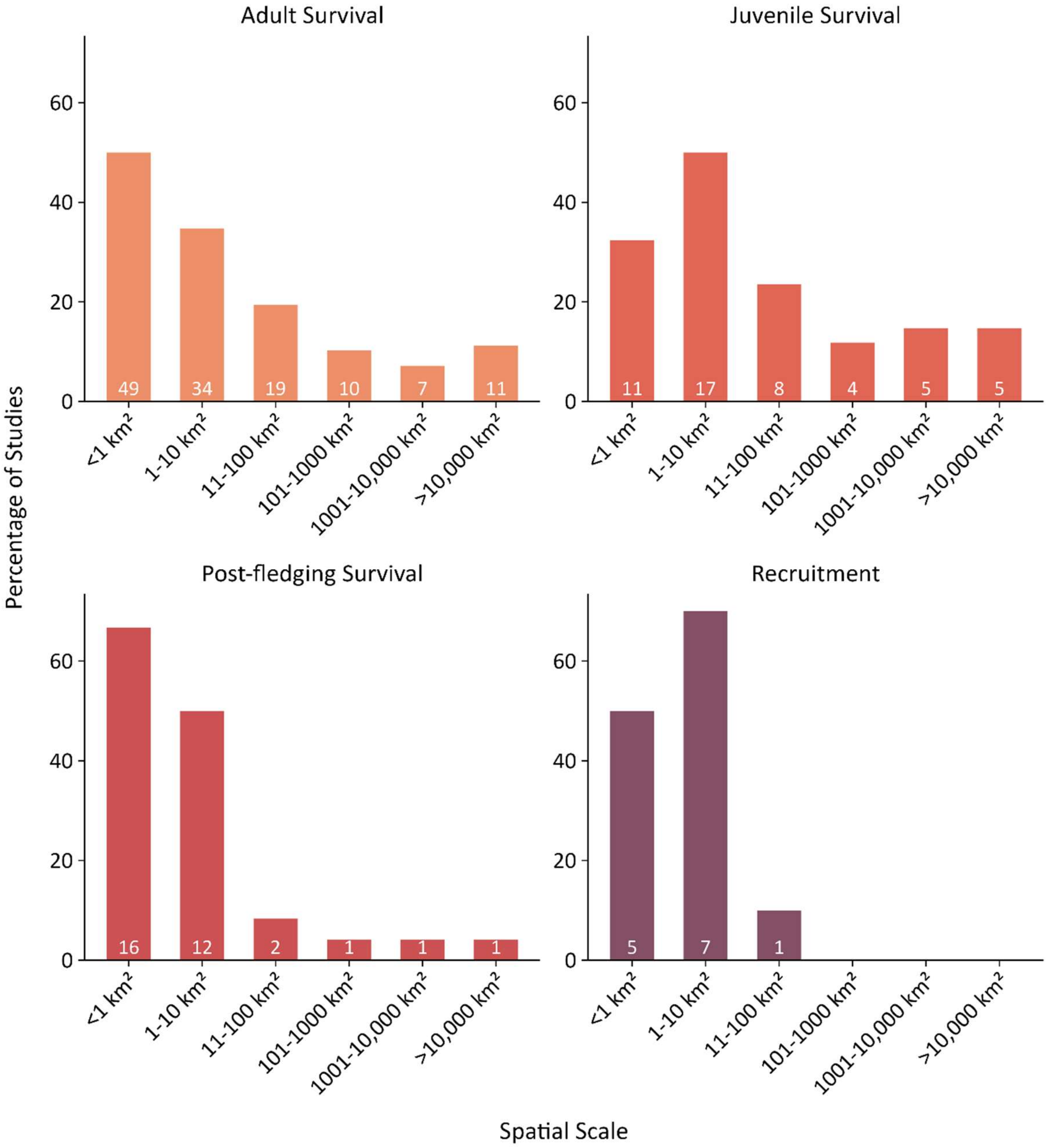


Figure 2.4: The percentage of reviewed studies measuring spatial variation in four survival metrics (adult survival, juvenile survival, post-fledging survival and recruitment) at different spatial scales. The number of studies is given at the base of each bar. Many studies measure variation at multiple scales and so the summed percentages are greater than 1.

Scales of Temporal Variation

For both survival and productivity, most studies explored annual variation (Figure 2.5). The temporal scales over which variation in productivity and survival have been examined differed significantly: survival analyses were more likely to examine annual/decadal variation than productivity analyses, which were more likely to examine sub-annual variation compared to survival analyses (LR statistic = 8.22, $p < 0.01$; see threshold coefficients in Table S2.11). There was no evidence of trends in any of the temporal scales of study (study year effect, LR statistic = 1.11, $p = 0.29$). Decadal variation was measured infrequently in both productivity and survival metrics.

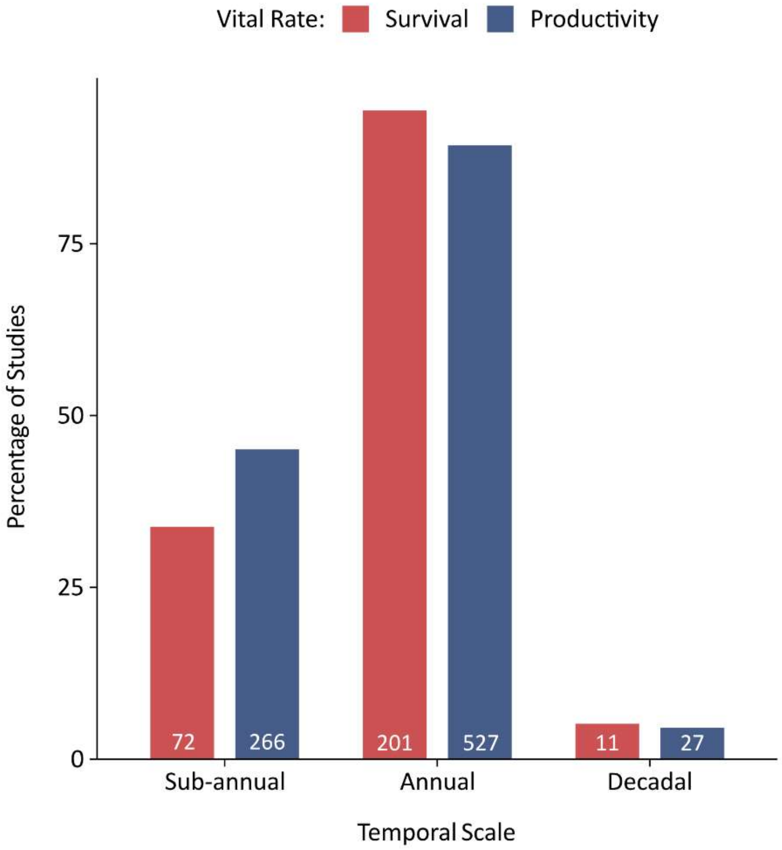


Figure 2.5: The percentage of reviewed studies measuring variation in productivity (blue) or survival (red) at different temporal scales. The number of studies is given at the base of each bar. Many studies measure variation at multiple scales and so the summed percentages are greater than 1.

Different metrics of productivity have also been explored at significantly different temporal scales (LR statistic = 59.12, $p < 0.0001$). Studies of variation in nest-level productivity were more likely to examine sub-annual variation compared to those measuring individual-level or population-level metrics (Figure 2.6; see threshold coefficients in Table S2.12). For population-level metrics, nearly all temporal analyses measured annual variation, with very few studies considering the other temporal scales.

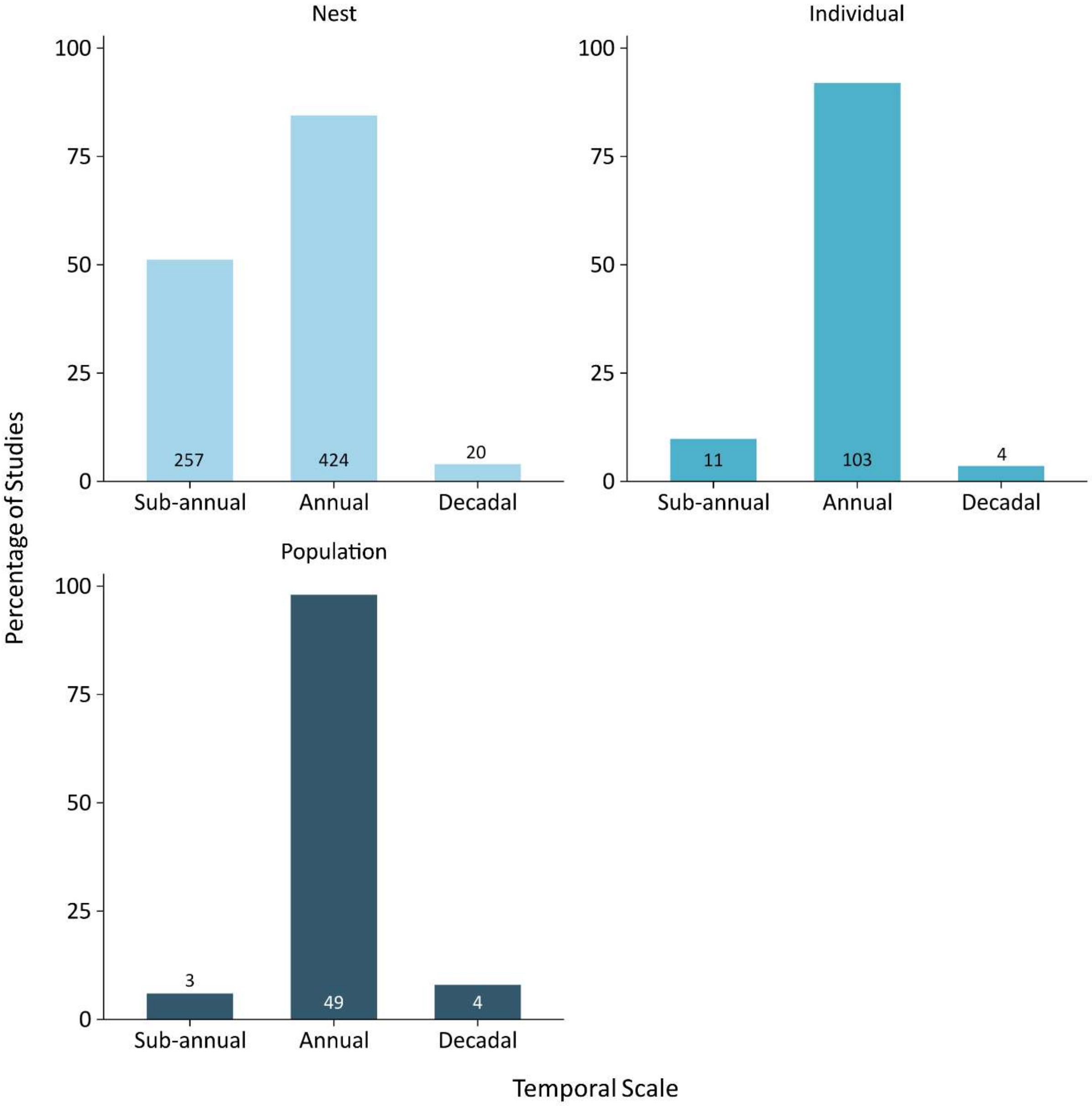


Figure 2.6: The percentage of reviewed studies measuring variation in nest, individual and population-level productivity metrics at different temporal scales. The number of studies is given at the base of each bar. Many studies measure variation at multiple scales and so the summed percentages are greater than 1.

Similarly, different survival metrics have been explored at significantly different temporal scales (LR statistic = 8.67, $p = 0.03$). Analyses of variation in post-fledging survival rates were significantly less likely to examine longer temporal scales compared to analyses of the other three metrics, which did not differ from one another (Table S2.13). Instead, a much greater percentage of post-fledging survival studies explored sub-annual variation (i.e. variation with fledging date) compared to the other metrics, whilst there were no studies exploring decadal variation (Figure 2.7).

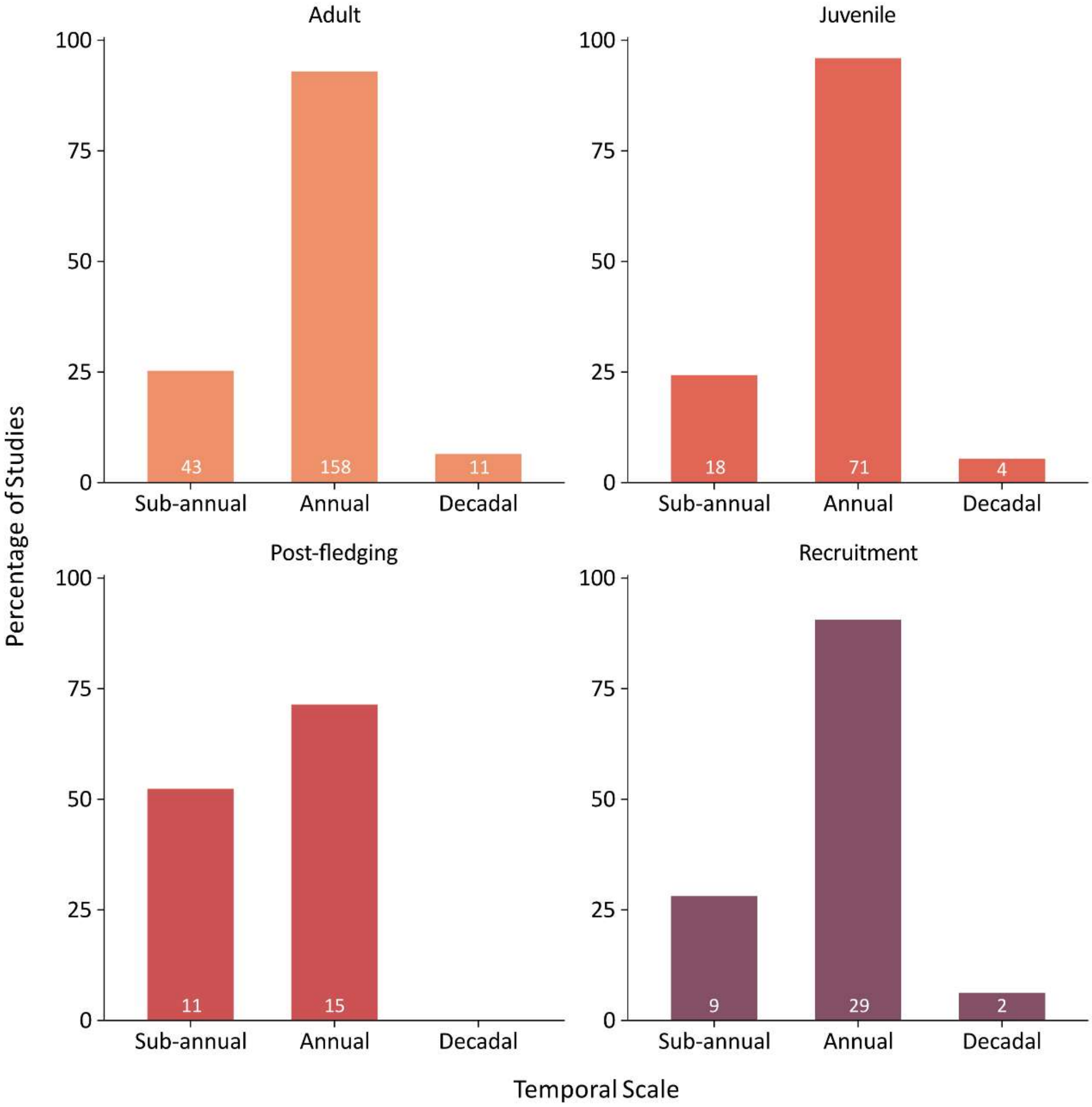


Figure 2.7: The percentage of reviewed studies measuring temporal variation in different survival metrics (adult, juvenile and post-fledging survival, recruitment) at different temporal scales. The number of studies is given at the base of each bar. Many studies measure variation at multiple scales and so the summed percentages are greater than 1.

2.4. Discussion

The demographic variation underlying population change can operate over different spatial and temporal scales. In this review, we show that most studies of variation in productivity and survival of bird populations have taken place over relatively small (≤ 10 km^2) spatial scales, and over annual timescales. We also found differences between productivity, survival and their component metrics in the extent to which spatial and temporal variation have been studied, and the scales at which this variation has been measured. Here, we discuss how this might impact our current understanding of demographic variation in birds and potential implications for their conservation.

Productivity vs Survival

Considerably more research effort has been dedicated to measuring spatiotemporal variation in productivity than in survival rates. This disparity may reflect the substantial effort required for mark-recapture programmes (Chandler et al., 2018), although nest monitoring or following the reproductive success of marked individuals can also be demanding (Etterson et al., 2011). Information on spatiotemporal variation in both survival and productivity provides important insights into population-level processes (Robinson et al., 2014). For example, work on willow warblers (*Phylloscopus trochilus*) in the U.K. demonstrated that while periods of low adult survival may have initiated population declines, years with high productivity rates were likely to have driven recovery in some regions (Morrison et al., 2016). Studies like this one which combine data on multiple demographic rates in Integrated Population Models (IPMs) can help to identify key vital rates driving population changes and associated effective targets for conservation action (e.g. Besbeas et al., 2002; Coates et al., 2018; Koons et al., 2017; Zhao et al., 2021; see Zipkin and Saunders 2018 for review). This is particularly valuable in scarce and difficult-to-study species, such as the Bearded Vulture (*Gypaetus barbatus*), for which IPMs have been used to improve estimates of spatiotemporal variation in demographic parameters and evaluate the impact of supplementary feeding efforts (Margalida et al., 2020).

Spatiotemporal Variation

Whilst spatial and temporal variation in productivity rates have been equally well-studied, we found spatial variation was less frequently examined in studies measuring survival rates. This could result from the prioritisation of accuracy in survival analyses, with intensive re-capture or re-sighting effort focused on single sites over long time periods, instead of replication over multiple sites. This is particularly likely in studies of survival rates in seabird species, for which it is logistically challenging to study multiple colonies congruently. Accordingly, within our sample of studies, those measuring variation in survival rates of seabirds showed an 81% probability of measuring temporal variation and a 19% probability of measuring spatial variation, and therefore showed a greater tendency towards studying temporal variation compared to the overall probabilities recorded across all species (62% temporal and 38% spatial). These studies often employ a “time-for-space” substitution, whereby the effects of environmental drivers on survival rates are studied by correlating temporal variation in demography and environmental variables, rather than measuring how these vary over space (e.g. Agnew et al., 2015; Barbraud et al., 2008; Jenouvrier et al., 2015; Quéroué et al., 2021). The validity of "time-for-space" or "space-for-time" substitutions have been questioned because they assume that spatial and temporal variation are equivalent, which is not necessarily the case (Bonthoux et al., 2013; Gaüzère and Devictor, 2021; although see Şen et al., 2025).

However, it could be argued that temporal variation is more relevant than spatial variation for survival rates. Findings from recent studies exploring spatiotemporal variation in large-scale monitoring datasets of Passeriformes (Morrison et al., 2022) and Galliformes (Nater et al., 2024) in Europe suggest that survival rates vary more over time than over space. This tendency towards the measurement of temporal variation could therefore reflect the main axis of variation in survival rates, but more studies examining spatial and temporal variation are needed to determine whether this is also the case in other bird Orders and regions.

Spatial Scales

We detected a strong tendency for studies of productivity and survival to take place over smaller spatial scales (≤ 10 km^2). This suggests that research has focused on understanding drivers of small-scale variation in demographic rates, such as patch- or site-level habitat characteristics (e.g. Belder et al., 2020), rather than drivers of large-scale variation, such as regional landscape composition (e.g. Rodgers et al., 2012). Grosbois et al., (2008) argue that mechanisms behind demographic variation are most easily studied and understood at local scales because drivers ultimately act on local demographic rates. Consistent with this, several studies collecting data over larger regional extents only analysed demographic variation at scales <1 km^2 (Anthony et al., 2021; Evans et al., 2015; Raybuck et al., 2020). In addition, the lower frequency of large-scale studies likely stems from practical constraints; due to the resource-intensive nature of demographic studies, most are geographically restricted in extent and so it is simply not possible to look at large-scale processes.

Analyses at larger spatial scales were at particularly low frequency for nest-level productivity metrics and post-fledging survival rates, which are typically viewed as being impacted by local conditions due to the static nature of nests and limited dispersal distances of fledglings. In comparison, analyses of variation in adult and juvenile survival rates, and population-level productivity, were less constrained to smaller spatial scales, possibly because processes affecting these rates occur over larger areas due to the movement of individuals. Choosing the appropriate spatial scale for analysis is challenging, and failure to do so can lead to inaccurate estimation of or failure to detect key processes (Wheatley and Johnson, 2009). For example, reviews on the effects of habitat fragmentation on avian nesting success (Stephens et al., 2004) and nest predator responses (Chalfoun et al., 2002) have shown that studies measuring fragmentation at the landscape scale were more likely to find effects than those examining the smaller edge and patch scales. Therefore, management strategies informed exclusively by studies at small spatial scales could be ineffective at reducing nest predation rates for species of conservation concern (Chiavacci et al., 2018).

Where *a priori* knowledge of the appropriate scale is lacking, the best approach might be to quantify demographic variation at multiple scales and compare results (Brickhill et al., 2015), although scales must be relevant to research questions and focal species' ecology to avoid indiscriminately searching for patterns in the data. For example, recent research into associations between landscape composition and nest predation rates of Snowy Plovers (*Charadrius nivosus*; Ellis et al., 2020), and shrub-nesting birds (Chiavacci et al., 2018) have demonstrated the importance of assessing multiple spatial scales to incorporate scale-dependence of different predator species' responses. A recently developed approach is to explicitly estimate the spatial scales at which species respond to their environment as parameters in analyses, which increases the likelihood of identifying the appropriate scale(s) for management interventions (Monroe et al., 2022).

Temporal Scales

Amongst temporal analyses, annual variation was the most well-studied scale for both survival and productivity. The measurement of annual survival rates is common because it accounts for conditions experienced by individuals across the complete seasonal cycle (Grosbois et al., 2008). In addition, annual time-scales are often the most practical, especially for migratory species and seabirds where studies tend to be restricted to breeding grounds due to uncertainty about the location of wintering grounds, the very low migratory connectivity in many species and difficulty in re-sighting individuals across vast areas (Clark et al., 2018; Finch et al., 2017; Wood et al., 2021). This is also the case for studies on juvenile survival in species with large natal dispersal distances (Anders and Marshall, 2005). However, the most critical time periods for mortality can be difficult to infer from annual survival estimates (Grosbois et al., 2008). A more precise understanding of the environmental conditions driving survival rates can be obtained by measuring within-season or inter-seasonal variation (Lavoie et al., 2017). For example, estimation of monthly survival rates in migratory Kirtland's warblers (*Setophaga kirtlandii*) revealed that most mortality occurs during migration rather than on breeding or wintering grounds (Rockwell et al., 2017). However, studies examining variation at these sub-annual timescales were relatively scarce. The deployment of tracking technologies, such as telemetry and geolocators, enables studies to estimate fine-scale temporal (and spatial) variation in survival rates and more accurately determine associations with environmental conditions, which is especially valuable for studies of wide-ranging (e.g. Greater Sage-Grouse, *Centrocercus urophasianus*; Coates et al., 2018) or migratory species (e.g. Afro-Palaearctic migratory raptors; Klaassen et al., 2014).

Several studies measuring the impact of climatic variation on productivity related annual productivity averages to mean weather conditions recorded in relevant time-windows, such as the pre-laying, incubation and nestling periods (e.g. Acquarone et al., 2003; DeSante and Saracco, 2021; Fantle-Lepczyk et al., 2016; Lehikoinen et al., 2013). Studies which examine how productivity varies within the breeding season allow variation to be more closely linked to the weather conditions directly experienced by breeding birds and their young. For example, many studies relate weather conditions measured during nest-specific time periods to the success of those individual nesting attempts (e.g. Shewring et al., 2020; Shiao et al., 2015; Weiser et al., 2018; Wright et al., 2009). Fullerton et al., (2021) examined temporal variation in productivity and weather at both of these temporal scales in order to assess the likelihood of different mechanisms driving these relationships. By measuring inter-annual variation in average nest success and early spring temperatures, they were able to explore the effect of phenological changes in average weather conditions on woodpeckers' ability to raise young, for example via impacts on food availability. Meanwhile, they related the success of individual nesting attempts to weather conditions during nest-specific time windows to examine whether discrete weather events directly affected nestling mortality. Thus, measurement of demographic variation at multiple temporal scales can help reveal a deeper understanding of processes driving population changes.

Decadal scale analyses are infrequent, even in long-term projects, where annual variation is often the focus. Averaging demographic rates across years can result in the loss of information, but can be valuable for comparing rates before and after a particular point-in-time, for example to monitor the impact of management actions, or adverse environmental events. Such comparisons combined with data across multiple sites have identified negative impacts of foraging habitat loss due to tidal management on winter survival in wading bird species (Burton et al., 2006; Duriez et al., 2009).

Conclusions and Recommendations

Most studies of variation in avian demographic rates have taken place over relatively small spatial scales and annual timescales. While this captures local, short-term effects well, we may be less able to detect the effects of changes operating over much larger spatial scales and longer timescales, such as land-use changes. Given that the majority of threatened seabirds and a fifth of threatened terrestrial birds require conservation action at the seascape or landscape scales (Boyd et al., 2008), it will be important to enable demographic research at larger spatial and temporal scales. Some of the practical barriers to large-scale studies can be overcome through collaborative research projects across institutes and regions. For example, the EuroCES (Europe; Robinson 2023) and MAPS (North America; DeSante and Saracco 2009) constant-effort bird ringing schemes each employ a vast network of volunteers to systematically collect demographic data in parallel at continent-wide scale. This has enabled numerous studies of large-scale processes, such as latitudinal variation in demographic responses to temperature (Eglington et al., 2015) and synchrony in vital rates across populations (Morrison et al., 2022). There have also been recent efforts to increase the sharing of data via FAIR repositories, such as the Studies of Populations of Individual Birds (SPI-Birds) network (Culina et al., 2021) and the COMADRE database for animal demography (Salguero-Gómez et al., 2016). Through such initiatives, disparate datasets can be integrated due to consistent data architecture and the development of integrative modelling approaches, allowing long-term, multi-population and even range-wide demographic studies (e.g. Nater et al., 2023; Woodman et al., 2025). We recommend that future work makes use of these data-sharing programmes to examine the extent to which local-scale studies can capture large-scale processes.

References

Acquarone, C., Cucco, M., Malacarne, G., 2003. Reproduction of the Crag Martin (Ptyonoprogne rupestris) in relation to weather and colony size. Ornis Fennica 80, 79–85.

Agnew, P., Lalas, C., Wright, J., Dawson, S., 2015. Variation in breeding success and survival of little penguins Eudyptula minor in response to environmental variation. Marine Ecology Progress Series 541, 219–229. https://doi.org/10.3354/meps11538

Anders, A.D., Marshall, M.R., 2005. Increasing the Accuracy of Productivity and Survival Estimates in Assessing Landbird Population Status. Conservation Biology 19, 66–74. https://doi.org/10.1111/j.1523-1739.2005.00543.x

Anthony, C.R., Hagen, C.A., Dugger, K.M., Elmore, R.D., 2021. Greater Sage-Grouse nest bowls buffer microclimate in a post-megafire landscape although effects on nest survival are marginal. Ornithological Applications 123, duaa068. https://doi.org/10.1093/ornithapp/duaa068

Arrondo, E., Sanz-Aguilar, A., Pérez-García, J.M., Cortés-Avizanda, A., Sánchez-Zapata, J.A., Donázar, J.A., 2020. Landscape anthropization shapes the survival of a top avian scavenger. Biodivers Conserv 29, 1411–1425. https://doi.org/10.1007/s10531-020-01942-6

Barbraud, C., Marteau, C., Ridoux, V., Delord, K., Weimerskirch, H., 2008. Demographic response of a population of white-chinned petrels Procellaria aequinoctialis to climate and longline fishery bycatch. Journal of Applied Ecology 45, 1460–1467. https://doi.org/10.1111/j.1365-2664.2008.01537.x

Bates, D., Maechler, M., Bolker [aut, B., cre, Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., simulate.formula), P.N.K. (shared copyright on, Tanaka, E., Jagan, M., 2025. lme4: Linear Mixed-Effects Models using “Eigen” and S4.

Belder, D.J., Pierson, J.C., Ikin, K., Lindenmayer, D.B., 2020. Revegetation and reproduction: do restoration plantings in agricultural landscapes support breeding populations of woodland birds? Oecologia 192, 865–878. https://doi.org/10.1007/s00442-020-04611-1

Besbeas, P., Freeman, S.N., Morgan, B.J.T., Catchpole, E.A., 2002. Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58, 540–547.

Bonthoux, S., Barnagaud, J.-Y., Goulard, M., Balent, G., 2013. Contrasting spatial and temporal responses of bird communities to landscape changes. Oecologia 172, 563–574. https://doi.org/10.1007/s00442-012-2498-2

Boyd, C., Brooks, T.M., Butchart, S.H.M., Edgar, G.J., Da Fonseca, G.A.B., Hawkins, F., Hoffmann, M., Sechrest, W., Stuart, S.N., Van Dijk, P.P., 2008. Spatial scale and the conservation of threatened species. Conservation Letters 1, 37–43. https://doi.org/10.1111/j.1755-263X.2008.00002.x

Bramer, W.M., Giustini, D., Jonge, G.B. de, Holland, L., Bekhuis, T., 2016. De-duplication of database search results for systematic reviews in EndNote. Journal of the Medical Library Association 104, 240–243. https://doi.org/10.5195/jmla.2016.24

Brickhill, D., Evans, P.G.H., Reid, J.M., 2015. Spatio-temporal variation in European starling reproductive success at multiple small spatial scales. Ecology and Evolution 5, 3364–3377. https://doi.org/10.1002/ece3.1615

Burgess, M.D., Eaton, M.A., Gregory, R.D., 2020. A review of spatial patterns across species ranges to aid the targeting of conservation interventions. Biological Conservation 251, 108755. https://doi.org/10.1016/j.biocon.2020.108755

Burton, N.H.K., Rehfisch, M.M., Clark, N.A., Dodd, S.G., 2006. Impacts of sudden winter habitat loss on the body condition and survival of redshank Tringa totanus. Journal of Applied Ecology 43, 464–473. https://doi.org/10.1111/j.1365-2664.2006.01156.x

Chalfoun, A.D., Thompson III, F.R., Ratnaswamy, M.J., 2002. Nest Predators and Fragmentation: a Review and Meta-Analysis. Conservation Biology 16, 306–318. https://doi.org/10.1046/j.1523-1739.2002.00308.x

Chandler, R.B., Hepinstall-Cymerman, J., Merker, S., Abernathy-Conners, H., Cooper, R.J., 2018. Characterizing spatio-temporal variation in survival and recruitment with integrated population models. The Auk 135, 409–426. https://doi.org/10.1642/AUK-17-181.1

Chiavacci, S.J., Benson, T.J., Ward, M.P., 2018. Linking landscape composition to predator-specific nest predation requires examining multiple landscape scales. Journal of Applied Ecology 55, 2082–2092. https://doi.org/10.1111/1365-2664.13090

Christensen, R.H.B., 2023. ordinal: Regression Models for Ordinal Data.

Clark, R.G., Winkler, D.W., Dawson, R.D., Shutler, D., Hussell, D.J.T., Lombardo, M.P., Thorpe, P.A., Dunn, P.O., Whittingham, L.A., 2018. Geographic variation and environmental correlates of apparent survival rates in adult tree swallows Tachycineta bicolor. Journal of Avian Biology 49, jav-012514. https://doi.org/10.1111/jav.01659

Coates, P.S., Prochazka, B.G., Ricca, M.A., Halstead, B.J., Casazza, M.L., Blomberg, E.J., Brussee, B.E., Wiechman, L., Tebbenkamp, J., Gardner, S.C., Reese, K.P., 2018. The relative importance of intrinsic and extrinsic drivers to population growth vary among local populations of Greater Sage-Grouse: An integrated population modeling approach. The Auk 135, 240–261. https://doi.org/10.1642/AUK-17-137.1

Culina, A., Adriaensen, F., Bailey, L.D., Burgess, M.D., Charmantier, A., Cole, E.F., Eeva, T., Matthysen, E., Nater, C.R., Sheldon, B.C., Sæther, B.-E., Vriend, S.J.G., Zajkova, Z., Adamík, P., Aplin, L.M., Angulo, E., Artemyev, A., Barba, E., Barišić, S., Belda, E., Bilgin, C.C., Bleu, J., Both, C., Bouwhuis, S., Branston, C.J., Broggi, J., Burke, T., Bushuev, A., Camacho, C., Campobello, D., Canal, D., Cantarero, A., Caro, S.P., Cauchoix, M., Chaine, A., Cichoń, M., Ćiković, D., Cusimano, C.A., Deimel, C., Dhondt, A.A., Dingemanse, N.J., Doligez, B., Dominoni, D.M., Doutrelant, C., Drobniak, S.M., Dubiec, A., Eens, M., Einar Erikstad, K., Espín, S., Farine, D.R., Figuerola, J., Kavak Gülbeyaz, P., Grégoire, A., Hartley, I.R., Hau, M., Hegyi, G., Hille, S., Hinde, C.A., Holtmann, B., Ilyina, T., Isaksson, C., Iserbyt, A., Ivankina, E., Kania, W., Kempenaers, B., Kerimov, A., Komdeur, J., Korsten, P., Král, M., Krist, M., Lambrechts, M., Lara, C.E., Leivits, A., Liker, A., Lodjak, J., Mägi, M., Mainwaring, M.C., Mänd, R., Massa, B., Massemin, S., Martínez-Padilla, J., Mazgajski, T.D., Mennerat, A., Moreno, J., Mouchet, A., Nakagawa, S., Nilsson, J.-Å., Nilsson, J.F., Cláudia Norte, A., van Oers, K., Orell, M., Potti, J., Quinn, J.L., Réale, D., Kristin Reiertsen, T., Rosivall, B., Russell, A.F., Rytkönen, S., Sánchez-Virosta, P., Santos, E.S.A., Schroeder, J., Senar, J.C., Seress, G., Slagsvold, T., Szulkin, M., Teplitsky, C., Tilgar, V., Tolstoguzov, A., Török, J., Valcu, M., Vatka, E., Verhulst, S., Watson, H., Yuta, T., Zamora-Marín, J.M., Visser, M.E., 2021. Connecting the data landscape of long-term ecological studies: The SPI-Birds data hub. Journal of Animal Ecology 90, 2147–2160. https://doi.org/10.1111/1365-2656.13388

Delgado, S., Zorrozua, N., Arizaga, J., 2021. NO EVIDENCE OF HABITAT EFFECT ON CLUTCH SIZE, EGG QUALITY, AND HATCHING SUCCESS OF THE YELLOW-LEGGED GULL LARUS MICHAHELLIS AT A MICRO-SPATIAL SCALE.

DeMay, S.M., Walters, J.R., 2019. Variable effects of a changing climate on lay dates and productivity across the range of the Red-cockaded Woodpecker. The Condor 121, duz048. https://doi.org/10.1093/condor/duz048

Desante, D.F., Saracco, J.F., 2009. POWER OF THE MAPS PROGRAM TO DETECT DIFFERENCES AND TRENDS IN SURVIVAL AND A VISION FOR PROGRAM EXPANSION. Bird Populations 9, 42–75.

DeSante, D.F., Saracco, J.F., 2021. Climate variation drives dynamics and productivity of a subalpine breeding bird community. Ornithological Applications 123, duab014. https://doi.org/10.1093/ornithapp/duab014

Duriez, O., Sæther, S.A., Ens, B.J., Choquet, R., Pradel, R., Lambeck, R.H.D., Klaassen, M., 2009. Estimating survival and movements using both live and dead recoveries: a case study of oystercatchers confronted with habitat change. Journal of Applied Ecology 46, 144–153. https://doi.org/10.1111/j.1365-2664.2008.01592.x

Eglington, S.M., Julliard, R., Gargallo, G., Jeugd, H.P., Pearce-Higgins, J.W., Baillie, S.R., Robinson, R.A., 2015. Latitudinal gradients in the productivity of European migrant warblers have not shifted northwards during a period of climate change. Global Ecology and Biogeography 24, 427–436.

Ellis, K.S., Larsen, R.T., Koons, D.N., 2020. Dependence of spatial scale in landscape associations with cause-specific predation of snowy plover nests. Ecosphere 11, e03257. https://doi.org/10.1002/ecs2.3257

Etterson, M.A., Ellis-Felege, S.N., Evers, D., Gauthier, G., Grzybowski, J.A., Mattsson, B.J., Nagy, L.R., Olsen, B.J., Pease, C.M., van der Burg, M.P., Potvien, A., 2011. Modeling fecundity in birds: Conceptual overview, current models, and considerations for future developments. Ecological Modelling 222, 2178–2190. https://doi.org/10.1016/j.ecolmodel.2010.10.013

Evans, B.S., Ryder, T.B., Reitsma, R., Hurlbert, A.H., Marra, P.P., 2015. Characterizing avian survival along a rural-to-urban land use gradient. Ecology 96, 1631–1640. https://doi.org/10.1890/14-0171.1

Fantle-Lepczyk, J., Taylor, A., Duffy, D., Crampton, L.H., Conant, S., 2016. Weather influences on nest success of the endangered Puaiohi (Myadestes palmeri). wils 128, 43–55. https://doi.org/10.1676/wils-128-01-43-55.1

Finch, T., Butler, S.J., Franco, A.M.A., Cresswell, W., 2017. Low migratory connectivity is common in long-distance migrant birds. Journal of Animal Ecology 86, 662–673. https://doi.org/10.1111/1365-2656.12635

Folk, T.H., Holmes, R.R., Grand, J.B., 2007. Variation in northern bobwhite demography along two temporal scales. Population Ecology 49, 211–219. https://doi.org/10.1007/s10144-007-0037-5

Frederiksen, M., Lebreton, J.-D., Pradel, R., Choquet, R., Gimenez, O., 2014. REVIEW: Identifying links between vital rates and environment: a toolbox for the applied ecologist. Journal of Applied Ecology 51, 71–81. https://doi.org/10.1111/1365-2664.12172

Fullerton, M.R., Walters, J.R., Will, R.E., Loss, S.R., 2021. Interannual climate variation influences nest initiation date and nest productivity of the Red-cockaded Woodpecker at the northwestern edge of its range. Ornithological Applications 123, duab013. https://doi.org/10.1093/ornithapp/duab013

Gaüzère, P., Devictor, V., 2021. Mismatches between birds' spatial and temporal dynamics reflect their delayed response to global changes. Oikos 130, 1284–1296. https://doi.org/10.1111/oik.08289

Green, R.E., 1999. Applications of large-scale studies of demographic rates to bird conservation. Bird Study 46, S279–S288. https://doi.org/10.1080/00063659909477255

Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P., Weimerskirch, H., 2008. Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews 83, 357–399. https://doi.org/10.1111/j.1469-185X.2008.00047.x

Gunnarsson, T.G., Gill, J.A., Newton, J., Potts, P.M., Sutherland, W.J., 2005. Seasonal matching of habitat quality and fitness in a migratory bird. Proceedings of The Royal Society B: Biological Sciences 272, 2319–2323. https://doi.org/10.1098/rspb.2005.3214

Gurevitch, J., Fox, G.A., Fowler, N.L., Graham, C.H., 2016. Landscape Demography: Population Change and its Drivers Across Spatial Scales. The Quarterly Review of Biology 91, 459–485. https://doi.org/10.1086/689560

Jenouvrier, S., Péron, C., Weimerskirch, H., 2015. Extreme climate events and individual heterogeneity shape life-history traits and population dynamics. Ecological Monographs 85, 605–624. https://doi.org/10.1890/14-1834.1

Klaassen, R.H.G., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.-M., Bairlein, F., Alerstam, T., 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. Journal of Animal Ecology 83, 176–184. https://doi.org/10.1111/1365-2656.12135

Koons, D.N., Arnold, T.W., Schaub, M., 2017. Understanding the demographic drivers of realized population growth rates. Ecological Applications 27, 2102–2115. https://doi.org/10.1002/eap.1594

Lavoie, M., Blanchette, P., Larivière, S., Tremblay, J.-P., 2017. Winter and summer weather modulate the demography of wild turkeys at the northern edge of the species distribution. Population Ecology 59, 239–249. https://doi.org/10.1007/s10144-017-0585-2

Lees, A.C., Haskell, L., Allinson, T., Bezeng, S.B., Burfield, I.J., Renjifo, L.M., Rosenberg, K.V., Viswanathan, A., Butchart, S.H.M., 2022. State of the World's Birds. Annual Review of Environment and Resources 47, 231–260. https://doi.org/10.1146/annurev-environ-112420-014642

Lehikoinen, A., Lindén, A., Byholm, P., Ranta, E., Saurola, P., Valkama, J., Kaitala, V., Lindén, H., 2013. Impact of climate change and prey abundance on nesting success of a top predator, the goshawk. Oecologia 171, 283–293. https://doi.org/10.1007/s00442-012-2411-z

Lenth, R.V., Banfai, B., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Piaskowski, J., Riebl, H., Singmann, H., 2024. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Margalida, A., Jiménez, J., Martínez, J.M., Sesé, J.A., García-Ferré, D., Llamas, A., Razin, M., Colomer, M., Arroyo, B., 2020. An assessment of population size and demographic drivers of the Bearded Vulture using integrated population models. Ecological Monographs 90, e01414. https://doi.org/10.1002/ecm.1414

Monroe, A.P., Heinrichs, J.A., Whipple, A.L., O'Donnell, M.S., Edmunds, D.R., Aldridge, C.L., 2022. Spatial scale selection for informing species conservation in a changing landscape. Ecosphere 13, e4320. https://doi.org/10.1002/ecs2.4320

Morrison, C.A., Butler, S.J., Clark, J.A., Arizaga, J., Baltà, O., Cepák, J., Nebot, A.L., Piha, M., Thorup, K., Wenninger, T., Robinson, R.A., Gill, J.A., 2022. Demographic variation in space and time: implications for conservation targeting. Royal Society Open Science 9, 211671. https://doi.org/10.1098/rsos.211671

Morrison, C.A., Robinson, R.A., Butler, S.J., Clark, J.A., Gill, J.A., 2016. Demographic drivers of decline and recovery in an Afro-Palaearctic migratory bird population. Proc. R. Soc. B. 283, 20161387. https://doi.org/10.1098/rspb.2016.1387

Morrison, C.A., Robinson, R.A., Clark, J.A., Gill, J.A., 2010. Spatial and temporal variation in population trends in a long-distance migratory bird. Diversity and Distributions 16, 620–627. https://doi.org/10.1111/j.1472-4642.2010.00663.x

Nater, C.R., Burgess, M.D., Coffey, P., Harris, B., Lander, F., Price, D., Reed, M., Robinson, R.A., 2023. Spatial consistency in drivers of population dynamics of a declining migratory bird. Journal of Animal Ecology 92, 97–111. https://doi.org/10.1111/1365-2656.13834

Nater, C.R., Frassinelli, F., Martin, J.A., Nilsen, E.B., 2024. Large-scale spatio-temporal variation in vital rates and population dynamics of an alpine bird. Peer Community Journal 4, e111. https://doi.org/10.24072/pcjournal.494

O'Dea, R.E., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H., Gurevitch, J., Page, M.J., Stewart, G., Moher, D., Nakagawa, S., 2021. Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. Biological Reviews 96, 1695–1722. https://doi.org/10.1111/brv.12721

Paquet, M., Arlt, D., Knape, J., Low, M., Forslund, P., Pärt, T., 2019. Quantifying the links between land use and population growth rate in a declining farmland bird. Ecology and Evolution. https://doi.org/10.1002/ece3.4766

Quéroué, M., Barbraud, C., Barraquand, F., Turek, D., Delord, K., Pacoureau, N., Gimenez, O., 2021. Multispecies integrated population model reveals bottom-up dynamics in a seabird predator–prey system. Ecological Monographs 91, e01459. https://doi.org/10.1002/ecm.1459

Raybuck, D.W., Larkin, J.L., Stoleson, S.H., Boves, T.J., 2020. Radio-tracking reveals insight into survival and dynamic habitat selection of fledgling Cerulean Warblers. The Condor 122, duz063. https://doi.org/10.1093/condor/duz063

Robinson, R.A., 2023. Understanding population change: the value of the EuroCES constant-effort ringing programme. Ringing & Migration 38, 29–37. https://doi.org/10.1080/03078698.2024.2311771

Robinson, R.A., Morrison, C.A., Baillie, S.R., 2014. Integrating demographic data: Towards a framework for monitoring wildlife populations at large spatial scales. Methods in Ecology and Evolution 5. https://doi.org/10.1111/2041-210X.12204

Rockwell, S.M., Wunderle, J.M., Sillett, T.S., Bocetti, C.I., Ewert, D.N., Currie, D., White, J.D., Marra, P.P., 2017. Seasonal survival estimation for a long-distance migratory bird and the influence of winter precipitation. Oecologia 183, 715–726. https://doi.org/10.1007/s00442-016-3788-x

Rodgers, J.A., Jr, Brooks, W.B., Barrett, M., 2012. Productivity and Habitat Modeling of Wood Storks Nesting in North and Central Florida. Journal of Fish and Wildlife Management 3, 252–265. https://doi.org/10.3996/022012-JFWM-016

Ruth, J.M., Skagen, S.K., 2018. Reproductive response of Arizona Grasshopper Sparrows to weather patterns and habitat structure. The Condor 120, 596–616. https://doi.org/10.1650/CONDOR-17-128.1

Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Vieregg, D., Buckley, Y.M., Che-Castaldo, J., Hodgson, D., Scheuerlein, A., Caswell, H., Vaupel, J.W., 2016. COMADRE: a global data base of animal demography. Journal of Animal Ecology 85, 371–384. https://doi.org/10.1111/1365-2656.12482

Selwood, K.E., McGeoch, M.A., Mac Nally, R., 2015. The effects of climate change and land-use change on demographic rates and population viability. Biol Rev Camb Philos Soc 90, 837–853. https://doi.org/10.1111/brv.12136

Şen, B., Che-Castaldo, C., LaRue, M.A., Krumhardt, K.M., Landrum, L., Holland, M.M., Lynch, H.J., Delord, K., Barbraud, C., Jenouvrier, S., 2025. Temporal and spatial equivalence in demographic responses of emperor penguins (Aptenodytes forsteri) to environmental change. Journal of Animal Ecology n/a. https://doi.org/10.1111/1365-2656.70025

Shewring, M., Jenks ,Paddy, Cross ,Anthony V., Vaughan ,Ian P., and Thomas, R.J., 2020. Testing for effects of tail-mounted radio tags and environmental variables on European Nightjar Caprimulgus europaeus nest survival. Bird Study 67, 429–439. https://doi.org/10.1080/00063657.2021.1927979

Shiao, M.-T., Chuang, M.-C., Yuan, H.-W., Wang, Y., 2015. Effects of weather variation on the timing and success of breeding in two cavity-nesting species in a subtropical montane forest in Taiwan. The Auk 132, 671–684. https://doi.org/10.1642/AUK-15-10.1

Stephens, S.E., Koons, D.N., Rotella, J.J., Willey, D.W., 2004. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115, 101–110. https://doi.org/10.1016/S0006-3207(03)00098-3

Weiser, E.L., Brown, S.C., Lanctot, R.B., Gates, H.R., Abraham, K.F., Bentzen, R.L., Bêty, J., Boldenow, M.L., Brook, R.W., Donnelly, T.F., English, W.B., Flemming, S.A., Franks, S.E., Gilchrist, H.G., Giroux, M.-A., Johnson, A., Kendall, S., Kennedy, L.V., Koloski, L., Kwon, E., Lamarre, J.-F., Lank, D.B., Latty, C.J., Lecomte, N., Liebezeit, J.R., McKinnon, L., Nol, E., Perz, J., Rausch, J., Robards, M., Saalfeld, S.T., Senner, N.R., Smith, P.A., Soloviev, M., Solovyeva, D., Ward, D.H., Woodard, P.F., Sandercock, B.K., 2018. Effects of environmental conditions on reproductive effort and nest success of Arctic-breeding shorebirds. Ibis 160, 608–623. https://doi.org/10.1111/ibi.12571

Wheatley, M., Johnson, C., 2009. Factors limiting our understanding of ecological scale. Ecological Complexity, Special Section: Environmental micro-simulation: From data approximation to theory assessment 6, 150–159. https://doi.org/10.1016/j.ecocom.2008.10.011

Wood, M.J., Canonne, C., Besnard, A., Lachish, S., Fairhurst, S.M., Liedvogel, M., Boyle, D., Patrick, S.C., Josey, S., Kirk, H., Dean, B., Guilford, T., McCleery, R.M., Perrins, C.M., Horswill, C., 2021. Demographic profiles and environmental drivers of variation relate to individual breeding state in a long-lived trans-oceanic migratory seabird, the Manx shearwater. PLOS ONE 16, e0260812. https://doi.org/10.1371/journal.pone.0260812

Woodman, J.P., Vriend, S.J.G., Adriaensen, F., Álvarez, E., Artemyev, A., Barba, E., Burgess, M.D., Caro, S.P., Cauchard, L., Charmantier, A., Cole, E.F., Dingemanse, N., Doligez, B., Eeva, T., Evans, S.R., Grégoire, A., Lambrechts, M., Leivits, A., Liker, A., Matthysen, E., Orell, M., Park, J.S., Rytkönen, S., Senar, J.C., Seress, G., Szulkin, M., van Oers, K., Vatka, E., Visser, M.E., Firth, J.A., Sheldon, B.C., 2025. Continent-Wide Drivers of Spatial Synchrony in Breeding Demographic Structure Across Wild Great Tit Populations. Ecology Letters 28, e70079. https://doi.org/10.1111/ele.70079

Wright, L.J., Hoblyn, R.A., Green, R.E., Bowden, C.G.R., Mallord, J.W., Sutherland, W.J., Dolman, P.M., 2009. Importance of climatic and environmental change in the demography of a multi-brooded passerine , the woodlark Lullula arborea 1191–1202. https://doi.org/10.1111/j.1365-2656.2009.01582.x

Zhao, Q., Heath-Acre, K., Collins, D., Conway, W., Weegman, M.D., 2021. Integrated population modelling reveals potential drivers of demography from partially aligned data: a case study of snowy plover declines under human stressors. PeerJ 9, e12475. https://doi.org/10.7717/peerj.12475

Zipkin, E.F., Saunders, S.P., 2018. Synthesizing multiple data types for biological conservation using integrated population models. Biological Conservation 217, 240–250. https://doi.org/10.1016/j.biocon.2017.10.017

Chapter 2 Supplementary Material

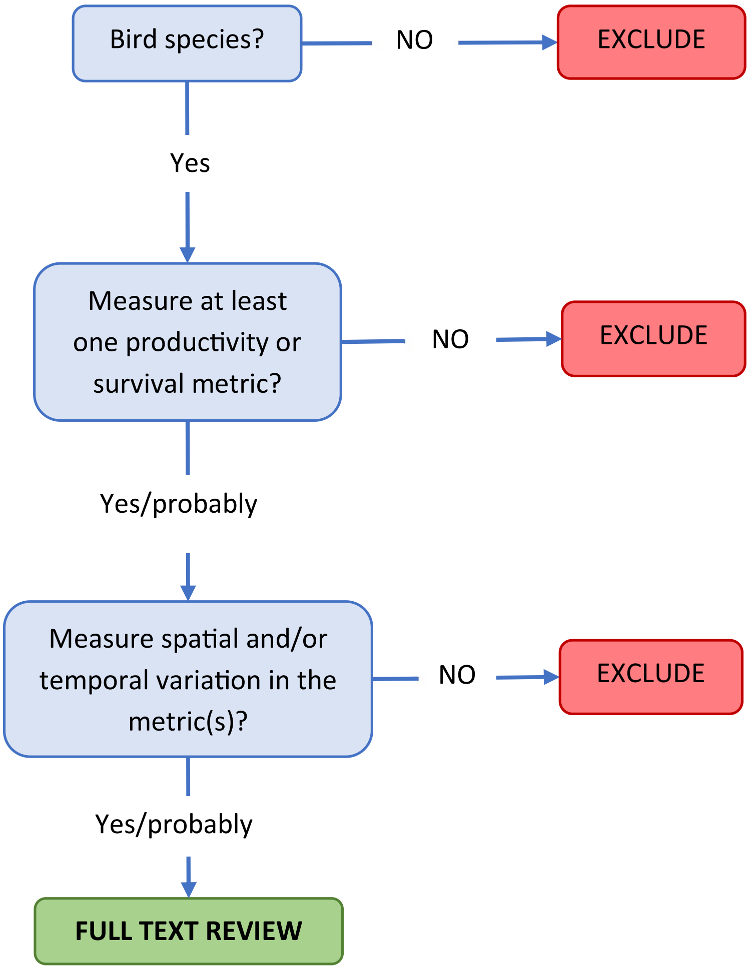


Figure S2.1: Decision tree used to evaluate studies identified by literature searches for inclusion and exclusion within a review of the spatial and temporal scales at which demographic rates of birds have been studied, at the stage of title and abstract screening.

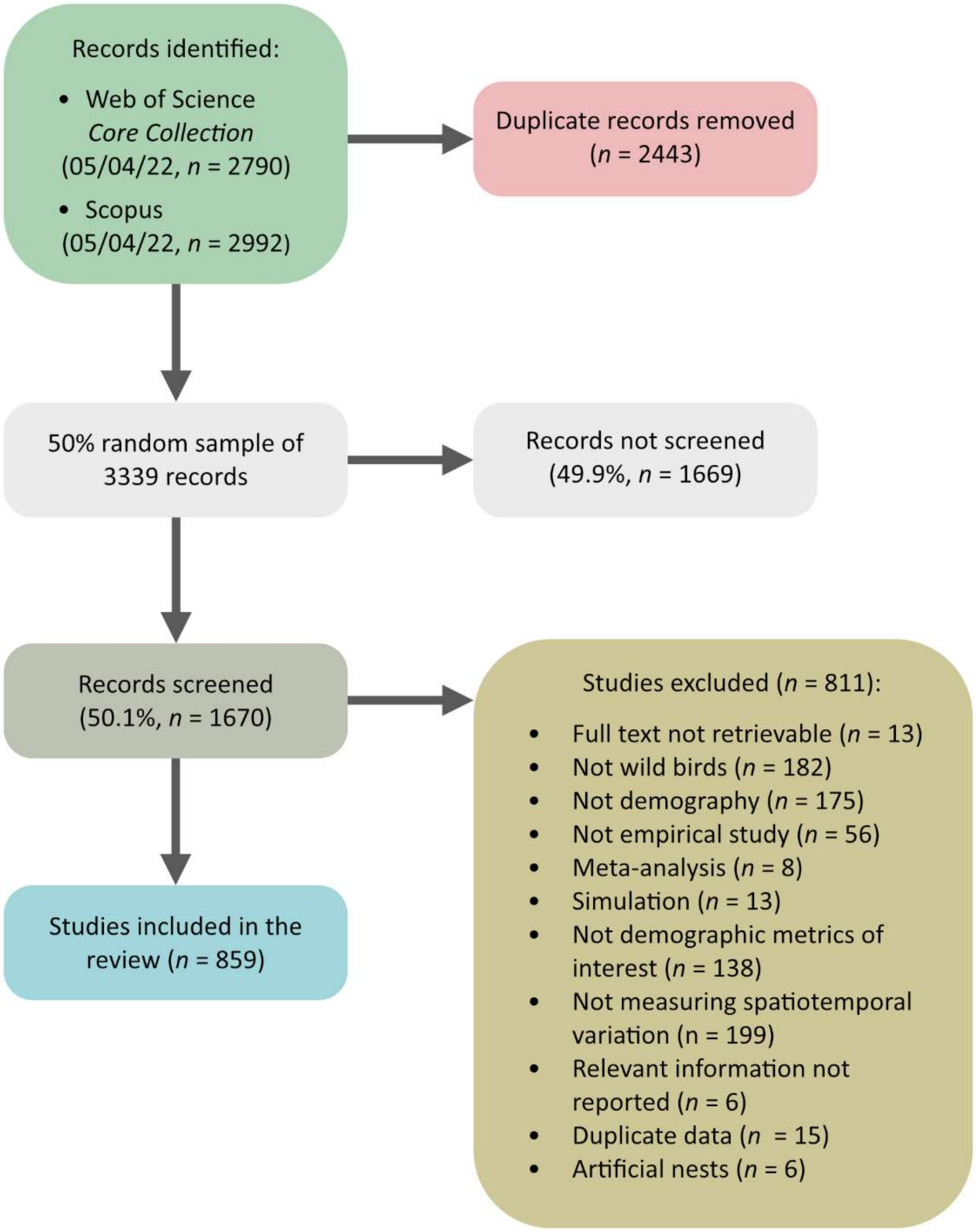


Figure S2.2: PRISMA flow chart summarising literature search and screening methods, plus reasons for study exclusion, for a review of the spatial and temporal scales at which demographic rates of birds have been studied, with the number of studies included and excluded at each stage.

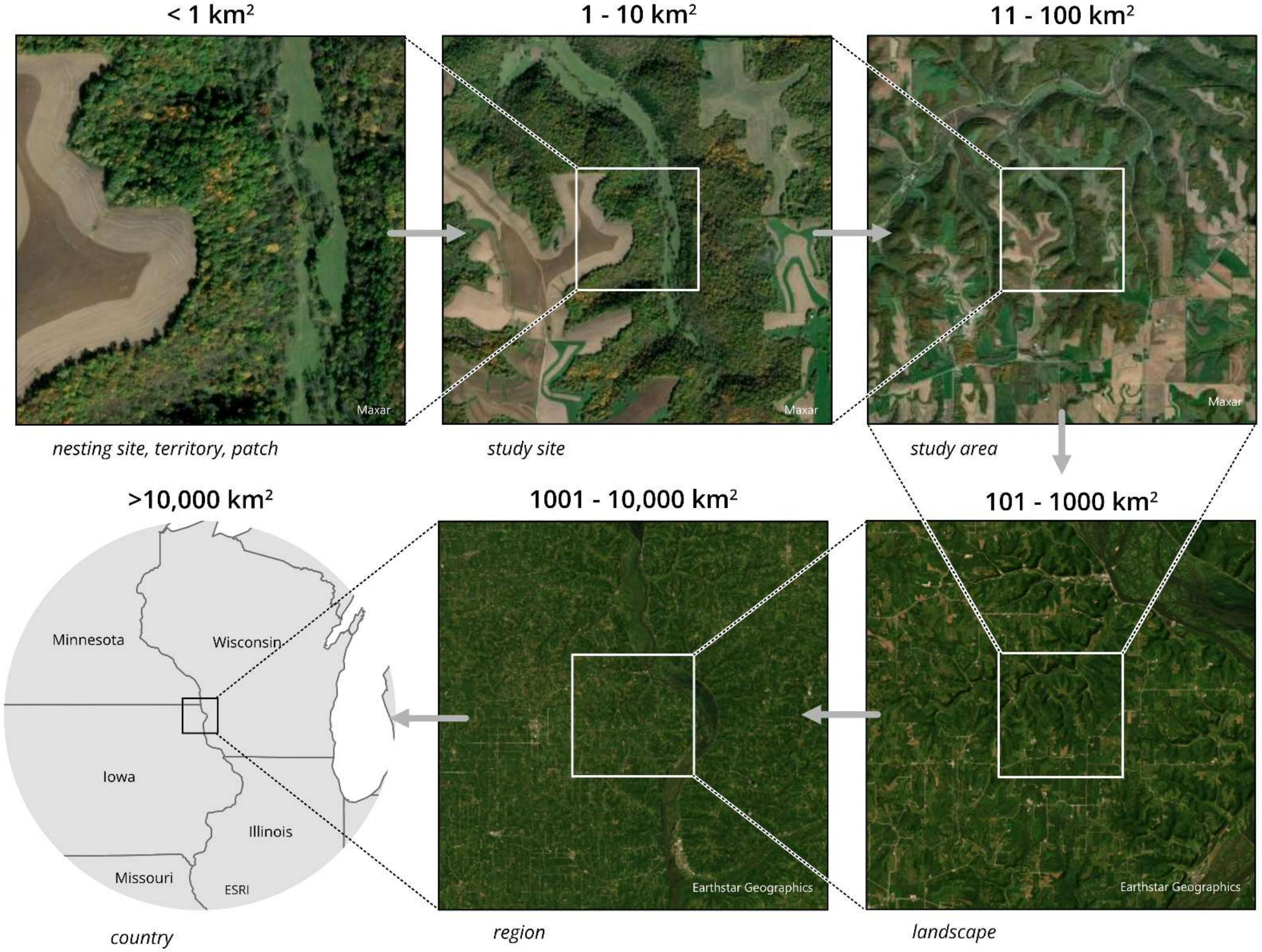


Figure S2.3: An example representation of the categories used to record the spatial scales at which demographic rates of birds have been studied, consisting of spatial ranges increasing in orders of magnitude. The white boxes represent the size of the previous scale in relation to the focal scale. Examples of terms used to describe these scales in the reviewed papers are given below each scale.

Table S2.1. Terminology used in the literature search string, grouped into 3 concept groups as well as exclusion terms.

Topic	AND	Title or Author Keywords				
Taxa		Demography	AND	Variation	NOT	Exclusion Terms
*bird$ OR "avian" OR "chick" OR passerine$		demograph* OR "vital rate" OR "vital rates" OR survival OR productivity OR reproduct* OR ((breeding OR nest*) AND (success OR performance OR phenology OR parameters)) OR recruitment OR "pairing success" OR “population dynamics” OR "brood size" OR "clutch size" OR "clutch initiation" OR ((fledg* OR "post- fledg*" OR hatch*) AND (rate OR success OR survival)) OR "lay* date" OR offspring		driv* OR climat* OR land* OR habitat OR weather OR (environmental AND (factor$ OR conditions OR variab* OR influences OR change OR correlates)) OR variation OR variability		genom* OR seedling OR embryo OR poultry OR captiv*

Search Strings

Web of Science Core Collection: Science Citation Index Expanded (SCI-EXPANDED), Conference Proceedings Citation Index – Science (CPCI-S), Emerging Sources Citation Index (ESCI):

TS=(*bird$ OR "avian" OR "chick" OR passerine$) AND ((TI=((demograph* OR "vital rate" OR "vital rates" OR survival OR productivity OR reproduct* OR ((breeding OR nest*) AND (success OR performance OR phenology OR parameters)) OR recruitment OR "pairing success" OR “population dynamics” OR "brood size" OR "clutch size" OR "clutch initiation" OR ((fledg* OR "post-fledg*" OR hatch*) AND (rate OR success OR survival)) OR "lay* date" OR offspring) AND (driv* OR climat* OR land* OR habitat OR weather OR (environmental AND (factor$ OR conditions OR variab* OR influences OR change OR correlates)) OR variation OR variability)) NOT TI=(genom* OR seedling OR embryo OR poultry OR captiv*)) OR (AK=((demograph* OR "vital rate" OR "vital rates" OR survival OR productivity OR reproduct* OR ((breeding OR nest*) AND (success OR performance OR phenology OR parameters)) OR recruitment OR "pairing success" OR “population dynamics” OR "brood size" OR "clutch size" OR "clutch initiation" OR ((fledg* OR "post-fledg*" OR hatch*) AND (rate OR success OR survival)) OR "lay* date" OR offspring) AND (driv* OR climat* OR land* OR habitat OR weather OR (environmental AND (factor$ OR conditions OR variab* OR influences OR change OR correlates)) OR variation OR variability)) NOT AK=(genom* OR seedling OR embryo OR poultry OR captiv*)))

Scopus:

TITLE-ABS-KEY (*bird OR avian OR chick OR passerine) AND ((TITLE ((demograph* OR "vital rate" OR survival OR productivity OR reproduct* OR ((breeding OR nest*) AND (success OR performance OR phenology OR parameters)) OR recruitment OR "pairing success" OR "population dynamics" OR "brood size" OR "clutch size" OR "clutch initiation" OR ((fledg* OR "post-fledg*" OR hatch*) AND (rate OR success OR survival)) OR "lay* date" OR offspring) AND (driv* OR climat* OR land* OR habitat OR weather OR (environmental AND (factor OR conditions OR variab* OR influences OR change OR correlates)) OR variation OR variability)) AND NOT TITLE (genom* OR seedling OR embryo OR poultry OR captiv*)) OR (AUTHKEY ((demograph* OR "vital rate" OR survival OR productivity OR reproduct* OR ((breeding OR nest*) AND (success OR performance OR phenology OR parameters)) OR recruitment OR "pairing success" OR "population dynamics" OR "brood size" OR "clutch size" OR "clutch initiation" OR ((fledg* OR "post-fledg*" OR hatch*) AND (rate OR success OR survival)) OR "lay* date" OR offspring) AND (driv* OR climat* OR land* OR habitat OR weather OR (environmental AND (factor OR conditions OR variab* OR influences OR change OR correlates)) OR variation OR variability)) AND NOT AUTHKEY (genom* OR seedling OR embryo OR poultry OR captiv*)))

Table S2.2: Each Order of birds studied by the reviewed papers which measure productivity, in descending order from the highest to the lowest number and percentage of studies (*n* = 721).

Order	Number of Studies	% of Studies
Passeriformes	336	46.6
Charadriiformes	100	13.9
Galliformes	56	7.8
Accipitriformes	41	5.7
Anseriformes	24	3.3
Procellariiformes	24	3.3
Sphenisciformes	21	2.9
Strigiformes	18	2.5
Pelecaniformes	18	2.5
Piciformes	18	2.5
Falconiformes	16	2.2
Ciconiiformes	15	2.1
Gruiformes	6	0.8
Suliformes	6	0.8
Caprimulgiformes	4	0.6
Gaviiformes	4	0.6
Podicipediformes	4	0.6
Bucerotiformes	3	0.4
Columbiformes	2	0.3
Coraciiformes	2	0.3
Otidiformes	2	0.3
Eurypygiformes	1	0.1
Phoenicopteriformes	1	0.1
Psittaciformes	1	0.1
Struthioniformes	1	0.1
Tinamiformes	1	0.1

Table S2.3: Each Order of birds studied by the reviewed papers which measure survival rates, in descending order from the highest to the lowest number and percentage of studies (*n* = 243).

Order	Number of Studies	% of Studies
Passeriformes	111	45.7
Charadriiformes	32	13.2
Galliformes	27	11.1
Anseriformes	20	8.2
Procellariiformes	18	7.4
Sphenisciformes	6	2.5
Falconiformes	5	2.1
Accipitriformes	4	1.6
Strigiformes	4	1.6
Suliformes	4	1.6
Ciconiiformes	3	1.2
Piciformes	4	1.6
Pelecaniformes	2	0.8
Bucerotiformes	1	0.4
Caprimulgiformes	1	0.4
Columbiformes	1	0.4
Cuculiformes	1	0.4
Gruiformes	1	0.4
Phaethontiformes	1	0.4

Table S2.4: The ten most-studied species amongst reviewed papers which measure productivity and survival rates.

Productivity	Number of Studies
White Stork, *Ciconia ciconia*	12
Blue Tit, *Cyanistes caeruleus*	12
Black-legged Kittiwake, *Rissa tridactyla*	12
Pied Flycatcher, *Ficedula hypoleuca*	11
Greater Sage-Grouse, *Centrocercus urophasianus*	10
Great Tit, *Parus major*	8
Barn Swallow, *Hirundo rustica*	7
European Goshawk, *Accipiter gentilis*	6
Florida Scrub-Jay, *Aphelocoma coerulescens*	6
Northern Bobwhite, *Colinus virginianus*	6
Survival	
Northern Bobwhite, *Colinus virginianus*	7
Greater Sage-Grouse, *Centrocercus urophasianus*	6
Ovenbird, *Seiurus aurocapilla*	6
Mallard, *Anas platyrhynchos*	4
Pied Flycatcher, *Ficedula hypoleuca*	4
Canada Goose, *Branta canadensis*	3
Cory's Shearwater, *Calonectris diomedea*	3
Stitchbird, *Notiomystis cincta*	3
Northern Wheatear, *Oenanthe oenanthe*	3
Cassin's Auklet, *Ptychoramphus aleuticus*	3

Table S2.5: Output from a generalised linear model with binomial error structure testing the effect of demographic rate type on the probability that a study measured spatial (0) or temporal (1) variation (*n* = 1453).

Prob Temporal	Estimate	Standard Error	Z value	p value
(Intercept) Productivity	0.12	0.06	2.07	0.04
Survival	0.38	0.13	2.98	**<0.01**

Table S2.6: Output from a generalised linear model with binomial error structure testing the effect of productivity metric type on the probability that a study measured spatial (0) or temporal (1) variation (*n* = 1240).

Prob Temporal	Estimate	Standard Error	Z value	p value
(Intercept) Individual	0.25	0.14	1.77	0.08
Nest	-0.18	0.16	-1.14	0.26
Population	0.52	0.29	1.81	0.07
RELEVELED				
(Intercept) Population	0.78	0.25	2.08	<0.01
Individual	-0.52	0.29	-1.81	0.07
Nest	-0.70	0.26	-2.70	**<0.01**

Table S2.7: Output from a generalised linear model with binomial error structure testing the effect of survival metric type on the probability that a study measured spatial (0) or temporal (1) variation (*n* = 463).

Prob Temporal	Estimate	Standard Error	Z value	p value
(Intercept) Adult	0.55	0.13	4.34	<0.001
Juvenile	0.23	0.24	0.93	0.35
Post-fledging	-0.68	0.33	-2.11	**0.04**
Recruitment	0.61	0.38	1.60	0.11
RELEVELED				
(Intercept) Post-fledging	-0.13	0.30	-0.45	0.66
Adult	0.68	0.33	2.11	**0.04**
Juvenile	0.91	0.36	2.51	**0.01**
Recruitment	1.30	0.47	2.76	**<0.01**
RELEVELED				
(Intercept) Recruitment	1.16	0.36	3.21	<0.01
Post-fledging	-1.30	0.47	-2.76	**<0.01**
Adult	-0.61	0.38	-1.60	0.11
Juvenile	-0.39	0.42	-0.92	0.36

Table S2.8: Output from a cumulative link mixed model testing the effect of demographic rate (Productivity or Survival), study year and their interaction on the probability a study measured demographic variation at increasing spatial scales (*n* = 881). Threshold coefficients represent the log-odds required to go from one spatial scale to the next.

Coefficients Relative to Productivity:	Estimate	Standard Error	Z value	p value
Survival	0.48	0.16	2.98	**<0.01**
Year	0.05	0.07	0.64	0.52
Survival:Year	0.03	0.17	0.18	0.86
Threshold Coefficients: (Productivity)				
<1km^2 | 1-10km^2	0.10	0.08	1.28	
1-10km^2 | 11-100km^2	1.16	0.10	11.41	
11-100km^2 | 101-1000km^2	1.97	0.13	15.03	
101-1000km^2 | 1001-10,000km^2	2.59	0.16	16.27	
1001-10,000km^2 | >10,000km^2	3.52	0.22	16.14	
Threshold Coefficients: (Survival)				
<1km^2 | 1-10km^2	-0.38	0.14	-2.61	
1-10km^2 | 11-100km^2	0.69	0.15	4.63	
11-100km^2 | 101-1000km^2	1.50	0.16	9.07	
101-1000km^2 | 1001-10,000km^2	2.12	0.19	11.42	
1001-10,000km^2 | >10,000km^2	3.04	0.24	12.89	
Random Effect	Variance	Standard Deviation		
Study ID (*n* = 560)	0.04	0.20		

Table S2.9: Output from a cumulative link mixed model testing the effect of productivity metric type, study year and their interaction on the probability a study measured increasing spatial scales (*n* = 780). Threshold coefficients represent the log-odds required to go from one spatial scale to the next.

Coefficients Relative to Individual	Estimate	Standard Error	Z value	p value
Nest	-0.32	0.20	-1.62	0.11
Population	0.74	0.38	1.96	0.05
Coefficients Relative to Population				
Individual	-0.74	0.38	-1.96	0.05
Nest	-1.06	0.34	-3.12	**<0.01**
Threshold Coefficients: (Individual)				
<1km^2 | 1-10km^2	0.16	0.19	-0.85	
1-10km^2 | 11-100km^2	0.91	0.20	4.54	
11-100km^2 | 101-1000km^2	1.78	0.22	8.03	
101-1000km^2 | 1001-10,000km^2	2.39	0.24	9.87	
1001-10,000km^2 | >10,000km^2	3.50	0.31	11.49	
Random Effect	Variance	Standard Deviation		
Study ID (*n* = 485)	0.16	0.40		

Table S2.10: Output from a cumulative link mixed model testing the effect of survival metric type, study year and their interaction on the probability a study measured increasing spatial scales (*n* = 225). Threshold coefficients represent the log-odds required to go from one spatial scale to the next.

Coefficients Relative to Adult	Estimate	Standard Error	Z value	p value
Juvenile	0.38	0.37	1.02	0.31
Post-fledging	-0.77	0.56	-1.37	0.17
Recruitment	-0.54	0.76	-0.71	0.48
Coefficients Relative to Post-fledging				
Adult	0.77	0.56	1.37	0.17
Juvenile	1.14	0.58	1.99	**0.05**
Recruitment	0.23	0.90	0.26	0.80
Coefficients Relative to Recruitment				
Adult	0.23	0.90	-0.26	0.80
Juvenile	0.54	0.76	0.71	0.48
Post-fledging	0.91	0.82	1.11	0.27
Threshold Coefficients: (Adult)				
<1km^2 | 1-10km^2	-0.87	0.29	-3.00	
1-10km^2 | 11-100km^2	1.08	0.32	3.43	
11-100km^2 | 101-1000km^2	2.24	0.39	5.71	
101-1000km^2 | 1001-10,000km^2	3.08	0.48	6.41	
1001-10,000km^2 | >10,000km^2	4.12	0.61	6.73	
Random Effect	Variance	Standard Deviation		
Study ID (*n* = 118)	3.40	1.84		

Table S2.11: Output from a cumulative link model testing the effect of demographic rate (Productivity vs Survival), study year and their interaction on the probability a study measured increasing temporal scales (*n* = 1066). Threshold coefficients represent the log-odds required to go from one temporal scale to the next.

Coefficients Relative to Productivity:	Estimate	Standard Error	Z value	p value
Survival	0.44	0.15	2.89	**<0.01**
Year	-0.06	0.07	-0.80	0.42
Survival:Year	-0.06	0.17	-0.34	0.73
Threshold Coefficients: (Productivity)				
Sub-annual | Annual	-0.72	0.07	-9.56	
Annual | Decadal	3.49	0.18	19.72	
Threshold Coefficients: (Survival)				
Sub-annual | Annual	-1.16	0.14	-8.45	
Annual | Decadal	3.04	0.20	15.28	

Table S2.12: Output from a cumulative link model testing the effect of productivity metric type on the probability a study measured increasing temporal scales (*n* = 872). Threshold coefficients represent the log-odds required to go from one temporal scale to the next.

Coefficients Relative to Individual	Estimate	Standard Error	Z value	p value
Nest	-1.36	0.25	-5.44	**<0.0001**
Population	0.54	0.41	1.32	0.19
Coefficients Relative to Population				
Individual	-0.54	0.41	-1.32	0.19
Nest	-1.89	0.36	-5.23	**<0.0001**
Threshold Coefficients: (Nest)				
Sub-annual | Annual	-0.57	0.08	-7.28	
Annual | Decadal	3.95	0.22	17.75	
Threshold Coefficients: (Individual)				
Sub-annual | Annual	-1.93	0.24	-8.03	
Annual | Decadal	2.60	0.27	9.69	
Threshold Coefficients: (Population)				
Sub-annual | Annual	-2.47	0.36	-6.89	
Annual | Decadal	2.06	0.35	5.97	

Table S2.13: Output from a cumulative link model testing the effect of survival metric type on the probability a study measured increasing temporal scales (*n* = 363). Threshold coefficients represent the log-odds required to go from one temporal scale to the next.

Coefficients Relative to Adult	Estimate	Standard Error	Z value	p value
Juvenile	0.05	0.30	-0.17	0.87
Post-fledging	-1.24	0.43	-2.91	**<0.01**
Recruitment	-0.23	0.40	-0.57	0.57
Coefficients Relative to Post-fledging				
Adult	1.24	0.43	2.91	**<0.01**
Juvenile	1.29	0.47	2.76	**<0.01**
Recruitment	1.01	0.53	1.90	0.06
Coefficients Relative to Recruitment				
Post-fledging	-1.01	0.53	1.90	0.06
Adult	0.23	0.40	-0.57	0.57
Juvenile	0.28	0.44	0.63	0.53
Threshold Coefficients: (Adult)				
Sub-annual | Annual	-1.51	0.17	-8.66	
Annual | Decadal	2.95	0.27	10.97	
Threshold Coefficients: (Post-Fledging)				
Sub-annual | Annual	-0.27	0.39	-0.71	
Annual | Decadal	4.18	0.47	8.92	
Threshold Coefficients: (Recruitment)				
Sub-annual | Annual	-1.28	0.36	-3.53	
Annual | Decadal	3.18	0.43	7.42	

List of Studies Included in the Review

ABADI, F., BARBRAUD, C. & GIMENEZ, O. 2017. Integrated population modeling reveals the impact of climate on the survival of juvenile emperor penguins. *Global Change Biology,* 23**,** 1353-1359.

ABDULLAH, M., KHAN, R. A., RAFAY, M., HUSSAIN, T., RUBY, T., REHMAN, F., KHALIL, S. & AKHTAR, S. 2017. Habitat Ecology and Breeding Performance of Cattle Egret (Bubulcus ibis) in Faisalabad, Pakistan. *Pakistan Journal of Zoology,* 49**,** 1863-1870.

ABRAHAM, C. L. & SYDEMAN, W. J. 2004. Ocean climate, euphausiids and auklet nesting: inter-annual trends and variation in phenology, diet and growth of a planktivorous seabird, Ptychoramphus aleuticus. *Marine Ecology Progress Series,* 274**,** 235-250.

ACKER, P., DAUNT, F., WANLESS, S., BURTHE, S. J., NEWELL, M. A., HARRIS, M. P., GRIST, H., STURGEON, J., SWANN, R. L., GUNN, C., PAYO-PAYO, A. & REID, J. M. 2021. Strong survival selection on seasonal migration versus residence induced by extreme climatic events. *Journal of Animal Ecology,* 90**,** 796-808.

ACQUARONE, C., CUCCO, M. & MALACARNE, G. 2003. Reproduction of the Crag Martin (Ptyonoprogne rupestris) in relation to weather and colony size. *Ornis Fennica,* 80**,** 79-85.

ADAMOU, A. E., KOUIDRI, M., BANBURA, A., OUAKID, M. L., CHABI, Y. & BANBURA, J. 2015. Variation in the timing of reproduction and clutch size of Afrocanarian blue tits Cyanistes teneriffae ultramarinus in the Saharan Atlas of Algeria. *Polish Journal of Ecology,* 63**,** 599-607.

ADAMOU, A. E., TABIB, R., KOUIDRI, M., OUAKID, M. L., GLADALSKI, M., BANBURA, A. & BANBURA, J. 2017. Inter-annual variation in clutch size and laying date of Rufous Bush Chats Cercotrichas galactotes inhabiting an Algerian oasis. *Journal of Arid Environments,* 141**,** 40-44.

ADAMS, H. L., BURGER, L. W. & RIFFELL, S. 2013. Disturbance and Landscape Effects on Avian Nests in Agricultural Conservation Buffers. *Journal of Wildlife Management,* 77**,** 1213-1220.

ADRIAENSEN, F. & DHONDT, A. A. 1990. Population dynamics and partial migration of the European robin (Erithacus rubecula) in different habitats. *Journal of Animal Ecology,* 59**,** 1077-1090.

AEBISCHER, N. J. & EWALD, J. A. 2004. Managing the UK Grey Partridge Perdix perdix recovery: population change, reproduction, habitat and shooting. *Ibis,* 146**,** 181-191.

AGNEW, P., HOUSTON, D., LALAS, C. & WRIGHT, J. 2014. Variation in reproductive performance of Little Penguins (Eudyptula minor) attributable to double brooding. *Journal of Ornithology,* 155**,** 101-109.

AGNEW, P., LALAS, C., WRIGHT, J. & DAWSON, S. 2015. Variation in breeding success and survival of little penguins Eudyptula minor in response to environmental variation. *Marine Ecology Progress Series,* 541**,** 219-229.

AHLEN, P. A., WILLEBRAND, T., SJOBERG, K. & HORNELL-WILLEBRAND, M. 2013. Survival of female capercaillie Tetrao urogallus in northern Sweden. *Wildlife Biology,* 19**,** 368-373.

AHOLA, M. P., LAAKSONEN, T., EEVA, T. & LEHIKOINEN, E. 2009. Great tits lay increasingly smaller clutches than selected for: a study of climate- and density-related changes in reproductive traits. *Journal of Animal Ecology,* 78**,** 1298-1306.

AHOLA, M. P., LAAKSONEN, T., EEVA, T. & LEHIKOINEN, E. 2012. Selection on laying date is connected to breeding density in the pied flycatcher. *Oecologia,* 168**,** 703-710.

AKRESH, M. E., KING, D. I. & BROOKS, R. T. 2015. Demographic response of a shrubland bird to habitat creation, succession, and disturbance in a dynamic landscape. *Forest Ecology and Management,* 336**,** 72-80.

AKRESH, M. E., KING, D. I. & MARRA, P. P. 2019. Examining carry-over effects of winter habitat on breeding phenology and reproductive success in prairie warblers Setophaga discolor. *Journal of Avian Biology,* 50**,** 13.

ALAYA-LTIFI, L., CHOKRI, M. A. & SELMI, S. 2012. Breeding performance of passerines in a polluted oasis habitat in southern Tunisia. *Ecotoxicology and Environmental Safety,* 79**,** 170-175.

ALBRECHT, T. 2004. Edge effect in wetland-arable land boundary determines nesting success of scarlet rosefinches (Carpodacus erythrinus) in the Czech Republic. *Auk,* 121**,** 361-371.

ALDINGER, K. R. & WOOD, P. B. 2014. Reproductive success and habitat characteristics of Golden-winged Warblers in high-elevation pasturelands. *Wilson Journal of Ornithology,* 126**,** 279-287.

ALDRIDGE, C. L. & BOYCE, M. S. 2008. ACCOUNTING FOR FITNESS: COMBINING SURVIVAL AND SELECTION WHEN ASSESSING WILDLIFE-HABITAT RELATIONSHIPS. *Israel Journal of Ecology & Evolution,* 54**,** 389-419.

ALLEN, J. H., NUECHTERLEIN, G. L. & BUITRON, D. 2008. Weathering the Storm: How Wind and Waves Impact Western Grebe Nest Placement and Success. *Waterbirds,* 31**,** 402-410.

ALTAMIRANO, T. A., IBARRA, J. T., DE LA MAZA, M., NAVARRETE, S. A. & BONACIC, C. 2015. Reproductive life-history variation in a secondary cavity-nester across an elevational gradient in Andean temperate ecosystems. *Auk,* 132**,** 826-835.

ALTMAN, B., BOULAY, M., DOWLAN, S., CRANNELL, D., RUSSELL, K., BEAL, K. & DILLON, J. 2003. Willow Flycatcher nesting ecology and habitat relationships in the Willamette Basin, Oregon. Conference on Ecology and Conservation of the Willow Flycatcher, Oct 24-25 2001 Tempe, Az. CAMARILLO: Cooper Ornitholigical Society, 73-80.

ALTWEGG, R., CRAWFORD, R. J. M., UNDERHILL, L. G., MARTIN, A. P. & WHITTINGTON, P. A. 2007. Geographic variation in reproduction and survival of kelp gulls Larus dominicanus vetula in southern Africa. *Journal of Avian Biology,* 38**,** 580-586.

ALTWEGG, R., DOUTRELANT, C., ANDERSON, M. D., SPOTTISWOODE, C. N. & COVAS, R. 2014. Climate, social factors and research disturbance influence population dynamics in a declining sociable weaver metapopulation. *Oecologia,* 174**,** 413-425.

ALTWEGG, R., ROULIN, A., KESTENHOLZ, M. & JENNI, L. 2006. Demographic effects of extreme winter weather in the barn owl. *Oecologia,* 149**,** 44-51.

ALVES, J. A., GUNNARSSON, T. G., SUTHERLAND, W. J., POTTS, P. M. & GILL, J. A. 2019. Linking warming effects on phenology, demography, and range expansion in a migratory bird population. *Ecology and Evolution,* 9**,** 2365-2375.

AMAR, A., ARROYO, B., MEEK, E., REDPATH, S. & RILEY, H. 2008. Influence of habitat on breeding performance of Hen Harriers Circus cyaneus in Orkney. *Ibis,* 150**,** 400-404.

AMBROSINI, R. & SAINO, N. 2010. Environmental effects at two nested spatial scales on habitat choice and breeding performance of barn swallow. *Evolutionary Ecology,* 24**,** 491-508.

AMININASAB, S. M., XU, C. C. Y., KINGMA, S. A. & KOMDEUR, J. 2017. Effect of tree logging on reproductive performance in Blue Tits (Cyanistes caeruleus). *Journal of Ornithology,* 158**,** 339-344.

ANCTIL, A., FRANKE, A. & BETY, J. 2014. Heavy rainfall increases nestling mortality of an arctic top predator: experimental evidence and long-term trend in peregrine falcons. *Oecologia,* 174**,** 1033-1043.

ANDERSON, H. B., MADSEN, J., FUGLEI, E., JENSEN, G. H., WOODIN, S. J. & VAN DER WAL, R. 2015. The dilemma of where to nest: influence of spring snow cover, food proximity and predator abundance on reproductive success of an arctic-breeding migratory herbivore is dependent on nesting habitat choice. *Polar Biology,* 38**,** 153-162.

ANTEAU, M. J., WILTERMUTH, M. T., SHERFY, M. H., SHAFFER, T. L. & PEARSE, A. T. 2014. The role of landscape features and density dependence in growth and fledging rates of Piping Plovers in North Dakota, USA. *Condor,* 116**,** 195-204.

ANTHONY, C. R., HAGEN, C. A., DUGGER, K. M. & ELMORE, R. D. 2021. Greater Sage-Grouse nest bowls buffer microclimate in a post-megafire landscape although effects on nest survival are marginal. *Ornithological Applications,* 123**,** 13.

ANTHONY, R. G. & WILLIS, M. J. 2009. Survival rates of female greater sage-grouse in autumn and winter in Southeastern Oregon. *Journal of Wildlife Management,* 73**,** 538-545.

ARBEITER, S., SCHULZE, M., TAMM, P. & HAHN, S. 2016. Strong cascading effect of weather conditions on prey availability and annual breeding performance in European bee-eaters Merops apiaster. *Journal of Ornithology,* 157**,** 155-163.

ARESU, M., PENNINO, M. G., DE ROSA, D., ROTTA, A. & BERLINGUER, F. 2022. Modelling the effect of environmental variables on the reproductive success of Griffon Vulture (Gyps fulvus) in Sardinia, Italy. *Ibis,* 164**,** 255-266.

ARLETTAZ, R., SCHAAD, M., REICHLIN, T. S. & SCHAUB, M. 2010. Impact of weather and climate variation on Hoopoe reproductive ecology and population growth. *Journal of Ornithology,* 151**,** 889-899.

ARLT, D. & PART, T. 2017. Marked reduction in demographic rates and reduced fitness advantage for early breeding is not linked to reduced thermal matching of breeding time. *Ecology and Evolution,* 7**,** 10782-10796.

ARMSTRONG, D. P., GORMAN, N., PIKE, R., KREIGENHOFER, B., MCARTHUR, N., GOVELLA, S., BARRETT, P. & RICHARD, Y. 2014. Strategic Rat Control for Restoring Populations of Native Species in Forest Fragments. *Conservation Biology,* 28**,** 713-723.

ARNOLD, T. W. 1992. VARIATION IN LAYING DATE, CLUTCH SIZE, EGG SIZE, AND EGG COMPOSITION OF YELLOW-HEADED BLACKBIRDS (XANTHOCEPHALUS-XANTHOCEPHALUS) - A SUPPLEMENTAL FEEDING EXPERIMENT. *Canadian Journal of Zoology,* 70**,** 1904-1911.

ARNOLD, T. W., ROCHE, E. A., DEVRIES, J. H. & HOWERTER, D. W. 2012. Costs of Reproduction in Breeding Female Mallards: Predation Risk during Incubation Drives Annual Mortality. *Avian Conservation and Ecology,* 7**,** 18.

ARRIERO, E., SANZ, J. J. & ROMERO-PUJANTE, M. 2006. Habitat structure in Mediterranean deciduous oak forests in relation to reproductive success in the Blue Tit Parus caeruleus. *Bird Study,* 53**,** 12-19.

ARRONDO, E., SANZ-AGUILAR, A., PEREZ-GARCIA, J. M., CORTES-AVIZANDA, A., SANCHEZ-ZAPATA, J. A. & DONAZAR, J. A. 2020. Landscape anthropization shapes the survival of a top avian scavenger. *Biodiversity and Conservation,* 29**,** 1411-1425.

ARROYO, B., MOUGEOT, F. & BRETAGNOLLE, V. 2017. Individual variation in behavioural responsiveness to humans leads to differences in breeding success and long-term population phenotypic changes. *Ecology Letters,* 20**,** 317-325.

ARTEMYEV, A. V. 2013. The influence of climate change on the ecology of the Pied Flycatcher (Ficedula hypoleuca) in Southern Karelia. *Russian Journal of Ecology,* 44**,** 239-246.

ARZEL, C., DESSBORN, L., POYSA, H., ELMBERG, J., NUMMI, P. & SJOBERG, K. 2014. Early springs and breeding performance in two sympatric duck species with different migration strategies. *Ibis,* 156**,** 288-298.

ATUO, F. A. & O'CONNELL, T. J. 2018. Superpredator proximity and landscape characteristics alters nest site selection and breeding success of a subordinate predator. *Oecologia,* 186**,** 817-829.

AUBRY, L. M., ROCKWELL, R. F., COOCH, E. G., BROOK, R. W., MULDER, C. P. H. & KOONS, D. N. 2013. Climate change, phenology, and habitat degradation: drivers of gosling body condition and juvenile survival in lesser snow geese. *Global Change Biology,* 19**,** 149-160.

AUSPREY, I. J. & RODEWALD, A. D. 2011. POSTFLEDGING SURVIVORSHIP AND HABITAT SELECTION ACROSS A RURAL-TO-URBAN LANDSCAPE GRADIENT. *Auk,* 128**,** 293-302.

AVILES, J. M., SANCHEZ, J. M. & PAREJO, D. 2001. Breeding rates of Eurasian Kestrels (Falco Tinnunculus) in relation to surrounding habitat in southwest Spain. *Journal of Raptor Research,* 35**,** 31-34.

BACHIR, A. S., CHENCHOUNI, H., DJEDDOU, N., BARBRAUD, C., CÉRÉGHINO, R. & SANTOUL, F. 2013. Using self-organizing maps to investigate environmental factors regulating colony size and breeding success of the White Stork (Ciconia ciconia). *Journal of Ornithology,* 154**,** 481-489.

BADYAEV, A. V. 1999. Nesting habitat and nesting success of eastern wild turkeys in the Arkansas Ozark highlands. *NCASI Technical Bulletin***,** 17.

BADYAEV, A. V., MARTIN, T. E. & ETGES, W. J. 1996. Habitat sampling and habitat selection by female wild turkeys: Ecological correlates and reproductive consequences. *Auk,* 113**,** 636-646.

BAGHBADARANI, F. A., BARATI, A., ABBASI, S., ETEZADIFAR, F. & AMIRI, A. 2014. Variability of daily nest survival and breeding success in relation to characteristics of Eurasian magpie (Pica pica) nests. *Journal of Natural History,* 48**,** 729-738.

BAILEY, B. A. & KING, D. I. 2019. Habitat selection and habitat quality for wintering wood thrushes in a coffee growing region in Honduras. *Global Ecology and Conservation,* 20**,** 10.

BAILLY, J., SCHEIFLER, R., BERTHE, S., CLEMENT-DEMANGE, V. A., LEBLOND, M., PASTEUR, B. & FAIVRE, B. 2016. From eggs to fledging: negative impact of urban habitat on reproduction in two tit species. *Journal of Ornithology,* 157**,** 377-392.

BAINES, D., AEBISCHER, N. J. & MACLEOD, A. 2016. Increased mammalian predators and climate ch1ange predict declines in breeding success and density of Capercaillie tetrao urogallus, an old stand specialist, in fragmented Scottish forests. *Biodiversity and Conservation,* 25**,** 2171-2186.

BAINES, D., WARREN, P. & RICHARDSON, M. 2007. Variations in the vital rates of black grouse Tetrao tetrix in the United Kingdom. *Wildlife Biology,* 13**,** 109-116.

BAKERMANS, M. H., RODEWALD, A. D. & VITZ, A. C. 2012. Influence of forest structure on density and nest success of mature forest birds in managed landscapes. *Journal of Wildlife Management,* 76**,** 1225-1234.

BALAZ, M., WEIDINGER, K., KOCIAN, L. & NEMETHOVA, D. 2007. Effect of habitat on blackcap, Sylvia atricapilla nest predation in the absence of corvid predators. *Folia Zoologica,* 56**,** 177-185.

BALBONTIN, J., MOLLER, A. P., HERMOSELL, I. G., MARZAL, A., REVIRIEGO, M. & DE LOPE, F. 2012. Geographical variation in reproductive ageing patterns and life-history strategy of a short-lived passerine bird. *Journal of Evolutionary Biology,* 25**,** 2298-2309.

BALENT, K. L. & NORMENT, C. J. 2003. Demographic characteristics of a Grasshopper Sparrow population in a highly fragmented landscape of western New York State. *Journal of Field Ornithology,* 74**,** 341-348.

BALESTRIERI, R., BASILE, M., ROMANO, S., FERRARO, S., IZZO, M., POSILLICO, M. & MATTEUCCI, G. 2018. Breeding performance of Blue tits Cyanistes caeruleus can be predicted from time since last logging in Mediterranean mixed oak forest. *Avocetta,* 42**,** 67-73.

BALL, I. J., ENG, R. L. & BALL, S. K. 1995. Population density and productivity of ducks on large grassland tracts in northcentral Montana. *Wildlife Society Bulletin,* 23**,** 767-773.

BALLANTYNE, K. & NOL, E. 2011. Nesting Habitat Selection and Hatching Success of Whimbrels Near Churchill, Manitoba, Canada. *Waterbirds,* 34**,** 151-159.

BARATI, A., ALIAKBARI, A. & GHASEMPOURI, S. M. 2011. Variations in breeding success and daily nest survival of Whiskered Tern (Chlidonias hybrida) at two Iranian colonies. *Russian Journal of Ecology,* 42**,** 315-320.

BARBOSA, A., BENZAL, J., DE LEÓN, A. & MORENO, J. 2012. Population decline of chinstrap penguins (Pygoscelis antarctica) on Deception Island, South Shetlands, Antarctica. *Polar Biology,* 35**,** 1453-1457.

BARBRAUD, C., MARTEAU, C., RIDOUX, V., DELORD, K. & WEIMERSKIRCH, H. 2008. Demographic response of a population of white-chinned petrels Procellaria aequinoctialis to climate and longline fishery bycatch. *Journal of Applied Ecology,* 45**,** 1460-1467.

BARBRAUD, C. & WEIMERSKIRCH, H. 2003. Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society B-Biological Sciences,* 270**,** 2111-2116.

BARNAGAUD, J. Y., CROCHET, P. A., MAGNANI, Y., LAURENT, A. B., MENONI, E., NOVOA, C. & GIMENEZ, O. 2011. Short-term response to the North Atlantic Oscillation but no long-term effects of climate change on the reproductive success of an alpine bird. *Journal of Ornithology,* 152**,** 631-641.

BARRAQUAND, F. & NIELSEN, O. K. 2021. Survival rates of adult and juvenile gyrfalcons in Iceland: estimates and drivers. *Peerj,* 9**,** 11.

BARRAS, A. G., BLACHE, S., SCHAUB, M. & ARLETTAZ, R. 2021. Variation in Demography and Life-History Strategies Across the Range of a Declining Mountain Bird Species. *Frontiers in Ecology and Evolution,* 9**,** 11.

BARRETT, R. T., ERIKSTAD, K. E. & REIERTSEN, T. K. 2017. Ocean climate and egg investment in the black-legged kittiwake Rissa tridactyla. *Marine Ecology Progress Series,* 579**,** 129-137.

BARRIENTOS, R., BARBOSA, A., VALERA, F. & MORENO, E. 2007. Temperature but not rainfall influences timing of breeding in a desert bird, the trumpeter finch (Bucanetes githagineus). *Journal of Ornithology,* 148**,** 411-416.

BARRIENTOS, R., BARBOSA, A., VALERA, F. & MORENO, E. 2009. Breeding parameters of the trumpeter finch at the periphery of its range: A case study with mainland expanding and island populations. *Journal of Arid Environments,* 73**,** 1177-1180.

BARROS, A., ROMERO, R., MUNILLA, I., PEREZ, C. & VELANDO, A. 2016. Behavioural plasticity in nest-site selection of a colonial seabird in response to an invasive carnivore. *Biological Invasions,* 18**,** 3149-3161.

BART, J. & EARNST, S. L. 2005. Breeding ecology of Spectacled Eiders Somateria fischeri in Northern Alaska. *Wildfowl,* 55**,** 83-98.

BASTIANELLI, G., TAVECCHIA, G., MELENDEZ, L., SEOANE, J., OBESO, J. R. & LAIOLO, P. 2017. Surviving at high elevations: an inter- and intra-specific analysis in a mountain bird community. *Oecologia,* 184**,** 293-303.

BAUDAINS, T. P. & LLOYD, P. 2007. Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. *Animal Conservation,* 10**,** 400-407.

BAYNE, E. M. & HOBSON, K. A. 2002. Apparent survival of male ovenbirds in fragmented and forested boreal landscapes. *Ecology,* 83**,** 1307-1316.

BEARS, H., MARTIN, K. & WHITE, G. C. 2009. Breeding in high-elevation habitat results in shift to slower life-history strategy within a single species. *Journal of Animal Ecology,* 78**,** 365-375.

BECK, M. L., HOPKINS, W. A., JACKSON, B. P. & HAWLEY, D. M. 2015. The effects of a remediated fly ash spill and weather conditions on reproductive success and offspring development in tree swallows. *Environmental Monitoring and Assessment,* 187.

BECK, N. R. & HEINSOHN, R. 2006. Group composition and reproductive success of cooperatively breeding white-winged choughs (Corcorax melanorhamphos) in urban and non-urban habitat. *Austral Ecology,* 31**,** 588-596.

BECKER, A. J., ROEDER, D. V., HUSAK, M. S. & MURPHY, M. T. 2018. Annual survival and breeding dispersal of a migratory passerine, the Scissor-tailed Flycatcher. *Journal of Field Ornithology,* 89**,** 22-36.

BECKER, B. H., PEERY, M. Z. & BEISSINGER, S. R. 2007. Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird. *Marine Ecology Progress Series,* 329**,** 267-279.

BECKER, M. E. & WEISBERG, P. J. 2015. Synergistic effects of spring temperatures and land cover on nest survival of urban birds. *Condor,* 117**,** 18-30.

BECKER, P. H. & FINCK, P. 1985. The influence of weather and food situation on the breeding success of Common Terns (Sterna hirundo). *Journal of Ornithology,* 126**,** 393-404.

BELDER, D. J., PIERSON, J. C., IKIN, K. & LINDENMAYER, D. B. 2020. Revegetation and reproduction: do restoration plantings in agricultural landscapes support breeding populations of woodland birds? *Oecologia,* 192**,** 865-878.

BELL, C. P. 1996. The relationship between geographic variation in clutch size and migration pattern in the yellow wagtail. *Bird Study,* 43**,** 333-341.

BELSKII, E. A., LUGAS'KOVA, N. V. & KARFIDOVA, A. A. 2005. Reproductive parameters of adult birds and morphophysiological characteristics of chicks in the pied flycatcher (Ficedula hypoleuca Pall.) in technogenically polluted habitats. *Russian Journal of Ecology,* 36**,** 329-335.

BELTRAO, P., GOMES, A. C. R., MARQUES, C. I., GUERRA, S., BATALHA, H. R. & CARDOSO, G. C. 2021. European breeding phenology of the invasive common waxbill, a sub-Saharan opportunistic breeder. *Acta Ethologica,* 24**,** 197-203.

BENNETTS, R. E., FASOLA, M., HAFNER, H. & KAYSER, Y. 2000. Influence of environmental and density-dependent factors on reproduction of Little Egrets. *Auk,* 117**,** 634-639.

BENSON, T. J., ANICH, N. M., BROWN, J. D. & BEDNARZ, J. C. 2010. Habitat and Landscape Effects on Brood Parasitism, Nest Survival, and Fledgling Production in Swainson's Warblers. *Journal of Wildlife Management,* 74**,** 81-93.

BENSON, T. J. & BEDNARZ, J. C. 2010. RELATIONSHIPS AMONG SURVIVAL, BODY CONDITION, AND HABITAT OF BREEDING SWAINSON'S WARBLERS. *Condor,* 112**,** 138-148.

BENSOUILAH, T. & BARRIENTOS, R. 2021. Greenfinches nesting in algerian orchards delayed their breeding and produced less fledglings in the driest of two years. *Journal of Arid Environments,* 184**,** 4.

BERG, A. 2008. Habitat selection and reproductive success of Ortolan Buntings Emberiza hortulana on farmland in central Sweden - the importance of habitat heterogeneity. *Ibis,* 150**,** 565-573.

BERG, A., LINDBERG, T. & KALLEBRINK, K. G. 1992. HATCHING SUCCESS OF LAPWINGS ON FARMLAND - DIFFERENCES BETWEEN HABITATS AND COLONIES OF DIFFERENT SIZES. *Journal of Animal Ecology,* 61**,** 469-476.

BERKELEY, L. I., MCCARTY, J. P. & WOLFENBARGER, L. L. 2007. Postfledging survival and movement in dickcissels (Spiza americana): Implications for habitat management and conservation. *Auk,* 124**,** 396-409.

BERL, J. L., EDWARDS, J. W., BOLSINGER, J. S. & KATZNER, T. E. 2014. SURVIVAL OF RED-HEADED WOODPECKERS' (MELANERPES ERYTHROCEPHALUS) NESTS IN NORTHERN NEW YORK. *Wilson Journal of Ornithology,* 126**,** 700-707.

BERLINCOURT, M. & ARNOULD, J. P. Y. 2015. Influence of environmental conditions on foraging behaviour and its consequences on reproductive performance in little penguins. *Marine Biology,* 162**,** 1485-1501.

BERROW, S. D., CROXALL, J. P. & GRANT, S. D. 2000. Status of white-chinned petrels Procellaria aequinoctialis Linnaeus 1758, at Bird Island, South Georgia. *Antarctic Science,* 12**,** 399-405.

BERTRAM, D. F., HARFENIST, A. & SMITH, B. D. 2005. Ocean climate and El Nino impacts on survival of Cassin's Auklets from upwelling and downwelling domains of British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences,* 62**,** 2841-2853.

BERZINS, L. L., DAWSON, R. D., MORRISSEY, C. A. & CLARK, R. G. 2020. The relative contribution of individual quality and changing climate as drivers of lifetime reproductive success in a short-lived avian species. *Scientific Reports,* 10**,** 12.

BERZINS, L. L., MAZER, A. K., MORRISSEY, C. A. & CLARK, R. G. 2021. Pre-fledging quality and recruitment in an aerial insectivore reflect dynamics of insects, wetlands and climate. *Oecologia,* 196**,** 89-100.

BESBEAS, P., FREEMAN, S. N., MORGAN, B. J. T. & CATCHPOLE, E. A. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics,* 58**,** 540-547.

BESTON, J. A., NICHOLS, T. C., CASTELLI, P. M. & WILLIAMS, C. K. 2014. Survival of Atlantic Flyway Resident Population Canada Geese in New Jersey. *Journal of Wildlife Management,* 78**,** 612-619.

BEZEL, V. S., BEL'SKII, E. A. & MUKHACHEVA, S. V. 1998. On the problem of variability in reproductive parameters of animal populations under toxic pollution of the environment. *Russian Journal of Ecology,* 29**,** 186-191.

BIANCHINI, K., TOZER, D. C., ALVO, R., BHAVSAR, S. P. & MALLORY, M. L. 2020. Drivers of declines in common loon (Gavia immer) productivity in Ontario, Canada. *Science of the Total Environment,* 738**,** 12.

BIELEFELD, R. R., GARRETTSON, P. R. & DOOLEY, J. L. 2020. Variation in Survival and Harvest Rates in Florida Mottled Duck. *Journal of Wildlife Management,* 84**,** 1515-1526.

BIONDA, R. & BRAMBILLA, M. 2012. Rainfall and landscape features affect productivity in an alpine population of Eagle Owl Bubo bubo. *Journal of Ornithology,* 153**,** 167-171.

BISSON, I. A. & STUTCHBURY, B. J. M. 2000. Nesting success and nest-site selection by a neotropical migrant in a fragmented landscape. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* 78**,** 858-863.

BJORKLUND, H., VALKAMA, J., SAUROLA, P. & LAAKSONEN, T. 2013. Evaluation of artificial nests as a conservation tool for three forest-dwelling raptors. *Animal Conservation,* 16**,** 546-555.

BJORKLUND, H., VALKAMA, J., TOMPPO, E. & LAAKSONEN, T. 2015. Habitat Effects on the Breeding Performance of Three Forest-Dwelling Hawks. *Plos One,* 10**,** 19.

BLAIR, R. 2004. The effects of urban sprawl on birds at multiple levels of biological organization. *Ecology and Society,* 9.

BLAKE, J. G. & LOISELLE, B. A. 2002. Manakins (Pipridae) in second-growth and old-growth forests: Patterns of habitat use, movement, and survival. *Auk,* 119**,** 132-148.

BLAKE, W. M., STONE, K. R., JANOUSEK, W. M. & MARTIN, T. E. 2021. Lewis's Woodpecker nest success and habitat selection in floodplain and burned forests in western Montana. *Journal of Field Ornithology***,** 15.

BLEWETT, C. M. & MARZLUFF, J. M. 2005. Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. *Condor,* 107**,** 678-693.

BLOMBERG, E. J., SEDINGER, J. S., GIBSON, D., COATES, P. S. & CASAZZA, M. L. 2014. Carryover effects and climatic conditions influence the postfledging survival of greater sage-grouse. *Ecology and Evolution,* 4**,** 4488-4499.

BLONDEL, J., PERRET, P., MAISTRE, M. & DIAS, P. C. 1992. DO HARLEQUIN MEDITERRANEAN ENVIRONMENTS FUNCTION AS SOURCE SINK FOR BLUE TITS (PARUS-CAERULEUS L). *Landscape Ecology,* 6**,** 213-219.

BLUMS, P., NICHOLS, J. D., HINES, J. E. & MEDNIS, A. 2002. Sources of variation in survival and breeding site fidelity in three species of European ducks. *Journal of Animal Ecology,* 71**,** 438-450.

BOANO, G., BRICHETTI, P. & FOSCHI, U. F. 2010. 'La Nina'-driven Atlantic storms affect winter survival of Mediterranean Cory's Shearwaters. *Italian Journal of Zoology,* 77**,** 460-468.

BOANO, G., PELLEGRINO, I., FERRI, M., CUCCO, M., MINELLI, F. & AKESSON, S. 2020. Climate anomalies affect annual survival rates of swifts wintering in sub-Saharan Africa. *Ecology and Evolution,* 10**,** 7916-7928.

BODEY, T. W., BARNETT, R., DU FEU, C. R., CLARK, J. R. & BEARHOP, S. 2021. Nesting outcomes under anthropogenic change - effects of changing climate and nestbox provision on the reproduction of Great Tits Parus major. *Ibis,* 163**,** 65-78.

BOERSMA, P. D. & REBSTOCK, G. A. 2009. Foraging distance affects reproductive success in Magellanic penguins. *Marine Ecology Progress Series,* 375**,** 263-275.

BOERSMA, P. D. & REBSTOCK, G. A. 2014. Climate Change Increases Reproductive Failure in Magellanic Penguins. *Plos One,* 9**,** 13.

BOGDANOVA, M. I., BUTLER, A., WANLESS, S., MOE, B., ANKER-NILSSEN, T., FREDERIKSEN, M., BOULINIER, T., CHIVERS, L. S., CHRISTENSEN-DALSGAARD, S., DESCAMPS, S., HARRIS, M. P., NEWELL, M., OLSEN, B., PHILLIPS, R. A., SHAW, D., STEEN, H., STROM, H., THORARINSSON, T. L. & DAUNT, F. 2017. Multi-colony tracking reveals spatio-temporal variation in carry-over effects between breeding success and winter movements in a pelagic seabird. *Marine Ecology Progress Series,* 578**,** 167-181.

BOILEAU, N., DELELIS, N. & HOEDE, C. 2006. Use of territory and habitat selection of breeding Kestrel Falco tinnunculus. *Alauda,* 74**,** 251-264.

BOLGER, D. T., PATTEN, M. A. & BOSTOCK, D. C. 2005. Avian reproductive failure in response to an extreme climatic event. *Oecologia,* 142**,** 398-406.

BOLLMANN, K. & REYER, H. U. 2001. Reproductive success of Water Pipits in an Alpine environment. *Condor,* 103**,** 510-520.

BOND, A. L., JONES, I. L., SYDEMAN, W. J., MAJOR, H. L., MINOBE, S., WILLIAMS, J. C. & BYRD, G. V. 2011. Reproductive success of planktivorous seabirds in the North Pacific is related to ocean climate on decadal scales. *Marine Ecology Progress Series,* 424**,** 205-U218.

BOND, A. L., WILHELM, S. I., ROBERTSON, G. J. & AVERY-GOMM, S. 2016. Differential Declines among Nesting Habitats of Breeding Herring Gulls (Larus argentatus) and Great Black-backed Gulls (Larus marinus) in Witless Bay, Newfoundland and Labrador, Canada. *Waterbirds,* 39**,** 143-151.

BOND, J. C., IVERSON, S. A., MACCALLUM, N. B., SMITH, C. M., BRUNER, H. J. & ESLER, D. 2009. Variation in Breeding Season Survival of Female Harlequin Ducks. *Journal of Wildlife Management,* 73**,** 965-972.

BONNEVIE, B. T. 2014. Variations in moult, morphology, movement and survival rates of the Sombre Greenbul Andropadus importunus within southern Africa. *Ostrich,* 85**,** 161-170.

BONTER, D. N., MACLEAN, S. A., SHAH, S. S. & MOGLIA, M. C. 2014. Storm-induced shifts in optimal nesting sites: a potential effect of climate change. *Journal of Ornithology,* 155**,** 631-638.

BORCHTCHEVSKI, V. G. 2017. Does Beginning of Spring Represent a Critical Period in Annual Cycle of Capercaillie (Tetrao urogallus, Tetronidae, Galliformes)? *Biology Bulletin,* 44**,** 751-760.

BORGMAN, C. C. & WOLF, B. O. 2016. The indirect effects of climate variability on the reproductive dynamics and productivity of an avian predator in the arid Southwest. *Oecologia,* 180**,** 279-291.

BORKHATARIA, R. R., FREDERICK, P. C., KELLER, R. A. & COLLAZO, J. A. 2012. TEMPORAL VARIATION IN LOCAL WETLAND HYDROLOGY INFLUENCES POSTDISPERSAL SURVIVAL OF JUVENILE WOOD STORKS (MYCTERIA AMERICANA). *Auk,* 129**,** 517-528.

BOSCH, J., MARTINEZ, J. E., CALVO, J. F., ZUBEROGOITIA, I. & JIMENEZ-FRANCO, M. V. 2015. Does rainfall affect the productivity of the Booted Eagle (Aquila pennata) during the breeding period in Mediterranean environments? *Journal of Ornithology,* 156**,** 1-8.

BOSCH, M. & SOL, D. 1998. Habitat selection and breeding success in yellow-legged gulls Larus cachinnans. *Ibis,* 140**,** 415-421.

BOST, C. A., COTTE, C., TERRAY, P., BARBRAUD, C., BON, C., DELORD, K., GIMENEZ, O., HANDRICH, Y., NAITO, Y., GUINET, C. & WEIMERSKIRCH, H. 2015. Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nature Communications,* 6**,** 9.

BOTH, C. 1998. Density dependence of clutch size: Habitat heterogeneity individual adjustment? *Journal of Animal Ecology,* 67**,** 659-666.

BOTH, C. & VISSER, M. E. 2005. The effect of climate change on the correlation between avian life-history traits. *Global Change Biology,* 11**,** 1606-1613.

BOUKHEDIM, A., BARA, M., CHAGRA, A., ROUAIGUIA, M., BOUDRAA, W., BOUAGUEL, L. & HOUHAMDI, M. 2018. Study of the affect of nesting environment on some aspects of the reproduction in the Eurasian blue tit, Cyanistes caeruleus, in the forest of Béni-Salah (Bouchegouf, northeast Algeria). *Bulletin de la Societe Zoologique de France,* 143**,** 187-198.

BOUKHRISS, J. & SELMI, S. 2018. Effects of temporal factors, nesting microhabitat and nest position on the survival of passerine nests in a Tunisian oasis habitat. *Ostrich,* 89**,** 321-328.

BOULTON, R. L., BAISER, B., DAVIS, M. J., VIRZI, T. & LOCKWOOD, J. L. 2011. VARIATION IN LAYING DATE AND CLUTCH SIZE: THE EVERGLADES ENVIRONMENT AND THE ENDANGERED CAPE SABLE SEASIDE SPARROW (AMMODRAMUS MARITIMUS MIRABILIS). *Auk,* 128**,** 374-381.

BOULTON, R. L. & POWLESLAND, R. G. 2008. Variation in egg size and nest survival with female age in the South Island Robin Petroica australis. *Ibis,* 150**,** 824-828.

BOURGEOIS, K., DROMZEE, S. & VIDAL, E. 2015. Are artificial burrows efficient conservation tools for seabirds? A case study of two sympatric shearwaters on neighbouring islands and guidelines for improvement. *Biological Conservation,* 191**,** 282-290.

BOURNE, A. R., CUNNINGHAM, S. J., SPOTTISWOODE, C. N. & RIDLEY, A. R. 2020. High temperatures drive offspring mortality in a cooperatively breeding bird. *Proceedings of the Royal Society B-Biological Sciences,* 287**,** 9.

BOURQUE, J. & VILLARD, M. A. 2001. Effects of selection cutting and landscape-scale harvesting on the reproductive success of two neotropical migrant bird species. *Conservation Biology,* 15**,** 184-195.

BOWERS, E. K., GRINDSTAFF, J. L., SOUKUP, S. S., DRILLING, N. E., ECKERLE, K. P., SAKALUK, S. K. & THOMPSON, C. F. 2016. Spring temperatures influence selection on breeding date and the potential for phenological mismatch in a migratory bird. *Ecology,* 97**,** 2880-2891.

BOWMAN, R., POWELL, G. V. N., HOVIS, J. A., KLINE, N. C. & WILMERS, T. 1989. Variations in reproductive success between subpopulations of the osprey (Pandion haliaetus) in south Florida. *Bulletin of Marine Science,* 44**,** 245-250.

BOYD, H. & PIERSMA, T. 2001. Changing balance between survival and recruitment explains population trends in Red Knots Calidris canutus islandica wintering in Britain, 1969-1995. *Ardea,* 89**,** 301-317.

BOYNTON, C. K., MAHONY, N. A. & WILLIAMS, T. D. 2020. Barn Swallow (Hirundo rustica) fledglings use crop habitat more frequently in relation to its availability than pasture and other habitat types. *Condor,* 122**,** 14.

BRADBURY, R. B., KYRKOS, A., MORRIS, A. J., CLARK, S. C., PERKINS, A. J. & WILSON, J. D. 2000. Habitat associations and breeding success of yellowhammers on lowland farmland. *Journal of Applied Ecology,* 37**,** 789-805.

BRAHMIA, H., ELAFRI, A., HALASSI, I. & KHEMIS, M. D. E. H. 2021. Local climate conditions impact on breeding performance of house martin (Delichon urbica) populations in Algeria. *Biologia,* 76**,** 1715-1725.

BRAIDWOOD, J., KUNZ, J. & WILSON, K. J. 2011. Effect of habitat features on the breeding success of the blue penguin (Eudyptula minor) on the West Coast of New Zealand. *New Zealand Journal of Zoology,* 38**,** 131-141.

BRAWN, J. D. 1991. ENVIRONMENTAL-EFFECTS ON VARIATION AND COVARIATION IN REPRODUCTIVE TRAITS OF WESTERN BLUEBIRDS. *Oecologia,* 86**,** 193-201.

BRAWN, J. D. 2006. Effects of restoring oak savannas on bird communities and populations. *Conservation Biology,* 20**,** 460-469.

BRAWN, J. D., ANGEHR, G., DAVROS, N., ROBINSON, W. D., STYRSKY, J. N. & TARWATER, C. E. 2011. Sources of variation in the nesting success of understory tropical birds. *Journal of Avian Biology,* 42**,** 61-68.

BRAZILL-BOAST, J., PRYKE, S. R. & GRIFFITH, S. C. 2013. Provisioning habitat with custom-designed nest-boxes increases reproductive success in an endangered finch. *Austral Ecology,* 38**,** 405-412.

BREININGER, D. R., LARSON, V. L., DUNCAN, B. W. & SMITH, R. B. 1998. Linking habitat suitability to demographic success in Florida scrub-jays. *Wildlife Society Bulletin,* 26**,** 118-128.

BREININGER, D. R., LARSON, V. L., DUNCAN, B. W., SMITH, R. B., ODDY, D. M. & GOODCHILD, M. F. 1995. Landscape patterns of Florida Scrub Jay habitat use and demographic success. *Conservation Biology,* 9**,** 1442-1453.

BREININGER, D. R. & ODDY, D. M. 2004. Do habitat potential, population density, and fires influence Scrub-Jay source-sink dynamics? *Ecological Applications,* 14**,** 1079-1089.

BREININGER, D. R., TOLAND, B., ODDY, D. M. & LEGARE, M. L. 2006. Landcover characterizations and Florida scrub-jay (Aphelocoma coerulescens) population dynamics. *Biological Conservation,* 128**,** 169-181.

BRETON, A. R., FOX, G. A. & CHARDINE, J. W. 2008. Survival of adult Herring Gulls (Larus argentatus) from a Lake Ontario colony over two decades of environmental change. *Waterbirds,* 31**,** 15-23.

BRICKHILL, D., EVANS, P. G. H. & REID, J. M. 2015. Spatio-temporal variation in European starling reproductive success at multiple small spatial scales. *Ecology and Evolution,* 5**,** 3364-3377.

BRIGGS, K. B. & MAINWARING, M. 2021. The orientation of nestboxes influences their occupation rates and the breeding success of passerine birds. *Ornis Hungarica,* 29**,** 107-121.

BRINKHOF, M. W. G. 1997. Seasonal variation in food supply and breeding success in European Coots Fulica atra. *Ardea,* 85**,** 51-65.

BRINKHOF, M. W. G. & CAVE, A. J. 1997. Food supply and seasonal variation in breeding success: An experiment in the European coot. *Proceedings of the Royal Society B-Biological Sciences,* 264**,** 291-296.

BRO, E., BRILLARD, J. P. & MULOT, F. 2014. Impact of heavy rains and wet cold weather on grey partridge Perdix perdix clutch desertion and breeding success. *Alauda,* 82**,** 51-62.

BRODMANN, P. A., REYER, H. U., BOLLMANN, K., SCHLAPFER, A. R. & RAUTER, C. 1997. The importance of food quantity and quality for reproductive performance in alpine water pipits (Anthus spinoletta). *Oecologia,* 109**,** 200-208.

BROMMER, J. E., PIETIAINEN, H. & KOKKO, H. 2002. Cyclic variation in seasonal recruitment and the evolution of the seasonal decline in Ural owl clutch size. *Proceedings of the Royal Society B-Biological Sciences,* 269**,** 647-654.

BROOK, R. W., LEAFLOOR, J. O., ABRAHAM, K. F. & DOUGLAS, D. C. 2015. Density dependence and phenological mismatch: consequences for growth and survival of sub-arctic nesting Canada Geese. *Avian Conservation and Ecology,* 10**,** 15.

BROOKE, J. M., TANNER, E. P., PETERS, D. C., TANNER, A. M., HARPER, C. A., KEYSER, P. D., CLARK, J. D. & MORGAN, J. J. 2017. Northern bobwhite breeding season ecology on a reclaimed surface mine. *Journal of Wildlife Management,* 81**,** 73-85.

BROOKE, M. D. L. 2019. Extreme rainfall-related clutch size variation in the Critically Endangered Raso Lark Alauda razae of the arid Cape Verde islands. *Bird Conservation International,* 29**,** 321-326.

BROOKER, M. & BROOKER, L. 2001. Breeding biology, reproductive success and survival of blue-breasted fairy-wrens in fragmented habitat in the Western Australian wheatbelt. *Wildlife Research,* 28**,** 205-214.

BROUWER, L., RICHARDSON, D. S., EIKENAAR, C. & KOMDEUR, J. 2006. The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. *Journal of Animal Ecology,* 75**,** 1321-1329.

BROWN, C. R., BROWN, M. B. & DANCHIN, E. 2000. Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. *Journal of Animal Ecology,* 69**,** 133-142.

BROWN, D. R., STRONG, C. M. & STOUFFER, P. C. 2002. Demographic effects of habitat selection by hermit thrushes wintering in a pine plantation landscape. *Journal of Wildlife Management,* 66**,** 407-416.

BROWN, J. L. & LI, S. H. 1996. Delayed effect of monsoon rains influences laying date of a passerine bird living in an arid environment. *Condor,* 98**,** 879-884.

BRZEZINSKI, M., CHIBOWSKI, P., GORNIA, J., GORECKI, G. & ZALEWSKI, A. 2018. Spatio-temporal variation in nesting success of colonial waterbirds under the impact of a non-native invasive predator. *Oecologia,* 188**,** 1037-1047.

BUCK, C. L., O'REILLY, K. A. & KILDAW, S. D. 2007. Interannual variability of Black-legged Kittiwake productivity is reflected in baseline plasma corticosterone. *General and Comparative Endocrinology,* 150**,** 430-436.

BUDNIK, J. M., RYAN, M. R. & THOMPSON, F. R. 2000. Demography of Bell's Vireos in Missouri grassland-shrub habitats. *Auk,* 117**,** 925-935.

BULLUCK, L., BUEHLER, D., VALLENDER, R. & ROBERTSON, R. J. 2013. DEMOGRAPHIC COMPARISON OF GOLDEN-WINGED WARBLER (VERMIVORA CHRYSOPTERA) POPULATIONS IN NORTHERN AND SOUTHERN EXTREMES OF THEIR BREEDING RANGE. *Wilson Journal of Ornithology,* 125**,** 479-490.

BURANT, J. B., HEISEY, E. W., WHEELWRIGHT, N. T., NEWMAN, A. E. M., WHELAN, S., MENNILL, D. J., DOUCET, S. M., MITCHELL, G. W., WOODWORTH, B. K. & NORRIS, D. R. 2022. Natal experience and pre-breeding environmental conditions affect lay date plasticity in Savannah Sparrows. *Ecology,* 103**,** 11.

BURGESS, M. D., NICOLL, M. A. C., JONES, C. G. & NORRIS, K. 2011. Multiple environmental gradients affect spatial variation in the productivity of a tropical bird population. *Journal of Animal Ecology,* 80**,** 688-695.

BURHANS, D. E. & THOMPSON, F. R. 2006. Songbird abundance and parasitism differ between urban and rural shrublands. *Ecological Applications,* 16**,** 394-405.

BURKE, D. M. & NOL, E. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. *Ecological Applications,* 10**,** 1749-1761.

BURKE, T. R., CADMAN, M. D. & NOL, E. 2019. Reproductive success and health of breeding Bank Swallows (Riparia riparia) in aggregate (sand and gravel) pit and natural lakeshore habitats. *Condor,* 121**,** 10.

BURR, P. C., ROBINSON, A. C., LARSEN, R. T., NEWMAN, R. A. & ELLIS-FELEGE, S. N. 2017. Sharp-Tailed Grouse Nest Survival and Nest Predator Habitat Use in North Dakota's Bakken Oil Field. *Plos One,* 12**,** 19.

BURTON, N. H. K. 2009. Reproductive success of Tree Pipits Anthus trivialis in relation to habitat selection in conifer plantations. *Ibis,* 151**,** 361-372.

BURTON, N. H. K., REHFISCH, M. M., CLARK, N. A. & DODD, S. G. 2006. Impacts of sudden winter habitat loss on the body condition and survival of redshank Tringa totanus. *Journal of Applied Ecology,* 43**,** 464-473.

BUSTNES, J. O., BARDSEN, B. J. & HELBERG, M. 2020. To Hide or Not to Hide: Nesting Habitat Dynamics in a Threatened Gull. *Waterbirds,* 43**,** 163-173.

BYHOLM, P., NIKULA, A., KENTTA, J. & TAIVALMAKI, J. P. 2007. Interactions between habitat heterogeneity and food affect reproductive output in a top predator. *Journal of Animal Ecology,* 76**,** 392-401.

BYRD, G. V., SYDEMAN, W. J., RENNER, H. M. & MINOBE, S. 2008. Responses of piscivorous seabirds at the Pribilof Islands to ocean climate. *Deep-Sea Research Part Ii-Topical Studies in Oceanography,* 55**,** 1856-1867.

CALDWELL, L., BAKKER, V. J., SILLETT, T. S., DESROSIERS, M. A., MORRISON, S. A. & ANGELONI, L. M. 2013. REPRODUCTIVE ECOLOGY OF THE ISLAND SCRUB-JAY. *Condor,* 115**,** 603-613.

CAMERON, M. 2009. The influence of climate on Glossy Black-cockatoo reproduction. *Pacific Conservation Biology,* 15**,** 65-71.

CAMPBELL, B. H. 1990. FACTORS AFFECTING THE NESTING SUCCESS OF DUSKY CANADA GEESE, BRANTA-CANADENSIS-OCCIDENTALIS, ON THE COPPER RIVER DELTA, ALASKA. *Canadian Field-Naturalist,* 104**,** 567-576.

CAPILLA-LASHERAS, P., BONDIA, B. & AGUIRRE, J. I. 2021. Environmental conditions but not nest composition affect reproductive success in an urban bird. *Ecology and Evolution,* 11**,** 3084-3092.

CARBONERAS, C., TAVECCHIA, G., GENOVART, M., REQUENA, S., OLIVE, M. & ORO, D. 2013. Inferring geographic origin, population structure and migration routes of a wintering population of Mediterranean gulls from resightings data. *Population Ecology,* 55**,** 343-351.

CARDONI, D. A., ISACCH, J. P. & IRIBARNE, O. 2012. EFFECTS OF CATTLE GRAZING AND FIRE ON THE ABUNDANCE, HABITAT SELECTION, AND NESTING SUCCESS OF THE BAY-CAPPED WREN-SPINETAIL (SPARTONOICA MALUROIDES) IN COASTAL SALTMARSHES OF THE PAMPAS REGION. *Condor,* 114**,** 803-811.

CARLE, R. D., HESTER, M. M., COLETTA, E. & BECK, J. N. 2019. Cassin's Auklet (Ptychoramphus aleuticus) Population Size, Reproduction, and Habitat Management on a Recently Colonized Island in California, USA. *Waterbirds,* 42**,** 366-379.

CARLINI, A. R., CORIA, N. R., SANTOS, M. M., NEGRETE, J., JUARES, M. A. & DANERI, G. A. 2009. Responses of Pygoscelis adeliae and P. papua populations to environmental changes at Isla 25 de Mayo (King George Island). *Polar Biology,* 32**,** 1427-1433.

CARNEIRO, C., CORREIA, E., GONCALVES, D., BRITO, R., LUIS, A. & ALVES, J. A. 2016. Weather mediated impacts on the breeding output of an Afro-Palearctic migratory waterbird. *Avian Biology Research,* 9**,** 167-173.

CARRETE, M., SANCHEZ-ZAPATA, J. A., MARTINEZ, J. E., SANCHEZ, M. A. & CALVO, J. F. 2002. Factors influencing the decline of a Bonelli's eagle Hieraaetus fasciatus population in southeastern Spain: demography, habitat or competition? *Biodiversity and Conservation,* 11**,** 975-985.

CARRILLO, J. & GONZALEZ-DAVILA, E. 2010. Impact of weather on breeding success of the Eurasian Kestrel Falco tinnunculus in a semi-arid island habitat. *Ardea,* 98**,** 51-58.

CARRLSON, K. M., KESLER, D. C. & THOMPSON, T. R. 2014. Survival and habitat use in translocated and resident greater prairie-chickens. *Journal for Nature Conservation,* 22**,** 405-412.

CARRO, M. E., MERMOZ, M. E. & FERNANDEZ, G. J. 2014. Factors affecting the probability of double brooding by Southern House Wrens. *Journal of Field Ornithology,* 85**,** 227-236.

CARROLL, J. M., HOVICK, T. J., DAVIS, C. A., ELMORE, R. D. & FUHLENDORF, S. D. 2017. Reproductive plasticity and landscape heterogeneity benefit a ground-nesting bird in a fire-prone ecosystem. *Ecological Applications,* 27**,** 2234-2244.

CARTWRIGHT, S. J., NICOLL, M. A. C., JONES, C. G., TATAYAH, V. & NORRIS, K. 2014. Agriculture modifies the seasonal decline of breeding success in a tropical wild bird population. *Journal of Applied Ecology,* 51**,** 1387-1395.

CARVER, A. R., ROSS, J. D., AUGUSTINE, D. J., SKAGEN, S. K., DWYER, A. M., TOMBACK, D. F. & WUNDER, M. B. 2017. Weather radar data correlate to hail-induced mortality in grassland birds. *Remote Sensing in Ecology and Conservation,* 3**,** 90-101.

CASAS, F. & VINUELA, J. 2010. Agricultural practices or game management: which is the key to improve red-legged partridge nesting success in agricultural landscapes? *Environmental Conservation,* 37**,** 177-186.

CATALAN, R. M. & HAEGER, J. F. 1999. Breeding performance of the Blue Tit Parus caeruleus in a patchy Mediterranean landscape. *Revue D Ecologie-La Terre Et La Vie,* 54**,** 167-185.

CATLIN, D., GIBSON, D., FRIEDRICH, M. J., HUNT, K. L., KARPANTY, S. M. & FRASER, J. D. 2019. Habitat selection and potential fitness consequences of two early-successional species with differing life-history strategies. *Ecology and Evolution,* 9**,** 13966-13978.

CATLIN, D. H., FRASER, J. D. & FELIO, J. H. 2015. Demographic Responses of Piping Plovers to Habitat Creation on the Missouri River. *Wildlife Monographs,* 192**,** 1-42.

CATRY, I., AMANO, T., FRANCO, A. M. A. & SUTHERLAND, W. J. 2012. Influence of spatial and temporal dynamics of agricultural practices on the lesser kestrel. *Journal of Applied Ecology,* 49, 99-108.

CATRY, T., RAMOS, J. A., MONTICELLI, D., BOWLER, J., JUPITER, T. & LE CORRE, M. 2009. Demography and conservation of the White-tailed Tropicbird Phaethon lepturus on Aride Island, Western Indian Ocean. *Journal of Ornithology,* 150**,** 661-669.

CATSADORAKIS, G. & CRIVELLI, A. J. 2001. Nesting habitat characteristics and breeding performance of Dalmatian Pelicans in Lake Mikri Prespa, NW Greece. *Waterbirds,* 24, 386-393.

CERNY, M., RYMESOVA, D. & SALEK, M. 2020. Habitat scarcity forms an ecological trap for the grey partridge (Perdix perdix) within a central European agricultural landscape. *European Journal of Wildlife Research,* 66**,** 13.

CEZILLY, F., BOY, V. & GREEN, R. E. 1995. INTERANNUAL VARIATION IN GREATER FLAMINGO BREEDING SUCCESS IN RELATION TO WATER LEVELS. *Ecology,* 76**,** 20-26.

CHAIYARAT, R. & EIAM-AMPAI, K. 2014. Effects of Grazing on Nesting of the Oriental Pratincole (Glareola maldivarum) in Bueng Boraphet Wetland, Thailand. *Zoological Science,* 31**,** 77-82.

CHAMBERLAIN, D. E. & CRICK, H. Q. P. 1999. Population declines and reproductive performance of Skylarks Alauda arvensis in different regions and habitats of the United Kingdom. *Ibis,* 141**,** 38-51.

CHAMBERLAIN, D. E., HATCHWELL, B. J. & PERRINS, C. M. 1999. Importance of feeding ecology to the reproductive success of Blackbirds Turdus merula nesting in rural habitats. *Ibis,* 141**,** 415-427.

CHAMPAGNON, J., LEBRETON, J. D., DRUMMOND, H. & ANDERSON, D. J. 2018. Pacific Decadal and El Nino oscillations shape survival of a seabird. *Ecology,* 99**,** 1063-1072.

CHANDLER, R. B., KING, D. I. & CHANDLER, C. C. 2009. Effects of management regime on the abundance and nest survival of shrubland birds in wildlife openings in northern New England, USA. *Forest Ecology and Management,* 258**,** 1669-1676.

CHANTEPIE, S., TEPLITSKY, C., PAVARD, S., SARRAZIN, F., DESCAVES, B., LECUYER, P. & ROBERT, A. 2016. Age-related variation and temporal patterns in the survival of a long-lived scavenger. *Oikos,* 125**,** 167-178.

CHAPA-VARGAS, L. & ROBINSON, S. K. 2006. Nesting success of a songbird in a complex floodplain forest landscape in Illinois, USA: local fragmentation vs. vegetation structure. *Landscape Ecology,* 21**,** 525-537.

CHAPA-VARGAS, L. & ROBINSON, S. K. 2013. Large forests enhance songbird nesting success in agricultural- dominated landscapes of the Midwestern US. *Ecography,* 36**,** 383-392.

CHARMAN, E. C., SMITH, K. W., DILLON, I. A., DODD, S., GRUAR, D. J., CRISTINACCE, A., GRICE, P. V. & GREGORY, R. D. 2012. Drivers of low breeding success in the Lesser Spotted Woodpecker Dendrocopos minor in England: testing hypotheses for the decline. *Bird Study,* 59**,** 255-265.

CHASE, M. K., NUR, N. & GEUPEL, G. R. 2005. Effects of weather and population density on reproductive success and population dynamics in a song sparrow (Melospiza melodia) population: A long-term study. *Auk,* 122**,** 571-592.

CHASTEL, O., WEIMERSKIRCH, H. & JOUVENTIN, P. 1993. HIGH ANNUAL VARIABILITY IN REPRODUCTIVE SUCCESS AND SURVIVAL OF AN ANTARCTIC SEABIRD, THE SNOW PETREL PAGODROMA-NIVEA - A 27-YEAR STUDY. *Oecologia,* 94**,** 278-285.

CHAUVENET, A. L. M., EWEN, J. G., ARMSTRONG, D. & PETTORELLI, N. 2013. Saving the hihi under climate change: a case for assisted colonization. *Journal of Applied Ecology,* 50**,** 1330-1340.

CHERNYSHOV, V. M. 2010. Seasonal phenomena of the year cycle of the whitethroat (Sylvia communis) in the south of West Siberia. *Contemporary Problems of Ecology,* 3**,** 100-107.

CHERNYSHOV, V. M. 2013. The ecological features of the booted warbler (Hippolais caligata) in the Baraba forest-steppe. *Contemporary Problems of Ecology,* 6**,** 77-84.

CHIFFARD, J., DELESTRADE, A., YOCCOZ, N. G., LOISON, A. & BESNARD, A. 2019. Warm temperatures during cold season can negatively affect adult survival in an alpine bird. *Ecology and Evolution,* 9**,** 12531-12543.

CHMURA, H. E., KRAUSE, J. S., PEREZ, J. H., ASMUS, A., SWEET, S. K., HUNT, K. E., MEDDLE, S. L., MCELREATH, R., BOELMAN, N. T., GOUGH, L. & WINGFIELD, J. C. 2018. Late-season snowfall is associated with decreased offspring survival in two migratory arctic-breeding songbird species. *Journal of Avian Biology,* 49**,** 13.

CHRISTENSEN-DALSGAARD, S., MAY, R. F., BARRETT, R. T., LANGSET, M., SANDERCOCK, B. K. & LORENTSEN, S. H. 2018. Prevailing weather conditions and diet composition affect chick growth and survival in the black-legged kittiwake. *Marine Ecology Progress Series,* 604**,** 237-249.

CHRISTIANS, J. K., EVANSON, M. & AIKEN, J. J. 2001. Seasonal decline in clutch size in European starlings: a novel randomization test to distinguish between the timing and quality hypotheses. *Journal of Animal Ecology,* 70**,** 1080-1087.

CHRISTMAN, B. J. 2002. Extreme between-year variation in productivity of a bridled titmouse (Baeolophus wollweberi) population. *Auk,* 119**,** 1149-1154.

CHYB, A. & MINIAS, P. Complex associations of weather conditions with reproductive performance in urban population of a common waterbird. *International Journal of Biometeorology***,** 10.

CIMADOM, A., ULLOA, A., MEIDL, P., ZOTTL, M., ZOTTL, E., FESSL, B., NEMETH, E., DVORAK, M., CUNNINGHAME, F. & TEBBICH, S. 2014. Invasive Parasites, Habitat Change and Heavy Rainfall Reduce Breeding Success in Darwin's Finches. *Plos One,* 9**,** 10.

CIMINO, M. A., PATTERSON-FRASER, D. L., STAMMERJOHN, S. & FRASER, W. R. 2019. The interaction between island geomorphology and environmental parameters drives Adelie penguin breeding phenology on neighboring islands near Palmer Station, Antarctica. *Ecology and Evolution,* 9**,** 9334-9349.

CIRULE, D., KRAMA, T., KRAMS, R., ELFERTS, D., KAASIK, A., RANTALA, M. J., MIERAUSKAS, P., LUOTO, S. & KRAMS, I. A. 2017. Habitat quality affects stress responses and survival in a bird wintering under extremely low ambient temperatures. *Science of Nature,* 104**,** 13.

CLAASSEN, A. H., FORESTER, J. D., ARNOLD, T. W. & CUTHBERT, F. J. 2018. Consequences of multi-scale habitat selection on reproductive success of riverine sandbar-nesting birds in Cambodia. *Avian Biology Research,* 11**,** 108-122.

CLARK, R. G., WINKLER, D. W., DAWSON, R. D., SHUTLER, D., HUSSELL, D. J. T., LOMBARDO, M. P., THORPE, P. A., DUNN, P. O. & WHITTINGHAM, L. A. 2018. Geographic variation and environmental correlates of apparent survival rates in adult tree swallows Tachycineta bicolor. *Journal of Avian Biology,* 49**,** 13.

CLARK, W. R., SCHMITZ, R. A. & BOGENSCHUTZ, T. R. 1999. Site selection and nest success of ring-necked pheasants as a function of location in Iowa landscapes. *Journal of Wildlife Management,* 63**,** 976-989.

CLEELAND, J. B., PARDO, D., RAYMOND, B., TUCK, G. N., MCMAHON, C. R., PHILLIPS, R. A., ALDERMAN, R., LEA, M. A. & HINDELL, M. A. 2021. Disentangling the Influence of Three Major Threats on the Demography of an Albatross Community. *Frontiers in Marine Science,* 8**,** 14.

CLERMONT, J., REALE, D. & GIROUX, J. F. 2018. Plasticity in laying dates of Canada Geese in response to spring phenology. *Ibis,* 160**,** 597-607.

COATES, P. S., PROCHAZKA, B. G., RICCA, M. A., HALSTEAD, B. J., CASAZZA, M. L., BLOMBERG, E. J., BRUSSEE, B. E., WIECHMAN, L., TEBBENKAMP, J., GARDNER, S. C. & REESE, K. P. 2018. The relative importance of intrinsic and extrinsic drivers to population growth vary among local populations of Greater Sage-Grouse: An integrated population modeling approach. *Auk,* 135**,** 240-261.

COCKLE, K. L., BODRATI, A., LAMMERTINK, M. & MARTIN, K. 2015. Cavity characteristics, but not habitat, influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic Forest. *Biological Conservation,* 184**,** 193-200.

COHEN, E. B. & LINDELL, C. A. 2004. Survival, habitat use, and movements of fledgling White-Throated Robins (Turdus assimilis) in a Costa Rican agricultural landscape. *Auk,* 121**,** 404-414.

COHEN, J. B., HOUGHTON, L. M. & FRASER, J. D. 2009. Nesting Density and Reproductive Success of Piping Plovers in Response to Storm- and Human-Created Habitat Changes. *Wildlife Monographs***,** 1-24.

COLLAZO, J. A., AGARDY, T., KLAAS, E. E., SALIVA, J. E. & PIERCE, J. 1998. An interdecadal comparison of population parameters of Brown Pelicans in Puerto Rico and the U.S. Virgin Islands. *Waterbirds,* 21**,** 61-65.

COLOMBO, M. A. & SEGURA, L. N. 2021. Forest edges negatively influence daily nest survival rates of a grassland Tinamou, the Spotted Nothura (Nothura maculosa). *Canadian Journal of Zoology,* 99**,** 573-579.

COLWELL, M. A., BURRELL, N. S., HARDY, M. A., KAYANO, K., MUIR, J. J., PEARSON, W. J., PETERSON, S. A. & SESSER, K. A. 2010. Arrival times, laying dates, and reproductive success of Snowy Plovers in two habitats in coastal northern California. *Journal of Field Ornithology,* 81**,** 349-360.

COLWELL, M. A., HURLEY, S. J., HALL, T. N. & DINSMORE, S. J. 2007. Age-related survival and behavior of snowy plover chicks. *Condor,* 109**,** 638-647.

COLWELL, M. A., MEYER, J. J., HARDY, M. A., MCALLISTER, S. E., TRANSOU, A. N., LEVALLEY, R. R. & DINSMORE, S. J. 2011. Western Snowy Plovers Charadrius alexandrinus nivosus select nesting substrates that enhance egg crypsis and improve nest survival. *Ibis,* 153**,** 303-311.

COMBRINK, L., COMBRINK, H. J., BOTHA, A. J. & DOWNS, C. T. 2017. Habitat structure and diversity influence the nesting success of an endangered large cavity-nesting bird, the Southern Ground-hornbill. *Koedoe,* 59**,** 8.

CONENNA, I., VALKAMA, J. & CHAMBERLAIN, D. 2017. Interactive effects of climate and forest canopy cover on Goshawk productivity. *Journal of Ornithology,* 158**,** 799-809.

CONFER, J. L., BARNES, K. W. & ALVEY, E. C. 2010. Golden- and Blue-winged Warblers: Distribution, nesting success, and genetic differences in two habitats. *Wilson Journal of Ornithology,* 122**,** 273-278.

CONKLING, T. J., BELANT, J. L., DEVAULT, T. L., WANG, G. M. & MARTIN, J. A. 2015. Assessment of variation of nest survival for grassland birds due to method of nest discovery. *Bird Study,* 62**,** 223-231.

CONOVER, M. R., DINKINS, J. B. & RUZICKA, R. E. 2015. Consequences of hunter harvest, winter weather, and increasing population size on survival of non-migratory Canada geese in Connecticut. *Journal of Wildlife Management,* 79**,** 1239-1245.

CONOVER, R. R., BURGER, L. W. & LINDER, E. T. 2011. Grassland Bird Nest Ecology and Survival in Upland Habitat Buffers Near Wooded Edges. *Wildlife Society Bulletin,* 35**,** 353-361.

CONRAD, K. F. & ROBERTSON, R. J. 1993. CLUTCH SIZE IN EASTERN PHOEBES (SAYORNIS-PHOEBE) .2. AGE EFFECTS AND SEASONAL-VARIATION. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* 71**,** 1738-1742.

CONREY, R. Y., SKAGEN, S. K., ADAMS, A. A. Y. & PANJABI, A. O. 2016. Extremes of heat, drought and precipitation depress reproductive performance in shortgrass prairie passerines. *Ibis,* 158**,** 614-629.

COOK, A., BURTON, N. H. K., DODD, S. G., FOSTER, S., PELL, R. J., WARD, R. M., WRIGHT, L. J. & ROBINSON, R. A. 2021. Temperature and density influence survival in a rapidly declining migratory shorebird. *Biological Conservation,* 260**,** 9.

COOK-HALEY, B. S. & MILLENBAH, K. F. 2002. Impacts of vegetative manipulations on Common Tern nest success at Lime Island, Michigan. *Journal of Field Ornithology,* 73**,** 174-179.

COPPES, J., KAMMERLE, J. L., SCHROTH, K. E., BRAUNISCH, V. & SUCHANT, R. 2021. Weather conditions explain reproductive success and advancement of the breeding season in Western Capercaillie (Tetrao urogallus). *Ibis,* 163**,** 990-1003.

CORBETT, L. & HERTOG, T. 2012. Impact of feral Water Buffalo Bubalus bubalis grazing on White-bellied Sea-Eagle Haliaeetus leucogaster breeding success in subtropical river habitat in the Northern Territory, Australia. *Corella,* 36**,** 24-26.

CORNELL, K. L. & DONOVAN, T. M. 2010. Effects of spatial habitat heterogeneity on habitat selection and annual fecundity for a migratory forest songbird. *Landscape Ecology,* 25**,** 109-122.

CORNULIER, T., ELSTON, D. A., ARCESE, P., BENTON, T. G., DOUGLAS, D. J. T., LAMBIN, X., REID, J., ROBINSON, R. A. & SUTHERLAND, W. J. 2009. Estimating the annual number of breeding attempts from breeding dates using mixture models. *Ecology Letters,* 12**,** 1184-1193.

CORREIA, D. L. P., CHAUVENET, A. L. M., ROWCLIFFE, J. M. & EWEN, J. G. 2015. Targeted management buffers negative impacts of climate change on the hihi, a threatened New Zealand passerine. *Biological Conservation,* 192**,** 145-153.

CORSINI, M., DUBIEC, A., MARROT, P. & SZULKIN, M. 2017. Humans and Tits in the City: Quantifying the Effects of Human Presence on Great Tit and Blue Tit Reproductive Trait Variation. *Frontiers in Ecology and Evolution,* 5**,** 12.

COSTANTINI, D., CARELLO, L. & DELL'OMO, G. 2010. Patterns of covariation among weather conditions, winter North Atlantic Oscillation index and reproductive traits in Mediterranean kestrels. *Journal of Zoology,* 280**,** 177-184.

COTTAM, M. R., ROBINSON, S. K., HESKE, E. J., BRAWN, J. D. & ROWE, K. C. 2009. Use of landscape metrics to predict avian nest survival in a fragmented midwestern forest landscape. *Biological Conservation,* 142**,** 2464-2475.

COULSON, J. C. 1999. Variation in clutch size of the Common Eider: A study based on 41 breeding seasons on Coquet Island, Northumberland, England. *Waterbirds,* 22**,** 225-238.

COWLEY, E. & SIRIWARDENA, G. M. 2005. Long-term variation in survival rates of Sand Martins Riparia riparia: dependence on breeding and wintering ground weather, age and sex, and their population consequences. *Bird Study,* 52**,** 237-251.

COX, A. R., ROBERTSON, R. J., FEDY, B. C., RENDELL, W. B. & BONIER, F. 2018. Demographic drivers of local population decline in Tree Swallows (Tachycineta bicolor) in Ontario, Canada. *Condor,* 120**,** 842-851.

COX, J. 1999. Land-cover correlates of wood stork productivity in north and central Florida. *NCASI Technical Bulletin***,** 108.

COX, W. A., DELLINGER, T. A., KILTIE, R., BANKOVICH, B. & TORNWALL, B. 2020. Factors associated with local and statewide population trends of the Florida Sandhill Crane (Antigone canadensis pratensis). *Avian Conservation and Ecology,* 15**,** 16.

COX, W. A., SCHWARZER, Y. C., TORNWALL, B. & CHICALO, R. 2020. Tide and habitat features affect salt marsh songbird nest survival in northeast Florida, USA. *Endangered Species Research,* 41**,** 119-129.

COX, W. A., THOMPSON, F. R., REIDY, J. L. & FAABORG, J. 2013. Temperature can interact with landscape factors to affect songbird productivity. *Global Change Biology,* 19**,** 1064-1074.

CRAIG, C., MAZEROLLE, M. J., TAYLOR, P. D., TREMBLAY, J. A. & VILLARD, M. A. 2019. Predictors of habitat use and nesting success for two sympatric species of boreal woodpeckers in an unburned, managed forest landscape. *Forest Ecology and Management,* 438**,** 134-141.

CRANDALL, R. H., BEDROSIAN, B. E. & CRAIGHEAD, D. 2015. HABITAT SELECTION AND FACTORS INFLUENCING NEST SURVIVAL OF GOLDEN EAGLES IN SOUTH-CENTRAL MONTANA. *Journal of Raptor Research,* 49**,** 413-428.

CRAWFORD, R. J. M., MAKHADO, A. B., UPFOLD, L. & DYER, B. M. 2008. Mass on arrival of rockhopper penguins at Marion Island correlated with breeding success. *African Journal of Marine Science,* 30**,** 185-188.

CRESPIN, L., HARRIS, M. P., LEBRETON, J. D., FREDERIKSEN, M. & WANLESS, S. 2006. Recruitment to a seabird population depends on environmental factors and on population size. *Journal of Animal Ecology,* 75**,** 228-238.

CRICK, H. Q. P., GIBBONS, D. W. & MAGRATH, R. D. 1993. SEASONAL-CHANGES IN CLUTCH SIZE IN BRITISH BIRDS. *Journal of Animal Ecology,* 62**,** 263-273.

CRIMMINS, S. M., MCKANN, P. C., ROBB, J. R., LEWIS, J. P., VANOSDOL, T., WALKER, B. A., WILLIAMS, P. J. & THOGMARTIN, W. E. 2016. FACTORS AFFECTING NEST SURVIVAL OF HENSLOW'S SPARROWS (AMMODRAMUS HENSLOWII) IN SOUTHERN INDIANA. *Wilson Journal of Ornithology,* 128**,** 108-119.

CROLL, D. A., DEMER, D. A., HEWITT, R. P., JANSEN, J. K., GOEBEL, M. E. & TERSHY, B. R. 2006. Effects of variability in prey abundance on reproduction and foraging in chinstrap penguins (Pygoscelis antarctica). *Journal of Zoology,* 269**,** 506-513.

CROMBIE, M. D. & ARCESE, P. 2018. Temporal variation in the effects of individual and environmental factors on nest success. *Auk,* 135**,** 326-341.

CROUCH, C. G., BENSON, R. H., BRENNAN, L. A. & GRAHMANN, E. D. 2019. SURVIVAL, SITE FIDELITY, AND TERRITORY SIZE OF AMERICAN KESTRELS WINTERING IN AN AGRICULTURAL LANDSCAPE OF SOUTH TEXAS. *Journal of Raptor Research,* 53**,** 334-342.

CUCCO, M., MALACARNE, G., ORECCHIA, G. & BOANO, G. 1992. INFLUENCE OF WEATHER CONDITIONS ON PALLID SWIFT APUS-PALLIDUS BREEDING SUCCESS. *Ecography,* 15**,** 184-189.

CULLEN, J. M., CHAMBERS, L. E., COUTIN, P. C. & DANN, P. 2009. Predicting onset and success of breeding in little penguins Eudyptula minor from ocean temperatures. *Marine Ecology Progress Series,* 378**,** 269-278.

CURRY, R. L. & GRANT, P. R. 1989. DEMOGRAPHY OF THE COOPERATIVELY BREEDING GALAPAGOS MOCKINGBIRD, NESOMIMUS-PARVULUS, IN A CLIMATICALLY VARIABLE ENVIRONMENT. *Journal of Animal Ecology,* 58**,** 441-463.

CURTIS, O. E., HOCKEY, P. A. R. & KOESLAG, A. 2007. Competition with Egyptian Geese Alopochen aegyptiaca overrides environmental factors in determining productivity of Black Sparrowhawks Accipiter melanoleucus. *Ibis,* 149**,** 502-508.

CUTHBERT, R. J., COOPER, J. & RYAN, P. G. 2014. Population trends and breeding success of albatrosses and giant petrels at Gough Island in the face of at-sea and on-land threats. *Antarctic Science,* 26**,** 163-171.

CZESZCZEWIK, D., CZORTEK, P., JAROSZEWICZ, B., ZUB, K., ROWINSKI, P. & WALANKIEWICZ, W. 2020. Climate change has cascading effects on tree masting and the breeding performance of a forest songbird in a primeval forest. *Science of the Total Environment,* 747**,** 13.

DA SILVA, L. P., ALVES, J., DA SILVA, A. A., RAMOS, J. A. & FONSECA, C. 2012. Variation in the abundance and reproductive characteristics of Great Tits Parus major in forest and monoculture plantations. *Acta Ornithologica,* 47**,** 147-155.

DALBECK, L. & HEG, D. 2006. Reproductive success of a reintroduced population of Eagle Owls Bubo bubo in relation to habitat characteristics in the Eifel, Germany. *Ardea,* 94**,** 3-21.

DANCHIN, E., BOULINIER, T. & MASSOT, M. 1998. Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. *Ecology,* 79**,** 2415-2428.

DAROLOVA, A., KRISTOFIK, J. & HOI, H. 2014. Vegetation type variation in marsh habitats: does it affect nest site selection, reproductive success, and maternal investment in Reed Warblers? *Journal of Ornithology,* 155**,** 997-1008.

DARRAH, A. J. 2020. Mixed evidence for effects of stewardship on Least Tern reproductive success in coastal Mississippi. *Condor,* 122**,** 13.

DAVIES, J., ARTHUR, D. & WHITE, S. 2014. Effects of variation in breeding habitat on Ring Ouzel Turdus torquatus productivity and chick condition. *Bird Study,* 61**,** 162-170.

DAVIS, D. M., REESE, K. P. & GARDNER, S. C. 2014. Demography, reproductive ecology, and variation in survival of greater sage-grouse in northeastern California. *Journal of Wildlife Management,* 78**,** 1343-1355.

DAVIS, J. B., COX, R. R., KAMINSKI, R. M. & LEOPOLD, B. D. 2007. Survival of wood duck ducklings and broods in Mississippi and Alabama. *Journal of Wildlife Management,* 71**,** 507-517.

DAVIS, S. K., LUDLOW, S. M. & MCMASTER, G. 2016. Reproductive success of songbirds and waterfowl in native mixed-grass pasture and planted grasslands used for pasture and hay. *Condor,* 118**,** 815-834.

DAVISON, M. A. & FITZPATRICK, J. W. 2010. Role of human-modified habitat in protecting specialist species: A case study in the threatened Florida Scrub-Jay. *Biological Conservation,* 143**,** 2815-2822.

DAWSON, R. D. & CLARK, R. G. 1996. Effects of variation in egg size and hatching date on survival of Lesser Scaup Aythya affinis ducklings. *Ibis,* 138**,** 693-699.

DE SANTO, T. L., WILLSON, M. F., BARTECCHI, K. M. & WEINSTEIN, J. 2003. Variation in nest sites, nesting success, territory size, and frequency of polygyny in Winter Wrens in northern temperate coniferous forests. *Wilson Bulletin,* 115**,** 29-37.

DE VILLEMEREUIL, P., RUTSCHMANN, A., EWEN, J. G., SANTURE, A. W. & BREKKE, P. 2019. Can threatened species adapt in a restored habitat? No expected evolutionary response in lay date for the New Zealand hihi. *Evolutionary Applications,* 12**,** 482-497.

DEBUS, S. J. S. 2006. Breeding-habitat and nest-site characteristics of Scarlet Robins and Eastern Yellow Robins near Armidale, New South Wales. *Pacific Conservation Biology,* 12**,** 261-271.

DEHNHARD, N., POISBLEAU, M., DEMONGIN, L., LUDYNIA, K., LECOQ, M., MASELLO, J. F. & QUILLFELDT, P. 2013. Survival of rockhopper penguins in times of global climate change. *Aquatic Conservation-Marine and Freshwater Ecosystems,* 23**,** 777-789.

DELGADO, S., ZORROZUA, N. & ARIZAGA, J. 2021. NO EVIDENCE OF HABITAT EFFECT ON CLUTCH SIZE, EGG QUALITY, AND HATCHING SUCCESS OF THE YELLOW-LEGGED GULL LARUS MICHAHELLIS AT A MICRO-SPATIAL SCALE. *Marine Ornithology,* 49**,** 241-246.

DELHEY, K., CARRIZO, M., VERNIERE, L. C., MAHLER, B. & PETERS, A. 2010. SEASONAL VARIATION IN REPRODUCTIVE OUTPUT OF A NEOTROPICAL TEMPERATE SUROSCINE, THE FIREWOOD-GATHERER (ANUMBIUS ANNUMBI). *Auk,* 127**,** 222-231.

DELORD, K., KAYSER, Y., BARBRAUD, C. & HAFNER, H. 2003. Variability in breeding parameters of the Squacco Heron Ardeola ralloides. *Bird Study,* 50**,** 300-305.

DEMAY, S. M. & WALTERS, J. R. 2019. Variable effects of a changing climate on lay dates and productivity across the range of the Red-cockaded Woodpecker. *Condor,* 121**,** 14.

DEMERDZHIEV, D., STOYCHEV, S., DOBREV, D., SPASOV, S. & OPPEL, S. 2015. Studying the demographic drivers of an increasing Imperial Eagle population to inform conservation management. *Biodiversity and Conservation,* 24**,** 627-639.

DEMONGIN, L., POISBLEAU, M., STRANGE, I. J. & QUILLFELDT, P. 2010. Effects of severe rains on the mortality of southern rockhopper penguin (Eudyptes chrysocome) chicks and its impact on breeding success. *Ornitologia Neotropical,* 21**,** 439-443.

DENAC, D. 2006. Resource-dependent weather effect in the reproduction of the White Stork Ciconia ciconia. *Ardea,* 94**,** 233-240.

DENG, W. H. & ZHANG, K. Q. 2016. Breeding habitat characteristics and nest survival of yellow-rumped flycatcher (Ficedula zanthopygia) in natural tree-cavities. *Russian Journal of Ecology,* 47**,** 194-199.

DENNIS, T. E., MCINTOSH, R. R. & SHAUGHNESSY, P. D. 2011. Effects of human disturbance on productivity of White-bellied Sea-Eagles (Haliaeetus leucogaster). *Emu,* 111**,** 179-185.

D'ENTREMONT, K. J. N., GUZZWELL, L. M., WILHELM, S. I., FRIESEN, V. L., DAVOREN, G. K., WALSH, C. J. & MONTEVECCHI, W. A. 2022. Northern Gannets (Morus bassanus) breeding at their southern limit struggle with prey shortages as a result of warming waters. *Ices Journal of Marine Science,* 79**,** 50-60.

DEROSE-WILSON, A., FRASER, J. D., KARPANTY, S. M. & CATLIN, D. H. 2013. Nest-site selection and demography of Wilson's Plovers on a North Carolina barrier island. *Journal of Field Ornithology,* 84**,** 329-344.

DESANTE, D. F., NOTT, M. P. & O'GRADY, D. R. 2001. Identifying the proximate demographic cause(s) of population change by modelling spatial variation in productivity, survivorship, and population trends. *Ardea,* 89**,** 185-207.

DESANTE, D. F. & SARACCO, J. F. 2021. Climate variation drives dynamics and productivity of a subalpine breeding bird community. *Ornithological Applications,* 123**,** 16.

DESCAMPS, S., TARROUX, A., LORENTSEN, S. H., LOVE, O. P., VARPE, O. & YOCCOZ, N. G. 2016. Large-scale oceanographic fluctuations drive Antarctic petrel survival and reproduction. *Ecography,* 39**,** 496-505.

DEVRIES, J. H., CLARK, R. G. & ARMSTRONG, L. M. 2018. Dynamics of habitat selection in birds: adaptive response to nest predation depends on multiple factors. *Oecologia,* 187**,** 305-318.

DHONDT, A. A. 2010. Effects of competition on great and blue tit reproduction: intensity and importance in relation to habitat quality. *Journal of Animal Ecology,* 79**,** 257-265.

DHONDT, A. A., KAST, T. L. & ALLEN, P. E. 2002. Geographical differences in seasonal clutch size variation in multi-brooded bird species. *Ibis,* 144**,** 646-651.

DI MAGGIO, R., CAMPOBELLO, D., TAVECCHIA, G. & SARA, M. 2016. Habitat- and density-dependent demography of a colonial raptor in Mediterranean agro-ecosystems. *Biological Conservation,* 193**,** 116-123.

DIAS, R. I., KUHLMANN, M., LOURENCO, L. R. & MACEDO, R. H. 2009. TERRITORIAL CLUSTERING IN THE BLUE-BLACK GRASSQUIT: REPRODUCTIVE STRATEGY IN RESPONSE TO HABITAT AND FOOD REQUIREMENTS? *Condor,* 111**,** 706-714.

DICKEY, M. H., GAUTHIER, G. & CADIEUX, M. C. 2008. Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. *Global Change Biology,* 14**,** 1973-1985.

DIETZ, M. S., MURDOCK, C. C., ROMERO, L. M., OZGUL, A. & FOUFOPOULOS, J. 2013. DISTANCE TO A ROAD IS ASSOCIATED WITH REPRODUCTIVE SUCCESS AND PHYSIOLOGICAL STRESS RESPONSE IN A MIGRATORY LANDBIRD. *Wilson Journal of Ornithology,* 125**,** 50-61.

DIJKSTRA, C. & ZIJLSTRA, M. 1997. Reproduction of the marsh harrier Circus aeruginosus in recent land reclamations in the Netherlands. *Ardea,* 85**,** 37-50.

DINKINS, J. B., CONOVER, M. R., KIROL, C. P., BECK, J. L. & FREY, S. N. 2014. Greater Sage-Grouse (Centrocercus urophasianus) hen survival: Effects of raptors, anthropogenic and landscape features, and hen behavior. *Canadian Journal of Zoology,* 92**,** 319-330.

DINSMORE, S. J., LAUTEN, D. J., CASTELEIN, K. A., GAINES, E. P. & STERN, M. A. 2014. Predator exclosures, predator removal, and habitat improvement increase nest success of Snowy Plovers in Oregon, USA. *Condor,* 116**,** 619-628.

DIRKSEN, S., BOUDEWIJN, T. J., SLAGER, L. K., MES, R. G., VANSCHAICK, M. J. M. & DEVOOGT, P. 1995. REDUCED BREEDING SUCCESS OF CORMORANTS (PHALACROCORAX-CARBO SINENSIS) IN RELATION TO PERSISTENT ORGANOCHLORINE POLLUTION OF AQUATIC HABITATS IN THE NETHERLANDS. *Environmental Pollution,* 88**,** 119-132.

DJEMADI, I., BOUZID, S. & BOUSLAMA, Z. 2015. Influence of nest position on blackbird's turdus merla breeding success in urban habitats. *Advances in Environmental Biology,* 9**,** 103-108.

DOHERTY, K. E., BECK, J. L. & NAUGLE, D. E. 2011. Comparing ecological site descriptions to habitat characteristics influencing greater sage-grouse nest site occurrence and success. *Rangeland Ecology and Management,* 64**,** 344-351.

DOLBEER, R. A. 1976. REPRODUCTIVE RATE AND TEMPORAL SPACING OF NESTING OF RED-WINGED BLACKBIRDS IN UPLAND HABITAT. *Auk,* 93**,** 343-355.

DOLENEC, Z., DOLENEC, P. & MOLLER, A. P. 2011. Warmer springs, laying date and clutch size of tree sparrows Passer montanus in Croatia. *Current Zoology,* 57**,** 414-418.

DOLIGEZ, B., DANCHIN, E., CLOBERT, J. & GUSTAFSSON, L. 1999. Tbe use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology,* 68**,** 1193-1206.

DONAZAR, J. A., CEBALLOS, O., TRAVAINI, A., RODRIGUEZ, A., FUNES, M. & HIRALDO, F. 1994. BREEDING PERFORMANCE IN RELATION TO NEST-SITE SUBSTRATUM IN A BUFF-NECKED IBIS (THERISTICUS-CAUDATUS) POPULATION IN PATAGONIA. *Condor,* 96**,** 994-1002.

DONOVAN, T. M., THOMPSON, F. R., FAABORG, J. & PROBST, J. R. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology,* 9**,** 1380-1395.

DORNAK, L. L., BURT, D. B., COBLE, D. W. & CONNER, R. N. 2004. Relationships between habitat and snag characteristics and the reproductive success of the brown-headed nuthatch (Sitta pusilla) in eastern Texas. *Southeastern Naturalist,* 3**,** 683-694.

DOUGLAS, D. J. T. & PEARCE-HIGGINS, J. W. 2019. Variation in ectoparasitic sheep tick Ixodes ricinus infestation on European Golden Plover chicks Pluvialis apricaria and implications for growth and survival. *Bird Study,* 66**,** 92-102.

DOXA, A., THEODOROU, K., CRIVELLI, A. J., HATZILACOU, D., CATSADORAKIS, G., MALAKOU, M., NAZIRIDES, T. & ROBERT, A. 2012. Spatially correlated environmental factors drive synchronisation in populations of the Dalmatian Pelican. *Population Ecology,* 54**,** 499-507.

DOYLE, S., CABOT, D., WALSH, A., INGER, R., BEARHOP, S. & MCMAHON, B. J. 2020. Temperature and precipitation at migratory grounds influence demographic trends of an Arctic-breeding bird. *Global Change Biology,* 26**,** 5447-5458.

DRAKE, A. & MARTIN, K. 2020. Rainfall and nest site competition delay Mountain Bluebird and Tree Swallow breeding but do not impact productivity. *Auk,* 137**,** 18.

DRAKE, A., MARTIN, M. & GREEN, D. J. 2014. Winter habitat use does not influence spring arrival dates or the reproductive success of Yellow Warblers breeding in the arctic. *Polar Biology,* 37**,** 181-191.

DREITZ, V. J., CONREY, R. Y. & SKAGEN, S. K. 2012. Drought and Cooler Temperatures Are Associated with Higher Nest Survival in Mountain Plovers. *Avian Conservation and Ecology,* 7**,** 13.

DRISCOLL, M. J. L. & DONOVAN, T. M. 2004. Landscape context moderates edge effects: Nesting success of wood thrushes in central New York. *Conservation Biology,* 18**,** 1330-1338.

DRUMMOND, B. A. & LEONARD, M. L. 2010. Reproductive Consequences of Nest Site Use in Fork-tailed Storm-Petrels in the Aleutian Islands, Alaska: Potential Lasting Effects of an Introduced Predator. *Avian Conservation and Ecology,* 5**,** 20.

DRUZYAKA, V. 2015. Reduction in variability of individual colonization programs in black-headed gulls (Larus ridibundus) leads to reproductive success diminishing. *Zhurnal Obshchei Biologii,* 76**,** 339-354.

DUCA, C. M., M. A. 2005. Temporal variation in the reproductive success of Cacicus haemorrhous(Linnaeus) (Aves, Icterinae) in an Atlantic Forest reserve in Southeast Brazil. *Revista Brasileira De Zoologia,* 22**,** 484-489.

DUCHARDT, C. J., BECK, J. L. & AUGUSTINE, D. J. 2020. Mountain Plover habitat selection and nest survival in relation to weather variability and spatial attributes of black-tailed prairie dog disturbance. *Condor,* 122**,** 15.

DUCHATEAU, S. & DELAGE, F. 2006. Black-shouldered Kite Elanus caeruleus in South-West France: Population variations, breeding success and limiting factors. *Alauda,* 74**,** 385-398.

DUFOUR, K. W. & CLARK, R. G. 2002. Differential survival of yearling and adult female mallards and its relation to breeding habitat conditions. *Condor,* 104**,** 297-308.

DUFVA, R. & ALLANDER, K. 1996. Variable effects of the Hen Flea Ceratophyllus gallinae on the breeding success of the Great Tit Parus major in relation to weather conditions. *Ibis,* 138**,** 772-777.

DUGGER, K. M., AINLEY, D. G., LYVER, P. O., BARTON, K. & BALLARD, G. 2010. Survival differences and the effect of environmental instability on breeding dispersal in an Adelie penguin meta-population. *Proceedings of the National Academy of Sciences of the United States of America,* 107**,** 12375-12380.

DUGGER, K. M., FAABORG, J., ARENDT, W. J. & HOBSON, K. A. 2004. Understanding survival and abundance of overwintering Warblers: Does rainfall matter? *Condor,* 106**,** 744-760.

DUNN, J. C., MORRIS, A. J., GRICE, P. V. & PEACH, W. J. 2021. Effects of seed-rich habitat provision on territory density, home range and breeding performance of European Turtle Doves Streptopelia turtur. *Bird Conservation International,* 31**,** 620-639.

DUNN, P. O., THUSIUS, K. J., KIMBER, K. & WINKLER, D. W. 2000. Geographic and ecological variation in clutch size of tree swallows. *Auk,* 117**,** 215-221.

DURANT, J. M., ANKER-NILSSEN, T. & STENSETH, N. C. 2003. Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proceedings of the Royal Society B-Biological Sciences,* 270**,** 1461-1466.

DURIEZ, O., SAETHER, S. A., ENS, B. J., CHOQUET, R., PRADEL, R., LAMBECK, R. H. D. & KLAASSEN, M. 2009. Estimating survival and movements using both live and dead recoveries: a case study of oystercatchers confronted with habitat change. *Journal of Applied Ecology,* 46**,** 144-153.

DWIGHT, I. A., VOGT, J. H., COATES, P. S., FLESKES, J. P., CONNELLY, D. P. & GARDNER, S. C. 2020. Linking nest microhabitat selection to nest survival within declining pheasant populations in the Central Valley of California. *Wildlife Research,* 47**,** 391-403.

DWYER, T. J., SEPIK, G. F., DERLETH, E. L. & MCAULEY, D. G. 1988. Demographic characteristics of a Maine woodcock population and effects of habitat management. *Fish & Wildlife Research - US Fish & Wildlife Service,* 4.

DYBALA, K. E., EADIE, J. M., GARDALI, T., SEAVY, N. E. & HERZOG, M. P. 2013. Projecting demographic responses to climate change: adult and juvenile survival respond differently to direct and indirect effects of weather in a passerine population. *Global Change Biology,* 19, 2688-2697.

DYKSTRA, C. R., HAYS, J. L., SIMON, M. M., WEGMAN, A. R., DYKSTRA, L. R. & WILLIAMS, K. A. 2021. Habitat and weather conditions influence reproductive rates of suburban and rural Red-shouldered HawksButeo lineatus. *Ibis,* 163, 623-640.

DYRCZ, A. & HALUPKA, L. 2009. The response of the Great Reed Warbler Acrocephalus arundinaceus to climate change. *Journal of Ornithology,* 150, 39-44.

DZIEWIATY, K. 2002. Significance of the Elbe dyke foreshore and hinterland as feeding habitats for White Storks (Ciconia ciconia). *Vogelwarte,* 41, 221-230.

EERKES-MEDRANO, D., FRYER, R. J., COOK, K. B. & WRIGHT, P. J. 2017. Are simple environmental indicators of food web dynamics reliable: Exploring the kittiwake–temperature relationship. *Ecological Indicators,* 75, 36-47.

EEVA, T., LEHIKOINEN, E. & POHJALAINEN, T. 1997. Pollution-related variation in food supply and breeding success in two hole-nesting passerines. *Ecology,* 78, 1120-1131.

EEVA, T., LEHIKOINEN, E. & VEISTOLA, S. 1989. HABITAT PREFERENCE AND BREEDING PERFORMANCE IN 4 HOLE-NESTING PASSERINES AT THE NORTHERN LIMIT OF THEIR RANGE. *Ornis Fennica,* 66, 142-150.

EGGERS, U., ARENS, M., FIRLA, M. & WALLSCHLAGER, D. 2015. To fledge or not to fledge: factors influencing the number of eggs and the eggs-to-fledglings rate in White Storks Ciconia ciconia in an agricultural environment. *Journal of Ornithology,* 156, 711-723.

EGLINGTON, S. M., JULLIARD, R., GARGALLO, G., VAN DER JEUGD, H. P., PEARCE-HIGGINS, J. W., BAILLIE, S. R. & ROBINSON, R. A. 2015. Latitudinal gradients in the productivity of European migrant warblers have not shifted northwards during a period of climate change. *Global Ecology and Biogeography,* 24, 427-436.

EKROOS, J., ÖST, M., KARELL, P., JAATINEN, K. & KILPI, M. 2012. Philopatric predisposition to predation-induced ecological traps: Habitat-dependent mortality of breeding eiders. *Oecologia,* 170, 979-986.

EL MALKI, S., HANANE, S., JOULAMI, L. & EL HAMOUMI, R. 2013. Nesting performance of the black-winged stilt and collared pratincole on a moroccan coastal wetland: A comparison between natural and artificial habitats. *Wader Study Group Bulletin,* 120, 47-52.

ELHASSAN, E. E. M., SLADECEK, M., BADAAM, S., BRYNYCHOVA, K., CHAJMA, P., FIRLOVA, V., JANATOVA, V., KUBELKA, V., PESKOVA, L., VOZABULOVA, E., ALMUHERY, A. & SALEK, M. 2021. An artificial lakes system Intended for human recreation supports a vital breeding population of Red-wattled Lapwing in the Arabian Desert. *Avian Conservation and Ecology,* 16, 19.

ELIAS, S. P., FRASER, J. D. & BUCKLEY, P. A. 2000. Piping plover brood foraging ecology on New York barrier islands. *Journal of Wildlife Management,* 64, 346-354.

ELIOTOUT, B., LECUYER, P. & DURIEZ, O. 2007. First results on the breeding biology of black vulture Aegypius monochus in France. *Alauda,* 75, 253-264.

ELLIS, L. A., STUMP, S. D. & WEDDLE, D. M. 2009. Southwestern willow flycatcher population and habitat response to reservoir inundation. *Journal of Wildlife Management,* 73, 946-954.

EMMERSON, L. & SOUTHWELL, C. 2011. Adelie penguin survival: age structure, temporal variability and environmental influences. *Oecologia,* 167, 951-965.

ENG, M. L., STUTCHBURY, B. J. M., BURKE, D. M. & ELLIOTT, K. A. 2011. Influence of forest management on pre- and post-fledging productivity of a Neotropical migratory songbird in a highly fragmented landscape. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 41, 2009-2019.

EPPLEY, Z. A. 1992. ASSESSING INDIRECT EFFECTS OF OIL IN THE PRESENCE OF NATURAL VARIATION - THE PROBLEM OF REPRODUCTIVE FAILURE IN SOUTH POLAR SKUAS DURING THE BAHIA-PARAISO OIL-SPILL. *Marine Pollution Bulletin,* 25, 307-312.

ERAUD, C. & BOUTIN, J. M. 2002. Density and productivity of breeding Skylarks Alauda arvensis in relation to crop type on agricultural lands in western France. *Bird Study,* 49, 287-296.

ERAUD, C., BOUTIN, J. M., RIVIERE, M., BRUN, J., BARBRAUD, C. & LORMEE, H. 2009. Survival of Turtle Doves Streptopelia turtur in relation to western Africa environmental conditions. *Ibis,* 151, 186-190.

ERIKSTAD, K. E. 1985. Growth and survival of willow grouse chicks in relation to home range size, brood movements and habitat selection. *Ornis Scandinavica,* 16, 181-190.

ESELY JR, J. D. & BOLLINGER, E. K. 2001. Habitat selection and reproductive success of Loggerhead Shrikes in northwest Missouri: A hierarchical approach. *Wilson Bulletin,* 113, 290-296.

ESTADES, C. F., LAZZONI, I. & AGUIRRE, J. 2019. NESTING ECOLOGY OF THE ENDANGERED CHILEAN WOODSTAR (EULIDIA YARRELLII). *Ornitologia Neotropical,* 30, 11-18.

EVANS, A. D., SMITH, K. W., BUCKINGHAM, D. L. & EVANS, J. 1997. Seasonal variation in breeding performance and nestling diet of Cirl Buntings Emberiza cirlus in England. *Bird Study,* 44, 66-79.

EVANS, B. S., RYDER, T. B., REITSMA, R., HURLBERT, A. H. & MARRA, P. P. 2015. Characterizing avian survival along a rural-to-urban land use gradient. *Ecology,* 96, 1631-1640.

EVANS, K. L., DUNCAN, R. P., BLACKBURN, T. M. & CRICK, H. Q. P. 2005. Investigating geographic variation in clutch size using a natural experiment. *Functional Ecology,* 19, 616-624.

EVANS, M. R. 2003. Survival of male scarlet-tufted malachite sunbirds (Nectarinia johnstoni) on Mount Kenya and the influence of ornamentation. *Biological Journal of the Linnean Society,* 80, 125-133.

EWING, S. R., BENN, S., COWIE, N., WILSON, L. & WILSON, J. D. 2013. Effects of weather variation on a declining population of Slavonian Grebes Podiceps auritus. *Journal of Ornithology,* 154, 995-1006.

FAIR, J. M. & MYERS, O. B. 2002. Early reproductive success of western bluebirds and ash-throated flycatchers: a landscapecontaminant perspective. *Environmental Pollution,* 118**,** 321-330.

FALK, K. J., NOL, E. & BURKE, D. M. 2011. Weak effect of edges on avian nesting success in fragmented and forested landscapes in Ontario, Canada. *Landscape Ecology,* 26**,** 239-251.

FANFANI, A., MANES, F., RANAZZI, L., ZITTI, M. & SALVATI, L. 2008. Exploring the relationship between climate aridity, vegetation stress, and the demographic performance of Tawny Owl Strix aluco in Castelporziano forest (Central Italy). *Biota,* 9**,** 15-23.

FANTLE-LEPCZYK, J., TAYLOR, A., DUFFY, D., CRAMPTON, L. H. & CONANT, S. 2016. WEATHER INFLUENCES ON NEST SUCCESS OF THE ENDANGERED PUAIOHI (MYADESTES PALMERI). *Wilson Journal of Ornithology,* 128**,** 43-55.

FARIA, N. & MORALES, M. B. 2018. Population productivity and late breeding habitat selection by the threatened Little Bustard: the importance of grassland management. *Bird Conservation International,* 28**,** 521-533.

FARRELL, P. D., BAASCH, D. M., FARNSWORTH, J. M. & SMITH, C. B. 2018. Interior Least Tern and Piping Plover nest and brood survival at managed, off-channel sites along the central Platte River, Nebraska, USA 2001-2015. *Avian Conservation and Ecology,* 13**,** 10.

FASOLA-MATASARU, L., BALTAG, E. S., ICHIM, P. & COJOCARU, D. 2018. FACTORS INFLUENCING THE BREEDING SUCCESS OF WHITE STORKS CICONIA CICONIA IN EASTERN ROMANIA. *Ardeola-International Journal of Ornithology,* 65**,** 271-282.

FAUTH, P. T., GUSTAFSON, E. J. & RABENOLD, K. N. 2000. Using landscape metrics to model source habitat for Neotropical migrants in the midwestern US. *Landscape Ecology,* 15**,** 621-631.

FAY, R., WEIMERSKIRCH, H., DELORD, K. & BARBRAUD, C. 2015. Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. *Journal of Animal Ecology,* 84**,** 1423-1433.

FAYET, A. L., CLUCAS, G. V., ANKER-NILSSEN, T., SYPOSZ, M. & HANSEN, E. S. 2021. Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. *Journal of Animal Ecology,* 90**,** 1152-1164.

FAYET, A. L., SHIRAI, M., MATSUMOTO, S., VAN TATENHOVE, A., YODA, K. & SHOJI, A. 2020. Differences in breeding success between neighbouring Streaked Shearwater subcolonies correlate with egg size and quality of parental care. *Ornithological Science,* 18**,** 189-195.

FENN, S. R., BIGNAL, E. M., BIGNAL, S., TRASK, A. E., MCCRACKEN, D. I., MONAGHAN, P. & REID, J. M. 2021. Within-year and among-year variation in impacts of targeted conservation management on juvenile survival in a threatened population. *Journal of Applied Ecology,* 58**,** 2722-2733.

FERNANDEZ, C., AZKONA, P. & DONAZAR, J. A. 1998. Density-dependent effects on productivity in the Griffon vulture Gyps fulvus: the role of interference and habitat heterogeneity. *Ibis,* 140**,** 64-69.

FERNANDEZ-BELLON, D., CORTES-AVIZANDA, A., ARENAS, R. & DONAZAR, J. A. 2016. Density-dependent productivity in a colonial vulture at two spatial scales. *Ecology,* 97**,** 406-416.

FERREIRA, D. D., DE AQUINO, M. M., HEMING, N. M., MARINI, M. A., LEITE, F. S. F. & LOPES, L. E. 2019. Breeding in the gray-headed tody-flycatcher (Aves: Tyrannidae) with comments on geographical variation in reproductive traits within the genus Todirostrum. *Journal of Natural History,* 53**,** 595-610.

FERRER, M., MORANDINI, V. & NEWTON, I. 2015. Floater interference reflects territory quality in the Spanish Imperial Eagle Aquila adalberti: a test of a density-dependent mechanism. *Ibis,* 157**,** 849-859.

FIEHLER, C. M., TIETJE, W. D. & FIELDS, W. R. 2006. Nesting success of Western Bluebirds (Sialia mexicana) using nest boxes in vineyard and oak-savannah habitats of California. *Wilson Journal of Ornithology,* 118**,** 552-557.

FIELD, R. H., ANDERSON, G. Q. A. & GRUAR, D. J. 2008. Land-use correlates of breeding performance and diet in Tree Sparrows Passer montanus. *Bird Study,* 55**,** 280-289.

FIERRO-CALDERON, K. & MARTIN, T. E. 2020. Does vegetation change over 28 years affect habitat use and reproductive success? *Auk,* 137**,** 9.

FIFE, D. T., DAVIS, S. E., ROBERTSON, G. J., GILCHRIST, H. G., STENHOUSE, I. J., SHUTLER, D. & MALLORY, M. L. 2018. Correlating tropical climate with survival of an Arctic-breeding, trans-equatorial migrant seabird. *Arctic Science,* 4**,** 656-668.

FINCH, T., PEARCE-HIGGINS, J. W., LEECH, D. I. & EVANS, K. L. 2014. Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. *Biodiversity and Conservation,* 23**,** 2427-2444.

FINK, A. D., THOMPSON, F. R. & TUDOR, A. A. 2006. Songbird use of regenerating forest, glade, and edge habitat types. *Journal of Wildlife Management,* 70**,** 180-188.

FISCHER, K., BUSCH, R., FAHL, G., KUNZ, M. & KNOPF, M. 2013. Habitat preferences and breeding success of Whinchats (Saxicola rubetra) in the Westerwald mountain range. *Journal of Ornithology,* 154**,** 339-349.

FISH, A. C., DEPERNO, C. S., SCHILLACI, J. M. & MOORMAN, C. E. 2020. Fledgling Bachman's Sparrows in a longleaf pine ecosystem: survival, movements, and habitat selection. *Journal of Field Ornithology,* 91**,** 354-366.

FISHER, R. J. & DAVIS, S. K. 2011. Post-fledging dispersal, habitat use, and survival of Sprague's pipits: Are planted grasslands a good substitute for native? *Biological Conservation,* 144**,** 263-271.

FLANDERS-WANNER, B. L., WHITE, G. C. & MCDANIEL, L. L. 2004. Weather and prairie grouse: Dealing with effects beyond our control. *Wildlife Society Bulletin,* 32**,** 22-34.

FORBES, S. 2010. Family structure and variation in reproductive success in blackbirds. *Behavioral Ecology and Sociobiology,* 64**,** 475-483.

FORMAN, D. W. & BRAIN, P. F. 2004. Reproductive strategies used by moorhens (Gallinula chloropus) colonizing an artificial wetland habitat in south Wales. *Journal of Natural History,* 38**,** 389-401.

FORSCHLER, M., BORRAS, A., CABRERA, J., CABRERA, T. & SENAR, J. 2005. Inter-locality variation in reproductive success of the citril finch Serinus citrinella. *Journal of Ornithology,* 146**,** 137-140.

FOSSOY, F., STOKKE, B. G., KASI, T. K., DYRSET, K., ESPMARK, Y., HOSET, K. S., WEDEGE, M. I. & MOKSNES, A. 2015. Reproductive success is strongly related to local and regional climate in the Arctic snow bunting (Plectrophenax nivalis). *Polar Biology,* 38**,** 393-400.

FRANKS, S. E., PEARCE-HIGGINS, J. W., ATKINSON, S., BELL, J. R., BOTHAM, M. S., BRERETON, T. M., HARRINGTON, R. & LEECH, D. I.

2018. The sensitivity of breeding songbirds to changes in seasonal timing is linked to population change but cannot be directly attributed to the effects of trophic asynchrony on productivity. *Global Change Biology,* 24**,** 957-971.

FRAUENDORF, M., ALLEN, A. M., JONGEJANS, E., ENS, B. J., TEUNISSEN, W., KAMPICHLER, C., VAN TURNHOUT, C. A. M., BAILEY, L. D., DE KROON, H., CREMER, J., KLEYHEEG, E., NIENHUIS, J. & VAN DE POL, M. 2022. Love thy neighbour?-Spatial variation in density dependence of nest survival in relation to predator community. *Diversity and Distributions,* 28**,** 624-635.

FREDERIKSEN, M., ANKER-NILSSEN, T., BEAUGRAND, G. & WANLESS, S. 2013. Climate, copepods and seabirds in the boreal Northeast Atlantic - current state and future outlook. *Global Change Biology,* 19**,** 364-372.

FREDERIKSEN, M., DAUNT, F., HARRIS, M. P. & WANLESS, S. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology,* 77**,** 1020-1029.

FREED, L. A., CANN, R. L. & BODNER, G. R. 2008. Incipient extinction of a major population of the Hawaii akepa owing to introduced species. *Evolutionary Ecology Research,* 10**,** 931-965.

FRERE, E., GANDINI, P. & BOERSMA, D. 1998. The breeding ecology of Magellanic Penguins at Cabo Virgenes, Argentina: What factors determine reproductive success? *Colonial Waterbirds,* 21**,** 205-210.

FRETWELL, S. D. 1969. On territorial behavior and other factors influencing habitat distribution in birds - III. Breeding success in a local population of Field Sparrows (Spiza americana Gmel). *Acta Biotheoretica,* 19**,** 45-52.

FREY, C., SONNAY, C., DREISS, A. & ROULIN, A. 2011. Habitat, breeding performance, diet and individual age in Swiss Barn Owls (Tyto alba). *Journal of Ornithology,* 152**,** 279-290.

FRIESEN, L., CADMAN, M. D. & MACKAY, R. J. 1999. Nesting success of neotropical migrant songbirds in a highly fragmented landscape. *Conservation Biology,* 13**,** 338-346.

FUFACHEV, I. A., EHRICH, D., SOKOLOVA, N. A., SOKOLOV, V. A. & SOKOLOV, A. A. 2019. Flexibility in a changing arctic food web: Can rough-legged buzzards cope with changing small rodent communities? *Global Change Biology,* 25**,** 3669-3679.

FULLERTON, M. R., WALTERS, J. R., WILL, R. E. & LOSS, S. R. 2021. Interannual climate variation influences nest initiation date and nest productivity of the Red-cockaded Woodpecker at the northwestern edge of its range. *Ornithological Applications,* 123**,** 17.

GALE, G. A., HANNERS, L. A. & PATTON, S. R. 1997. Reproductive success of Worm-eating Warblers in a forested landscape. *Conservation Biology,* 11**,** 246-250.

GARCIA-PEREZ, B., HOBSON, K. A., ALBRECHTS, G., CADMAN, M. D. & SALVADORIS, A. 2014. Influence of climate on annual survival of Barn Swallows (Hirundo rustica) breeding in North America. *Auk,* 131**,** 351-362.

GARDARSSON, A. & JONSSON, J. E. 2019. Numbers and distribution of the Great Cormorant in Iceland: Limitation at the regional and metapopulation level. *Ecology and Evolution,* 9**,** 3984-4000.

GAUDET, C. A., GREEN, E. N., BRIGHAM, R. M. & DAVIS, S. K. 2020. Nesting ecology and reproductive success of mixed-grass prairie songbirds. *Wilson Journal of Ornithology,* 132**,** 952-966.

GAUTHIER, G., LEGAGNEUX, P., VALIQUETTE, M. A., CADIEUX, M. C. & THERRIEN, J. F. 2015. Diet and reproductive success of an Arctic generalist predator: Interplay between variations in prey abundance, nest site location, and intraguild predation. *Auk,* 132**,** 735-747.

GAUTSCHI, D., HEINSOHN, R., MURPHY, L. & CRATES, R. 2021. Landscape-scale distribution of nest predators and its relationship with regent honeyeater nest success. *Austral Ecology,* 46**,** 1322-1334.

GENOVART, M., BECARES, J., IGUAL, J. M., MARTINEZ-ABRAIN, A., ESCANDELL, R., SANCHEZ, A., RODRIGUEZ, B., ARCOS, J. M. & ORO, D. 2018. Differential adult survival at close seabird colonies: The importance of spatial foraging segregation and bycatch risk during the breeding season. *Global Change Biology,* 24**,** 1279-1290.

GIBSON, D., BLOMBERG, E. J., ATAMIAN, M. T. & SEDINGER, J. S. 2016. Nesting habitat selection influences nest and early offspring survival in Greater Sage-Grouse. *Condor,* 118**,** 689-702.

GIBSON, D., BLOMBERG, E. J., ATAMIAN, M. T. & SEDINGER, J. S. 2017. Weather, habitat composition, and female behavior interact to modify offspring survival in Greater Sage-Grouse. *Ecological Applications,* 27**,** 168-181.

GIBSON, K. F. & WILLIAMS, T. D. 2017. Intraclutch egg size variation is independent of ecological context among years in the European Starling Sturnus vulgaris. *Journal of Ornithology,* 158**,** 1099-1110.

GILBERT, G., TYLER, G. A., DUNN, C. J., RATCLIFFE, N. & SMITH, K. W. 2007. The influence of habitat management on the breeding success of the Great Bittern Botaurus stellaris in Britain. *Ibis,* 149**,** 53-66.

GIL-DELGADO, J. A., MARCO, E., PAREDES, M. & VIVES-FERRANDIZ, C. 2005. Seasonal clutch size variation of multi-brooded bird species: comparisons between breeding season and latitudes. *Ibis,* 147**,** 206-212.

GIMENEZ, O., CRAINICEANU, C., BARBRAUD, C., JENOUVRIER, S. & MORGAN, B. J. T. 2006. Semiparametric regression in capture-recapture modeling. *Biometrics,* 62**,** 691-698.

GIORDANO, O., FICETTO, G. & TIZZANI, P. 2013. Influence of weather-climate conditions on the breeding success of rock partridge Alectoris graeca in a population of the western Alps. *Avocetta,* 37**,** 125-127.

GLADALSKI, M., BANBURA, M., KALINSKI, A., MARKOWSKI, M., SKWARSKA, J., WAWRZYNIAK, J., ZIELINSKI, P., CYZEWSKA, I., MANKOWSKA, D. & BANBURA, J. 2016. Effects of human-related disturbance on breeding success of urban and non-urban blue tits (Cyanistes caeruleus). *Urban Ecosystems,* 19**,** 1325-1334.

GLADALSKI, M., CYZEWSKA, I., BANBURA, M., KALISKI, A., MARKOWSKI, M., SKWARSKA, J., WAWRZYNIAK, J. & BANBURA, J. 2019. Influence of habitat composition on nestling body condition and breeding success in European Pied Flycatchers (Ficedula hypoleuca). *Avian Biology Research,* 12**,** 67-72.

GOGUEN, C. B. & MURRAY, L. D. 2020. Nest survival, predator assemblage, and patterns of predation at Veery (Catharus fuscescens) nests in a mature forest landscape. *Wilson Journal of Ornithology,* 132**,** 284-294.

GOUTTE, A., ANGELIER, F., BECH, C., CLEMENT-CHASTEL, C., DELL'OMO, G., GABRIELSEN, G. W., LENDVAI, A. Z., MOE, B., NOREEN, E., PINAUD, D., TARTU, S. & CHASTEL, O. 2014. Annual variation in the timing of breeding, pre-breeding foraging areas and corticosterone levels in an Arctic population of black-legged kittiwakes. *Marine Ecology Progress Series,* 496**,** 233-247.

GREEN, R. E. 1988. Effects of environmental factors on the timing and success of breeding of common snipe Gallinago gallinago

(Aves: Scolopacidae). *Journal of Applied Ecology,* 25**,** 79-93.

GRENDELMEIER, A., ARLETTAZ, R., GERBER, M. & PASINELLI, G. 2015. Reproductive Performance of a Declining Forest Passerine in Relation to Environmental and Social Factors: Implications for Species Conservation. *Plos One,* 10**,** 23.

GRIFFIN, E., DESMOND, M. & VAN LEEUWEN, D. 2017. Juvenile Burrowing Owl Movement and Survival in a Human-Altered Landscape. *Wildlife Society Bulletin,* 41**,** 649-658.

GROSBOIS, V. & THOMPSON, P. M. 2005. North Atlantic climate variation influences survival in adult fulmars. *Oikos,* 109**,** 273-290.

GRUBER-HADDEN, N. W., MESSMER, T. A., MAXFIELD, B. D., KOONS, D. N. & GUTTERY, M. R. 2016. Population vital rates of resident and translocated female greater sage-grouse. *Journal of Wildlife Management,* 80**,** 753-760.

GRUEBLER, M. U., KORNER-NIEVERGELT, F. & VON HIRSCHHEYDT, J. 2010. The reproductive benefits of livestock farming in barn swallows Hirundo rustica: quality of nest site or foraging habitat? *Journal of Applied Ecology,* 47**,** 1340-1347.

GRUEBLER, M. U., MULLER, M., MICHEL, V. T., PERRIG, M., KEIL, H., NAEF-DAENZER, B. & KORNER-NIEVERGELT, F. 2018. Brood provisioning and reproductive benefits in relation to habitat quality: a food supplementation experiment. *Animal Behaviour,* 141**,** 45-55.

GRYZ, J. & KRAUZE-GRYZ, D. 2018. Influence of habitat urbanisation on time of breeding and productivity of tawny owl (Strix aluco). *Polish Journal of Ecology,* 66**,** 153-161.

GULLETT, P., EVANS, K. L., ROBINSON, R. A. & HATCHWELL, B. J. 2014. Climate change and annual survival in a temperate passerine: partitioning seasonal effects and predicting future patterns. *Oikos,* 123**,** 389-400.

GUZMAN, J. L., VINUELA, J., CARRANZA, J., PORRAS, J. T. & ARROYO, B. 2020. Red-legged partridge Alectoris rufa productivity in relation to weather, land use, and releases of farm-reared birds. *European Journal of Wildlife Research,* 66**,** 15.

HACHE, S., BAYNE, E. M. & VILLARD, M. A. 2014. Postharvest regeneration, sciurid abundance, and postfledging survival and movements in an Ovenbird population. *Condor,* 116**,** 102-112.

HACHE, S. & VILLARD, M. A. 2010. Age-specific response of a migratory bird to an experimental alteration of its habitat. *Journal of Animal Ecology,* 79**,** 897-905.

HAGELIN, J. C., PERRY, M. L., EWEN-CAMPEN, B. S., SIKES, D. S. & SHARBAUGH, S. 2010. HABITAT TYPE IS RELATED TO NEST MASS AND FLEDGING SUCCESS OF ARCTIC WARBLERS. *Wilson Journal of Ornithology,* 122**,** 699-705.

HAHN, S., REINHARDT, K., RITZ, M. S., JANICKE, T., MONTALTI, D. & PETER, H. U. 2007. Oceanographic and climatic factors differentially affect reproduction performance of Antarctic skuas. *Marine Ecology Progress Series,* 334**,** 287-297.

HALL, K. R. 2008. Comparing geographic boundaries in songbird demography data with vegetation boundaries: a new approach to evaluating habitat quality. *Environmental and Ecological Statistics,* 15**,** 491-521.

HALUPKA, L., BOROWIEC, M., NEUBAUER, G. & HALUPKA, K. 2021. Fitness consequences of longer breeding seasons of a migratory passerine under changing climatic conditions. *Journal of Animal Ecology,* 90**,** 1655-1665.

HALUPKA, L., WIERUCKA, K., SZTWIERTNIA, H. & KLIMCZUK, E. 2017. Conditions at autumn stopover sites affect survival of a migratory passerine. *Journal of Ornithology,* 158**,** 979-988.

HAMILTON, S. & HAMILTON, S. 1998. Determining burrow occupancy, fledging success and land-based threats to mainland and near-shore island sooty shearwater (Puffinus griseus) colonies. *New Zealand Journal of Zoology,* 25**,** 443-453.

HARROD, S. E. & ROLLAND, V. 2020. Demographic responses of eastern bluebirds to climatic variability in northeastern Arkansas. *Population Ecology,* 62**,** 317-331.

HENDERSON, L. J., EVANS, N. P., HEIDINGER, B. J., HERBORN, K. A. & ARNOLD, K. E. 2017. Do glucocorticoids predict fitness? Linking environmental conditions, corticosterone and reproductive success in the blue tit, Cyanistes caeruleus. *Royal Society Open Science,* 4**,** 11.

HERNÁNDEZ, F., HERNÁNDEZ, F., ARREDONDO, J. A., BRYANT, F. C., BRENNAN, L. A. & BINGHAM, R. L. 2005. Influence of precipitation on demographics of northern bobwhites in southern Texas. *Wildlife Society Bulletin,* 33**,** 1071-1079.

HERNANDEZ, N., ORO, D. & SANZ-AGUILAR, A. 2017. Environmental conditions, age, and senescence differentially influence survival and reproduction in the Storm Petrel. *Journal of Ornithology,* 158**,** 113-123.

HILL, J. M., LLOYD, J. D., MCFARLAND, K. P. & RIMMER, C. C. 2019. Apparent survival of a range-restricted montane forest bird species is influenced by weather throughout the annual cycle. *Avian Conservation and Ecology,* 14**,** 12.

HINSLEY, S. A., HILL, R. A., BELLAMY, P. E., HARRISON, N. M., SPEAKMAN, J. R., WILSON, A. K. & FERNS, P. N. 2008. Effects of structural and functional habitat gaps on breeding woodland birds: working harder for less. *Landscape Ecology,* 23**,** 615-626.

HOBART, B. K., ROBERTS, K. N., DOTTERS, B. P., BERIGAN, W. J., WHITMORE, S. A., RAPHAEL, M. G., KEANE, J. J., GUTIÉRREZ, R. J. & PEERY, M. Z. 2019. Site occupancy and reproductive dynamics of California spotted owls in a mixed-ownership landscape. *Forest Ecology and Management,* 437**,** 188-200.

HOEKMAN, S. T., GABOR, T. S., MAHER, R., MURKIN, H. R. & LINDBERG, M. S. 2006. Demographics of breeding female mallards in southern Ontario, Canada. *Journal of Wildlife Management,* 70**,** 111-120.

HOLLENBECK, J. P., SAAB, V. A. & FRENZEL, R. W. 2011. Habitat Suitability and Nest Survival of White-Headed Woodpeckers in Unburned Forests of Oregon. *Journal of Wildlife Management,* 75**,** 1061-1071.

HOLMES, R. T., MARRA, P. P. & SHERRY, T. W. 1996. Habitat-specific demography of breeding black-throated blue warblers (Dendroica caerulescens): Implications for population dynamics. *Journal of Animal Ecology,* 65**,** 183-195.

HOLOUBEK, N. S. & JENSEN, W. E. 2016. Avian Nest Success along a Habitat Gradient in the Cross Timbers Oak Savanna. *American Midland Naturalist,* 176**,** 234-246.

HOMAN, H. J., LINZ, G. M. & BLEIER, W. J. 2000. Winter habitat use and survival of female ring-necked pheasants (Phasianus colchicus) in southeastern North Dakota. *American Midland Naturalist,* 143**,** 463-480.

HORAK, D., SEDLACEK, O., TOSZOGYOVA, A., ALBRECHT, T., FERENC, M., JELINEK, V. & STORCH, D. 2011. Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa. *Ostrich,* 82**,** 175-183.

HORSWILL, C., MATTHIOPOULOS, J., GREEN, J. A., MEREDITH, M. P., FORCADA, J., PEAT, H., PRESTON, M., TRATHAN, P. N. & RATCLIFFE, N. 2014. Survival in macaroni penguins and the relative importance of different drivers: individual traits, predation pressure and environmental variability. *Journal of Animal Ecology,* 83**,** 1057-1067.

HOSET, K. S., ESPMARK, Y., LIER, M., HAUGAN, T., WEDEGE, M. I. & MOKSNES, A. 2009. The effects of male mating behaviour and food provisioning on breeding success in snow buntings Plectrophenax nivalis in the high Arctic. *Polar Biology,* 32**,** 1649-1656.

HOTKER, H. 2000. Intraspecific variation in size and density of Avocet colonies: effects of nest-distances on hatching and breeding success. *Journal of Avian Biology,* 31**,** 387-398.

HOWERTER, D. W., ANDERSON, M. G., DEVRIES, J. H., JOYNT, B. L., ARMSTRONG, L. M., EMERY, R. B. & ARNOLD, T. W. 2014. Variation in mallard vital rates in Canadian Aspen Parklands: The Prairie Habitat Joint Venture assessment. *Wildlife Monographs,* 188**,** 1-37.

HUNT, V. M. 2016. Reproductive Success and Habitat Selection in Black-crowned Night-Herons (Nycticorax nycticorax) in a City Park. *American Midland Naturalist,* 175**,** 168-182.

ILES, D. T., ROCKWELL, R. F., MATULONIS, P., ROBERTSON, G. J., ABRAHAM, K. F., DAVIES, J. C. & KOONS, D. N. 2013. Predators, alternative prey and climate influence annual breeding success of a long-lived sea duck. *Journal of Animal Ecology,* 82**,** 683-693.

JACKSON, D. B. 2005. Environmental correlates of lake occupancy and chick survival of Black-throated Divers Gavia arctica in Scotland. *Bird Study,* 52**,** 225-236.

JAHN, A. E., TUERO, D. T., MAMANI, A. M., BEJARANO, V., MASSON, D. A. & AGUILAR, E. 2014. Drivers of clutch-size in Fork-tailed Flycatchers (Tyrannus savana) at temperate and tropical latitudes in South America. *Emu-Austral Ornithology,* 114**,** 337-342.

JAKUBAS, D. 2011. THE INFLUENCE OF CLIMATE CONDITIONS ON BREEDING PHENOLOGY OF THE GREY HERON ARDEA CINEREA L. IN NORTHERN POLAND. *Polish Journal of Ecology,* 59**,** 179-192.

JANISZEWSKI, T., MINIAS, P. & WOJCIECHOWSKI, Z. 2015. Selective forces responsible for transition to nesting on electricity poles in the White Stork Ciconia ciconia. *Ardea,* 103**,** 39-50.

JANISZEWSKI, T., MINIAS, P., WOJCIECHOWSKI, Z. & PODLASZCZUK, P. 2014. Habitat Selection by White Storks Breeding in a Mosaic Agricultural Landscape of Central Poland. *Wilson Journal of Ornithology,* 126**,** 591-599.

JANKE, A. K., GATES, R. J. & TERHUNE, T. M. 2015. Habitat influences Northern Bobwhite survival at fine spatiotemporal scales. *Condor,* 117**,** 41-52.

JENOUVRIER, S., PERON, C. & WEIMERSKIRCH, H. 2015. Extreme climate events and individual heterogeneity shape life-history traits and population dynamics. *Ecological Monographs,* 85**,** 605-624.

JENOUVRIER, S., THIBAULT, J. C., VIALLEFONT, A., VIDALS, P., RISTOW, D., MOUGIN, J. L., BRICHETTI, P., BORG, J. J. & BRETAGNOLLE, V. 2009. Global climate patterns explain range-wide synchronicity in survival of a migratory seabird. *Global Change Biology,* 15**,** 268-279.

JOHNS, M. E., WARZYBOK, P., JAHNCKE, J., DOAK, P., LINDBERG, M. & BREED, G. A. 2022. Episodes of high recruitment buffer against climate-driven mass mortality events in a North Pacific seabird population. *Journal of Animal Ecology,* 91**,** 345-355.

JONES, I. L., HUNTER, F. M. & ROBERTSON, G. J. 2002. Annual adult survival of Least Auklets (Aves, Alcidae) varies with large-scale climatic conditions of the North Pacific Ocean. *Oecologia,* 133**,** 38-44.

JONES, I. L., HUNTER, F. M., ROBERTSON, G. J. & FRASER, G. 2004. Natural variation in the sexually selected feather ornaments of crested auklets (Aethia cristatella) does not predict future survival. *Behavioral Ecology,* 15**,** 332-337.

JONES, I. L., HUNTER, F. M., ROBERTSON, G. J., WILLIAMS, J. C. & BYRD, G. V. 2007. Covariation among demographic and climate parameters in whiskered auklets Aethia pygmaea. *Journal of Avian Biology,* 38**,** 450-461.

JONES, S. L. & WHITE, G. C. 2012. THE EFFECT OF HABITAT EDGES ON NEST SURVIVAL OF SPRAGUE'S PIPITS. *Wilson Journal of Ornithology,* 124**,** 310-315.

JORGENSEN, P. S., TOTTRUP, A. P., RAHBEK, C. & GEERTSMA, M. 2013. Effects of summer weather on reproductive success of the Red-backed Shrike (Lanius collurio). *Bird Study,* 60**,** 1-10.

KAPLAN, R. H., ROSAMOND, K. M., GODED, S., SOULTAN, A., GLASS, A., KIM, D. H. & ARCILLA, N. 2021. Bobolink (Dolichonyx oryzivorus) Declines Follow Bison (Bison bison) Reintroduction on Private Conservation Grasslands. *Animals,* 11**,** 21.

KASPRZYKOWSKI, Z. 2007. Reproduction of the rook, Corvus frugilegus in relation to the colony size and foraging habitats. *Folia Zoologica,* 56**,** 186-193.

KAUFFMAN, M. J., FRICK, W. F. & LINTHICUM, J. 2003. Estimation of habitat-specific demography and population growth for peregrine falcons in California. *Ecological Applications,* 13**,** 1802-1816.

KEANE, J. J., MORRISON, M. L. & FRY, D. M. 2006. Prey and weather factors associated with temporal variation in Northern Goshawk reproduction in the Sierra Nevada, California. *Studies in Avian Biology.*

KEARNS, L. J. & RODEWALD, A. D. 2017. Does nest predator activity predict the location and survival of songbird nests in urbanizing landscapes? *Condor,* 119**,** 745-760.

KELLETT, D. K. & ALISAUSKAS, R. T. 1997. Breeding biology of king eiders nesting on Karrak Lake, Northwest Territories. *Arctic,* 50**,** 47-54.

KELLEY, S. W., RANSOM, D., BUTCHER, J. A., SCHULZ, G. G., SURBER, B. W., PINCHAK, W. E., SANTAMARIA, C. A. & HURTADO, L. A. 2011. Home range dynamics, habitat selection, and survival of Greater Roadrunners. *Journal of Field Ornithology,* 82**,** 165-174.

KERN, R. A., SHRIVER, W. G., BOWMAN, J. L., MITCHELL, L. R. & BOUNDS, D. L. 2012. Seaside Sparrow Reproductive Success in Relation to Prescribed Fire. *Journal of Wildlife Management,* 76**,** 932-939.

KETTEL, E. F., GENTLE, L. K., YARNELL, R. W. & QUINN, J. L. 2019. Breeding performance of an apex predator, the peregrine falcon, across urban and rural landscapes. *Urban Ecosystems,* 22**,** 117-125.

KIDAWA, D., JAKUBAS, D., WOJCZULANIS-JAKUBAS, K., STEMPNIEWICZ, L., TRUDNOWSKA, E., BOEHNKE, R., KESLINKA-NAWROT, L. & BLACHOWIAK-SAMOLYK, K. 2015. Parental efforts of an Arctic seabird, the little auk Alle alle, under variable foraging conditions. *Marine Biology Research,* 11**,** 349-360.

KILDAW, S. D., IRONS, D. B., NYSEWANDER, D. R. & BUCK, C. L. 2005. Formation and growth of new seabird colonies: The significance of habitat quality. *Marine Ornithology,* 33**,** 49-58.

KING, D. I. & DEGRAAF, R. M. 2002. The effect of forest roads on the reproductive success of forest-dwelling passerine birds. *Forest Science,* 48**,** 391-396.

KING, D. I. & DEGRAAF, R. M. 2004. Effects of group-selection opening size on the distribution and reproductive success of an early-successional shrubland bird. *Forest Ecology and Management,* 190**,** 179-185.

KING, D. I., DEGRAAF, R. M., SMITH, M. L. & BUONACCORSI, J. P. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (Seiurus aurocapilla). *Journal of Zoology,* 269**,** 414-421.

KING, D. I., GRIFFIN, C. R. & DEGRAAF, R. M. 1996. Effects of clearcutting on habitat use and reproductive success of the ovenbird in forested landscapes. *Conservation Biology,* 10**,** 1380-1386.

KISS, O., ELEK, Z. & MOSKAT, C. 2014. High breeding performance of European Rollers Coracias garrulus in heterogeneous farmland habitat in southern Hungary. *Bird Study,* 61**,** 496-505.

KNIGHT, E. C., VENNESLAND, R. G. & WINCHESTERS, N. N. 2016. Importance of Proximity to Foraging Areas for the Pacific Great Blue Heron (Ardea herodias fannini) Nesting in a Developed Landscape. *Waterbirds,* 39**,** 165-174.

KNUDSON, T. W., LOVVORN, J. R., LAWONN, M. J., CORCORAN, R. M., ROBY, D. D., PIATT, J. F. & PYLE, W. H. 2020. Can oceanic prey effects on growth and time to fledging mediate terrestrial predator limitation of an at-risk seabird? *Ecosphere,* 11**,** 20.

KNUTSON, M. G., NIEMI, G. J., NEWTON, W. E. & FRIBERG, M. A. 2004. Avian nest success in midwestern forests fragmented by agriculture. *Condor,* 106**,** 116-130.

KORFANTA, N. M., NEWMARK, W. D. & KAUFFMAN, M. J. 2012. Long-term demographic consequences of habitat fragmentation to a tropical understory bird community. *Ecology,* 93**,** 2548-2559.

KOSICKI, J. Z. 2012. Effect of weather conditions on nestling survival in the White Stork Ciconia ciconia population. *Ethology Ecology & Evolution,* 24**,** 140-148.

KOSTIN, I. O. & MOOIJ, J. H. 1995. Influence of weather conditions and other factors on the reproductive cycle of red-breasted geese Branta ruficollis on the Taymyr Peninsula. *Wildfowl,* 46**,** 43-54.

KOVAR, D. G., SPERRY, J. H. & CIMPRICH, D. A. 2018. Comparative reproductive ecology of co-occurring rare and common vireos in shrublands and woodlands. *Wilson Journal of Ornithology,* 130**,** 410-426.

KOWALCZYK, N. D., REINA, R. D., PRESTON, T. J. & CHIARADIA, A. 2015. Environmental variability drives shifts in the foraging behaviour and reproductive success of an inshore seabird. *Oecologia,* 178**,** 967-979.

KOZULIN, A. & VERGEICHYK, L. 2006. Dynamics of the aquatic warbler (acrocephalus paludicola) population at the zvanets mire (belarus). *Acta Zoologica Lituanica,* 16**,** 261-270.

KROLL, A. J. & HAUFLER, J. B. 2006. Development and evaluation of habitat models at multiple spatial scales: A case study with the dusky flycatcher. *Forest Ecology and Management,* 229**,** 161-169.

KROLL, A. J. & HAUFLER, J. B. 2007. Evaluating habitat quality for the dusky flycatcher. *Journal of Wildlife Management,* 71**,** 14-22.

KROLL, A. J. & HAUFLER, J. B. 2009. Age and clutch size variation in dusky flycatcher nest survival. *Journal of Ornithology,* 150**,** 409-417.

KUIPER, M. W., OTTENS, H. J., VAN RUIJVEN, J., KOKS, B. J., DE SNOO, G. R. & BERENDSE, F. 2015. Effects of breeding habitat and field margins on the reproductive performance of Skylarks (Alauda arvensis) on intensive farmland. *Journal of Ornithology,* 156**,** 557-568.

KURANOV, B. D., NEKHOROSHEV, O. G., GUREEV, S. P. & KILIN, S. V. 2019. Nesting of the Pied Flycatcher (Ficedula hypoleuca Pall.) in the Southeast of Western Siberia. *Contemporary Problems of Ecology,* 12**,** 607-620.

LAAKSONEN, T., LYYTINEN, S. & KORPIMAKI, E. 2004. Sex-specific recruitment and brood sex ratios of Eurasian kestrels in a seasonally and annually fluctuating northern environment. *Evolutionary Ecology,* 18**,** 215-230.

LABROUSSE, S., FRASER, A. D., SUMNER, M., LE MANACH, F., SAUSER, C., HORSTMANN, I., DEVANE, E., DELORD, K., JENOUVRIER, S. & BARBRAUD, C. 2021. Landfast ice: a major driver of reproductive success in a polar seabird. *Biology Letters,* 17**,** 7.

LAHOZ-MONFORT, J. J., HARRIS, M. P., MORGAN, B. J. T., FREEMAN, S. N. & WANLESS, S. 2014. Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival. *Journal of Applied Ecology,* 51**,** 534-543.

LAMBRECHTS, M. M., BLONDEL, J., DE FRANCESCHI, C. & DOUTRELANT, C. 2017. Nest size is positively correlated with fledging success in Corsican Blue Tits (Cyanistes caeruleus) in an insular oak-dominated habitat mosaic. *Journal of Ornithology,* 158**,** 125-132.

LAMBRECHTS, M. M., CARO, S. P., CHARMANTIER, A., GROSS, N., GALAN, M. J., PERRET, P., CARTAN-SON, M., DIAS, P. C., BLONDEL, J. & THOMAS, D. W. 2004. Habitat quality as a predictor of spatial variation in blue tit reproductive performance: a multi-plot analysis in a heterogeneous landscape. *Oecologia,* 141**,** 555-561.

LATIMER, C. E. & ZUCKERBERG, B. 2019. How extreme is extreme? Demographic approaches inform the occurrence and ecological relevance of extreme events. *Ecological Monographs,* 89**,** 15.

LATTA, S. C. & FAABORG, J. 2002. Demographic and population responses of cape may warblers wintering in multiple habitats. *Ecology,* 83**,** 2502-2515.

LAUTENBACH, J. M., HAUKOS, D. A., SULLINS, D. S., HAGEN, C. A., LAUTENBACH, J. D., PITMAN, J. C., PLUMB, R. T., ROBINSON, S. G. & KRAFT, J. D. 2019. Factors influencing nesting ecology of lesser prairie-chickens. *Journal of Wildlife Management,* 83**,** 205-215.

LAUTENBACH, J. M., PLUMB, R. T., ROBINSON, S. G., HAGEN, C. A., HAUKOS, D. A. & PITMAN, J. C. 2017. Lesser Prairie-Chicken Avoidance of Trees in a Grassland Landscape. *Rangeland Ecology & Management,* 70**,** 78-86.

LAVOIE, M., BLANCHETTE, P., LARIVIERE, S. & TREMBLAY, J. P. 2017. Winter and summer weather modulate the demography of wild turkeys at the northern edge of the species distribution. *Population Ecology,* 59**,** 239-249.

LEBLANC, J. P., BURKE, D. M. & NOL, E. 2011. Ovenbird (Seiurus aurocapilla) demography and nest-site selection in response to single-tree selection silviculture in a northern hardwood managed forest landscape. *Ecoscience,* 18**,** 26-36.

LEE, D. E., NUR, N. & SYDEMAN, W. J. 2007. Climate and demography of the planktivorous Cassin's auklet Ptychoramphus aleuticus off northern California: implications for population change. *Journal of Animal Ecology,* 76**,** 337-347.

LEHIKOINEN, A., LINDEN, A., BYHOLM, P., RANTA, E., SAUROLA, P., VALKAMA, J., KAITALA, V. & LINDEN, H. 2013. Impact of climate change and prey abundance on nesting success of a top predator, the goshawk. *Oecologia,* 171**,** 283-293.

LEHIKOINEN, A., RANTA, E., PIETIAINEN, H., BYHOLM, P., SAUROLA, P., VALKAMA, J., HUITU, O., HENTTONEN, H. & KORPIMAKI, E. 2011. The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. *Oecologia,* 165**,** 349-355.

LENGYEL, S. 2006. Spatial differences in breeding success in the pied avocet Recurvirostra avosetta: effects of habitat on hatching success and chick survival. *Journal of Avian Biology,* 37**,** 381-395.

L'HERAULT, V., FRANKE, A., LECOMTE, N., ALOGUT, A. & BETY, J. 2013. Landscape heterogeneity drives intra-population niche variation and reproduction in an arctic top predator. *Ecology and Evolution,* 3**,** 2867-2879.

LIBERATORI, F. & PENTERIANI, V. 2001. A long-term analysis of the declining population of the Egyptian vulture in the Italian peninsula: distribution, habitat preference, productivity and conservation implications. *Biological Conservation,* 101**,** 381-389.

LIMINANA, R., ARROYO, B. E., SURROCA, M., URIOS, V. & REIG-FERRER, A. 2011. Influence of habitat on nest location and reproductive output of Montagu's Harriers breeding in natural vegetation. *Journal of Ornithology,* 152**,** 557-565.

LINDBLOOM, A. J., REESE, K. P. & ZAGER, P. 2003. Nesting and brood-rearing characteristics of Chukars in West Central Idaho. *Western North American Naturalist,* 63**,** 429-439.

LINDELL, C. & SMITH, M. 2003. Nesting bird species in sun coffee, pasture, and understory forest in southern Costa Rica. *Biodiversity and Conservation,* 12**,** 423-440.

LIU, C. Y., GELIN, U., HE, R. C., LI, H. & QUAN, R. C. 2021. Flexible breeding performance under unstable climatic conditions in a tropical passerine in Southwest China. *Zoological Research,* 42**,** 221-226.

LLEDÓ, Á. O., MATEO, J. V. & MOLINER, V. U. 2018. Reproductive success of Whiskered Tern Chlidonias hybrida in eastern Spain in relation to water level variation. *PeerJ,* 2018.

LLOYD, P., MARTIN, T. E., REDMOND, R. L., LANGNER, U. & HART, M. M. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. *Ecological Applications,* 15**,** 1504-1514.

LOCKYER, Z. B., COATES, P. S., CASAZZA, M. L., ESPINOSA, S. & DELEHANTY, D. J. 2015. Nest-site selection and reproductive success of greater sage-grouse in a fire-affected habitat of northwestern Nevada. *Journal of Wildlife Management,* 79**,** 785-797.

LOHR, M., COLLINS, B. M., CASTELLI, P. M. & WILLIAMS, C. K. 2011. Life on the Edge: Northern Bobwhite Ecology at the Northern Periphery of Their Range. *Journal of Wildlife Management,* 75**,** 52-60.

LOISON, A., SAETHER, B. E., JERSTAD, K. & ROSTAD, O. W. 2002. Disentangling the sources of variation in the survival of the European dipper. *Journal of Applied Statistics,* 29**,** 289-304.

LONDE, D. W., ELMORE, R. D., DAVIS, C. A., FUHLENDORF, S. D., HOVICK, T. J., LUTTBEG, B. & RUTLEDGE, J. 2021. Weather Influences Multiple Components of Greater Prairie-Chicken Reproduction. *Journal of Wildlife Management,* 85**,** 121-134.

LÓPEZ-SEPULCRE, A., KOKKO, H. & NORRIS, K. 2010. Evolutionary conservation advice for despotic populations: Habitat heterogeneity favours conflict and reduces productivity in Seychelles magpie robins. *Proceedings of the Royal Society B: Biological Sciences,* 277**,** 3477-3482.

LORENTSEN, S. H., MATTISSON, J. & CHRISTENSEN-DALSGAARD, S. 2019. Reproductive success in the European shag is linked to annual variation in diet and foraging trip metrics. *Marine Ecology Progress Series,* 619**,** 137-147.

LOW, M., ARLT, D., EGGERS, S. & PART, T. 2010. Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. *Journal of Animal Ecology,* 79**,** 214-224.

LUCK, G. W. 2003. Differences in the reproductive success and survival of the rufous treecreeper (Climacteris rufa) between a fragmented and unfragmented landscape. *Biological Conservation,* 109**,** 1-14.

LUDWIG, G. X., ALATALO, R. V., HELLE, P. & SIITARI, H. 2010. Individual and environmental determinants of early brood survival in black grouse Tetrao tetrix. *Wildlife Biology,* 16**,** 367-378.

LUDWIG, S. C., AEBISCHER, N. J., BUBB, D., RICHARDSON, M., ROOS, S., WILSON, J. D. & BAINES, D. 2018. Population responses of Red Grouse Lagopus lagopus scotica to expansion of heather Calluna vulgaris cover on a Scottish grouse moor. *Avian Conservation and Ecology,* 13**,** 14.

LUDWIG, S. C., AEBISCHER, N. J., BUBB, D., ROOS, S. & BAINES, D. 2018. Survival of chicks and adults explains variation in population growth in a recovering red grouse Lagopus lagopus scotica population. *Wildlife Biology***,** 10.

LUO, R. S., SU, T. P., NIU, N. & LIANG, W. 2016. Effect of temperature on timing of reproduction and nesting success in a tropical population of barn swallows in South China. *Chinese Journal of Ecology,* 35**,** 2159-2163.

LUSIGNAN, A. P., MEHL, K. R., JONES, I. L. & GLOUTNEY, M. L. 2010. CONSPECIFIC BROOD PARASITISM IN COMMON EIDERS (SOMATERIA MOLLISSIMA): DO BROOD PARASITES TARGET SAFE NEST SITES? *Auk,* 127**,** 765-772.

MACDONALD, E. C., CAMFIELD, A. F., MARTIN, M., WILSON, S. & MARTIN, K. 2016. Nest-site selection and consequences for nest survival among three sympatric songbirds in an alpine environment. *Journal of Ornithology,* 157**,** 393-405.

MACFARLAND, L., MAHONY, N. A., HARRISON, M. & GREEN, D. 2019. Habitat-mediated breeding performance of Lewis's Woodpeckers (Melanerpes lewis) in British Columbia. *Plos One,* 14**,** 13.

MACHIN, P., FERNANDEZ-ELIPE, J., HUNGAR, J., ANGERBJORN, A., KLAASSEN, R. H. G. & AGUIRRE, J. I. 2019. The role of ecological and environmental conditions on the nesting success of waders in sub-Arctic Sweden. *Polar Biology,* 42**,** 1571-1579.

MACIAS-DUARTE, A., MONTOYA, A. B., HUNT, W. G., LAFON-TERRAZAS, A. & TAFANELLI, R. 2004. Reproduction, prey, and habitat of the Aplomado Falcon (Falco femoralis) in desert grasslands of Chihuahua, Mexico. *Auk,* 121**,** 1081-1093.

MACIAS-DUARTE, A., PANJABI, A. O., STRASSER, E. H., LEVANDOSKI, G. J., RUVALCABA-ORTEGA, I., DOHERTY, P. F. & ORTEGA-ROSAS, C. I. 2017. Winter survival of North American grassland birds is driven by weather and grassland condition in the Chihuahuan Desert. *Journal of Field Ornithology,* 88**,** 374-386.

MACLEOD, C. J., PARISH, D. M. B. & HUBBARD, S. F. 2004. Habitat associations and breeding success of the Chaffinch Fringilla coelebs. *Bird Study,* 51**,** 239-247.

MAHON, C. L. & MARTIN, K. 2006. Nest survival of chickadees in managed forests: Habitat, predator, and year effects. *Journal of Wildlife Management,* 70**,** 1257-1265.

MAICAS, R., BONILLO, J. C. & HAEGER, J. F. 2014. The effects of resprouting natural forest on reproductive traits of blue tits (Cyanistes caeruleus) in a stone pine afforestation. *Forest Ecology and Management,* 326**,** 117-124.

MAKAN, T., CASTRO, I., ROBERTSON, A. W., JOY, M. K. & LOW, M. 2014. Habitat complexity and management intensity positively influence fledging success in the endangered hihi (Notiomystis cincta). *New Zealand Journal of Ecology,* 38**,** 53-63.

MALLORY, M. L., GASTON, A. J., FORBES, M. R. & GILCHRIST, H. G. 2009. Influence of weather on reproductive success of northern fulmars in the Canadian high Arctic. *Polar Biology,* 32**,** 529-538.

MANIKOWSKA-SLEPOWRONSKA, B., SLEPOWRONSKI, K. & JAKUBAS, D. 2016. Grey Heron Ardea cinerea productivity in relation to habitat features and different spatial scales. *Polish Journal of Ecology,* 64**,** 384-398.

MANSOURI, I., SQUALLI, W., EL AGY, A., EL-HASSANI, A., EL GHADRAOUI, L. & DAKKI, M. 2021. Comparison of Nesting Features and Breeding Success of Turtle Dove Streptopelia turtur between Orchards and Riparian Habitats. *International Journal of Zoology,* 2021.

MANZER, D. L. & HANNON, S. J. 2005. Relating grouse nest success and corvid density to habitat: A multi-scale approach. *Journal of Wildlife Management,* 69**,** 110-123.

MANZER, D. L. & HANNON, S. J. 2008. Survival of sharp-tailed grouse Tympanuchus phasianellus chicks and hens in a fragmented prairie landscape. *Wildlife Biology,* 14**,** 16-25.

MARGALIDA, A., JIMENEZ, J., MARTINEZ, J. M., SESE, J. A., GARCIA-FERRE, D., LLAMAS, A., RAZIN, M., COLOMER, M. A. & ARROYO, B. 2020. An assessment of population size and demographic drivers of the Bearded Vulture using integrated population models. *Ecological Monographs,* 90**,** 17.

MARQUES-SANTOS, F., WISCHHOFF, U. & RODRIGUES, M. 2021. Weather fluctuations are linked to nesting success and renesting decisions in saffron finches. *Journal of Avian Biology,* 52**,** 12.

MARTIN, J. M., BRANCH, L. C., RAID, R. N. & BEYELER, S. C. 2010. TEMPORAL INSTABILITY OF AGRICULTURAL HABITAT REDUCES REPRODUCTIVE SUCCESS OF BARN OWLS (TYTO ALBA). *Auk,* 127**,** 909-916.

MARTIN, K. & WIEBE, K. L. 2004. Coping mechanisms of alpine and arctic breeding birds: Extreme weather and limitations to reproductive resilience. *Integrative and Comparative Biology,* 44**,** 177-185.

MARTINEZ, G., BALADRON, A. V., CAVALLI, M., BO, M. S. & ISACCH, J. P. 2017. MICROSCALE NEST SITE SELECTION BY THE BURROWING OWL (ATHENE CUNICULARIA) IN THE PAMPAS OF ARGENTINA. *Wilson Journal of Ornithology,* 129**,** 62-70.

MARZLUFF, J. M., WITHEY, J. C., WHITTAKER, K. A., OLEYAR, M. D., UNFRIED, T. M., RULLMAN, S. & DELAP, J. 2007. Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanizing landscape. *Condor,* 109**,** 516-534.

MASSA, B., CUSIMANO, C. A., MARGAGLIOTTA, B. & GALICI, R. 2011. Reproductive characteristics and differential response to seasonal temperatures of blue and great TITS (Cyanistes caeruleus & parus major) in three neighbouring mediterranean habitats. *Revue d'Ecologie (La Terre et la Vie),* 66**,** 157-172.

MASSOM, R. A., HILL, K., BARBRAUD, C., ADAMS, N., ANCEL, A., EMMERSON, L. & POOK, M. J. 2009. Fast ice distribution in Adelie Land, East Antarctica: interannual variability and implications for emperor penguins Aptenodytes forsteri. *Marine Ecology Progress Series,* 374**,** 243-257.

MATSUOKA, S. M. & HANDEL, C. M. 2007. Nesting ecology of boreal forest birds following a massive outbreak of spruce beetles. *Journal of Wildlife Management,* 71**,** 51-63.

MATTHYSEN, E., ADRIAENSEN, F., VAN DE KERCKHOVE, P. & VANDEKERKHOVE, K. 2021. Great and blue tit laying dates vary with fine-scale variation in local tree composition but not tree budburst. *Journal of Ornithology,* 162**,** 709-722.

MATTSSON, B. J., LATTA, S. C., COOPER, R. J. & MULVIHILL, R. S. 2011. LATITUDINAL VARIATION IN REPRODUCTIVE STRATEGIES BY THE MIGRATORY LOUISIANA WATERTHRUSH. *Condor,* 113**,** 412-418.

MCCREEDY, C. & VAN RIPER, C. 2015. Drought-caused delay in nesting of Sonoran Desert birds and its facilitation of parasite- and predator-mediated variation in reproductive success. *Auk,* 132**,** 235-247.

MCFARLAND, H. R., KENDALL, S. & POWELL, A. N. 2017. Nest-site selection and nest success of an Arctic-breeding passerine, Smith's Longspur, in a changing climate. *Condor,* 119**,** 85-97.

MCHUGH, N. M., PRIOR, M., LEATHER, S. R. & HOLLAND, J. M. 2018. Relationships between tree sparrow Passer montanus fledging success and the quantity and quality of agricultural habitats - A model comparison study. *Ecological Informatics,* 47**,** 73-76.

MCINTYRE, A. F. & HEATH, J. A. 2011. Evaluating the effects of foraging habitat restoration on shorebird reproduction: the importance of performance criteria and comparative design. *Journal of Coastal Conservation,* 15**,** 151-157.

MCKELLAR, A. E., REUDINK, M. W., MARRA, P. P., RATCLIFFE, L. M. & WILSON, S. 2015. Climate and density influence annual survival and movement in a migratory songbird. *Ecology and Evolution,* 5**,** S892-S904.

MCLEAN, I. G. & FLEMING, A. 2018. Successful restoration of an unnatural breeding habitat for white-fronted terns (Sterna striata). *Notornis,* 65**,** 54-58.

MCLEAN, N., LAWSON, C. R., LEECH, D. I. & VAN DE POL, M. 2016. Predicting when climate-driven phenotypic change affects population dynamics. *Ecology Letters,* 19**,** 595-608.

MCMASTER, D. G., DEVRIES, J. H. & DAVIS, S. K. 2005. Grassland birds nesting in haylands of southern Saskatchewan: Landscape influences and conservation priorities. *Journal of Wildlife Management,* 69**,** 211-221.

MCNEIL, D. J., RODEWALD, A. D., ROBINSON, O. J., FISS, C. J., ROSENBERG, K. V., RUIZ-GUTIERREZ, V., ALDINGER, K. R., DHONDT, A. A., PETZINGER, S. & LARKIN, J. L. 2020. Regional abundance and local breeding productivity explain occupancy of restored habitats in a migratory songbird. *Biological Conservation,* 245**,** 13.

MEEK, W. R., BURMAN, P. J., NOWAKOWSKI, M., SPARKS, T. H., HILL, R. A., SWETNAM, R. D. & BURMAN, N. J. 2009. Habitat does not influence breeding performance in a long-term Barn Owl Tyto alba study. *Bird Study,* 56**,** 369-380.

MEGANATHAN, T. & URFI, A. J. 2009. Inter-colony Variations in Nesting Ecology of Painted Stork (Mycteria leucocephala) in the Delhi Zoo (North India). *Waterbirds,* 32**,** 352-356.

MEZQUIDA, E. T. & VILLARAN, A. 2006. Abundance variations, survival and site fidelity of Reed Buntings Emberiza schoeniclus wintering in central Spain. *Ornis Fennica,* 83**,** 11-19.

MIKULA, P., HROMADA, M., ALBRECHT, T. & TRYJANOWSKI, P. 2014. Nest site selection and breeding success in three Turdus thrush species coexisting in an urban environment. *Acta Ornithologica,* 49**,** 83-92.

MOHR, L. R. D., PERICO, E., FONSECA, V. S. D. & MOHR, A. R. 2017. The breeding biology, nest success, habitat and behavior of the endangered Saffron-cowled Blackbird, Xanthopsar flavus (Aves: Icteridae), at an Important Bird Area (IBA) in Rio Grande do Sul, Brazil. *Zoologia,* 34**,** 10.

MOLLER, A. P. 2008. Climate change and micro-geographic variation in laying date. *Oecologia,* 155**,** 845-857.

MONROE, A. P., BURGER, L. W. & MARTIN, J. A. 2019. Pasture-scale vegetation predicts Dickcissel nest-site selection and success in native and exotic grass pastures. *Condor,* 121**,** 14.

MONTICELLI, D., RAMOS, J. A. & DOUCET, J. L. 2008. Influence of woodland cover on habitat selection and reproductive parameters of tropical roseate terns: Implications for colony management. *Endangered Species Research,* 4**,** 257-266.

MONTICELLI, D., RAMOS, J. A., HINES, J. E., NICHOLS, J. D. & SPENDELOW, J. A. 2008. Juvenile survival in a tropical population of roseate terns: interannual variation and effect of tick parasitism. *Marine Ecology Progress Series,* 365**,** 277-287.

MONTICELLI, D., RAMOS, J. A. & QUARTLY, G. D. 2007. Effects of annual changes in primary productivity and ocean indices on breeding performance of tropical roseate terns in the western Indian Ocean. *Marine Ecology Progress Series,* 351**,** 273-286.

MORAN-LOPEZ, R., SANCHEZ, J. M., COSTILLO, E., CORBACHO, C. & VILLEGAS, A. 2006. Spatial variation in anthropic and natural factors regulating the breeding success of the cinereous vulture (Aegypius monachus) in the SW Iberian Peninsula. *Biological Conservation,* 130**,** 169-182.

MORRISON, C. A., ROBINSON, R. A., BUTLER, S. J., CLARK, J. A. & GILL, J. A. 2016. Demographic drivers of decline and recovery in an Afro-Palaearctic migratory bird population. *Proceedings of the Royal Society B-Biological Sciences,* 283**,** 8.

MORRISON, S. A. & BOLGER, D. T. 2002. Lack of an urban edge effect on reproduction in a fragmentation-sensitive sparrow. *Ecological Applications,* 12**,** 398-411.

MORTON, M. L., SOCKMAN, K. W. & PETERSON, L. E. 1993. NEST PREDATION IN THE MOUNTAIN WHITE-CROWNED SPARROW. *Condor,* 95**,** 72-82.

MOSS, R., OSWALD, J. & BAINES, D. 2001. Climate change and breeding success: decline of the capercaillie in Scotland. *Journal of Animal Ecology,* 70**,** 47-61.

MOYNAHAN, B. J., LINDBERG, M. S. & THOMAS, J. W. 2006. Factors contributing to process variance in annual survival of female Greater Sage-Grouse in Montana. *Ecological Applications,* 16**,** 1529-1538.

MURPHY, E. C., SPRINGER, A. M. & ROSENEAU, D. G. 1991. HIGH ANNUAL VARIABILITY IN REPRODUCTIVE SUCCESS OF KITTIWAKES (RISSA-TRIDACTYLA L) AT A COLONY IN WESTERN ALASKA. *Journal of Animal Ecology,* 60**,** 515-534.

MURPHY, M. T. 1986. TEMPORAL COMPONENTS OF REPRODUCTIVE VARIABILITY IN EASTERN KINGBIRDS (TYRANNUS-TYRANNUS). *Ecology,* 67**,** 1483-1492.

MURPHY, M. T. 2004. Intrapopulation variation in reproduction by female eastern kingbirds Tyrannus tyrannus: the impacts of age, individual performance, and breeding site. *Journal of Avian Biology,* 35**,** 252-261.

MURPHY, M. T., CUMMINGS, C. L. & PALMER, M. S. 1997. Comparative analysis of habitat selection, nest site and nest success by cedar waxwings (Bombycilla cedrorum) and eastern kingbirds (Tyrannus tyrannus). *American Midland Naturalist,* 138**,** 344-356.

MURPHY, R. K., SHAFFER, T. L., GRANT, T. A., DERRIG, J. L., RUBIN, C. S. & KERNS, C. K. 2017. Sparrow Nest Survival in Relation to Prescribed Fire and Woody Plant Invasion in a Northern Mixed-Grass Prairie. *Wildlife Society Bulletin,* 41**,** 442-452.

MUSILOVA, Z., MUSIL, P., ZOUHAR, J. & POLAKOVA, S. 2014. Nest survival in the Reed Bunting Emberiza schoeniclus in fragmented wetland habitats: the effect of nest-site selection. *Ornis Fennica,* 91**,** 138-148.

NAPPI, A. & DRAPEAU, P. 2009. Reproductive success of the black-backed woodpecker (Picoides arcticus) in burned boreal forests: Are burns source habitats? *Biological Conservation,* 142**,** 1381-1391.

NEATE-CLEGG, M. H. C., HORNS, J. J., BUCHERT, M., POPE, T. L., NORVELL, R., PARRISH, J. R., HOWE, F. & SEKERCIOGLU, C. H. The effects of climate change and fluctuations on the riparian bird communities of the arid Intermountain West. *Animal Conservation***,** 17.

NEATE-CLEGG, M. H. C., STANLEY, T. R., SEKERCIOGLU, C. H. & NEWMARK, W. D. 2021. Temperature-associated decreases in demographic rates of Afrotropical bird species over 30 years. *Global Change Biology,* 27**,** 2254-2268.

NEL, D. C., TAYLOR, F., RYAN, P. G. & COOPER, J. 2003. Population dynamics of the wandering albatross Diomedea exulans at Marion Island: Longline fishing and environmental influences. *African Journal of Marine Science,* 25**,** 503-517.

NEVOUX, M., BARBRAUD, J. C. & BARBRAUD, C. 2008. Breeding experience and demographic response to environmental variability in the White Stork. *Condor,* 110**,** 55-62.

NEVOUX, M., WEIMERSKIRCH, H. & BARBRAUD, C. 2010. Long- and short-term influence of environment on recruitment in a species with highly delayed maturity. *Oecologia,* 162**,** 383-392.

NEWHOUSE, M. J., MARRA, P. P. & JOHNSON, L. S. 2008. Reproductive success of House Wrens in suburban and rural landscapes. *Wilson Journal of Ornithology,* 120**,** 99-104.

NGUYEN, L. P., NOL, E. & ABRAHAM, K. F. 2003. Nest success and habitat selection of the semipalmated plover on Akimiski Island, Nunavut. *Wilson Bulletin,* 115**,** 285-291.

NICOLAU, P. G., BURGESS, M. D., MARQUES, T. A., BAILLIE, S. R., MORAN, N. J., LEECH, D. I. & JOHNSTON, A. 2021. Latitudinal variation in arrival and breeding phenology of the pied flycatcher Ficedula hypoleuca using large-scale citizen science data. *Journal of Avian Biology,* 52**,** 12.

NIEDERHAUSER, J. M. & BOWMAN, R. 2014. Testing sources of variation in nestling-stage nest success of Florida Scrub-Jays in suburban and wildland habitats. *Journal of Field Ornithology,* 85**,** 180-195.

NILSSON, L. & PERSSON, H. 1993. Variation in survival in an increasing population of the greylag goose Anser anser in Scania, southern Sweden. *Ornis Svecica,* 3**,** 137-146.

NOA, L. A., HIRTH, D. H., DONOVAN, T. M. & CIMPRICH, D. 2007. Demographic differences of black-capped vireos in 2 habitat types in central Texas. *Journal of Wildlife Management,* 71**,** 1042-1049.

NORRIS, D. R., FLOCKHART, D. T. T. & STRICKLAND, D. 2013. Contrasting patterns of survival and dispersal in multiple habitats reveal an ecological trap in a food-caching bird. *Oecologia,* 173**,** 827-835.

NORRIS, D. R., MARRA, P. P., KYSER, T. K., SHERRY, T. W. & RATCLIFFE, L. M. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B-Biological Sciences,* 271**,** 59-64.

NOTT, M. P., DESANTE, D. F., SIEGEL, R. B. & PYLE, P. 2002. Influences of the El Nino/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. *Global Ecology and Biogeography,* 11**,** 333-342.

NUIJTEN, R. J. M., VRIEND, S. J. G., WOOD, K. A., HAITJEMA, T., REES, E. C., JONGEJANS, E. & NOLET, B. A. 2020. Apparent breeding success drives long-term population dynamics of a migratory swan. *Journal of Avian Biology,* 51**,** 12.

OGUTU, J. O., PIEPHO, H. P. & DUBLIN, H. T. 2012. Ostrich recruitment dynamics in relation to rainfall in the Mara-Serengeti ecosystem. *Ostrich,* 83**,** 119-136.

OKADA, S., LINDENMAYER, D. B., WOOD, J. T., CRANE, M. J. & PIERSON, J. C. 2017. How does a transforming landscape influence bird breeding success? *Landscape Ecology,* 32**,** 1039-1048.

OLIVIER, F., VAN FRANEKER, J. A., CREUWELS, J. C. S. & WOEHLER, E. J. 2005. Variations of snow petrel breeding success in relation to sea-ice extent: detecting local response to large-scale processes? *Polar Biology,* 28**,** 687-699.

OLMASTRONI, S., PEZZO, F., VOLPI, V. & FOCARDI, S. 2004. Effects of weather and sea-ice on the reproductive performance of the Adélie penguin at Edmonson Point, Ross Sea. *CCAMLR Science,* 11**,** 99-109.

OLSEN, P. & MARPLES, T. G. 1993. GEOGRAPHIC-VARIATION IN EGG SIZE, CLUTCH SIZE AND DATE OF LAYING OF AUSTRALIAN RAPTORS (FALCONIFORMES AND STRIGIFORMES). *Emu-Austral Ornithology,* 93**,** 167-179.

OLSSON, O., WIKTANDER, U., MALMQVIST, A. & NILSSON, S. G. 2001. Variability of patch type preferences in relation to resource availability and breeding success in a bird. *Oecologia,* 127**,** 435-443.

O'NEIL, S. T., COATES, P. S., BRUSSEE, B. E., RICCA, M. A., ESPINOSA, S. P., GARDNER, S. C. & DELEHANTY, D. J. 2020. Wildfire and the ecological niche: Diminishing habitat suitability for an indicator species within semi-arid ecosystems. *Global Change Biology,* 26**,** 6296-6312.

ORLOWSKI, G., KARG, J., JERZAK, L., BOCHENSKI, M., PROFUS, P., KSIAZKIEWICZ-PARULSKA, Z., ZUB, K., EKNER-GRZYB, A. & CZARNECKA, J. 2019. Linking land cover satellite data with dietary variation and reproductive output in an opportunistic forager: Arable land use can boost an ontogenetic trophic bottleneck in the White Stork Ciconia ciconia. *Science of the Total Environment,* 646**,** 491-502.

ORO, D., TORRES, R., RODRIGUEZ, C. & DRUMMOND, H. 2010. Climatic influence on demographic parameters of a tropical seabird varies with age and sex. *Ecology,* 91**,** 1205-1214.

ÖST, M., LEHIKOINEN, A. & JAATINEN, K. 2022. Top–down effects override climate forcing on reproductive success in a declining sea duck. *Oikos,* 2022.

OST, M., WICKMAN, M., MATULIONIS, E. & STEELE, B. 2008. Habitat-specific clutch size and cost of incubation in eiders reconsidered. *Oecologia,* 158**,** 205-216.

OWEN, T. M. & PIERCE, A. R. 2013. Hatching Success and Nest Site Characteristics of Black Skimmer (Rynchops niger) on the Isles Dernieres Barrier Island Refuge, Louisiana. *Waterbirds,* 36**,** 342-347.

PAIJMANS, D. M., LOEWENTHAL, D., RYAN, P. G. & HOCKEY, P. A. R. 2015. Temporal and spatial differences in three-egg clutch frequency of the African Black Oystercatcher. *Ostrich,* 86**,** 35-41.

PAKANEN, V. M., HAGSTEDT, R., PAULINY, A. & BLOMQVIST, D. 2021. Survival during the pre-fledging period rather than during post-fledging drives variation in local recruitment of an endangered migratory shorebird, the Southern DunlinCalidris alpina schinzii. *Journal of Ornithology,* 162**,** 119-124.

PALMER, W. E., PUCKETT, K. M., ANDERSON, J. R. & BROMLEY, P. T. 1998. Effects of foliar insecticides on survival of northern bobwhite quail chicks. *Journal of Wildlife Management,* 62**,** 1565-1573.

PANEK, M. 1997. The effect of agricultural landscape structure on food resources and survival of grey partridge Perdix perdix chicks in Poland. *Journal of Applied Ecology,* 34**,** 787-792.

PAQUET, M., ARLT, D., KNAPE, J., LOW, M., FORSLUND, P. & PART, T. 2019. Quantifying the links between land use and population growth rate in a declining farmland bird. *Ecology and Evolution,* 9**,** 868-879.

PAREDES, R., HARDING, A. M. A., IRONS, D. B., ROBY, D. D., SURYAN, R. M., ORBEN, R. A., RENNER, H., YOUNG, R. & KITAYSKY, A. 2012. Proximity to multiple foraging habitats enhances seabirds' resilience to local food shortages. *Marine Ecology Progress Series,* 471**,** 253-269.

PASITSCHNIAK-ARTS, M., CLARK, R. G. & MESSIER, F. 1998. Duck nesting success in a fragmented prairie landscape: is edge effect important? *Biological Conservation,* 85**,** 55-62.

PATERSON, I. W., BOYER, P. R. & MASSEN, D. D. 1990. Variations in clutch size and breeding success of greylag geese Anser anser in the Uists, Scotland. *Wildfowl,* 41**,** 18-22.

PAYO-PAYO, A., GENOVART, M., BERTOLERO, A., PRADEL, R. & ORO, D. 2016. Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird. *Proceedings of the Royal Society B-Biological Sciences,* 283**,** 6.

PEARCE, J. M., REED, J. A. & FLINT, P. L. 2005. Geographic variation in survival and migratory tendency among North American Common Mergansers. *Journal of Field Ornithology,* 76**,** 109-118.

PENTERIANI, V., DELGADO, M. D., GALLARDO, M. & FERRER, M. 2004. Spatial heterogeneity and structure of bird populations: a case example with the eagle owl. *Population Ecology,* 46**,** 185-192.

PERKINS, D. W., VICKERY, P. D. & SHRIVER, W. G. 2003. Spatial dynamics of source-sink habitats: Effects on rare grassland birds. *Journal of Wildlife Management,* 67**,** 588-599.

PERSSON, M. 2003. Habitat quality, breeding success and density in Tawny Owl Strix aluco. *Ornis Svecica,* 13**,** 137-143.

PETERS, D. C., BROOKE, J. M., TANNER, E. P., UNGER, A. M., KEYSER, P. D., HARPER, C. A., CLARK, J. D. & MORGAN, J. J. 2015. Impact of experimental habitat manipulation on northern bobwhite survival. *Journal of Wildlife Management,* 79**,** 605-617.

PEZZO, F., OLMASTRONI, S., CORSOLINI, S. & FOCARDI, S. 2001. Factors affecting the breeding success of the south polar skua Catharacta maccormicki at Edmonson Point, Victoria Land, Antarctica. *Polar Biology,* 24**,** 389-393.

PIDGEON, A. M., RADELOFF, V. C. & MATHEWS, N. E. 2003. Landscape-scale patterns of black-throated sparrow (Amphispiza bilineata) abundance and nest success. *Ecological Applications,* 13**,** 530-542.

PIERSMA, T., LOK, T., CHEN, Y., HASSELL, C. J., YANG, H. Y., BOYLE, A., SLAYMAKER, M., CHAN, Y. C., MELVILLE, D. S., ZHANG, Z. W. & MA, Z. J. 2016. Simultaneous declines in summer survival of three shorebird species signals a flyway at risk. *Journal of Applied Ecology,* 53**,** 479-490.

PIPER, S. E. 2002. Survival of adult, territorial Longtailed Wagtails Motacilla clara: the effects of environmental factors and individual covariates. *Journal of Applied Statistics,* 29**,** 107-124.

PLEASANT, G. D., DABBERT, C. B. & MITCHELL, R. B. 2006. Nesting ecology and survival of scaled quail in the Southern High Plains of Texas. *Journal of Wildlife Management,* 70**,** 632-640.

POLAK, M. 2016. Nest survival patterns in Eurasian Bittern: effect of nest age, time and habitat variables. *Peerj,* 4**,** 14.

POLLOCK, H. S., SAVIDGE, J. A., KASTNER, M., SEIBERT, T. F. & JONES, T. M. 2019. Pervasive impacts of invasive brown treesnakes drive low fledgling survival in endangered Micronesian Starlings (Aplonis opaca) on Guam. *Condor,* 121**,** 11.

PONCHON, A., GREMILLET, D., CHRISTENSEN-DALSGAARD, S., ERIKSTAD, K. E., BARRETT, R. T., REIERTSEN, T. K., MCCOY, K. D., TVERAA, T. & BOULINIER, T. 2014. When things go wrong: intra-season dynamics of breeding failure in a seabird. *Ecosphere,* 5**,** 19.

POSADAS-LEAL, C., CHAPA-VARGAS, L., ARREDONDO-MORENO, J. T. & HUBER-SANNWALD, E. 2010. Effects of habitat type on bird nesting in the desert grasslands of central Mexico: conservation implications. *Oryx,* 44**,** 448-454.

POWELL, G. V. N. & POWELL, A. H. 1986. Reproduction by great white herons Ardea herodias in Florida Bay as an indicator of habitat quality. *Biological Conservation,* 36**,** 101-113.

PRETELLI, M. G., ISACCH, J. P. & CARDONI, D. A. 2015. Effects of fragmentation and landscape matrix on the nesting success of grassland birds in the Pampas grasslands of Argentina. *Ibis,* 157**,** 688-699.

PROETT, M., ROBERTS, S. B., HORNE, J. S., KOONS, D. N. & MESSMER, T. A. 2019. Columbian sharp-tailed grouse nesting ecology: wind energy and habitat. *Journal of Wildlife Management,* 83**,** 1214-1225.

PROKOSCH, J., BERNITZ, Z., BERNITZ, H., ERNI, B. & ALTWEGG, R. 2019. Are animals shrinking due to climate change? Temperature-mediated selection on body mass in mountain wagtails. *Oecologia,* 189**,** 841-849.

QUEROUE, M., BARBRAUD, C., BARRAQUAND, F., TUREK, D., DELORD, K., PACOUREAU, N. & GIMENEZ, O. 2021. Multispecies integrated population model reveals bottom-up dynamics in a seabird predator-prey system. *Ecological Monographs,* 91**,** 17.

RACKETE, C., PONCET, S., GOOD, S. D., PHILLIPS, R. A., PASSFIELD, K. & TRATHAN, P. 2021. Variation among colonies in breeding success and population trajectories of wandering albatrosses Diomedea exulans at South Georgia. *Polar Biology,* 44**,** 221-227.

RAMIREZ, F., AFAN, I., TAVECCHIA, G., CATALAN, I. A., ORO, D. & SANZ-AGUILAR, A. 2016. Oceanographic drivers and mistiming processes shape breeding success in a seabird. *Proceedings of the Royal Society B-Biological Sciences,* 283**,** 7.

RAMOS, J. A. 2001. Seasonal variation in reproductive measures of tropical Roseate Terns Sterna dougallii: previously undescribed breeding patterns in a seabird. *Ibis,* 143**,** 83-91.

RAMOS, J. A., MAUL, A. M., BOWLER, J., WOOD, L., THREADGOLD, R., JOHNSON, S., BIRCH, D. & WALKER, S. 2006. Annual variation in laying date and breeding success of Brown Noddies on Aride Island, Seychelles. *Emu-Austral Ornithology,* 106**,** 81-86.

RANGEL-SALAZAR, J. L., MARTIN, K., MARSHALL, P. & ELNER, R. W. 2008. Influence of habitat variation, nest-site selection, and parental behavior on breeding success of Ruddy-capped Nightingale Thrushes (Catharus frantzii) in Chiapas, Mexico. *Auk,* 125**,** 358-367.

RANGEL-SALAZAR, J. L., MARTIN, K., MARSHALL, P. & ELNER, R. W. 2008. Population dynamics of the ruddy-capped nightingale thrush (Catharus frantzil) in Chiapas, Mexico: influences of density, productivity and survival. *Journal of Tropical Ecology,* 24**,** 583-593.

RANTANEN, E. M., BUNER, F., RIORDAN, P., SOTHERTON, N. & MACDONALD, D. W. 2010. Habitat preferences and survival in wildlife reintroductions: an ecological trap in reintroduced grey partridges. *Journal of Applied Ecology,* 47**,** 1357-1364.

RAYBUCK, D. W., LARKIN, J. L., STOLESON, S. H. & BOVES, T. J. 2020. Radio-tracking reveals insight into survival and dynamic habitat selection of fledgling Cerulean Warblers. *Condor,* 122**,** 1-15.

REED, T. E., JENOUVRIER, S. & VISSER, M. E. 2013. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology,* 82**,** 131-144.

REID, T., LADA, H., SELWOOD, K. E., HORROCKS, G. F. B., THOMSON, J. R. & MAC NALLY, R. Responses of floodplain birds to high-amplitude precipitation fluctuations over two decades. *Austral Ecology***,** 13.

REIDY, J. L., THOMPSON, F. R., CONNETTE, G. M. & O'DONNELL, L. 2018. Demographic rates of Golden-cheeked Warblers in an urbanizing woodland preserve. *Condor,* 120**,** 249-264.

RICKETTS, C. E., KURIMO-BEECHUK, E., MILLS, W. E., COOPER, R. J., SCHWEITLER, S. H., WIGGERS, E. P. & HEPINSTALL-CYMERMAN, J. 2020. Local and Landscape Analyses of Habitat Selection of South Carolina Clapper Rails (Rallus crepitans). *Waterbirds,* 43**,** 281-291.

RIDDINGTON, R. & GOSLER, A. G. 1995. DIFFERENCES IN REPRODUCTIVE SUCCESS AND PARENTAL QUALITIES BETWEEN HABITATS IN THE GREAT TIT PARUS-MAJOR. *Ibis,* 137**,** 371-378.

RIDLEY, A. R. 2007. Factors affecting offspring survival and development in a cooperative bird: social, maternal and environmental effects. *Journal of Animal Ecology,* 76, 750-760.

RILEY, T. Z., CLARK, W. R., EWING, D. E. & VOHS, P. A. 1998. Survival of ring-necked pheasant chicks during brood rearing. *Journal of Wildlife Management,* 62, 36-44.

RINGSBY, T. H., SÆTHER, B. E., ALTWEGG, R. & SOLBERG, E. J. 1999. Temporal and spatial variation in survival rates of a house sparrow, Passer domesticus, metapopulation. *Oikos,* 85, 419-425.

ROBINSON, D. H., MATHEWSON, H. A., MORRISON, M. L. & WILKINS, R. N. 2018. Habitat Effects on Golden-cheeked Warbler Productivity in an Urban Landscape. *Wildlife Society Bulletin,* 42, 48-56.

ROBINSON, R. A., BAILLIE, S. R. & KING, R. 2012. Population processes in European Blackbirds Turdus merula: a state-space approach. *Journal of Ornithology,* 152, S419-S433.

ROBLES, H., CIUDAD, C., VERA, R. & BAGLIONE, V. 2007. No effect of habitat fragmentation on post-fledging, first-year and adult survival in the middle spotted woodpecker. *Ecography,* 30, 685-694.

ROBLES, H., CIUDAD, C., VERA, R., OLEA, P. P. & MATTHYSEN, E. 2008. Demographic responses of Middle Spotted Woodpeckers (Dendrocopos medius) to habitat fragmentation. *Auk,* 125, 131-139.

RODEWALD, A. D. 2002. Nest predation in forested regions: Landscape and edge effects. *Journal of Wildlife Management,* 66, 634-640.

RODGERS, J. A., BROOKS, W. B. & BARRETT, M. 2012. Productivity and Habitat Modeling of Wood Storks Nesting in North and Central Florida. *Journal of Fish and Wildlife Management,* 3, 252-265.

RODRIGUEZ, B., RODRIGUEZ, A., LORENZO, J. A. & MARTINEZ, J. M. 2021. Exotic tree plantations as alternative breeding habitat for an endemic avian predator. *Journal of Avian Biology,* 52, 15.

RODWAY, M. S. & REGEHR, H. M. 1999. Habitat selection and reproduction performance of food-stressed herring gulls. *Condor,* 101, 566-576.

ROGERS, C. M. 2013. MINIMUM ANNUAL SURVIVAL ESTIMATES OF MALE CERULEAN WARBLERS (SETOPHAGA CERULEA) IN SOUTHWESTERN MICHIGAN. *Wilson Journal of Ornithology,* 125, 370-375.

ROGERS, C. M., SMITH, J. N. M., HOCHACHKA, W. M., CASSIDY, A., TAITT, M. J., ARCESE, P. & SCHLUTER, D. 1991. SPATIAL VARIATION IN WINTER SURVIVAL OF SONG SPARROWS MELOSPIZA-MELODIA. *Ornis Scandinavica,* 22, 387-395.

ROLLAND, V., HOSTETLER, J. A., HINES, T. C., JOHNSON, F. A., PERCIVAL, H. F. & OLI, M. K. 2011. Effects of harvest and climate on population dynamics of northern bobwhites in south Florida. *Wildlife Research,* 38, 396-407.

ROONEY, E., REID, N. & MONTGOMERY, W. I. 2015. Supplementary feeding increases Common Buzzard Buteo buteo productivity but only in poor-quality habitat. *Ibis,* 157, 181-185.

RORVIK, K. A., PEDERSEN, H. C. & STEEN, J. B. 1999. An impact of genetic variation and predation on chick survival in willow ptarmigan Lagopus l. lagopus. *Wildlife Biology,* 5, 129-135.

ROSENFIELD, R. N., BIELEFELDT, J., ROSENFIELD, L. J., STEWART, A. C., NENNEMAN, M. P., MURPHY, R. K. & BOZEK, M. A. 2007. Variation in reproductive indices in three populations of Cooper's Hawks. *Wilson Journal of Ornithology,* 119, 181-188.

ROUNDS, R. A., ERWIN, R. M. & PORTER, J. H. 2004. Nest-site selection and hatching success of waterbirds in coastal Virginia: some results of habitat manipulation. *Journal of Field Ornithology,* 75, 317-329.

RUSH, S. A. & STUTCHBURY, B. J. M. 2008. Survival of fledgling Hooded Warblers (Wilsonia citrina) in small and large forest fragments. *Auk,* 125, 183-191.

RUSKIN, K. J., ETTERSON, M. A., HODGMAN, T. P., BOROWSKE, A. C., COHEN, J. B., ELPHICK, C. S., FIELD, C. R., LONGENECKER, R. A., KING, E., KOCEK, A. R., KOVACH, A. I., O'BRIEN, K. M., PAU, N., SHRIVER, W. G., WALSH, J. & OLSEN, B. J. 2017. Demographic analysis demonstrates systematic but independent spatial variation in abiotic and biotic stressors across 59 percent of a global species range. *Auk,* 134, 903-916.

RUSKIN, K. J., HODGMAN, T. P., ETTERSON, M. A. & OLSEN, B. J. 2015. Divergent oviposition preferences of sister species are not driven by nest survival: the evidence for neutrality. *Behavioral Ecology and Sociobiology,* 69, 1639-1647.

RUSTICALI, R., SCARTON, F. & VALLE, R. 1999. Habitat selection and hatching success of Eurasian Oystercatchers in relation to nesting Yellow-legged Gulls and human presence. *Waterbirds,* 22, 367-375.

RUTH, J. M. & SKAGEN, S. K. 2018. Reproductive response of Arizona Grasshopper Sparrows to weather patterns and habitat structure. *Condor,* 120, 596-616.

RUTHRAUFF, D. R., KELLER, J. N. & RIZZOLO, D. J. 2009. Ecological factors regulating brood attendance patterns of the Western Sandpiper Calidris mauri. *Ibis,* 151, 523-534.

SAAB, V. A. & VIERLING, K. T. 2001. Reproductive success of Lewis's Woodpecker in burned pine and cottonwood riparian forests. *Condor,* 103, 491-501.

SADOTI, G., POLLOCK, M. G., VIERLING, K. T., ALBRIGHT, T. P. & STRAND, E. K. 2014. Variogram models reveal habitat gradients predicting patterns of territory occupancy and nest survival among vesper sparrows. *Wildlife Biology,* 20, 97-107.

SALAFSKY, S. R., REYNOLDS, R. T., NOON, B. R. & WIENS, J. A. 2007. Reproductive responses of northern goshawks to variable prey populations. *Journal of Wildlife Management,* 71, 2274-2283.

SALVATI, L., MANGANARO, A., FATTORINI, S. & PIATTELLA, E. 1999. Population features of Kestrels Falco tinnunculus in urban, suburban and rural areas in Central Italy. *Acta Ornithologica,* 34, 53-58.

SANCHEZ, R., BLENDINGER, P. G., WAGNER, E. M. & MARTIN, E. 2013. HIERARCHICAL HABITAT SELECTION AND REPRODUCTIVE SUCCESS OF THE RINGED WARBLING-FINCH IN CHACO WOODLANDS. *Condor,* 115, 893-901.

SANTISTEBAN, L., BENKMAN, C. W., FETZ, T. & SMITH, J. W. 2012. Survival and population size of a resident bird species are declining as temperature increases. *Journal of Animal Ecology,* 81, 352-363.

SANZ, J. J., POTTI, J., MORENO, J., MERINO, S. & FRIAS, O. 2003. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Global Change Biology,* 9, 461-472.

SARA, M., CAMPOBELLO, D. & ZANCA, L. 2012. Effects of nest and colony features on Lesser Kestrel (Falco naumanni) reproductive success. *Avian Biology Research,* 5, 209-217.

SARACCO, J. F., RADLEY, P., PYLE, P., ROWAN, E., TAYLOR, R. & HELTON, L. 2016. Linking Vital Rates of Landbirds on a Tropical Island to Rainfall and Vegetation Greenness. *Plos One,* 11**,** 18.

SASVARI, L. & HEGYI, Z. 2005. Effects of breeding experience on nest-site choice and the reproductive performance of tawny owls (Strix aluco). *Journal of Raptor Research,* 39**,** 26-35.

SAUSER, C., DELORD, K. & BARBRAUD, C. 2021. Sea ice and local weather affect reproductive phenology of a polar seabird with breeding consequences. *Ornithological Applications,* 123**,** 13.

SCHAEFER, T., LEDEBUR, G., BEIER, J. & LEISLER, B. 2006. Reproductive responses of two related coexisting songbird species to environmental changes: global warming, competition, and population sizes. *Journal of Ornithology,* 147**,** 47-56.

SCHAUB, M., JAKOBER, H. & STAUBER, W. 2011. Demographic response to environmental variation in breeding, stopover and non-breeding areas in a migratory passerine. *Oecologia,* 167**,** 445-459.

SCHAUB, M., KANIA, W. & KOPPEN, U. 2005. Variation of primary production during winter induces synchrony in survival rates in migratory white storks Ciconia ciconia. *Journal of Animal Ecology,* 74**,** 656-666.

SCHAUB, M., REICHLIN, T. S., ABADI, F., KERY, M., JENNI, L. & ARLETTAZ, R. 2012. The demographic drivers of local population dynamics in two rare migratory birds. *Oecologia,* 168**,** 97-108.

SCHIFFERLI, L., RICKENBACH, O., KOLLER UND, A. & GRÜEBLER, M. 2009. Nest protection from agriculture and predation to improve nest and chick survival of the Northern Lapwing Vanellus vanellus in Swiss farmland. *Ornithologische Beobachter,* 106**,** 311-326.

SCHLESSELMANN, A. K. V., O'DONNELL, C. F. J., MONKS, J. M. & ROBERTSON, B. C. 2018. Clearing islands as refugia for black-fronted tern (Chlidonias albostriatus) breeding colonies in braided rivers. *New Zealand Journal of Ecology,* 42**,** 137-148.

SCOTT, J. L., HERNÁNDEZ, F., BRENNAN, L. A., BALLARD, B. M., JANIS, M. & FORRESTER, N. D. 2013. Population demographics of translocated northern bobwhites on fragmented habitat. *Wildlife Society Bulletin,* 37**,** 168-176.

SEAGLE, S. W. & STURTEVANT, B. R. 2005. Forest productivity predicts invertebrate biomass and ovenbird (Seiurus aurocapillus) reproduction in Appalachian landscapes. *Ecology,* 86**,** 1531-1539.

SECKINGER, E. M., BURGER JR, L. W., WHITTINGTON, R., HOUSTON, A. & CARLISLE, R. 2008. Effects of landscape composition on winter survival of northern bobwhites. *Journal of Wildlife Management,* 72**,** 959-969.

SEGURA, L. N. & BERKUNSKY, I. 2012. Nest survival of the Red-crested Cardinal (Paroaria coronata) in a modified habitat in Argentina. *Ornitologia Neotropical,* 23**,** 489-498.

SELAS, V., SONERUD, G. A., FRAMSTAD, E., KALAS, J. A., KOBRO, S., PEDERSEN, H. B., SPIDSO, T. K. & WIIG, O. 2011. Climate change in Norway: warm summers limit grouse reproduction. *Population Ecology,* 53**,** 361-371.

SEWARD, A. M., BEALE, C. M., GILBERT, L., JONES, T. H. & THOMAS, R. J. 2014. The Impact of Increased Food Availability on Reproduction in a Long-Distance Migratory Songbird: Implications for Environmental Change? *Plos One,* 9**,** 11.

SHAVE, A., GARROWAY, C. J., SIEGRIST, J. & FRASER, K. C. 2019. Timing to temperature: Egg-laying dates respond to temperature and are under stronger selection at northern latitudes. *Ecosphere,* 10**,** 15.

SHELDON, R. D., KAMP, J., KOSHKIN, M. A., URAZALIEV, R. S., ISKAKOV, T. K., FIELD, R. H., SALEMGAREEV, A. R., KHROKOV, V. V., ZHULY, V. A., SKLYARENKO, S. L. & DONALD, P. F. 2013. Breeding ecology of the globally threatened Sociable Lapwing Vanellus gregarius and the demographic drivers of recent declines. *Journal of Ornithology,* 154**,** 501-516.

SHERLEY, R. B., BARHAM, B. J., BARHAM, P. J., LESHORO, T. M. & UNDERHILL, L. G. 2012. Artificial nests enhance the breeding productivity of African Penguins (Spheniscus demersus) on Robben Island, South Africa. *Emu,* 112**,** 97-106.

SHERRY, T. W., WILSON, S., HUNTER, S. & HOLMES, R. T. 2015. Impacts of nest predators and weather on reproductive success and population limitation in a long-distance migratory songbird. *Journal of Avian Biology,* 46**,** 559-569.

SHEWRING, M., JENKS, P., CROSS, A. V., VAUGHAN, I. P. & THOMAS, R. J. 2020. Testing for effects of tail-mounted radio tags and environmental variables on European Nightjar Caprimulgus europaeus nest survival. *Bird Study,* 67**,** 429-439.

SHIAO, M. T., CHUANG, M. C., YUAN, H. W. & WANG, Y. 2015. Effects of weather variation on the timing and success of breeding in two cavity-nesting species in a subtropical montane forest in Taiwan. *Auk,* 132**,** 671-684.

SHIPLEY, K. L. & SCOTT, D. P. 2006. Survival and nesting habitat use by Sichuan and ring-necked pheasants released in Ohio. *Ohio Journal of Science,* 106**,** 78-85.

SICURELLA, B., CAFFI, M., CAPRIOLI, M., RUBOLINI, D., SAINO, N. & AMBROSINI, R. 2015. Weather conditions, brood size and hatching order affect Common Swift Apus apus nestlings survival and growth. *Bird Study,* 62**,** 64-77.

SILLETT, T. S., HOLMES, R. T. & SHERRY, T. W. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science,* 288**,** 2040-2042.

SIM, I. M. W., REBECCA, G. W., LUDWIG, S. C., GRANT, M. C. & REID, J. M. 2011. Characterizing demographic variation and contributions to population growth rate in a declining population. *Journal of Animal Ecology,* 80**,** 159-170.

SIRIWARDENA, G. M., BAILLIE, S. R. & WILSON, J. D. 1999. Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. *Ibis,* 141**,** 621-636.

SIRIWARDENA, G. M., CRICK, H. Q. P., BAILLIE, S. R. & WILSON, J. D. 2000. Agricultural habitat-type and the breeding performance of granivorous farmland birds in Britain. *Bird Study,* 47**,** 66-81.

SIRKIA, P. M., VIROLAINEN, M. & LAAKSONEN, T. 2010. Melanin coloration has temperature-dependent effects on breeding performance that may maintain phenotypic variation in a passerine bird. *Journal of Evolutionary Biology,* 23**,** 2385-2396.

SJOBERG, K., PETTERSSON, R. & ATLEGRIM, O. 1993. Differences in bird habitat quality between plantations of Scots and lodgepole pine measured in terms of pied flycatcher Ficedula hypoleuca breeding success. *Ornis Svecica,* 3**,** 59-68.

SLOBODNIK, R., BALAZOVA, M., JANDZIK, D. & BALAZ, M. 2013. Local weather differently affects collared flycatcher reproduction at different altitudes. *Central European Journal of Biology,* 8**,** 1145-1152.

SMART, J., GILL, J. A., SUTHERLAND, W. J. & WATKINSON, A. R. 2006. Grassland-breeding waders: identifying key habitat requirements for management. *Journal of Applied Ecology,* 43**,** 454-463.

SMITH, R. J., HATCH, M. I. & CAREY, M. 2020. Arrival timing and the influence of weather experienced during the nonbreeding and breeding periods on correlates of reproductive success in female field sparrows (Spizella pusilla) breeding in northeastern

Pennsylvania, USA. *International Journal of Biometeorology,* 64**,** 1285-1293.

SMITH, R. J. & MOORE, F. R. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behavioral Ecology and Sociobiology,* 57**,** 231-239.

SOFAER, H. R., SILLETT, T. S., LANGIN, K. M., MORRISON, S. A. & GHALAMBOR, C. K. 2014. Partitioning the sources of demographic variation reveals density-dependent nest predation in an island bird population. *Ecology and Evolution,* 4**,** 2738-2748.

SOVADA, M. A., IGL, L. D., PIETZ, P. J. & BARTOS, A. J. 2014. Influence of Climate Change on Productivity of American White Pelicans, Pelecanus erythrorhynchos. *Plos One,* 9**,** 8.

SPENDELOW, J. A., HINES, J. E., NICHOLS, J. D., NISBET, I. C. T., CORMONS, G., HAYS, H., HATCH, J. J. & MOSTELLO, C. S. 2008. Temporal Variation in Adult Survival Rates of Roseate Terns During Periods of Increasing and Declining Populations. *Waterbirds,* 31**,** 309-319.

SPERRY, J. H., BARRON, D. G. & WEATHERHEAD, P. J. 2012. Snake behavior and seasonal variation in nest survival of northern cardinals Cardinalis cardinalis. *Journal of Avian Biology,* 43**,** 496-502.

STALWICK, J. A. & WIEBE, K. L. 2019. Lower reproductive output of Mountain Bluebirds (Sialia currucoides) in clearcut versus grassland habitat is consistent with a passive ecological trap. *Canadian Journal of Zoology,* 97**,** 895-903.

STANBACK, M. T. & SEIFERT, M. L. 2005. A comparison of eastern bluebird reproductive parameters in golf and rural habitats. *Wildlife Society Bulletin,* 33**,** 471-482.

STEEN, H. & ERIKSTAD, K. E. 1996. Sensitivity of willow grouse Lagopus lagopus population dynamics to variations in demographic parameters. *Wildlife Biology,* 2**,** 27-35.

STERNALSKI, A., BLANC, J. F., AUGIRON, S., ROCHETEAU, V. & BRETAGNOLLE, V. 2013. Comparative breeding performance of Marsh Harriers Circus aeruginosus along a gradient of land-use intensification and implications for population management. *Ibis,* 155**,** 55-67.

STEVENS, D. K., ANDERSON, G. Q. A., GRICE, P. V. & NORRIS, K. 2007. Breeding success of Spotted Flycatchers Muscicapa striata in southern England - is woodland a good habitat for this species? *Ibis,* 149**,** 214-223.

STILLMAN, A. N., LORENZ, T. J., FISCHER, P. C., SIEGEL, R. B., WILKERSON, R. L., JOHNSON, M. & TINGLEY, M. W. 2021. Juvenile survival of a burned forest specialist in response to variation in fire characteristics. *Journal of Animal Ecology,* 90**,** 1317-1327.

STILLMAN, A. N., SIEGEL, R. B., WILKERSON, R. L., JOHNSON, M., HOWELL, C. A. & TINGLEY, M. W. 2019. Nest site selection and nest survival of Black-backed Woodpeckers after wildfire. *Condor,* 121**,** 13.

STRASSER, E. H. & HEATH, J. A. 2013. Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. *Journal of Applied Ecology,* 50**,** 912-919.

STREBY, H. M. & ANDERSEN, D. E. 2013. Movements, cover-type selection, and survival of fledgling Ovenbirds in managed deciduous and mixed coniferous-deciduous forests. *Forest Ecology and Management,* 287**,** 9-16.

STRINELLA, E., SCRIDEL, D., BRAMBILLA, M., SCHANO, C. & KORNER-NIEVERGELT, F. 2020. Potential sex-dependent effects of weather on apparent survival of a high-elevation specialist. *Scientific Reports,* 10**,** 13.

SUAREZ-SEOANE, S., ALVAREZ-MARTINEZ, J. M., WINTLE, B. A., PALACIN, C. & ALONSO, J. C. 2017. Modelling the spatial variation of vital rates: An evaluation of the strengths and weaknesses of correlative species distribution models. *Diversity and Distributions,* 23**,** 841-853.

SUTER, C., REHSTEINER, U. & ZBINDEN, N. 2002. Habitat selection and breeding success of Corn Buntings Miliaria calandra in an intensively cultivated, arable landscape in Switzerland. *Ornithologische Beobachter,* 99**,** 105-115.

SWENSON, J. E., SAARI, L. & BONCZAR, Z. 1994. EFFECTS OF WEATHER ON HAZEL GROUSE REPRODUCTION - AN ALLOMETRIC PERSPECTIVE. *Journal of Avian Biology,* 25**,** 8-14.

SYDEMAN, W. J., HESTER, M. M., THAYER, J. A., GRESS, F., MARTIN, P. & BUFFA, J. 2001. Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969-1997. *Progress in Oceanography,* 49**,** 309-329.

SYROECHKOVSKIY, Y. V., LITVIN, K. Y. & EBBINGE, B. S. 1991. BREEDING SUCCESS OF GEESE AND SWANS ON VAYGACH ISLAND (USSR) DURING 1986-1988 - INTERPLAY OF WEATHER AND ARCTIC FOX PREDATION. *Ardea,* 79**,** 373-382.

TAKAGI, M. 2001. Some effects of inclement weather conditions on the survival and condition of bull-headed shrike nestlings. *Ecological Research,* 16**,** 55-63.

TANEDO, S. A., HOLLMEN, T. E., MANISCALCO, J. M. & ULMAN, S. E. G. 2021. USING REMOTE VIDEO TECHNOLOGY TO STUDY ENVIRONMENTAL FACTORS INFLUENCING PRODUCTIVITY OF BLACK-LEGGED KITTIWAKES RISSA TRIDACTYLA. *Marine Ornithology,* 49**,** 293-299.

TERRAUBE, J., ARROYO, B. E., BRAGIN, A., BRAGIN, E. & MOUGEOT, F. 2012. Ecological factors influencing the breeding distribution and success of a nomadic, specialist predator. *Biodiversity and Conservation,* 21**,** 1835-1852.

TEWKSBURY, J. J., HEJL, S. J. & MARTIN, T. E. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology,* 79**,** 2890-2903.

THEUERKAUF, J., HANEDA, T., OKAHISA, Y., SATO, N. J., ROUYS, S., BLOC, H., UEDA, K., WATANABE, I., KUEHN, R. & GULA, R. 2017. Elevated concentrations of naturally occurring heavy metals inversely correlate with reproductive output and body mass of the Kagu Rhynochetos jubatus. *Ibis,* 159**,** 580-587.

THINGSTAD, P. G. 1997. Annual and local reproductive variations of a Pied Flycatcher Ficedula hypoleuca population near a subalpine lake in Central Norway. *Ornis Fennica,* 74**,** 39-49.

THOMPSON, P. M. & OLLASON, J. C. 2001. Lagged effects of ocean climate change on fulmar population dynamics. *Nature,* 413**,** 417-420.

THORUP, K., SUNDE, P., JACOBSEN, L. B. & RAHBEK, C. 2010. Breeding season food limitation drives population decline of the Little Owl Athene noctua in Denmark. *Ibis,* 152**,** 803-814.

THYEN, S. & BECKER, P. H. 2006. Effects of individual life-history traits and weather on reproductive output of Black-headed Gulls Larus ridibundus breeding in the Wadden Sea, 1991-97. *Bird Study,* 53**,** 132-141.

TILGAR, V., MAND, R. & LEIVITS, A. 1999. Effect of calcium availability and habitat quality on reproduction in Pied Flycatcher Ficedula hypoleuca and Great Tit Paras major. *Journal of Avian Biology,* 30**,** 383-391.

TINOCO, B. A., GRAHAM, L., ASTUDILLO, P. X., NIETO, A., AGUILAR, J. M., LATTA, S. C. & GRAHAM, C. H. 2019. Survival estimates of bird species across altered habitats in the tropical Andes. *Journal of Field Ornithology,* 90**,** 105-116.

TITEUX, N., DUFRENE, M., RADOUX, J., HIRZEL, A. H. & DEFOURNY, P. 2007. Fitness-related parameters improve presence-only distribution modelling for conservation practice: The case of the red-backed shrike. *Biological Conservation,* 138**,** 207-223.

TOBOLKA, M., ZOLNIEROWICZ, K. M. & REEVE, N. F. 2015. The effect of extreme weather events on breeding parameters of the White Stork Ciconia ciconia. *Bird Study,* 62**,** 377-385.

TOME, R., BLOISE, C. & KORPIMAKI, E. 2004. Nest-site selection and nesting success of Little Owls (Athene noctua) in Mediterranean woodland and open habitats. *Journal of Raptor Research,* 38**,** 35-46.

TORNBERG, R., KORPIMÄKI, E. & BYHOLM, P. 2006. Ecology of the Northern Goshawk in Fennoscandia. *Studies in Avian Biology.*

TOSSAS, A. G. 2008. Reproductive success of the Puerto Rican Vireo in a montane habitat. *Wilson Journal of Ornithology,* 120**,** 460-466.

TRAYLOR, J. J., ALISAUSKAS, R. T., SLATTERY, S. M. & DRAKE, K. L. 2012. Comparative survival and recovery of Ross's and lesser snow geese from Canada's central arctic. *Journal of Wildlife Management,* 76**,** 1135-1144.

TREINYS, R., DEMENTAVICIUS, D., RUMBUTIS, S., SVAZAS, S., BUTKAUSKAS, D., SRUOGA, A. & DAGYS, M. 2016. Settlement, habitat preference, reproduction, and genetic diversity in recovering the white-tailed eagle Haliaeetus albicilla population. *Journal of Ornithology,* 157**,** 311-323.

TREMBLAY, I., THOMAS, D. W., LAMBRECHTS, M. M., BLONDEL, J. & PERRET, P. 2003. Variation in Blue Tit breeding performance across gradients in habitat richness. *Ecology,* 84**,** 3033-3043.

TRUMBO, E. M., WARD, M. P., MACEY, J. N., GRIGSBY, N. A. & BRAWN, J. D. 2021. Post-fledging ecology of endangered Golden-cheeked Warblers. *Journal of Field Ornithology,* 92**,** 417-430.

TRYJANOWSKI, P. & SPARKS, T. H. 2008. The relationship between phenological traits and brood size of the white stork Ciconia ciconia in western Poland. *Acta Oecologica-International Journal of Ecology,* 33**,** 203-206.

TWEDT, D. J., SOMERSHOE, S. G., HAZLER, K. R. & COOPER, R. J. 2010. Landscape and Vegetation Effects on Avian Reproduction on Bottomland Forest Restorations. *Journal of Wildlife Management,* 74**,** 423-436.

UHER-KOCH, B. D., WRIGHT, K. G. & SCHMUTZ, J. A. 2019. The influence of chick production on territory retention in Arctic-breeding Pacific and Yellow-billed loons. *Condor,* 121**,** 11.

ULENAERS, P. & DHONDT, A. A. 1991. PHENOLOGY, HABITAT CHOICE AND REPRODUCTION OF THE GREAT CRESTED GREBE PODICEPS-CRISTATUS L, ON A FISH-FARM. *Ardea,* 79**,** 395-408.

UNANDER, S., PEDERSEN, A. O., SOININEN, E. M., DESCAMPS, S., HORNELL-WILLEBRAND, M. & FUGLEI, E. 2016. Populations on the limits: survival of Svalbard rock ptarmigan. *Journal of Ornithology,* 157**,** 407-418.

VALI, U. 2012. Factors limiting reproductive performance and nestling sex ratio in the Lesser Spotted Eagle Aquila pomarina at the northern limit of its range: the impact of weather and prey abundance. *Acta Ornithologica,* 47**,** 157-168.

VAN DE POL, M., ENS, B. J., HEG, D., BROUWER, L., KROL, J., MAIER, M., EXO, K. M., OOSTERBEEK, K., LOK, T., EISING, C. M. & KOFFIJBERG, K. 2010. Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *Journal of Applied Ecology,* 47**,** 720-730.

VAN DEN HOUT, P. J., PIERSMA, T., TEN HORN, J., SPAANS, B. & LOK, T. 2017. Individual shifts toward safety explain age-related foraging distribution in a gregarious shorebird. *Behavioral Ecology,* 28**,** 419-428.

VAN OUDENHOVE, L., GAUTHIER, G. & LEBRETON, J. D. 2014. Year-round effects of climate on demographic parameters of an arctic-nesting goose species. *Journal of Animal Ecology,* 83**,** 1322-1333.

VAN VESSEM, J. & DRAULANS, D. 1986. The adaptive significance of colonial breeding in the grey heron Ardea cinerea: inter- and intra-colony variability in breeding success. *Ornis Scandinavica,* 17**,** 356-362.

VANDER HAEGEN, W. M., SCHROEDER, M. A., CHANG, W. Y. & KNAPP, S. M. 2015. Avian Abundance and Reproductive Success in the Intermountain West: Local-Scale Response to the Conservation Reserve Program. *Wildlife Society Bulletin,* 39**,** 276-291.

VANDERWERF, E. A., TAYLOR, P. E. & DITTMAR, E. 2020. Breeding season shift by the Oahu Elepaio (Chasiempis ibidis) in response to changing rainfall patterns. *Wilson Journal of Ornithology,* 132**,** 924-933.

VASSEUR, P. L. & LEBERG, P. L. 2015. Effects of habitat edges and nest-site characteristics on Painted Bunting nest success. *Journal of Field Ornithology,* 86**,** 27-40.

VEISTOLA, S., LEHIKOINEN, E. & EEVA, T. 1997. Weather and breeding success at high latitudes - The pied flycatcher Ficedula hypoleuca and the Siberian tit Parus cinctus. *Ornis Fennica,* 74**,** 89-98.

VERBOVEN, N. & VISSER, M. E. 1998. Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos,* 81**,** 511-524.

VERMEER, K., MORGAN, K. H. & SMITH, G. E. J. 1992. BLACK OYSTERCATCHER HABITAT SELECTION, REPRODUCTIVE SUCCESS, AND THEIR RELATIONSHIP WITH GLAUCOUS-WINGED GULLS. *Colonial Waterbirds,* 15**,** 14-23.

VERNASCO, B. J., SILLETT, T. S., MARRA, P. P. & RYDER, T. B. 2018. Environmental predictors of nestling condition, postfledging movement, and postfledging survival in a migratory songbird, the Wood Thrush (Hylocichla mustelina). *Auk,* 135**,** 15-24.

VERNOUILLET, A., FORTIN, M. J., FIOLA, M. L. & VILLARD, M. A. 2020. Do Female Songbirds Avoid a Mammalian Nest Predator When Selecting Their Nest Site? *Frontiers in Ecology and Evolution,* 8**,** 10.

VERNOUILLET, A., VILLARD, M. A. & HACHE, S. 2014. ENSO, Nest Predation Risk, Food Abundance, and Male Status Fail to Explain Annual Variations in the Apparent Survival Rate of a Migratory Songbird. *Plos One,* 9**,** 17.

VIGFUSDOTTIR, F., GUNNARSSON, T. G. & GILL, J. A. 2013. Annual and between-colony variation in productivity of Arctic Terns in West Iceland. *Bird Study,* 60**,** 289-297.

VOLKOV, S. V. & POZDNYAKOV, V. I. 2021. Effects of Environmental Conditions on Spring Arrival, the Timing of Nesting, and the Reproductive Effort of Ross's Gull (Phodostethia rosea) in the Delta of Lena River, Yakutia. *Biology Bulletin,* 48**,** 1332-1341.

VOTIER, S. C., HATCHWELL, B. J., BECKERMAN, A., MCCLEERY, R. H., HUNTER, F. M., PELLATT, J., TRINDER, M. & BIRKHEAD, T. R. 2005. Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecology Letters,* 8**,** 1157-1164.

WALK, J. W., KERSHNER, E. L., BENSON, T. J. & WARNER, R. E. 2010. NESTING SUCCESS OF GRASSLAND BIRDS IN SMALL PATCHES IN AN AGRICULTURAL LANDSCAPE. *Auk,* 127**,** 328-334.

WANG, G., HOBBS, N. T., GALBRAITH, H. & GIESEN, K. M. 2002. Signatures of large-scale and local climates on the demography of white-tailed ptarmigan in Rocky Mountain National Park, Colorado, USA. *International Journal of Biometeorology,* 46**,** 197-201.

WARD, D. H., SCHMUTZ, J. A., SEDINGER, J. S., BOLLINGER, K. S., MARTIN, P. D. & ANDERSON, B. A. 2004. Temporal and geographic variation in survival of juvenile Black Brant. *Condor,* 106**,** 263-274.

WATANUKI, Y., ITO, M., DEGUCHI, T. & MINOBE, S. 2009. Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. *Marine Ecology Progress Series,* 393**,** 259-271.

WAWRZYNIAK, J., KALINSKI, A., GLADALSKI, M., BANBURA, M., MARKOWSKI, M., SKWARSKA, J., ZIELINSKI, P., CYZEWSKA, I. & BANBURA, J. 2015. LONG-TERM VARIATION IN LAYING DATE AND CLUTCH SIZE OF THE GREAT TIT PARUS MAJOR IN CENTRAL POLAND: A COMPARISON BETWEEN URBAN PARKLAND AND DECIDUOUS FOREST. *Ardeola,* 62**,** 311-322.

WEBB, W. C., BOARMAN, W. I. & ROTENBERRY, J. T. 2004. Common raven juvenile survival in a human-augmented landscape. *Condor,* 106**,** 517-528.

WEISER, E. L., BROWN, S. C., LANCTOT, R. B., GATES, H. R., ABRAHAM, K. F., BENTZEN, R. L., BETY, J., BOLDENOW, M. L., BROOK, R. W., DONNELLY, T. F., ENGLISH, W. B., FLEMMING, S. A., FRANKS, S. E., GILCHRIST, H. G., GIROUX, M. A., JOHNSON, A., KENDALL, S., KENNEDY, L. V., KOLOSKI, L., KWON, E., LAMARRE, J. F., LANK, D. B., LATTY, C. J., LECOMTE, N., LIEBEZEIT, J. R., MCKINNON, L., NOL, E., PERZ, J., RAUSCH, J., ROBARDS, M., SAALFELD, S. T., SENNER, N. R., SMITH, P. A., SOLOVIEV, M., SOLOVYEVA, D., WARD, D. H., WOODARD, P. F. & SANDERCOCK, B. K. 2018. Effects of environmental conditions on reproductive effort and nest success of Arctic-breeding shorebirds. *Ibis,* 160**,** 608-623.

WEISER, E. L., LANCTOT, R. B., BROWN, S. C., GATES, H. R., BENTZEN, R. L., BETY, J., BOLDENOW, M. L., ENGLISH, W. B., FRANKS, S. E., KOLOSKI, L., KWON, E., LAMARRE, J. F., LANK, D. B., LIEBEZEIT, J. R., MCKINNON, L., NOL, E., RAUSCH, J., SAALFELD, S. T., SENNER, N. R., WARD, D. H., WOODARD, P. F. & SANDERCOCK, B. K. 2018. Environmental and ecological conditions at Arctic breeding sites have limited effects on true survival rates of adult shorebirds. *Auk,* 135**,** 29-43.

WESOLOWSKI, T. & MAZIARZ, M. 2009. Changes in breeding phenology and performance of Wood Warblers Phylloscopus sibilatrix in a primeval forest: a thirty-year perspective. *Acta Ornithologica,* 44**,** 69-80.

WESSELS, J. L. & BOVES, T. J. 2021. Cerulean Warblers in the Ozark region: habitat selection, breeding biology, survival, and space use. *Journal of Field Ornithology,* 92**,** 54-66.

WIACEK, J. 2015. Long-term changes of breeding success in Montagu's Harrier Circus pygargus. *Belgian Journal of Zoology,* 145**,** 103-114.

WIEBE, K. L. 2020. Local recruitment in Northern Flickers is related to environmental factors at multiple scales and provides reproductive benefits to yearling breeders settling close to home. *Auk,* 137**,** 10.

WIGHTMAN, C. S., SAAB, V. A., FORRISTAL, C., MELLEN-MCLEAN, K. & MARKUS, A. 2010. White-Headed Woodpecker Nesting Ecology After Wildfire. *Journal of Wildlife Management,* 74**,** 1098-1106.

WILLIAMS, K. A. & MILES, D. B. 2016. Demographic Costs Associated with Differences in Habitat Space Occupancy. *Plos One,* 11**,** 18.

WILLIAMS, T. D. & CROXALL, J. P. 1991. CHICK GROWTH AND SURVIVAL IN GENTOO PENGUINS (PYGOSCELIS-PAPUA) - EFFECT OF HATCHING ASYNCHRONY AND VARIATION IN FOOD-SUPPLY. *Polar Biology,* 11**,** 197-202.

WILSON, S. & MARTIN, K. 2011. Life-history and demographic variation in an alpine specialist at the latitudinal extremes of the range. *Population Ecology,* 53**,** 459-471.

WINDELS, S. K., BEEVER, E. A., PARUK, J. D., BRINKMAN, A. R., FOX, J. E., MACNULTY, C. C., EVERS, D. C., SIEGEL, L. S. & OSBORNE, D. C. 2013. Effects of Water-Level Management on Nesting Success of Common Loons. *Journal of Wildlife Management,* 77**,** 1626-1638.

WINFREE, R., DUSHOFF, J., ROBINSON, S. K. & BENGALI, D. 2006. A Monte Carlo model for estimating the productivity of a generalist brood parasite across multiple host species. *Evolutionary Ecology Research,* 8**,** 213-236.

WINIARSKI, J. M., MOORMAN, C. E., CARPENTER, J. P. & HESS, G. R. 2017. Reproductive consequences of habitat fragmentation for a declining resident bird of the longleaf pine ecosystem. *Ecosphere,* 8**,** 13.

WINKLER, D. W., HALLINGER, K. K., PEGAN, T. M., TAFF, C. C., VERHOEVEN, M. A., VAN OORDT, D. C., STAGER, M., UEHLING, J. J., VITOUSEK, M. N., ANDERSEN, M. J., ARDIA, D. R., BELMAKER, A., FERRETTI, V., FORSMAN, A. M., GAUL, J. R., LLAMBIAS, P. E., ORZECHOWSKI, S. C., SHIPLEY, J. R., WILSON, M. & YOON, H. S. 2020. Full lifetime perspectives on the costs and benefits of lay-date variation in tree swallows. *Ecology,* 101**,** 19.

WIRTITSCH, M., HOI, H., VALERA, F. & KRISTIN, A. 2001. Habitat composition and use in the lesser grey shrike Lanius minor. *Folia Zoologica,* 50**,** 137-150.

WOOD, K. A., NUIJTEN, R. J. M., NEWTH, J. L., HAITJEMA, T., VANGELUWE, D., IOANNIDIS, P., HARRISON, A. L., MACKENZIE, C., HILTON, G. M., NOLET, B. A. & REES, E. C. 2018. Apparent survival of an Arctic-breeding migratory bird over 44years of fluctuating population size. *Ibis,* 160**,** 413-430.

WOOD, M. J., CANONNE, C., BESNARD, A., LACHISH, S., FAIRHURST, S. M., LIEDVOGEL, M., BOYLE, D., PATRICK, S. C., JOSEY, S., KIRK, H., DEAN, B., GUILFORD, T., MCCLEERY, R. M., PERRINS, C. M. & HORSWILL, C. 2021. Demographic profiles and environmental drivers of variation relate to individual breeding state in a long-lived trans-oceanic migratory seabird, the Manx shearwater. *Plos One,* 16**,** 17.

WOODWORTH, B. K., FRANCIS, C. M. & TAYLOR, P. D. 2014. Inland flights of young red-eyed vireos Vireo olivaceus in relation to survival and habitat in a coastal stopover landscape. *Journal of Avian Biology,* 45**,** 387-395.

WRIGHT, L. J., HOBLYN, R. A., GREEN, R. E., BOWDEN, C. G. R., MALLORD, J. W., SUTHERLAND, W. J. & DOLMAN, P. M. 2009. Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark Lullula arborea. *Journal of Animal Ecology,* 78**,** 1191-1202.

YASUE, M. & DEARDEN, P. 2006. The potential impact of tourism development on habitat availability and productivity of Malaysian plovers Charadrius peronii. *Journal of Applied Ecology,* 43**,** 978-989.

YOUNG, A. C., COX, W. A., MCCARTY, J. P. & WOLFENBARGER, L. L. 2019. Postfledging habitat selection and survival of Henslow's Sparrow: management implications for a critical life stage. *Avian Conservation and Ecology,* 14**,** 12.

YOUNG, B. E. 1994. GEOGRAPHIC AND SEASONAL PATTERNS OF CLUTCH-SIZE VARIATION IN-HOUSE WRENS. *Auk,* 111**,** 545-555.

YOUNGFLESH, C., LI, Y., LYNCH, H. J., DELORD, K., BARBRAUD, C., JI, R. B. & JENOUVRIER, S. 2021. Lack of synchronized breeding success in a seabird community: extreme events, niche separation, and environmental variability. *Oikos,* 130**,** 1943-1953.

ZDUNIAK, P., CZECHOWSKI, P. & JEDRO, G. 2011. The effect of nesting habitat on reproductive output of the Barn Swallow (Hirundo rustica). A comparative study of populations from atypical and typical nesting habitats in western Poland. *Belgian Journal of Zoology,* 141**,** 38-43.

ZHANG, L., AN, B., SHU, M. & YANG, X. 2017. Nest-site selection, reproductive ecology and shifts within core-use areas of Black-necked Cranes at the northern limit of the Tibetan Plateau. *PeerJ,* 2017.

ZHAO, Q., HEATH-ACRE, K., COLLINS, D., CONWAY, W. & WEEGMAN, M. D. 2021. Integrated population modelling reveals potential drivers of demography from partially aligned data: a case study of snowy plover declines under human stressors. *Peerj,* 9**,** 24.

ZHU, X., SRIVASTAVA, D. S., SMITH, J. N. M. & MARTIN, K. 2012. Habitat Selection and Reproductive Success of Lewis's Woodpecker (Melanerpes lewis) at Its Northern Limit. *Plos One,* 7**,** 10.

ZINSSER, E., SANDERS, F. J., GERARD, P. & JODICE, P. G. R. 2017. Daily Survival Rate and Habitat Characteristics of Nests of Wilson's Plover. *Southeastern Naturalist,* 16**,** 149-156.

ZUBEN, V. V. & NOCERA, J. J. 2019. Drivers of Intra-Seasonal Variation in Black Tern (Chlidonias niger) Nest Survival. *Waterbirds,* 42**,** 112-121.

Chapter 3: Is Spatial Variation in the Productivity of European Passerines Associated with Landscape Structure?

A selection of birds in hand caught and ringed at Constant Effort Sites in Europe. All birds handled under licence. © Chas Holt and Matt Prior.

Abstract

Human land-use change is considered a key driver of biodiversity declines globally. There is an urgent need to address these large-scale threats, but identifying and targeting appropriate conservation actions is challenging because data with sufficient spatial and temporal coverage are rare. European landbirds have shown considerable population declines and have been well-studied compared to other taxonomic groups, providing an opportunity to examine these issues. Previous Pan-European research identified substantial site-level spatial variation in population trends and productivity of landbirds, consistent across species and years (Morrison et al., 2021, 2022). This suggests that local environmental conditions at breeding sites are key drivers of variation in population trends, through impacts on productivity, and are a realistic target for conservation actions. We aimed to identify features of the landscape surrounding sites which could be driving this spatial variation in productivity. For 843 Constant Effort bird ringing sites across 12 European countries, we measured mean productivity across 21 years for 90 species, and related this to characteristics of the surrounding 1, 5 and 10 km landscapes. At each scale, we measured the dominant land cover and management intensity, the prevalence of watercourses and inland water bodies, and two metrics of landscape configuration. We found that sites within landscapes locally dominated by wetlands and, at larger scales, low-intensity land-uses, are more frequently associated with higher mean productivity. Productivity was not always high in these conditions, with a large proportion of the variation left unexplained, likely driven by site-level characteristics. Whilst we did find some differences in the responses of residents, arid-zone migrants and humid-zone migrants, overall, the productivity of species in these migratory groups showed very similar associations with landscape structure. Our findings identify landscape-level conservation actions which could benefit both resident and migratory breeding bird populations across Europe. Future work should explore the role of site-level characteristics, especially those associated with high productivity sites, and the mechanisms driving these patterns, to inform management actions which could increase the number of sites achieving high productivity.

3.1. Introduction

Human land-use change is considered the greatest threat to global biodiversity (Davison et al., 2021; Sala et al., 2000), through the impacts of habitat loss, fragmentation and degradation (Heinrichs et al., 2016). There is an urgent need to address these large-scale threats, but identifying and targeting appropriate conservation actions is challenging because data with sufficient spatial and temporal coverage are rare. Compared to other taxa, birds have been well-studied over large scales and long time periods due to their visibility and developed census methods (Fraixedas et al. 2020). Bird species also serve as important indicators for ecological communities and wider ecosystem health (Gregory and van Strien, 2010), and so provide a key focus for understanding the impacts of land-use change and potential solutions.

Nearly half of all bird species are undergoing population declines, and over 80% of species threatened with extinction are impacted by land-use change (Lees et al., 2022). In Europe, breeding bird numbers have declined by nearly 20% since 1980, with especially strong declines in species associated with agricultural or grassland systems and long-distance migration (Burns et al., 2021; Vickery et al., 2023). Recent Pan-European research using long-term data on landbirds identified substantial site-level spatial variation in population trends and productivity, which covaries between residents and sub-Saharan migrants (Morrison et al., 2021), and is consistent across years (Morrison et al., 2022). This suggests that local environmental conditions at breeding sites are key drivers of variation in population trends, through impacts on productivity, and are a realistic target for conservation actions which could benefit the whole bird community. However, this depends on our ability to identify the conditions driving this spatial variation in productivity, which are not yet known (Morrison et al., 2022).

Productivity in bird populations often varies with landscape structure (Bionda and Brambilla, 2012; Cornell and Donovan, 2010; Lampila et al., 2005; Lande et al., 2014), which has two main qualities, composition and configuration (Adler and Jedicke, 2022; Hadley and Betts, 2016; Lustig et al., 2015). Landscape composition refers to the type and relative coverage of habitats, and includes both the classes of land cover and their level of human modification (i.e. land-use intensity) (Pellissier et al., 2017). Numerous studies have shown that productivity is higher in landscapes with greater coverage of preferred breeding habitat (Šálek et al., 2025; Tozer et al., 2010) and/or lower coverage of poor-quality matrix habitats, such as urban environments (Reidy et al., 2023) and intensive agriculture (Garrett et al., 2022; Ghilain and Bélisle, 2008).

Bird productivity is not only affected by the composition of terrestrial habitats, but also their interaction with aquatic habitats in the landscape. For example, the abundance of insectivorous birds has been shown to increase with stream length in study areas due to the foraging opportunities provided, including increased abundance of emergent aquatic insects (Iwata et al., 2010, 2003). In addition, water bodies have been shown to be important for nestling condition, reproductive success and annual recruitment rates in insectivorous birds in agricultural landscapes, due to increased aquatic insect food abundance (Berzins et al., 2021, 2022; Lewis-Phillips et al., 2020). Watercourses and water bodies can therefore act as resource subsidies, which may be particularly important in landscapes with reduced terrestrial insect abundance such as intensive agricultural land (Bradbury and Kirby, 2006; McKellar et al., 2025). Vegetation associated with water features may also provide nesting habitat (Bradbury and Kirby, 2006).

Landscape configuration refers to the spatial arrangement of landscape features, their shape and how they are connected. For specialist species reliant on a single habitat, productivity in landscapes with complex configurations may be lower because greater fragmentation of focal habitat leads to smaller patch sizes and greater edge effects (Akresh et al., 2024; Burke and Nol, 2000; Flaspohler et al., 2001; Harrod and Green, 2018). In contrast, complex landscape configurations can be beneficial for species which nest within habitat edges (Woodward et al., 2001), or for species which obtain different resources from contrasting habitats within heterogeneous landscapes (Dolman, 2012; Fahrig et al., 2019). Complexity is particularly important in agricultural landscapes, where many species benefit from the availability of diverse nesting and foraging habitats in close proximity (Siriwardena et al., 2000; Vickery and Arlettaz, 2012).

Several studies have highlighted the importance of spatial scale when exploring associations between landscape structure and bird productivity rates (Cornell and Donovan, 2010; Cox et al., 2012; Stephens et al., 2004). Results can vary with the landscape scale examined because the mechanisms involved often operate at different spatial scales (Siriwardena et al., 2000; Smith et al., 2011). For example, if resource availability is a key factor driving productivity rates and influenced by landscape structure, effects might be more apparent at scales equivalent to the foraging distances of the species examined (Ghilain and Bélisle, 2008). Meanwhile, where nest predation is important, effects are more likely to be detected at larger scales relevant to predators (Chalfoun et al., 2002).

To date, most studies of the relationship between landscape structure and productivity have focused on one or two species (e.g. Ghilain and Bélisle, 2008), or where a community-wide approach has been taken, only consider single ecosystems (e.g. Burke and Nol, 2000; Rodewald and Yahner, 2001), and so findings are relatively limited in generality. In this study, we used a large-scale, long-term citizen science dataset to examine whether spatial variation in cross-community productivity across Europe is related to landscape structure. We investigated whether site-level productivity is associated with the composition and configuration of the surrounding landscape, in particular, dominant land cover and its management intensity, prevalence of watercourses and inland water bodies, and two metrics of landscape configuration (patch density and mean patch perimeter-area ratio). We measured these components of landscape structure at 1, 5 and 10 km scales, in order to capture potentially scale-dependent processes that could be driving the local, site-level variation in productivity previously identified with this dataset (Morrison et al., 2021; 2022).

We were also interested in whether responses to landscape structure differed between species with different migratory strategies, because long-distance migrants are declining significantly faster than short-distance migrants and residents which remain within Europe (Burns et al., 2021; Vickery et al., 2023). Breeding sites in Europe tend to show consistently high or low productivity rates for both the resident and migrant species that occur in those sites (Morrison et al., 2021), and so we may expect to see similar landscape features associated with productivity for these species. However, residents and migrants might not respond to all landscape features in the same way. For instance, long-distance migrants in Europe favour open breeding habitats to a greater extent than residents and short-distance migrants and so may be more sensitive to changes in agricultural or grassland systems (Vickery et al., 2014). In addition, there might be additional variation amongst long-distance migrants overwintering in different parts of sub-Saharan Africa, because recent population declines have been greater in species travelling to the humid tropics than those wintering in the arid Sahel zone (Vickery et al., 2023). It is therefore important to identify which landscape features are associated with productivity across migratory groups in order to inform conservation actions which could benefit the whole bird community.

3.2. Methods

Quantifying Site-level Productivity

We use data from the European Constant Effort Sites (EuroCES) programme, which is a large network of constant-effort bird ringing sites across Europe. Site locations are determined by citizen scientist volunteers as those that are suitable for catching sufficient numbers of birds to measure demographic metrics, and where successional changes in habitat can be managed, and they occur in a variety of landscapes. Data were collated from 16 CES schemes spanning 12 countries, for the years of 1998 through to 2019 (Table S3.1). All EuroCES schemes follow a common protocol (Robinson et al., 2009; Robinson, 2023), in which licenced ringers deploy a series of mist nets in the same configurations, for the same length of time, during morning and/or evening visits evenly spaced throughout the breeding period, with individuals caught aged using plumage characteristics (Svensson, 1992). Net-length and operating times vary between sites but are kept constant within each site across sessions and years. Schemes operate between 7 and 12 visits a year, roughly every 10 days between April-May and July-August (with higher latitudes starting and ending later). Here, we quantify productivity at EuroCE sites as the number of juveniles caught per adult each breeding season (Robinson, 2023); this index of productivity integrates breeding success across the whole season, including the outcomes of multiple broods and early post-fledging mortality. To ensure captures were fully representative of the numbers of adults and juveniles on a site, we set a threshold for the minimum number of visits in the first and second halves of the season for a year's data at a site ("site-year") to be included. This was half of the maximum number of visits for each scheme minus two (e.g. a site in a twelve-visit scheme would require at least four "early" visits and four "late" visits, while a site in a seven-visit scheme would require at least two "early" and two "late" visits).

For each species, we only included site-years in which a minimum of three adults were caught, and only sites with a minimum of three such years were included. In addition, sites at which no juveniles had been caught across years were excluded from analyses for that species. Some species are known to occasionally form flocks after fledging, which could bias the age ratio, so we removed any site-years with productivity ratios above a maximum threshold expected for each species in Europe. This was calculated by multiplying the maximum clutch size reported in Storchová and Hořák (2018) by the maximum number of broods reported in Cramp (2006), and dividing by two to get a value per adult.

We restricted the species list to passerines because productivity rates for these species are most reliably measured with CES methodology, and excluded invasive non-native species, resulting in a final list of 90 species (Table S3.2). We classified each species into one of three migratory groups: (1) resident within Europe or short-distance migrant ("resident"), (2) long-distance migrant overwintering in the arid-zone of sub-Saharan Africa ("arid"), or (3) long-distance migrant overwintering in the more southerly humid-zone of sub-Saharan Africa ("humid"). We used the classifications from Morrison et al., (2021), resulting in 56 residents, 14 arid migrants and 20 humid migrants.

To estimate the mean juvenile-adult ratio across years for each species at each site, the number of juveniles was modelled in binomial generalised linear mixed models (GLMM), with the total number of birds (juveniles plus adults) as the binomial denominator and site as a fixed effect. Year nested within site was fitted as a random effect to account for the non-independence of birds sampled within the same year, while allowing this year effect to vary between sites. These models were constructed using the package 'glmmTMB' (Brooks et al., 2017). Before proceeding with the estimated site means, we checked each model for overdispersion. Subsequently, a standardisation procedure was employed to produce site-level productivity estimates that were relative within each species and scheme. Site estimates for each species were standardised by subtracting the overall species mean of the site-level estimates and dividing by the standard deviation within each scheme separately. This accounted for differences in species composition between sites, and prevented any methodological differences between schemes biasing the productivity values. This resulted in a total of 10,636 species site-level productivity estimates at 857 sites.

Landscape Characteristics

Landscape composition and configuration metrics were measured within 1, 5 and 10 km around each CES location (Table 3.1). The 1 km scale captures characteristics of the habitat in which the mist-nests are erected, as well as the immediate landscape surrounding the site, while the 5 and 10 km scales encompass processes occurring in the wider area around sites, but small enough to capture processes varying between nearby sites. Eleven coastal sites with >50% of the 1 km buffer area consisting of sea and ocean were excluded from the analyses because we did not consider these comparable to sites with fully terrestrial landscapes.

Table 3.1: Description of landscape composition and configuration variables measured at 1, 5 and 10 km scales around European Constant Effort Sites, plus the range of values recorded for each variable, before standardisation.

Predictor	Description	Range of Values (unscaled)
Landscape Composition		
Land System Type (System)	Land system category of 1 km square that site falls in, or dominant category of 1 km squares falling within and overlapping the 5 or 10 km buffers around sites	Arable Cropland, Forest, Grassland, Settlements, Wetland, Mosaics (1 km only)
Land System Intensity (Intensity)	Land management intensity of 1 km square that site falls in, or dominant category of 1 km squares falling within and overlapping the 5 or 10 km buffers around sites	Low, Medium, High
Water Course Length (WCL)	Total length of water courses within 1, 5 or 10 km buffers around sites	1 km: 0 – 8414 m 5 km: 0 – 83, 836 m 10 km: 5823 – 301,607 m
Inland Water Body Perimeter (IWP)	Total length of perimeters of inland water bodies within 1, 5 or 10 km buffers around sites	1 km: 0 – 15,883 m 5 km: 0 – 128,359 m 10 km: 0 – 465,538 m
Landscape Configuration		
Patch Density (PD)	Number of patches, scaled to area of landscape buffer; higher value = more patches	1 km: 0.317 – 5.161 5 km: 0.0891 – 2.130 10 km: 0.068 – 1.60
Mean Patch Perimeter - Area Ratio (MPPAR)	Perimeter to area ratio averaged across all patches within landscape buffer; higher value = more complex/more exposed to edge	1 km: 0.00252 – 0.0299 5 km: 0.00599 – 0.0264 10 km: 0.00811 – 0.0238

Landscape composition

Landscape composition was categorised using the Land System typology of Dou et al., (2021), under which each 1 km grid square in the EU is classified as belonging to a land system and sub-system based on finer resolution data on land cover and land use intensities (see Table 3.1 and Dou et al., (2021) for details). First, we categorised the system of each CE site as the land system assigned to the 1 km square in which it occurs (Table 3.2a); for the 5 and 10 km landscape scales, each CE site was categorised according to the dominant land system across all 1 km squares overlapped by the 5 and 10 km radii buffers. Only sites within system categories assigned to at least 30 sites were included at each scale to ensure sufficient sample sizes for analysis (Table 3.2a). There were approximately equal numbers of sites across the six system types at the 1 km scale, while at the larger scales most sites were within landscapes dominated by arable cropland, with relatively few within landscapes dominated by wetlands. There were too few sites within 5 and 10 km landscapes dominated by mosaics and so these sites were excluded at these scales. Secondly, management intensity was categorised according to the sub-system classification assigned to the 1 km square in which it occurs (Table 3.2b; see Table S3.3 for sub-system groupings used to define the intensity variable). Again, for the 5 and 10 km landscape scales, management intensity was categorised according to the dominant sub-system across all 1 km squares overlapped by the 5 and 10 km radii buffers. Most sites were within landscapes dominated by either low- or high-intensity land-uses at the 1 km scale, whilst at the larger scales, most sites were in medium- or high-intensity landscapes (Table 3.2b). Note that two sites in Andorra and one site on the Isle of Man were not covered by the Dou et al., (2021) dataset and so do not appear in subsequent analyses. Finally, we used the EU-Hydro dataset (European Environment Agency, 2020a) to measure the total length of watercourses and the total length of inland water body perimeters within each of the three buffers around each site. The R package ‘sf’ (Pebesma, 2018) was used to generate these datasets.

Table 3.2: The number (#) and percentage (%) of European Constant Effort Sites within landscapes dominated by each (a) land system type, and (b) land management intensity, at the 1, 5 and 10 km scales. Categories with fewer than 30 sites were excluded from the analyses at each scale, and are shown in brackets.

a)	System	1 km		5 km		10 km	
		# sites	% sites	# sites	% sites	# sites	% sites
	Arable Cropland	149	18	300	37	335	42
	Forest	115	14	171	21	184	23
	Grassland	88	11	102	13	107	13
	Settlement	164	20	158	20	124	16
	Wetland	164	20	71	9	50	6
	Mosaic	129	16	(16)	(0)	(13)	(0)
	(Permanent Crops)	(15)	(0)	(17)	(0)	(23)	(0)
	(Shrub)	(19)	(0)	(8)	(0)	(7)	(0)

b)	Intensity	1 km		5 km		10 km	
		# sites	% sites	# sites	% sites	# sites	% sites
	Low	221	34	77	11	74	10
	Medium	166	26	340	47	367	49
	High	258	40	314	43	309	41

Landscape configuration

We focused on two key metrics of landscape configuration: patch density and mean patch perimeter-area ratio (Table 3.1). Patch density directly measures habitat fragmentation (Püttker et al., 2020) but, when calculated across all habitat patch types in a landscape, serves as a general index of spatial heterogeneity (McGarigal et al., 2023). The mean patch perimeter-area ratio quantifies the extent of the edge effect in the landscape as well as providing a measure of overall shape complexity of patches (Harrod and Green, 2018). These two metrics were measured within the 1, 5 and 10 km buffers around each CES in the *landscapemetrics* package in R (Hesselbarth et al., 2019), from the CORINE Land Cover (CLC) 2012 raster dataset at 100 m resolution, using the level 3 classification (European Environment Agency, 2020b). We selected the 2012 version because it is the closest available to the midpoint of our CES dataset (2010). The "sea and ocean" class was excluded from the CLC dataset before calculating landscape configuration metrics because this does not form part of the terrestrial landscape.

Statistical Analysis

We used a linear mixed modelling (LMM) approach to examine the effects of landscape composition and configuration on bird productivity, and how these differ between migratory groups. All analyses were conducted in R 4.4.1 (R Core Team, 2024).

Data Preparation

Our response variable was the mean standardised productivity ratio for each species at each site. The final sample sizes were 10,111 species-site estimates for the 1 km analysis, 10,073 estimates for the 5 km analysis and 10,062 estimates for the 10 km analysis. In all models, the inverse of the standard error from the individual species-site productivity GLMMs was used as a weighting variable to account for uncertainty in the species-site estimates. We standardised all continuous predictors by subtracting the mean and dividing by the standard deviation to enable effect size comparison and improve model fit (Harrison et al., 2018). We checked for collinearity between continuous predictors by examining the Spearman's rank correlation coefficients (Table S3.4), and consider a *rho* value of 0.6 or more to indicate a strong correlation. Watercourse length and inland water body perimeter were weakly correlated (*rho* <0.2 for all scales) and were included in the same models. Patch density and mean patch perimeter-area ratio were more strongly correlated (*rho* = 0.531 – 0.637, p <0.001) and so were modelled separately in parallel models, with either one or the other as a predictor variable (see below), in order to examine their effects independently. In addition, because all wetland sites were classified as "low intensity", including system and intensity predictors in the same model would have confounded their effects, and so these were also modelled separately in parallel models.

Modelling

For each of the 1, 5 and 10 km scales, we ran eight LMMs (Table 3.2) using the *lmer* function in the 'lmerTest' package (Kuznetsova et al., 2017). All continuous predictors were fitted as orthogonal polynomials using the '*poly(x, 2)*' notation to test for quadratic effects. The first two models examined the effect of system, with either patch density or mean patch perimeter-area ratio as an additional predictor, and were run on all sites. We then examined the effect of intensity for sites within managed land systems (arable cropland, forest, grassland, settlements, mosaics), excluding wetland sites. The first four models examined the effects of the explanatory variables on the bird community as a whole, whilst models five to eight included interaction terms for migratory status (MigStatus) to assess whether landscape effects differed between residents, arid-zone migrants and humid-zone migrants. All models contained fixed effects of watercourse length, inland water body perimeter and elevation, in addition to random effects of site and species to account for non-independence.

We subsequently ran separate models for each of the land system categories to explore whether the effect of intensity on site-level productivity differed depending on the system type. We did not fit this as an interaction term within the main models because we did not have a balanced design for all categorical combinations, and to avoid over-parameterisation. These models followed the same structure as above, except where the species random effect was estimated as zero ("singular fit") and was therefore excluded. For mosaic systems, we combined medium and high intensity sites into a single category due to limited sample size.

Table 3.2: Linear mixed model structure used to examine the effect of landscape composition and configuration variables on the mean productivity ratio for each bird species at each Constant Effort Site. All continuous variables were fitted as orthogonal polynomial quadratic terms. PD = patch density, MPPAR = mean patch perimeter-area ratio, WCL = watercourse length, IWP = inland water body perimeter length, MigStatus = migratory group.

Model	Structure
1	System + PD + WCL + IWP + elevation + (1|site) + (1|species)
2	System + MPPAR + WCL + IWP + elevation + (1|site) + (1|species)
3	Intensity + PD + WCL + IWP + elevation + (1|site) + (1|species)
4	Intensity + MPPAR + WCL + IWP + elevation + (1|site) + (1|species)
5	System*MigStatus + PD + WCL*MigStatus + IWP*MigStatus + elevation + (1|site) + (1|species)
6	System*MigStatus + MPPAR + WCL*MigStatus + IWP*MigStatus + elevation + (1|site) + (1|species)
7	Intensity*MigStatus + PD + WCL*MigStatus + IWP*MigStatus + elevation + (1|site) + (1|species)
8	Intensity*MigStatus + MPPAR + WCL*MigStatus + IWP*MigStatus + elevation + (1|site) + (1|species)

We inspected the distribution of residuals and checked for influential points using the 'performance' package (Lüdecke et al., 2021). In addition, we calculated marginal and conditional R^2 using the Nakagawa and Schielzeth (2013) method. The landscape buffers of different sites inevitably overlapped, especially at the larger scales, but this has been shown not to violate statistical independence (Zuckerberg et al., 2020). Spatial autocorrelation of modelled residuals was examined by calculating Moran's *I* using the package 'ape' (Paradis and Schliep, 2019). The sizes of the estimates were negligible (<0.001) and tests non-significant ($p > 0.1$) for all models and so no further action was taken.

We used a full model approach without simplification because we asked hypothesis-driven questions (following Shutt et al., 2018 and Zielonka et al., 2024). We examined continuous predictor significance from 'lmerTest' model summaries with p-values calculated using Satterthwaite's method for estimation of degrees of freedom. We assessed categorical predictor significance using term deletion and likelihood ratio tests to obtain p-values. If categorical predictors were significant, we undertook post-hoc pairwise contrasts to determine which levels were significant from one-another using the 'emmeans' package (Lenth et al., 2024). In many cases we were making large numbers of comparisons, and so we undertook Tukey-Kramer p-value adjustment. Here, we discuss the non-adjusted results but also present the adjusted results.

We acknowledge that this does not account for the multiple testing of predictor variables across models, and employ a cautionary approach to interpreting predictor significance, as follows. The results from the models with patch density or mean patch perimeter-area ratio were almost identical, and so only the models with patch density as a predictor variable are used for interpretation of the other predictor effects going forwards (mean patch perimeter-area ratio model results are presented in the supplementary material). In addition, while the results of all tests conducted are reported, isolated predictor significance in a single or small number of models should be interpreted as of limited importance and are not carried through to our conclusions and recommendations.

3.3. Results

Neither patch density nor mean patch-perimeter area ratio showed a significant association with mean standardised productivity at any scale (Tables S3.20 – S3.43).

Dominant Land System

At the 1 km scale, mean standardised productivity across all species varied significantly with the dominant land system (LRT: $X^2 = 17.83$, df = 5, $p < 0.01$), with species in sites within wetland landscapes having significantly greater mean productivity than those in all other system types (Table S3.5). Mean productivity was lowest at sites within forest- and settlement-dominated landscapes (Figure 3.1a). These differences in productivity across landscapes varied between resident species, arid-zone migrants and humid-zone migrants (LRT for interaction between system and migratory status: $X^2 = 37.89$, df = 10, $p<0.001$; Table S3.6). For residents, mean productivity was greatest at sites within wetland landscapes and lowest at sites within forest landscapes (Figure 3.1b). Arid-zone and humid-zone migrants showed similar patterns to one another (Figures 3.1c-d), but sites within settlement landscapes were particularly poor for arid-zone migrants and sites within wetland landscapes particularly good for humid-zone migrants, relative to the other systems.

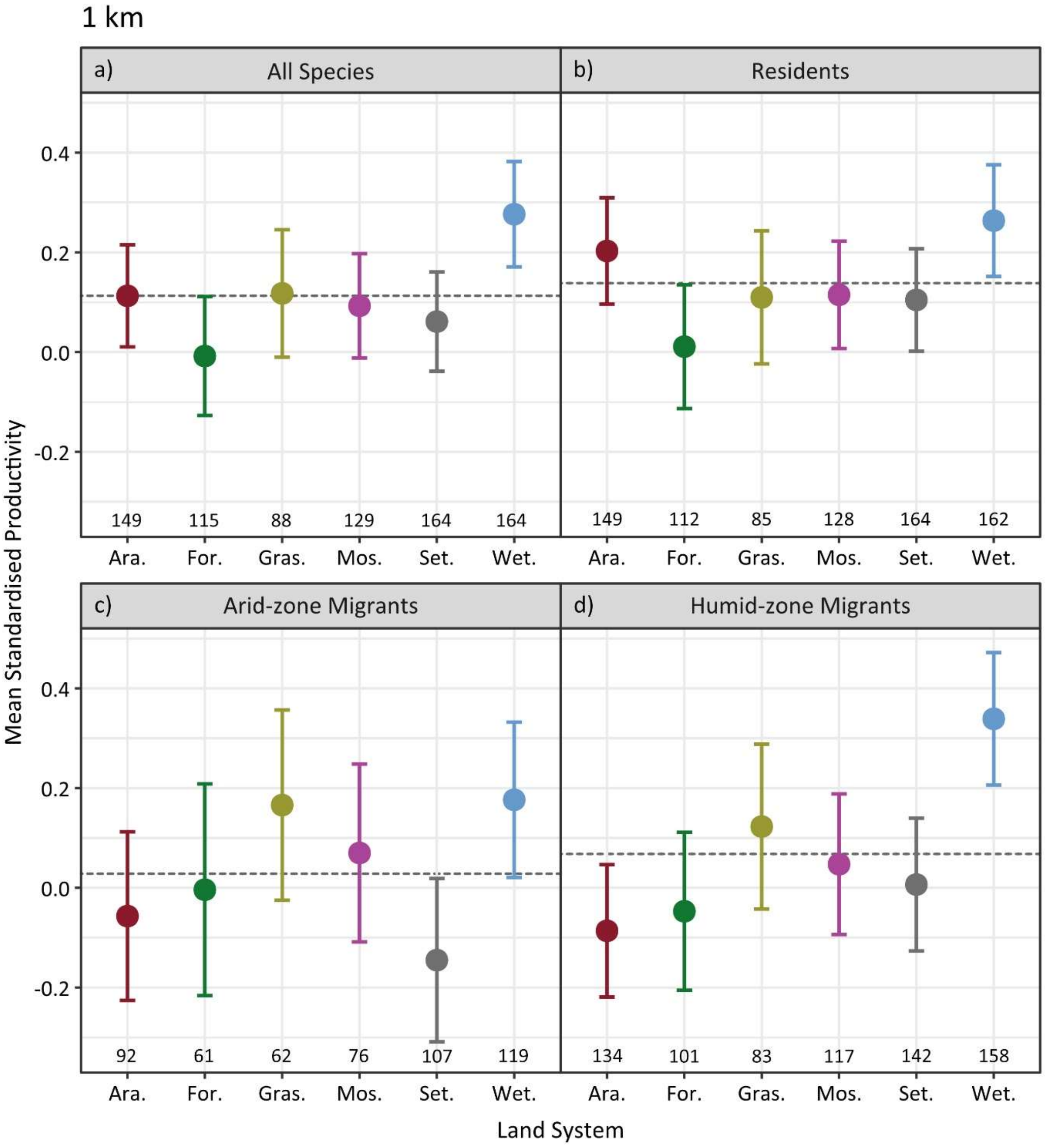


Figure 3.1: Mean standardised site-level productivity estimates and 95% Confidence Intervals at European Constant Effort Sites within landscapes dominated by different land system types at the 1 km scale. Productivity estimates are for a) all bird species, b) species that are residents within Europe or short-distance migrants, c) arid-zone sub-Saharan migrants or d) humid-zone sub-Saharan migrants. These are marginal means estimated from linear mixed models with system as a main effect (a), or with a system*migratory status interaction term (b, c & d). Horizontal dashed lines represent the overall mean productivity across all sites for each species group. The number of sites in each system type is given at the base of the plots. “Ara.” = Arable Cropland, “For.” = Forest. “Gras.” = Grassland, “Mos.” = Mosaic, “Sett.” = Settlement, “Wet.” = Wetland.

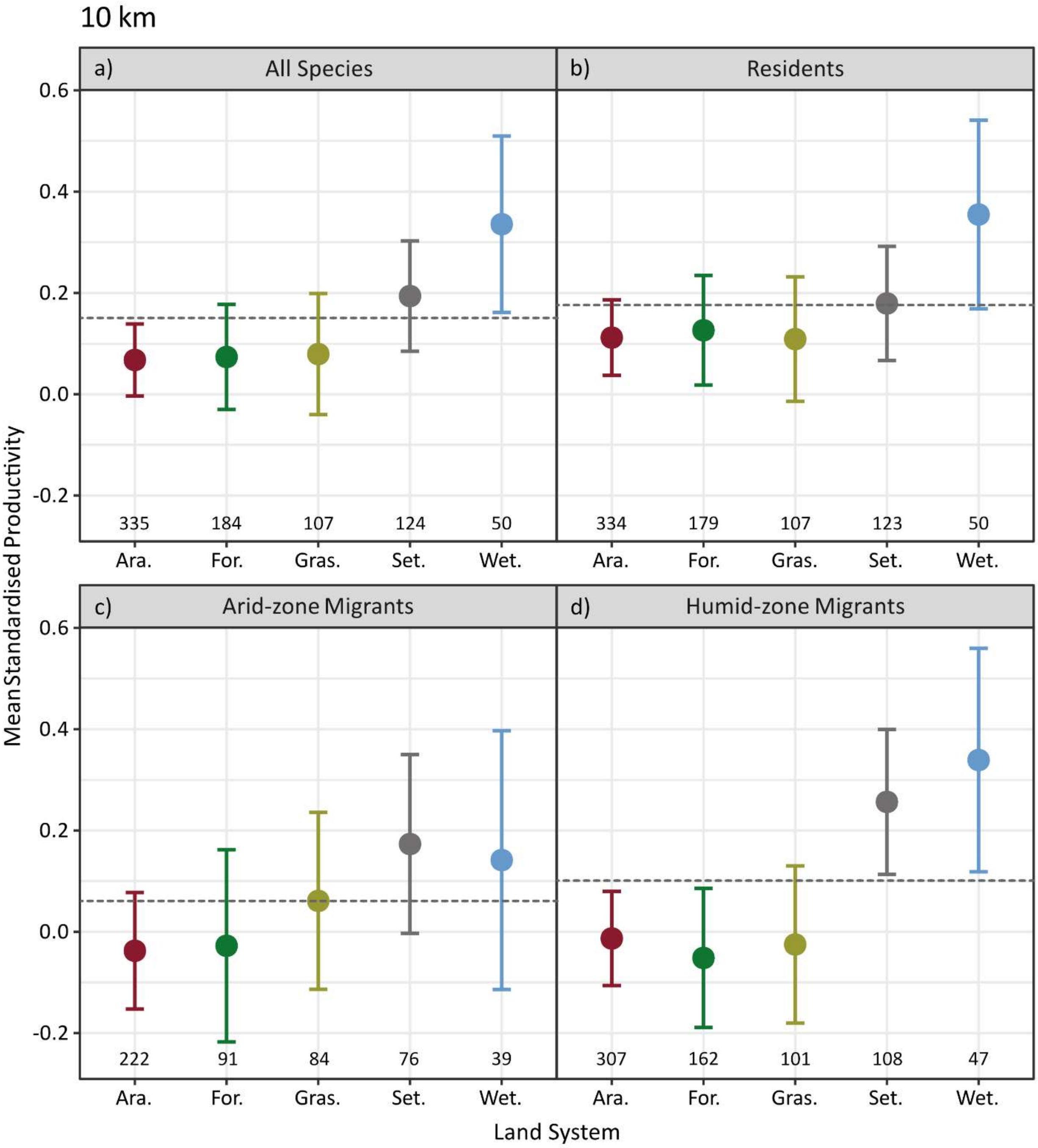


Figure 3.2: Mean standardised site-level productivity estimates and 95% Confidence Intervals at European Constant Effort Sites within landscapes dominated by different land system types at the 10 km scale. Productivity estimates are for a) all bird species, b) species that are residents within Europe or short-distance migrants, c) arid-zone sub-Saharan migrants or d) humid-zone sub-Saharan migrants. These are marginal means estimated from linear mixed models with system as a main effect (a), or with a system*migratory status interaction term (b, c & d). Horizontal dashed lines represent the overall mean productivity across all sites for each species group. The number of sites in each system type is given at the base of the plots. “Ara.” = Arable Cropland, “For.” = Forest. “Gras.” = Grassland, “Sett.” = Settlement, “Wet.” = Wetland.

Across all species, productivity did not vary significantly with the dominant land system in the surrounding 5 km (LRT: $X^2 = 6.92$, df = 4, $p = 0.14$), with only one weakly significant pairwise difference between sites in wetland (+) and forest (-) landscapes (Table S3.5). In addition, there was no significant interaction between the effect of system and migratory status (LRT: $X^2 = 10.17$, df = 8, $p = 0.25$), although there were some weakly significant differences between systems for humid-zone migrants (Table S3.7).

At the 10 km scale, mean standardised productivity across all species varied significantly with the dominant land system (LRT: $X^2 = 13.37$, df = 4, $p = 0.01$). Sites within wetland landscapes showed significantly greater productivity than those within arable, forest and grassland landscapes (Table S3.5, Figure 3.2a). Sites within settlement landscapes also showed greater productivity than those within arable landscapes (although with weak significance). Again, the differences in productivity across landscapes varied between the migratory groups (LRT: $X^2 = 18.16$, df = 8, $p = 0.02$). Arid-zone migrants and (especially) humid-zone migrants showed just as high productivity at sites within settlement-dominated landscapes as sites within wetland-dominated landscapes, a pattern not shown by residents (Figures 3.2b-d; Table S3.8 for pairwise comparisons). To further explore these patterns, we also compared productivity across sites of different 1 km systems within these 10 km settlement landscapes. Sites classified as wetland at 1 km and settlement at 10 km had significantly higher mean productivity across all species than sites classified as settlement at both 1 km and 10 km scales (Tables S3.9a and S3.9b), suggesting that these wetland 1 km sites were driving the high mean productivity within 10 km settlement landscapes. Additional exploration showed that mean productivity at sites classified as wetland at 1 km and settlement at 10 km was just as high as at sites classified as wetland at both 1 km and 10 km, and significantly greater than sites within 10 km landscapes classified as other system types (Tables S3.10a and S3.10b).

Intensity

At the 1 km scale, there was no significant overall effect of landscape intensity on the site-level productivity across all species (LRT: $X^2 = 1.96$, df = 2, $p = 0.37$, Table S3.11). There was, however, a significant interaction with migratory status (LRT: $X^2 = 10.51$, df = 4, $p = 0.03$); humid-zone migrants had significantly higher productivity at sites within low-intensity landscapes compared to sites within medium- and high-intensity landscapes (Table S3.12).

At the 5 km scale, productivity at sites in low-intensity landscapes was significantly higher than at sites in medium- and high-intensity landscapes (LRT: $X^2 = 12.48$, df = 2, $p < 0.01$, Table S3.11, Figure 3.3a). This general pattern was replicated for both residents and humid-zone migrants but there was no difference in productivity between low- and high-intensity landscapes for arid-zone migrants (Figures 3.3b-d, Table S3.13). Similar results were seen for the effect of intensity within a 10 km radius. Across species, productivity was again significantly higher at sites within low-intensity landscapes compared to high-intensity landscapes (LRT: $X^2 = 7.40$, df = 2, $p = 0.02$; Table S3.11, Figure 3.4a). This was also observed across all three migratory status groups (Table S3.14, Figures 3.4b-d).

When exploring these patterns at the individual land system level, the intensity effect was particularly pronounced in grassland-dominated landscapes. At the 5 km scale, for all species and for each migratory group, sites within low-intensity grassland landscapes had significantly greater productivity than sites within medium- and high-intensity grassland landscapes (Table S3.16, Figure S3.1). Meanwhile, at the 1 km and 10 km scales, productivity in sites within low-intensity grassland landscapes was significantly greater than at sites within high-intensity grassland for humid-zone migrants, but not for arid-zone migrants or residents (Tables S3.15 and S3.17). Productivity also varied significantly with management intensity for arable cropland and settlement landscapes, but this differed with migratory status and spatial scale. At the 5 km scale, resident species productivity was significantly greater at sites within low-intensity arable cropland landscapes compared to medium- and high-intensity arable landscapes (Table S3.18), but not at the other scales. Meanwhile, at the 1 km scale, arid-zone migrant productivity was greater at sites within high-intensity settlement landscapes compared to low-intensity landscapes (Table S3.19).

The frequency distributions of species-site productivity estimates within these different 1 km systems and 5 km intensities reveal that despite these differences between system and intensity categories, there was still a considerable amount of variation in productivity between sites within these categories (Figure 3.5, also see small model R^2 values).

Watercourse Length and Inland Water Body Perimeter

There were significant but small effects of watercourse length and inland water perimeter on the site-level productivity of migrants at the larger scales. Productivity of arid-zone and humid-zone migrants was lower at sites with longer watercourse lengths in the surrounding 5 km (Table S3.28, Figure S3.2) and 10 km landscapes (Table S3.30, Figure S3.3), with these effects stronger for sites within non-wetland landscapes (Tables S3.40 and S3.42). In contrast, resident species productivity was not significantly associated with watercourse length at any of the landscape scales. In addition, productivity did not significantly vary with watercourse length at the 1km landscape scale (Tables S3.20 and S3.32).

Across species, productivity did not significantly vary with inland water body perimeter within a 1 km radius (Tables S3.20 and S3.32) or 5km radius (Tables S23 and S3.34). However, at the 10 km scale, productivity showed a negative, non-linear relationship with increasing inland water perimeter, (Table S3.24; Figure S3.4), which was replicated in arid-zone and humid-zone migrants, but not residents (Table S3.30; Figure S3.5). This was small in size and was only detected in the system models, not the intensity models (Tables S3.36 and S3.42).

We found limited evidence that productivity varied with site elevation. Productivity was slightly but significantly lower at higher-elevation sites, when analysed at the 5 km scale amongst non-wetland sites (intensity LMM: $\beta = -4.58$, S.E. = 2.12, $t = -2.16$, $p = 0.03$). No effect of site elevation was detected in the models at the other scales.

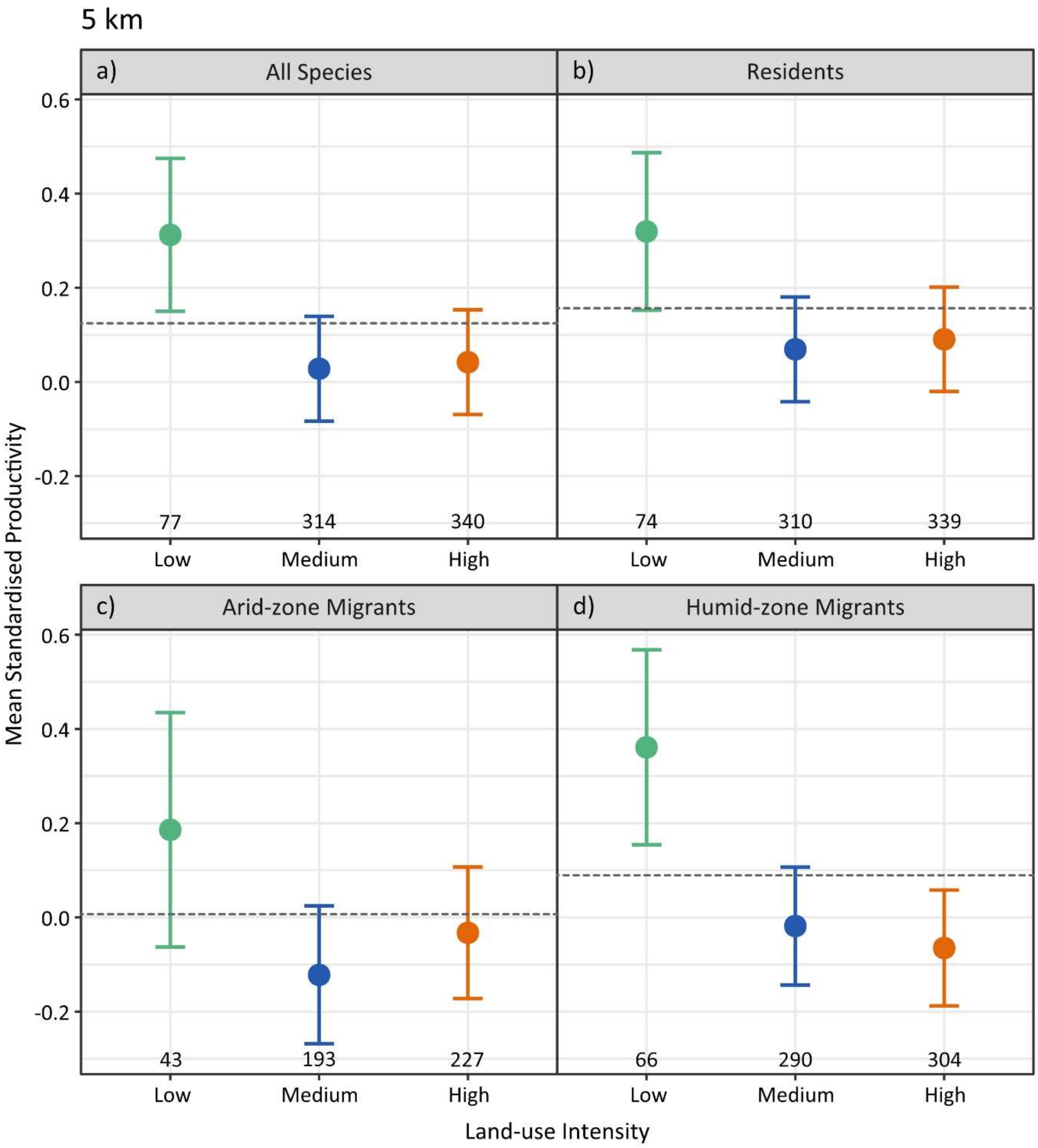


Figure 3.3: Mean standardised site-level productivity estimates and 95% Confidence Intervals at European Constant Effort Sites within landscapes dominated by different land-use intensities at the 5 km scale. Productivity estimates are for a) all bird species, b) species that are residents within Europe or short-distance migrants, c) arid-zone sub-Saharan migrants or d) humid-zone sub-Saharan migrants. These are marginal means estimated from linear mixed models with intensity as a main effect (a), or with an intensity*migratory status interaction term (b, c & d). Horizontal dashed lines represent the overall mean productivity across all sites for each species group. The number of sites in each intensity type is given at the base of the plots.

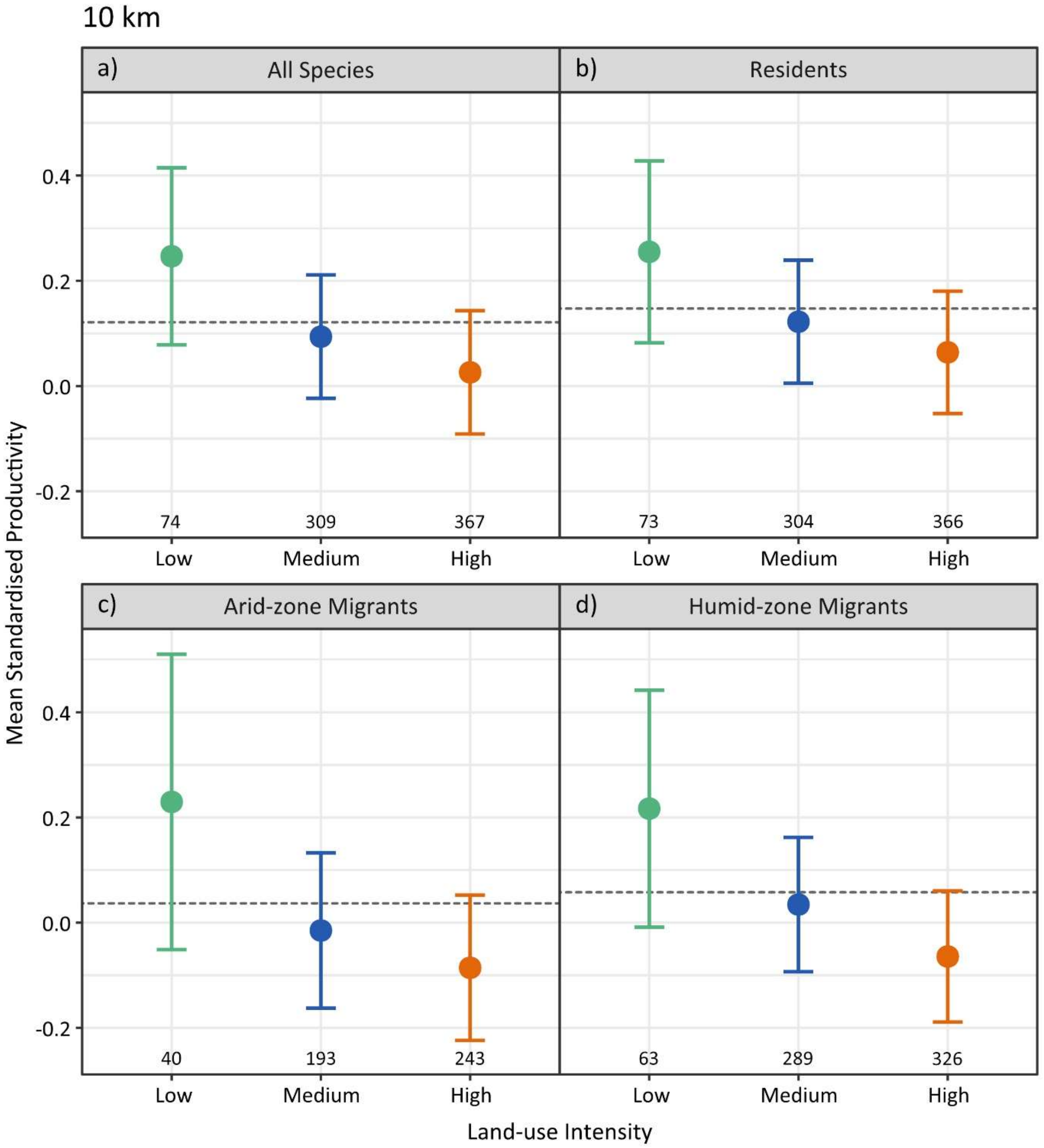


Figure 3.4: Mean standardised site-level productivity estimates and 95% Confidence Intervals at European Constant Effort Sites within landscapes dominated by different land-use intensities at the 10 km scale. Productivity estimates are for a) all bird species, b) species that are residents within Europe or short-distance migrants, c) arid-zone sub-Saharan migrants or d) humid-zone sub-Saharan migrants. These are marginal means estimated from linear mixed models with intensity as a main effect (a), or with an intensity*migratory status interaction term (b, c & d). Horizontal dashed lines represent the overall mean productivity across all sites for each species group. The number of sites in each intensity type is given at the base of the plots.

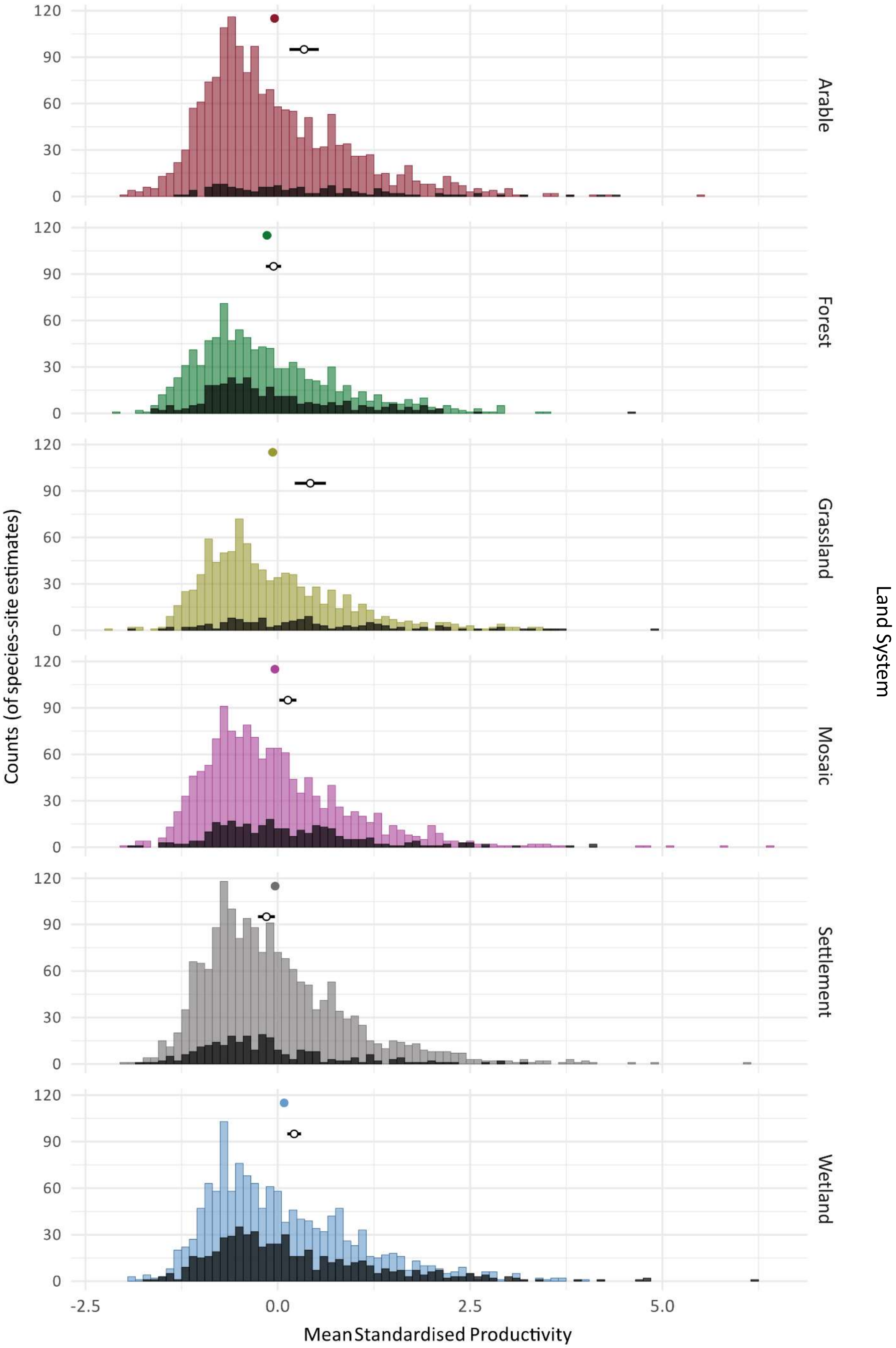


Figure 3.5: Frequency distributions of mean standardised productivity estimates for 90 species across 843 European Constant Effort Sites, split into sites within landscapes dominated by different land system types at the 1 km scale, and different land-use intensities at the 5 km scale (black = low intensity; coloured = medium/high intensity). Points and error bars represent means and 95% Confidence Intervals across species and sites (unfilled = low-intensity 5 km, filled = medium/high-intensity 5 km).

3.4. Discussion

The productivity of landbirds at European breeding sites varies with the land system and management intensity within the surrounding landscape. Across species, sites within landscapes dominated by wetlands nearly always showed the highest relative productivity, whilst those within landscapes dominated by other system types varied in their respective productivity levels across scales and between migratory groups. These land system effects were strongest at the local, 1 km landscape scale. Land-use intensity was more influential at larger scales, with sites within landscapes dominated by low-intensity land-uses demonstrating greater productivity compared to medium- and high-intensity landscapes, particularly in grasslands. In contrast to these aspects of landscape composition, we did not find evidence for effects of landscape configuration on site-level productivity.

Whilst we did find some differences in the responses of residents, arid-zone migrants and humid-zone migrants, the productivity of species in these migratory groups showed broadly similar associations with landscape structure. This is consistent with previous findings that productivity at CESs in Europe covaries between resident and migratory species (Morrison et al., 2021), and further demonstrates that common factors influence population trends and productivity across landbird communities. Importantly, these findings allow us to identify conservation policies and actions that would be beneficial for both residents and migrants at breeding sites.

Landscape Composition and Configuration

Our finding that productivity was highest at sites within wetland-dominated landscapes builds on the results of multiple previous studies demonstrating increased nestling condition, reproductive success and juvenile recruitment of landbird species in wetland habitats (Berzins et al., 2021, 2022; Tozer et al., 2010). This has been shown to be related to higher abundance of emergent aquatic insects (Berzins et al., 2022), which are of higher nutritional value compared to terrestrial insects due to their fatty-acid content (Twining et al., 2018). In addition, in wetland habitats, insect emergence occurs over a longer period compared to terrestrial habitats, providing extended feeding opportunities for provisioning parents (Both et al., 2010; Lewis-Phillips et al., 2020; although see Shipley et al., 2022). Most landbird species (excluding birds of prey) feed their chicks insects, and so our results may indicate increased fledging success and/or survival of fledglings due to increased availability of high-quality food in wetland-dominated landscapes. Contrary to this, we did not find a positive effect of inland water body perimeter or watercourse length in the landscape surrounding sites. This may be because the Europe-wide dataset we used is relatively coarse scale and did not include small water bodies like ponds, which are considerably undermapped (Biggs et al., 2017). Small water bodies have been suggested to be more productive than larger water bodies in their insect biomass (Berzins et al., 2022), and more research is needed into their role in supporting high productivity rates of bird species.

There are well-documented negative effects of increased land-use intensity on bird communities (Pellissier et al., 2017) and populations (Eglington and Pearce-Higgins, 2012; Zingg et al., 2018), especially in agricultural systems (Donald et al., 2001). Evidence for impacts on productivity itself is more mixed, with some studies demonstrating negative effects of agricultural intensity (Brickle et al., 2000; Britschgi et al., 2006; Garrett et al., 2022; Ghilain and Bélisle, 2008), whilst others have found limited evidence for an effect (Kusack et al., 2020; van Vliet et al., 2020; Zhao et al., 2022). We found an overall negative effect of increasing management intensity on productivity across species at the larger landscape scales, but not at the local 1 km scale. This indicates that, regardless of the local intensity, sites situated within intensive landscapes show reduced productivity. The evidence for negative impacts of increased management intensity was particularly strong within grassland-dominated landscapes. Studies which have explored the impact of grassland management intensity on bird productivity have tended to focus on farmland species which nest and forage directly in grassland, and are negatively impacted by reduced food availability for provisioning nestlings and higher nest predation rates in the structurally-uniform swards (Britschgi et al., 2006; Evans et al., 1997; van Vliet et al., 2020; Vickery et al., 2001). Here, we find negative effects on productivity across the bird community, especially in humid-zone migrants. While some of these species may forage for insects in the grassland itself, it is not likely that these impacts are entirely driven by these management practices. Instead, we suggest that this results from the lower heterogeneity of intensive grassland landscapes (Shipley et al., 2024), which have fewer semi-natural features such as scrub patches and grassy margins for nesting and foraging (Perkins et al., 2000; Rime et al., 2025; Vickery and Arlettaz, 2012). These impacts may be particularly strong in humid-zone migrants because their long migratory journeys mean they are more time-limited for breeding compared to other species, and so may be less able to lay replacement clutches following nest failure (Hoffmann et al., 2015; Morrison et al., 2019).

In contrast to landscape composition, we did not find an effect of patch density or mean patch perimeter-area ratio on productivity. Multiple studies have shown that landscape configuration is less important than composition for birds (Adler and Jedicke, 2022), and the evidence for configuration effects on bird productivity is mixed, differing between species and types of land cover (Harrod and Green, 2018; Harsh et al., 2022; Tewksbury et al., 1998). Therefore, the fact that we do not detect any effects may result from different species responses cancelling each other out so no overall pattern is seen across species (Betts et al., 2014). Overall patterns may also be obscured by the effects of increasing landscape complexity being positive or negative in different habitats (Fahrig, 2017). For example, increasing patch density in forest landscapes might indicate increased fragmentation, which can negatively impact bird productivity (Burke and Nol, 2000; Flaspohler et al., 2001). Meanwhile, increasing patch density in arable landscapes might indicate greater habitat heterogeneity and presence of semi-natural habitat, which can be beneficial for providing birds with multiple foraging and nesting resources (Vickery and Arlettaz, 2012). However, we did not find any effects within the individual system models, so this does not seem to be the case within our dataset. Alternatively, our ability to detect landscape configuration effects could have been reduced by mismatches in the year in which these metrics were measured (2012) and the years in which productivity was measured at each site (anywhere between 1998 and 2019). Temporal changes have been shown to be greater in CORINE land cover configuration compared to composition in western Europe (Mimet et al., 2016), and so it is more likely that temporal mismatch in the datasets affected the landscape configuration data than the composition data.

Whilst we have identified habitats and landscapes in which conditions associated with higher productivity occur more frequently, a large proportion of the variation in productivity amongst sites remains unexplained (Figure 3.5). This indicates that there are drivers of productivity we have not been able to account for. One such factor could be site-level characteristics, which may not be adequately represented within our broad-scale classifications of land system and intensity or by the 1 km resolution. For example, fine-scale habitat characteristics have frequently been shown to influence productivity rates (Conover et al., 2011; Darolová et al., 2014; Ruth and Skagen, 2018), and some studies have found that they explain more variation in nest success than landscape factors (Shew et al., 2019; Twedt et al., 2010). In addition, not only is the presence of small water bodies within sites a potentially important factor, but also their condition, because this determines their quality as foraging and nesting habitat for birds (Davies et al., 2016; Lewis-Phillips et al., 2020, 2019). Further work is therefore needed to identify site-level characteristics associated with productivity rates, using a similar approach to what we present here with landscape characteristics.

Implications of Analysis Approach

It is important to recognise that our multi-species models effectively average across species responses. As a consequence, a large proportion of the sites are determined as intermediate in quality, supporting high productivity for some species and low productivity for others. This combined with the standardisation process could partly explain why the effect sizes we detect are quite small. In addition, CE sites are not a random sample of the European landscape and are instead selected based on their suitability for catching sufficient numbers of birds to measure demographic metrics. These sites therefore represent relatively ‘good’ sites compared to the wider matrix, which might dilute the effect of the surrounding landscape on site-level productivity, as measured in this study. Taken together, this means that our results could be seen as relatively conservative, and the wider impacts of landscape composition on productivity may be much stronger than we present here. Another consequence of this modelling approach is that landscape characteristics associated with sites at the extremes, which are either consistently ‘good’ or ‘poor’ across species, are likely to be particularly informative for designing conservation actions.

An additional consideration is that the metric of productivity we use can be influenced by local movement patterns of dispersing juveniles, and may therefore be more indicative of productivity within a broader area around the CE sites rather than site-level productivity itself (Robinson, 2023). Inferences about the influence of landscape structure on productivity can still be made, but caution should be exercised because these patterns may also incorporate its influence on immigration rates into or emigration rates from sites. For example, there is some evidence that juveniles of migratory species perform pre-migration movements from their natal sites towards areas with higher-quality habitat with more abundant foraging resources for pre-migratory fuel-loading or greater shelter from predators (Mitchell et al., 2010; although see Hayes et al., 2024). The relatively high productivity of migrants in sites within urban wetland landscapes reported here may therefore be influenced, in part at least, by the congregation of juveniles from the wider urban landscape at higher-quality wetland habitat at the end of the season, before they begin their migratory journeys. The extent to which productivity estimates are affected by juvenile dispersal warrants further exploration because this influences the conclusions we can make about the scales over which environmental conditions influence productivity. This will be particularly important for studies on the effect of site-level characteristics on CES productivity, which could increase the likelihood of measuring true site-level productivity by removing captures from the end of the breeding season to avoid the inclusion of dispersing juveniles from elsewhere.

Conclusions

We show that examination of spatial variation in productivity rates can be used to identify target areas for the spatial prioritisation of limited conservation resources to benefit both resident and migratory breeding bird populations across Europe. Our findings demonstrate that there is an urgent need to protect and restore wetland habitats, and support low-intensity land uses, especially in grassland-dominated landscapes. This could partly be achieved through the expansion of protected sites networks to wetlands under threat from development and other anthropogenic impacts, but population-level benefits are likely to be limited for the common and widespread species studied here. More significant population recovery could be achieved through actions applied at large-scales to restore degraded and lost wetlands, and reduce the intensity of grassland management, through national and potentially continent-wide land management policies such as agri-environment schemes, and landscape recovery projects. Further work is needed to identify local-scale characteristics associated with high productivity, and the mechanistic processes driving these patterns, such as insect food availability, in order to inform specific management actions. It will be particularly important to focus on sites achieving consistently high productivity to identify actions which could be targeted at sites with consistently low productivity to replicate these conditions over large scales.

References

Adler, K., Jedicke, E., 2022. Landscape metrics as indicators of avian community structures – A state of the art review. Ecological Indicators 145, 109575. https://doi.org/10.1016/j.ecolind.2022.109575

Akresh, M.E., McInvale, S.L., King, D.I., 2024. A meta-analysis of edge effects on nesting success in forest and shrubland birds of eastern North America. Journal of Field Ornithology 95. https://doi.org/10.5751/JFO-00481-950212

Berzins, L.L., Mazer, A.K., Morrissey, C.A., Clark, R.G., 2021. Pre-fledging quality and recruitment in an aerial insectivore reflect dynamics of insects, wetlands and climate. Oecologia 196, 89–100. https://doi.org/10.1007/s00442-021-04918-7

Berzins, L.L., Morrissey, C.A., Howerter, D.W., Clark, R.G., 2022. Conserving wetlands in agroecosystems can sustain aerial insectivore productivity and survival. Can. J. Zool. 100, 617–629. https://doi.org/10.1139/cjz-2021-0204

Betts, M.G., Fahrig, L., Hadley, A.S., Halstead, K.E., Bowman, J., Robinson, W.D., Wiens, J.A., Lindenmayer, D.B., 2014. A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. Ecography 37, 517–527. https://doi.org/10.1111/ecog.00740

Biggs, J., von Fumetti, S., Kelly-Quinn, M., 2017. The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers. Hydrobiologia 793, 3–39. https://doi.org/10.1007/s10750-016-3007-0

Bionda, R., Brambilla, M., 2012. Rainfall and landscape features affect productivity in an alpine population of Eagle Owl Bubo bubo. J Ornithol 153, 167–171. https://doi.org/10.1007/s10336-011-0721-2

Both, C., Turnhout, C.A.M. van, Bijlsma, R.G., Siepel, H., Strien, A.J. van, Strien, A.J. van, Foppen, R.P.B., 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proceedings of The Royal Society B: Biological Sciences 277, 1259–1266. https://doi.org/10.1098/rspb.2009.1525

Bradbury, R.B., Kirby, W.B., 2006. Farmland birds and resource protection in the UK: Cross-cutting solutions for multi-functional farming? Biological Conservation 129, 530–542. https://doi.org/10.1016/j.biocon.2005.11.020

Brickle, N.W., Harper, D.G.C., Aebischer, N.J., Cockayne, S.H., 2000. Effects of agricultural intensification on the breeding success of corn buntings Miliaria calandra. Journal of Applied Ecology 37, 742–755. https://doi.org/10.1046/j.1365-2664.2000.00542.x

Britschgi, A., Spaar, R., Arlettaz, R., 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. Biological Conservation 130, 193–205. https://doi.org/10.1016/j.biocon.2005.12.013

Brooks, M., E., Kristensen, K., Benthem, K., J. ,van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., Bolker, B., M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9, 378. https://doi.org/10.32614/RJ-2017-066

Burke, D.M., Nol, E., 2000. Landscape and Fragment Size Effects on Reproductive Success of Forest-Breeding Birds in Ontario. Ecological Applications 10, 1749–1761. https://doi.org/10.1890/1051-0761(2000)010%255B1749:LAFSEO%255D2.0.CO;2

Burns, F., Eaton, M.A., Burfield, I.J., Klvaňová, A., Šilarová, E., Staneva, A., Gregory, R.D., 2021. Abundance decline in the avifauna of the European Union reveals cross-continental similarities in biodiversity change. Ecology and Evolution n/a. https://doi.org/10.1002/ece3.8282

Chalfoun, A.D., Thompson III, F.R., Ratnaswamy, M.J., 2002. Nest Predators and Fragmentation: a Review and Meta-Analysis. Conservation Biology 16, 306–318. https://doi.org/10.1046/j.1523-1739.2002.00308.x

Conover, R.R., Burger Jr., L.W., Linder, E.T., 2011. Grassland bird nest ecology and survival in upland habitat buffers near wooded edges. Wildlife Society Bulletin 35, 353–361. https://doi.org/10.1002/wsb.87

Cornell, K.L., Donovan, T.M., 2010. Scale-Dependent Mechanisms of Habitat Selection for a Migratory Passerine: An Experimental Approach. The Auk 127, 899–908. https://doi.org/10.1525/auk.2010.09171

Cox, W.A., Thompson, F.R., Faaborg, J., 2012. Landscape forest cover and edge effects on songbird nest predation vary by nest predator. Landscape Ecol 27, 659–669. https://doi.org/10.1007/s10980-012-9711-x

Cramp, S., 2006. The birds of the western Palearctic interactive. Oxford University Press and BirdGuides, Oxford, U.K.

Darolová, A., Krištofík, J., Hoi, H., 2014. Vegetation type variation in marsh habitats: does it affect nest site selection, reproductive success, and maternal investment in Reed Warblers? J Ornithol 155, 997–1008. https://doi.org/10.1007/s10336-014-1086-0

Davies, S.R., Sayer, C.D., Greaves, H., Siriwardena, G.M., Axmacher, J.C., 2016. A new role for pond management in farmland bird conservation. Agriculture, Ecosystems & Environment 233, 179–191. https://doi.org/10.1016/j.agee.2016.09.005

Davison, C.W., Rahbek, C., Morueta-Holme, N., 2021. Land-use change and biodiversity: Challenges for assembling evidence on the greatest threat to nature. Global Change Biology 27, 5414–5429. https://doi.org/10.1111/gcb.15846

Dolman, P.M., 2012. Mechanisms and processes underlying landscape structure effects on bird populations, in: Fuller, R.J. (Ed.), Birds and Habitat. Cambridge University Press, pp. 93–124. https://doi.org/10.1017/CBO9781139021654.006

Donald, P.F., Green, R.E., Heath, M., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of The Royal Society B: Biological Sciences 268, 25–29. https://doi.org/10.1098/rspb.2000.1325

Dou, Y., Cosentino, F., Malek, Z., Maiorano, L., Thuiller, W., Verburg, P.H., 2021. A new European land systems representation accounting for landscape characteristics. Landscape Ecol 36, 2215–2234. https://doi.org/10.1007/s10980-021-01227-5

Eglington, S.M., Pearce-Higgins, J.W., 2012. Disentangling the Relative Importance of Changes in Climate and Land-Use Intensity in Driving Recent Bird Population Trends. PLOS ONE 7. https://doi.org/10.1371/journal.pone.0030407

European Environment Agency, 2020a. EU-Hydro River Network Database 2006-2012 (vector), Europe. European Union's Copernicus Land Monitoring Service information. https://doi.org/10.2909/393359a7-7ebd-4a52-80ac-1a18d5f3db9c

European Environment Agency, 2020b. CORINE Land Cover 2012 (raster 100m). European Union's Copernicus Land Monitoring Service information. https://doi.org/10.2909/a84ae124-c5c5-4577-8e10-511bfe55cc0d

Evans, A.D., Smith, K.W., Buckingham, D.L., Evans, J., 1997. Seasonal variation in breeding performance and nestling diet of Cirl Buntings *Emberiza cirlus* in England. Bird Study 44, 66–79. https://doi.org/10.1080/00063659709461039

Fahrig, L., 2017. Ecological Responses to Habitat Fragmentation Per Se. Annu. Rev. Ecol. Evol. Syst. 48, 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J., Eigenbrod, F., Ford, A.T., Harrison, S.P., Jaeger, J.A.G., Koper, N., Martin, A.E., Martin, J.-L., Metzger, J.P., Morrison, P., Rhodes, J.R., Saunders, D.A., Simberloff, D., Smith, A.C., Tischendorf, L., Vellend, M., Watling, J.I., 2019. Is habitat fragmentation bad for biodiversity? Biological Conservation 230, 179–186. https://doi.org/10.1016/j.biocon.2018.12.026

Flaspohler, D.J., Temple, S.A., Rosenfield, R.N., 2001. Species-Specific Edge Effects on Nest Success and Breeding Bird Density in a Forested Landscape. Ecological Applications 11, 32–46. https://doi.org/10.1890/1051-0761

Fraixedas, S., Lindén, A., Piha, M., Cabeza, M., Gregory, R., Lehikoinen, A., 2020. A state-of-the-art review on birds as indicators of biodiversity: Advances, challenges, and future directions. Ecological Indicators 118, 106728. https://doi.org/10.1016/j.ecolind.2020.106728

Garrett, D.R., Pelletier, F., Garant, D., Bélisle, M., 2022. Combined influence of food availability and agricultural intensification on a declining aerial insectivore. Ecological Monographs 92, e1518. https://doi.org/10.1002/ecm.1518

Ghilain, A., Bélisle, M., 2008. Breeding success of tree swallows along a gradient of agricultural intensification. Ecological Applications 18, 1140–1154. https://doi.org/10.1890/07-1107.1

Gregory, R.D., van Strien, A., 2010. Wild Bird Indicators: Using Composite Population Trends of Birds as Measures of Environmental Health. Ornithological Science 9, 3–22. https://doi.org/10.2326/osj.9.3

Hadley, A.S., Betts, M.G., 2016. Refocusing Habitat Fragmentation Research Using Lessons from the Last Decade. Curr Landscape Ecol Rep 1, 55–66. https://doi.org/10.1007/s40823-016-0007-8

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6, e4794. https://doi.org/10.7717/peerj.4794

Harrod, S.E., Green, M.C., 2018. Effects of Class-level Vegetation Characteristics on Nesting Success of Bewick's Wrens. Southeastern Naturalist 17, 381–395.

Harsh, S., Lonsinger, R.C., Gregory, A.J., 2022. Habitat amount or landscape configuration: Emerging HotSpot analysis reveals the importance of habitat amount for a grassland bird in South Dakota. PLOS ONE 17, e0274808. https://doi.org/10.1371/journal.pone.0274808

Hayes, S., Boyd, B., Stutchbury, B., 2024. Why do juvenile Wood Thrushes make long-distance pre-migratory movements across a fragmented landscape? JFO 95, art9. https://doi.org/10.5751/JFO-00465-950209

Heinrichs, J.A., Bender, D.J., Schumaker, N.H., 2016. Habitat degradation and loss as key drivers of regional population extinction. Ecological Modelling 335, 64–73. https://doi.org/10.1016/j.ecolmodel.2016.05.009

Hesselbarth, M.H.K., Sciani, M., With, K.A., Wiegand, K., Nowosad, J., 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 1648–1657. https://doi.org/10.1111/ecog.04617

Hoffmann, J., Postma, E., Schaub, M., 2015. Factors influencing double brooding in Eurasian Hoopoes Upupa epops. Ibis 157, 17–30. https://doi.org/10.1111/ibi.12188

Iwata, T., Nakano, S., Murakami, M., 2003. Stream meanders increase insectivorous bird abundance in riparian deciduous forests. Ecography 26, 325–337. https://doi.org/10.1034/j.1600-0587.2003.03355.x

Iwata, T., Urabe, J., Mitsuhashi, H., 2010. Effects of Drainage-Basin Geomorphology on Insectivorous Bird Abundance in Temperate Forests. Conservation Biology 24, 1278–1289. https://doi.org/10.1111/j.1523-1739.2010.01493.x

Kusack, J.W., Mitchell, G.W., Evans, D.R., Cadman, M.D., Hobson, K.A., Keith A. Hobson, Keith A. Hobson, 2020. Effects of agricultural intensification on nestling condition and number of young fledged of barn swallows (Hirundo rustica). Science of The Total Environment 709, 136195. https://doi.org/10.1016/j.scitotenv.2019.136195

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82, 1–26. https://doi.org/10.18637/jss.v082.i13

Lampila, P., Mönkkönen, M., Desrochers, A., 2005. Demographic Responses by Birds to Forest Fragmentation. Conservation Biology 19, 1537–1546. https://doi.org/10.1111/j.1523-1739.2005.00201.x

Lande, U.S., Herfindal, I., Willebrand, T., Moa, P.F., Storaas, T., 2014. Landscape characteristics explain large-scale variation in demographic traits in forest grouse. Landscape Ecol 29, 127–139. https://doi.org/10.1007/s10980-013-9960-3

Lees, A.C., Haskell, L., Allinson, T., Bezeng, S.B., Burfield, I.J., Renjifo, L.M., Rosenberg, K.V., Viswanathan, A., Butchart, S.H.M., 2022. State of the World's Birds. Annual Review of Environment and Resources 47, 231–260. https://doi.org/10.1146/annurev-environ-112420-014642

Lenth, R.V., Banfai, B., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Piaskowski, J., Riebl, H., Singmann, H., 2024. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Lewis-Phillips, J., Brooks, S.J., Sayer, C.D., McCrea, R., Siriwardena, G., Robson, H., Harrison, A.L., Axmacher, J.C., 2019. Seasonal benefits of farmland pond management for birds. Bird Study 66, 342–352. https://doi.org/10.1080/00063657.2019.1688762

Lewis-Phillips, J., Brooks, S.J., Sayer, C.D., Patmore, I.R., Hilton, G.M., Harrison, A., Robson, H., Axmacher, J.C., 2020. Ponds as insect chimneys: Restoring overgrown farmland ponds benefits birds through elevated productivity of emerging aquatic insects. Biological Conservation 241, 108253. https://doi.org/10.1016/j.biocon.2019.108253

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software 6, 3139. https://doi.org/10.21105/joss.03139

Lustig, A., Stouffer, D.B., Roigé, M., Worner, S.P., 2015. Towards more predictable and consistent landscape metrics across spatial scales. Ecological Indicators 57, 11–21. https://doi.org/10.1016/j.ecolind.2015.03.042

McGarigal, K., Cushman, S.A., Ene, E., 2023. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical Maps.

McKellar, A.E., Berzins, L.L., Morrissey, C.A., Michelson, C.I., Clark, R.G., 2025. The positive influence of wetlands on reproductive success and body mass in an aerial insectivore is more pronounced in intensively cropped agroecosystems. Ornithological Applications duaf051. https://doi.org/10.1093/ornithapp/duaf051

Mimet, A., Pellissier, V., Houet, T., Julliard, R., Simon, L., 2016. A Holistic Landscape Description Reveals That Landscape Configuration Changes More over Time than Composition: Implications for Landscape Ecology Studies. PLOS ONE 11, e0150111. https://doi.org/10.1371/journal.pone.0150111

Mitchell, G.W., Taylor, P.D., Warkentin, I.G., 2010. Assessing the Function of Broad-Scale Movements Made by Juvenile Songbirds Prior to Migration. The Condor: Ornithological Applications 112, 644–654. https://doi.org/10.1525/cond.2010.090136

Morrison, C.A., Alves, J.A., Gunnarsson, T.G., Þórisson, B., Gill, J.A., 2019. Why do earlier-arriving migratory birds have better breeding success? Ecology and Evolution 9, 8856–8864. https://doi.org/10.1002/ece3.5441

Morrison, C.A., Butler, S.J., Clark, J.A., Arizaga, J., Baltà, O., Cepák, J., Nebot, A.L., Piha, M., Thorup, K., Wenninger, T., Robinson, R.A., Gill, J.A., 2022. Demographic variation in space and time: implications for conservation targeting. Royal Society Open Science 9, 211671. https://doi.org/10.1098/rsos.211671

Morrison, C.A., Butler, S.J., Robinson, R.A., Clark, J.A., Arizaga, J., Aunins, A., Baltà, O., Cepák, J., Chodkiewicz, T., Escandell, V., Foppen, R.P.B., Gregory, R.D., Husby, M., Jiguet, F., Kålås, J.A., Lehikoinen, A., Lindström, Å., Moshøj, C.M., Nagy, K., Nebot, A.L., Piha, M., Reif, J., Sattler, T., Škorpilová, J., Szép, T., Teufelbauer, N., Thorup, K., van Turnhout, C., Wenninger, T., Gill, J.A., 2021. Covariation in population trends and demography reveals targets for conservation action. Proceedings of the Royal Society B: Biological Sciences 288, 20202955. https://doi.org/10.1098/rspb.2020.2955

Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pebesma, E., 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10, 439–446. https://doi.org/10.32614/RJ-2018-009

Pellissier, V., Mimet, A., Fontaine, C., Svenning, J.-C., Couvet, D., 2017. Relative importance of the land-use composition and intensity for the bird community composition in anthropogenic landscapes. Ecol. Evol. 7, 10513–10535. https://doi.org/10.1002/ece3.3534

Perkins, A.J., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Morris, A.J., Barnett, P.R., 2000. Habitat characteristics affecting use of lowland agricultural grassland by birds in winter. Biological Conservation 95, 279–294. https://doi.org/10.1016/S0006-3207(00)00042-2

Püttker, T., Crouzeilles, R., Almeida-Gomes, M., Schmoeller, M., Maurenza, D., Alves-Pinto, H., Pardini, R., Vieira, M.V., Banks-Leite, C., Fonseca, C.R., Metzger, J.P., Accacio, G.M., Alexandrino, E.R., Barros, C.S., Bogoni, J.A., Boscolo, D., Brancalion, P.H.S., Bueno, A.A., Cambui, E.C.B., Canale, G.R., Cerqueira, R., Cesar, R.G., Colletta, G.D., Delciellos, A.C., Dixo, M., Estavillo, C., Esteves, C.F., Falcão, F., Farah, F.T., Faria, D., Ferraz, K.M.P.M.B., Ferraz, S.F.B., Ferreira, P.A., Graipel, M.E., Grelle, C.E.V., Hernández, M.I.M., Ivanauskas, N., Laps, R.R., Leal, I.R., Lima, M.M., Lion, M.B., Magioli, M., Magnago, L.F.S., Mangueira, J.R.A.S., Marciano-Jr, E., Mariano-Neto, E., Marques, M.C.M., Martins, S.V., Matos, M.A., Matos, F.A.R., Miachir, J.I., Morante-Filho, J.M., Olifiers, N., Oliveira-Santos, L.G.R., Paciencia, M.L.B., Paglia, A.P., Passamani, M., Peres, C.A., Pinto Leite, C.M., Porto, T.J., Querido, L.C.A., Reis, L.C., Rezende, A.A., Rigueira, D.M.G., Rocha, P.L.B., Rocha-Santos, L., Rodrigues, R.R., Santos, R.A.S., Santos, J.S., Silveira, M.S., Simonelli, M., Tabarelli, M., Vasconcelos, R.N., Viana, B.F., Vieira, E.M., Prevedello, J.A., 2020. Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species. Biological Conservation 241, 108368. https://doi.org/10.1016/j.biocon.2019.108368

R Core Team, 2024. R: A Language and Environment for Statistical Computing.

Reidy, J.L., Sinnott, E.A., Thompson III, F.R., O'Donnell, L., 2023. Urban land cover and El Niño events negatively impact population viability of an endangered North American songbird. Ecosphere 14, e4583. https://doi.org/10.1002/ecs2.4583

Rime, Y., Korner, P., Helm, B., Müller, T., Amrhein, V., Liechti, F., Meier, C.M., 2025. Drivers of nest site selection and breeding success in an Alpine ground-nesting songbird. J Ornithol 166, 357–370. https://doi.org/10.1007/s10336-024-02221-9

Robinson, R.A., 2023. Understanding population change: the value of the EuroCES constant-effort ringing programme. Ringing & Migration 38, 29–37. https://doi.org/10.1080/03078698.2024.2311771

Robinson, R.A., Julliard, R., Saracco, J.F., 2009. Constant effort: studying avian population processes using standardised ringing. Ringing & Migration 24, 199–204.

Rodewald, A.D., Yahner, R.H., 2001. Influence of Landscape Composition on Avian Community Structure and Associated Mechanisms. Ecology 82, 3493–3504. https://doi.org/10.1890/0012-9658(2001)082%255B3493:IOLCOA%255D2.0.CO;2

Ruth, J.M., Skagen, S.K., 2018. Reproductive response of Arizona Grasshopper Sparrows to weather patterns and habitat structure. The Condor 120, 596–616. https://doi.org/10.1650/CONDOR-17-128.1

Sala, O.E., Stuart Chapin, F., III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global Biodiversity Scenarios for the Year 2100. Science 287, 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Šálek, M., Mayer, S.S., Rymešová, D., Černý, M., Mikula, P., Sládeček, M., 2025. Synergistic effects of habitat composition and weather on reproduction of a sharply declining farmland bird in Central Europe. Landsc Ecol 40, 1–17. https://doi.org/10.1007/s10980-025-02110-3

Shew, J.J., Nielsen, C.K., Sparling, D.W., 2019. Finer-scale habitat predicts nest survival in grassland birds more than management and landscape: A multi-scale perspective. Journal of Applied Ecology 56, 929–945. https://doi.org/10.1111/1365-2664.13317

Shipley, J.R., Frei, E.R., Bergamini, A., Boch, S., Schulz, T., Ginzler, C., Barandun, M., Bebi, P., Bolliger, J., Bollmann, K., Delpouve, N., Gossner, M.M., Graham, C., Krumm, F., Marty, M., Pichon, N., Rigling, A., Rixen, C., 2024. Agricultural practices and biodiversity: Conservation policies for semi-natural grasslands in Europe. Current Biology 34, R753–R761. https://doi.org/10.1016/j.cub.2024.06.062

Shipley, J.R., Twining, C.W., Mathieu-Resuge, M., Parmar, T.P., Kainz, M., Martin-Creuzburg, D., Weber, C., Winkler, D.W., Graham, C.H., Matthews, B., 2022. Climate change shifts the timing of nutritional flux from aquatic insects. Current Biology 32, 1342-1349.e3. https://doi.org/10.1016/j.cub.2022.01.057

Shutt, J.D., Bolton, M., Cabello, I.B., Burgess, M.D., Phillimore, A.B., 2018. The effects of woodland habitat and biogeography on blue tit Cyanistes caeruleus territory occupancy and productivity along a 220 km transect. Ecography 41, 1967–1978. https://doi.org/10.1111/ecog.03573

Siriwardena, G.M., Crick, H.Q.P., Baillie, S.R., Wilson, J.D., 2000. Agricultural habitat-type and the breeding performance of granivorous farmland birds in Britain. Bird Study 47, 66–81. https://doi.org/10.1080/00063650009461161

Smith, A.C., Fahrig, L., Francis, C.M., 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. Ecography 34, 103–113. https://doi.org/10.1111/j.1600-0587.2010.06201.x

Stephens, S.E., Koons, D.N., Rotella, J.J., Willey, D.W., 2004. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115, 101–110. https://doi.org/10.1016/S0006-3207(03)00098-3

Storchová, L., Hořák, D., 2018. Life-history characteristics of European birds. Global Ecology and Biogeography 27, 400–406. https://doi.org/10.1111/geb.12709

Svensson, L., 1992. Identification Guide to European Passerines. The author.

Tewksbury, J.J., Hejl, S.J., Martin, T.E., 1998. Breeding Productivity Does Not Decline with Increasing Fragmentation in a Western Landscape. Ecology 79, 2890–2903. https://doi.org/10.1890/0012-9658(1998)079%255B2890:BPDNDW%255D2.0.CO;2

Tozer, D.C., Nol, E., Abraham, K.F., 2010. Effects of local and landscape-scale habitat variables on abundance and reproductive success of wetland birds. Wetlands Ecol Manage 18, 679–693. https://doi.org/10.1007/s11273-010-9187-x

Twedt, D.J., Somershoe, S.G., Hazler, K.R., Cooper, R.J., 2010. Landscape and Vegetation Effects on Avian Reproduction on Bottomland Forest Restorations. The Journal of Wildlife Management 74, 423–436. https://doi.org/10.2193/2008-563

Twining, C.W., Shipley, J.R., Winkler, D.W., 2018. Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. Ecology Letters 21, 1812–1820. https://doi.org/10.1111/ele.13156

van Vliet, H.E.J., Stutchbury, B.J.M., Newman, A.E.M., Norris, D.R., 2020. The impacts of agriculture on an obligate grassland bird of North America. Agriculture, Ecosystems & Environment 287, 106696. https://doi.org/10.1016/j.agee.2019.106696

Vickery, J. a., Tallowin, J. r., Feber, R. e., Asteraki, E. j., Atkinson, P. w., Fuller, R. j., Brown, V. k., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology 38, 647–664. https://doi.org/10.1046/j.1365-2664.2001.00626.x

Vickery, J., Arlettaz, R., 2012. The importance of habitat heterogeneity at multiple scales for birds in European agricultural landscapes, in: Fuller, R.J. (Ed.), Birds and Habitat. Cambridge University Press, pp. 177–204. https://doi.org/10.1017/CBO9781139021654.009

Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J., Gregory, R.D., 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156, 1–22. https://doi.org/10.1111/ibi.12118

Vickery, J.A., Mallord, J.W., Adams, W.M., Beresford, A.E., Both, C., Cresswell, W., Diop, N., Ewing, S.R., Gregory, R.D., Morrison, C.A., Sanderson, F.J., Thorup, K., Van Wijk, R.E., Hewson, C.M., 2023. The conservation of Afro-Palaearctic migrants: What we are learning and what we need to know? Ibis n/a. https://doi.org/10.1111/ibi.13171

Woodward, A.A., Fink, A.D., Thompson, F.R., 2001. Edge Effects and Ecological Traps: Effects on Shrubland Birds in Missouri. The Journal of Wildlife Management 65, 668. https://doi.org/10.2307/3803018

Zhao, Q., Mitchell, G.W., Cadman, M.D., Kusack, J.W., Evans, D.R., Bumelis, K., Hobson, K.A., Weegman, M.D., Salvadori, A., Wilson, S., 2022. Integrating regional and site-level data to assess drivers of population decline in a threatened aerial insectivorous bird. Biological Conservation 265, 109424. https://doi.org/10.1016/j.biocon.2021.109424

Zielonka, N.B., Shutt, J.D., Butler, S.J., Dicks, L.V., 2024. Management practices, and not surrounding habitats, drive bird and arthropod biodiversity within vineyards. Agriculture, Ecosystems & Environment 367, 108982. https://doi.org/10.1016/j.agee.2024.108982

Zingg, S., Grenz, J., Humbert, J.-Y., 2018. Landscape-scale effects of land use intensity on birds and butterflies. Agriculture, Ecosystems & Environment 267, 119–128. https://doi.org/10.1016/j.agee.2018.08.014

Zuckerberg, B., Cohen, J.M., Nunes, L.A., Bernath-Plaisted, J., Clare, J.D.J., Gilbert, N.A., Kozidis, S.S., Maresh Nelson, S.B., Shipley, A.A., Thompson, K.L., Desrochers, A., 2020. A Review of Overlapping Landscapes: Pseudoreplication or a Red Herring in Landscape Ecology? Curr Landscape Ecol Rep 5, 140–148. https://doi.org/10.1007/s40823-020-00059-4

Chapter 3 Supplementary Material

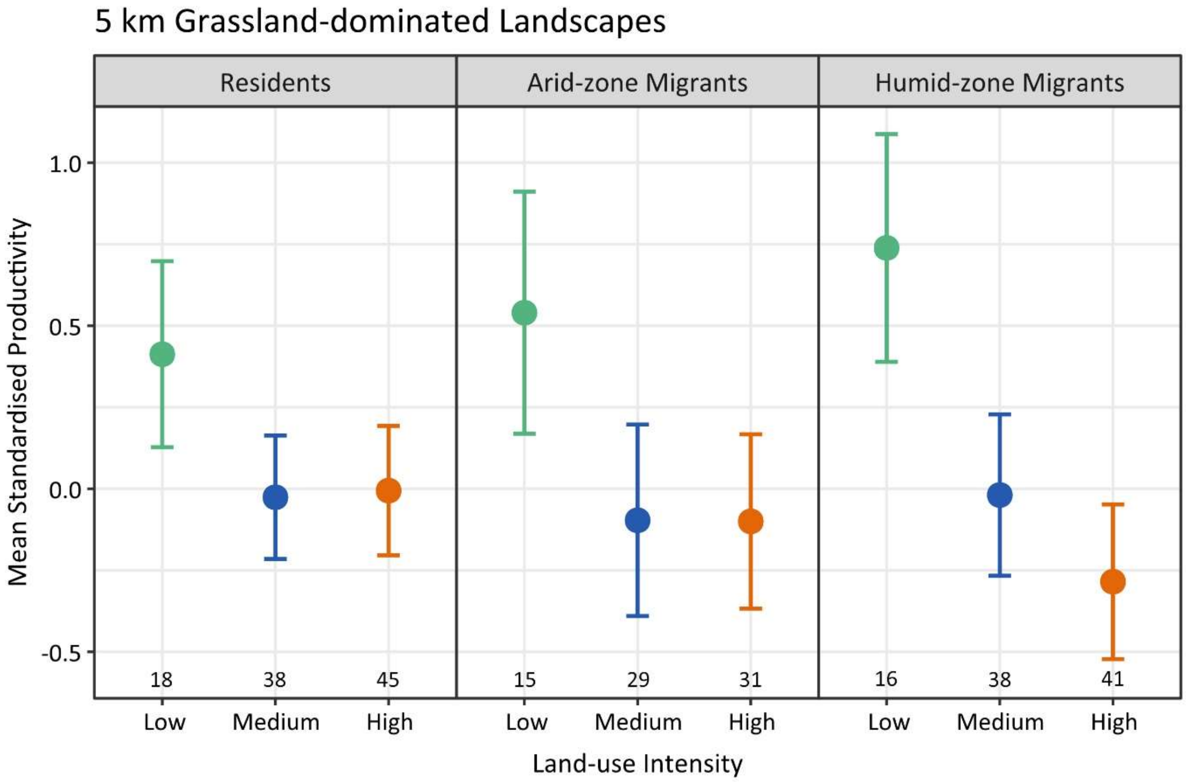


Figure S3.1: Mean standardised site-level productivity estimates and 95% Confidence Intervals at European Constant Effort Sites within landscapes dominated by low-, medium- and high-intensity grassland at the 5 km scale. Productivity estimates are for species that are resident within Europe or short-distance migrants (left), arid-zone sub-Saharan migrants (middle) or humid-zone sub-Saharan migrants (right). These are marginal means estimated from linear mixed models with an intensity*migratory status interaction term (b, c & d). The number of sites in each intensity type is given at the base of the plots.

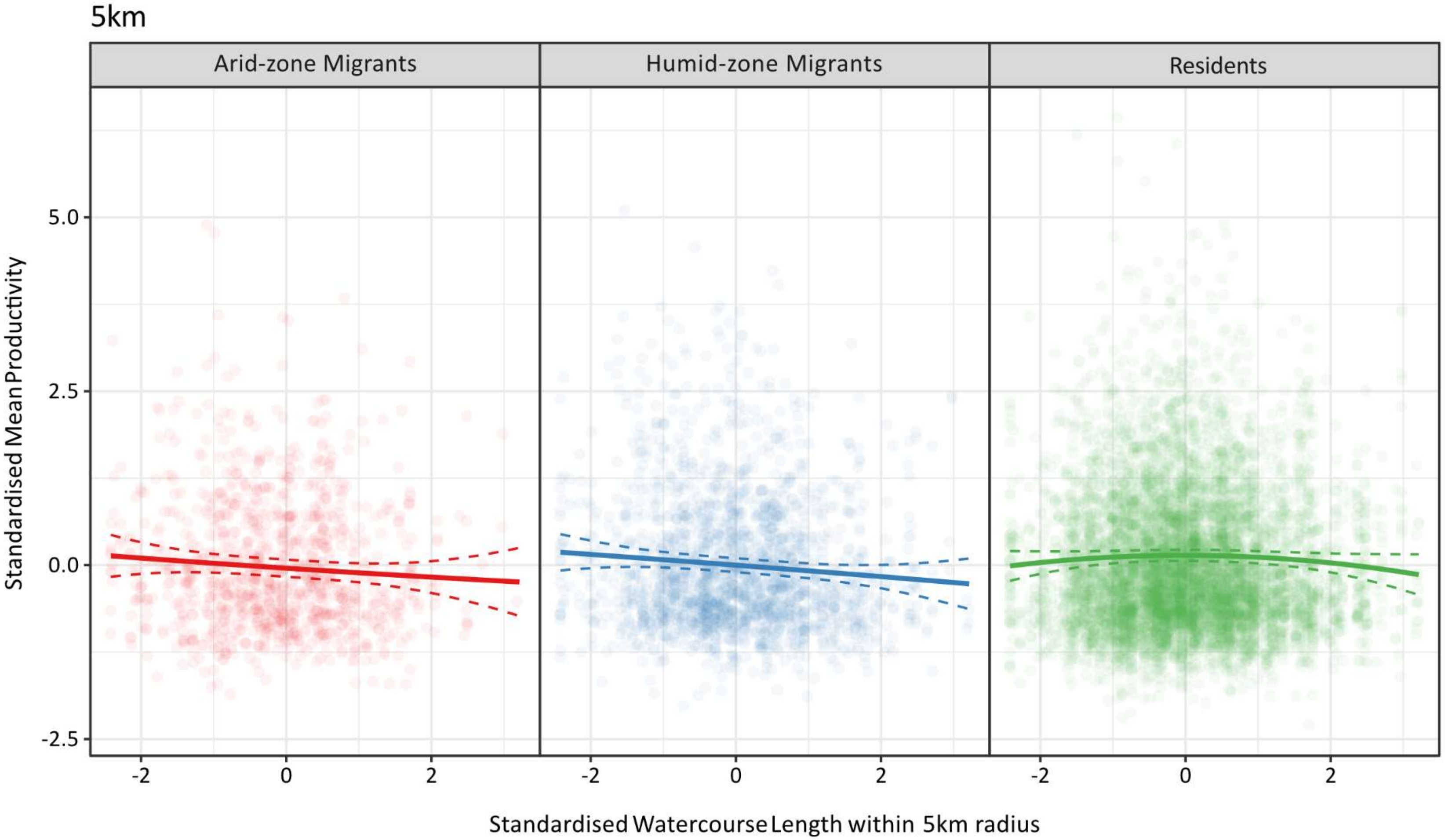


Figure S3.2: Predicted standardised site-level mean productivity of arid-zone migrant, humid-zone migrant and resident bird species, as a function of the standardised watercourse length within a 5 km radius around 802 Constant Effort Sites in Europe.

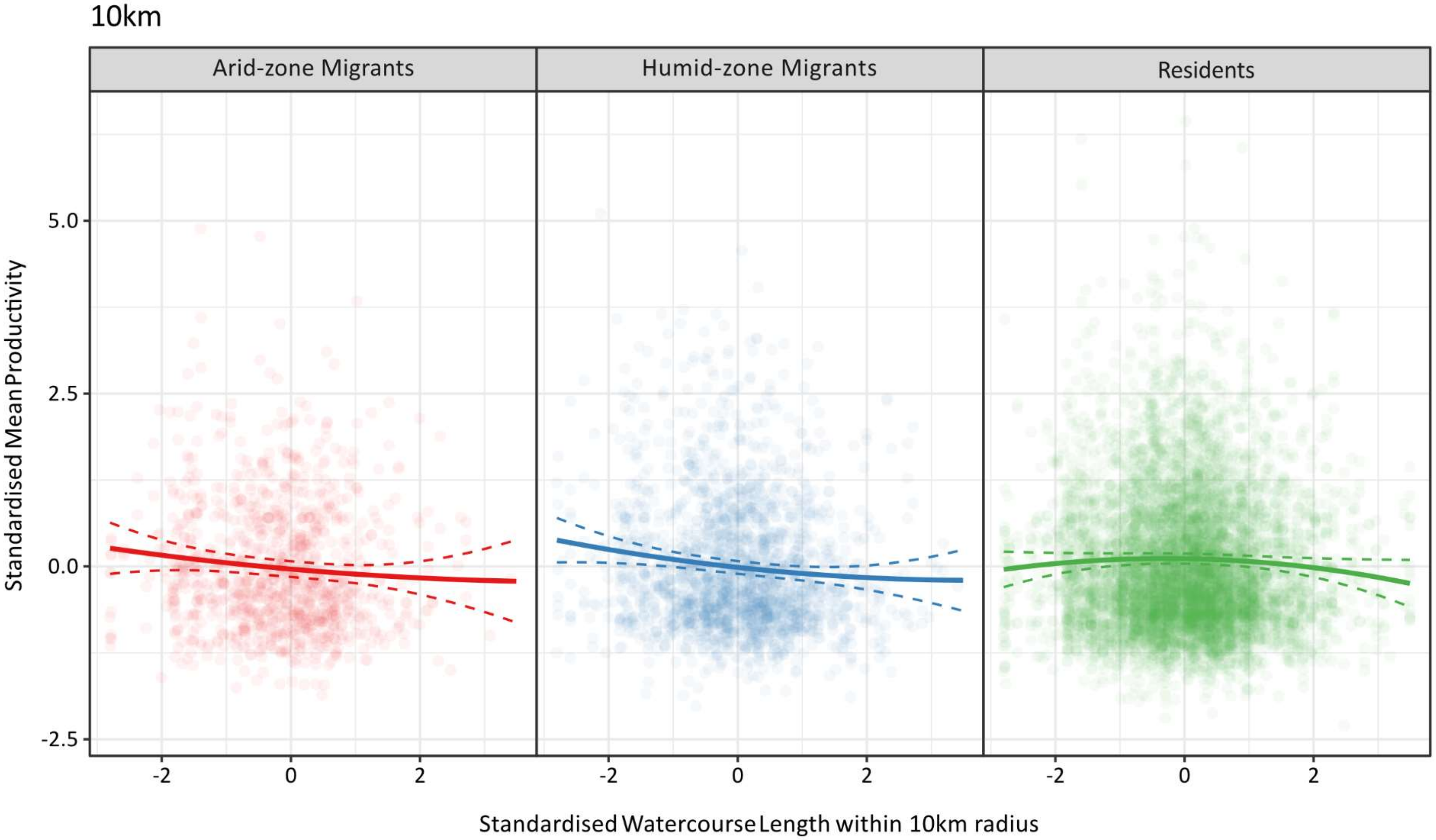


Figure S3.3: Predicted standardised site-level mean productivity of arid-zone migrant, humid-zone migrant and resident bird species, as a function of the standardised watercourse length within a 10 km radius around 800 Constant Effort Sites in Europe.

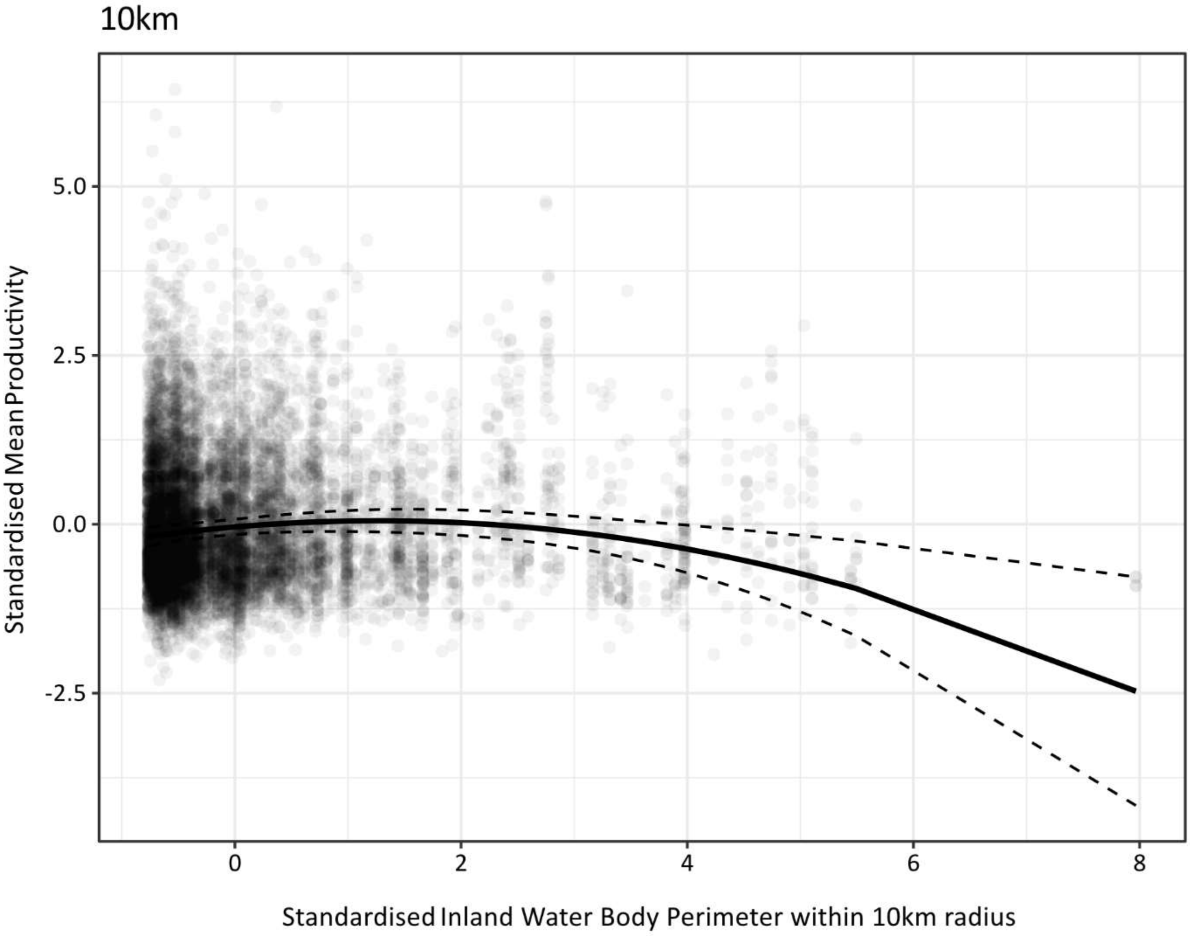


Figure S3.4: Predicted standardised site-level mean productivity across bird species, as a function of the standardised inland water body perimeter within a 10 km radius around 800 Constant Effort Sites in Europe.

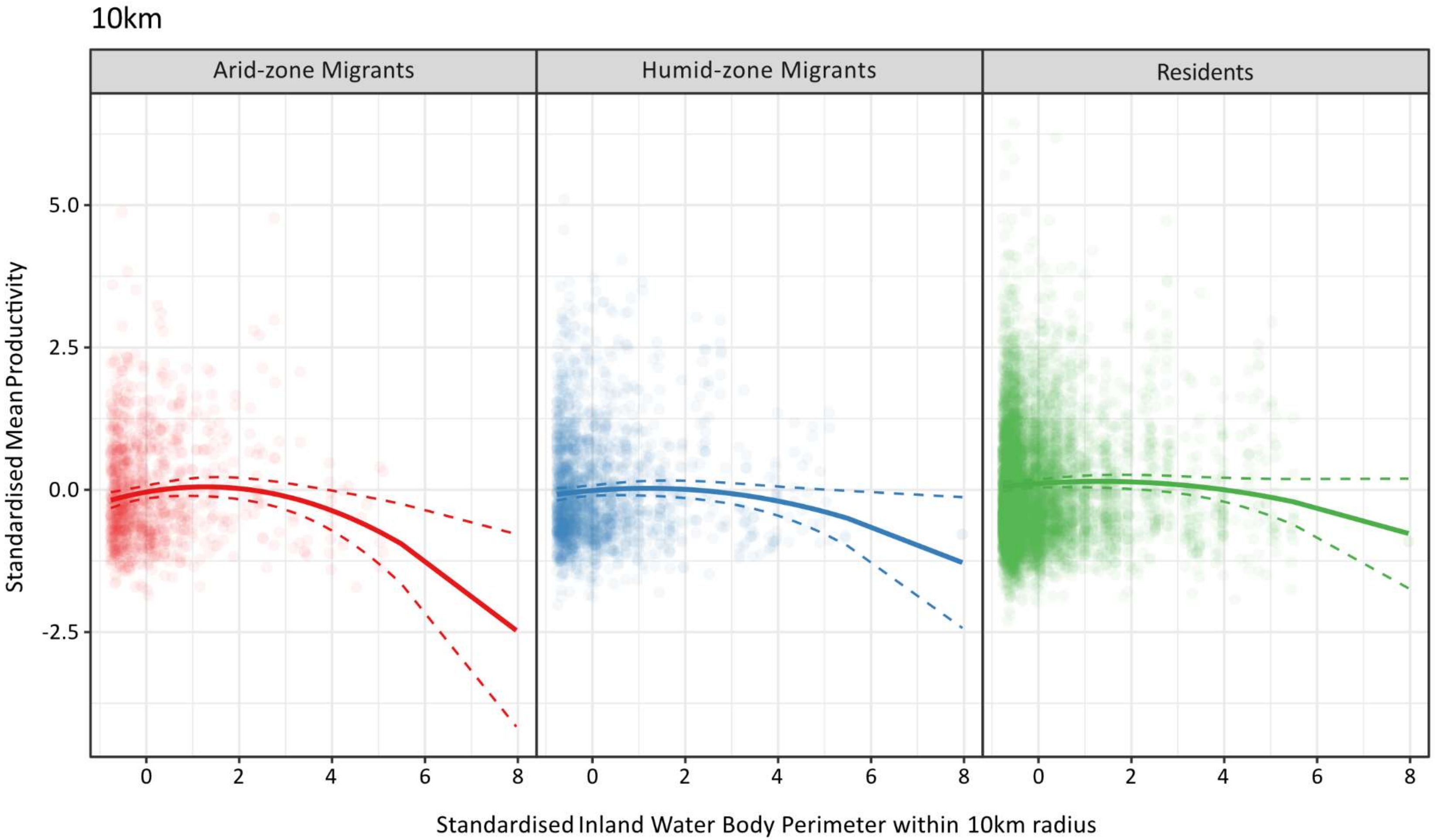


Figure S3.5: Predicted standardised site-level mean productivity of arid-zone migrant, humid-zone migrant and resident bird species, as a function of the standardised inland water body perimeter within a 10 km radius around 800 Constant Effort Sites in Europe.

Table S3.1: The number of sites, seasonal visits, species, adults and juveniles captured in each of the European Constant Effort Site Schemes from 1998 - 2019 that contributed to productivity models.

Scheme	Number of sites	Number of visits	Number of species	Number of adults	Number of juveniles	Range of years
Britain & Ireland	253	12	47	299792	464667	1998 - 2019
Czech Republic	39	9	51	55713	48526	2004 – 2019
Denmark	9	12	35	12053	12558	2004 – 2019
Finland	52	12	42	49423	63449	1998 - 2019
France	95	7	61	49554	34900	1998 – 2019
Germany (DEH)	50	12	55	69985	70506	1999 - 2019
Germany (DER)	10	12	30	7632	8044	2000 - 2019
Germany (DEW)	19	12	43	24023	29864	2001 - 2019
Hungary	40	9	48	61005	47914	2004 - 2019
Italy	21	12	33	8904	11201	2015 - 2019
Netherlands	72	12	50	152085	166243	1998 - 2019
Portugal	8	12	27	3743	2531	2007 - 2019
Spain (Basque Country)	17	7	38	11634	9252	2010 - 2019
Spain (Madrid)	80	12	59	81412	45755	1999 - 2019
Spain (Catalonia)	50	10	55	44792	37725	1998 - 2019
Sweden	42	12	43	30397	32808	2004 - 2019

Table S3.2: Species, their migratory status (extracted from Morrison et al., 2021) and number of Constant Effort Sites at which species were recorded in sufficient numbers to measure productivity.

English name	Latin name	Migratory status	Number of sites
Eurasian Blackbird	*Turdus merula*	Resident	681
Eurasian Blackcap	*Sylvia atricapilla*	Resident	664
Great Tit	*Parus major*	Resident	621
Eurasian Blue Tit	*Cyanistes caeruleus*	Resident	561
European Robin	*Erithacus rubecula*	Resident	509
Common Chiffchaff	*Phylloscopus collybita*	Resident	453
Eurasian Reed Warbler	*Acrocephalus scirpaceus*	Humid	430
Willow Warbler	*Phylloscopus trochilus*	Humid	412
Common Chaffinch	*Fringilla coelebs*	Resident	408
Dunnock	*Prunella modularis*	Resident	406
Garden Warbler	*Sylvia borin*	Humid	396
Eurasian Wren	*Troglodytes troglodytes*	Resident	378
Song Thrush	*Turdus philomelos*	Resident	357
Long-tailed Tit	*Aegithalos caudatus*	Resident	313
Reed Bunting	*Emberiza schoeniclus*	Resident	309
Greater Whitethroat	*Curruca communis*	Arid	307
Sedge Warbler	*Acrocephalus schoenobaenus*	Arid	294
European Greenfinch	*Chloris chloris*	Resident	276
Eurasian Bullfinch	*Pyrrhula pyrrhula*	Resident	236
Common Nightingale	*Luscinia megarhynchos*	Humid	212
European Goldfinch	*Carduelis carduelis*	Resident	196
Marsh Warbler	*Acrocephalus palustris*	Humid	185
Lesser Whitethroat	*Curruca curruca*	Arid	166
Cetti's Warbler	*Cettia cetti*	Resident	127
House Sparrow	*Passer domesticus*	Resident	119
Yellowhammer	*Emberiza citrinella*	Resident	118
Melodious Warbler	*Hippolais polyglotta*	Humid	108
European Serin	*Serinus serinus*	Resident	97
Eurasian Tree Sparrow	*Passer montanus*	Resident	93
Great Reed Warbler	*Acrocephalus arundinaceus*	Humid	89
European Pied Flycatcher	*Ficedula hypoleuca*	Humid	77
Red-backed Shrike	*Lanius collurio*	Humid	74
Barn Swallow	*Hirundo rustica*	Humid	68
Bluethroat	*Luscinia svecica*	Arid	67
Common Grasshopper-Warbler	*Locustella naevia*	Arid	62

Eurasian Linnet	*Linaria cannabina*	Resident	61
Sardinian Warbler	*Curruca melanocephala*	Resident	61
Spotted Flycatcher	*Muscicapa striata*	Humid	58
Icterine Warbler	*Hippolais icterina*	Humid	57
Marsh Tit	*Poecile palustris*	Resident	50
Short-toed Treecreeper	*Certhia brachydactyla*	Resident	48
Eurasian Siskin	*Spinus spinus*	Resident	44
Bearded Reedling	*Panurus biarmicus*	Resident	43
Savi's Warbler	*Locustella luscinioides*	Arid	43
Common Redstart	*Phoenicurus phoenicurus*	Arid	42
European Starling	*Sturnus vulgaris*	Resident	42
Redpoll	*Acanthis flammea/cabaret*	Resident	42
Redwing	*Turdus iliacus*	Resident	42
Fieldfare	*Turdus pilaris*	Resident	40
Hawfinch	*Coccothraustes coccothraustes*	Resident	40
Thrush Nightingale	*Luscinia luscinia*	Humid	34
Willow Tit	*Poecile montanus*	Resident	31
Coal Tit	*Periparus ater*	Resident	29
Eurasian Treecreeper	*Certhia familiaris*	Resident	29
Bonelli's Warbler	*Phylloscopus bonelli/orientalis*	Arid	28
Subalpine Warbler	*Curruca cantillans/iberiae/subalpina*	Arid	26
Cirl Bunting	*Emberiza cirlus*	Resident	25
Eurasian Nuthatch	*Sitta europaea*	Resident	25
Goldcrest	*Regulus regulus*	Resident	24
Tree Pipit	*Anthus trivialis*	Humid	22
Eurasian Penduline-Tit	*Remiz pendulinus*	Resident	19
White Wagtail	*Motacilla alba*	Resident	19
Barred Warbler	*Curruca nisoria*	Arid	18
Crested Tit	*Lophophanes cristatus*	Resident	15
Moustached Warbler	*Acrocephalus melanopogon*	Resident	15
Spotless Starling	*Sturnus unicolor*	Resident	15
Western Yellow Wagtail	*Motacilla flava*	Arid	14
Common Firecrest	*Regulus ignicapilla*	Resident	13
Woodchat Shrike	*Lanius senator*	Arid	13
Western Orphean Warbler	*Curruca hortensis*	Arid	12
Bank Swallow	*Riparia riparia*	Arid	11
Spanish Sparrow	*Passer hispaniolensis*	Resident	10
Whinchat	*Saxicola rubetra*	Humid	9

Common House-Martin	*Delichon urbicum*	Humid	8
European Stonechat	*Saxicola rubicola*	Resident	8
Eastern Olivaceous Warbler	*Iduna pallida*	Humid	7
Grey Wagtail	*Motacilla cinerea*	Resident	6
Meadow Pipit	*Anthus pratensis*	Resident	6
Rock Sparrow	*Petronia petronia*	Resident	6
Black Redstart	*Phoenicurus ochruros*	Resident	5
Collared Flycatcher	*Ficedula albicollis*	Humid	5
Corn Bunting	*Emberiza calandra*	Resident	5
Eurasian Golden Oriole	*Oriolus oriolus*	Humid	5
Mistle Thrush	*Turdus viscivorus*	Resident	5
Rock Bunting	*Emberiza cia*	Resident	5
Zitting Cisticola	*Cisticola juncidis*	Resident	5
Citril Finch	*Carduelis citrinella*	Resident	4
River Warbler	*Locustella fluviatilis*	Humid	4
Dartford Warbler	*Curruca undata*	Resident	3
Red Crossbill	*Loxia curvirostra*	Resident	3

Table S3.3: The number of Constant Effort Sites in landscapes dominated by different land sub-systems from Dou et al., (2021) classification, and the higher level system and intensity groupings used in this study.

System	Sub-system	Intensity	# sites 1km	# sites 5km	# sites 10km
arable cropland	low-intensity cropland	low	11	11	8
arable cropland	medium-intensity cropland	medium	64	137	151
arable cropland	high-intensity cropland	high	74	152	176
forest	low-intensity forest	low	38	45	49
forest	medium-intensity forest	medium	51	57	57
forest	high-intensity forest	high	26	69	78
grassland	low-intensity grassland	low	32	19	17
grassland	medium-intensity grassland	medium	31	38	41
grassland	high-intensity grassland	high	25	45	49
mosaic	forest/shrubs and cropland mosaics	low	50	(4)	(4)
mosaic	forest/shrubs and grassland mosaics	low	25	(4)	(3)
mosaic	forest/shrubs and mixed agriculture mosaics	low	9	(0)	(0)
mosaic	low-intensity agricultural mosaics	low	21	(0)	(0)
mosaic	medium-intensity agricultural mosaics	medium	19	(7)	(5)
mosaic	high-intensity agricultural mosaics	high	5	(1)	(1)
settlement	low-intensity settlement	low	35	2	0
settlement	medium-intensity settlement	medium	93	82	60
settlement	high-intensity settlement	high	36	74	64
wetland	water body	low	60	35	26
wetland	wetland	low	104	36	24
(permanent crops)	extensive perm-crops	NA	(11)	(13)	(18)
(permanent crops)	intensive perm-crops	NA	(4)	(4)	(5)
(shrub)	shrub	NA	(19)	(8)	(7)

Table S3.4: Spearman's rank correlation coefficients for continuous explanatory variables at the 1 km, 5 km and 10 km scales. Calculated using the *cor.test* function in R. PD = patch density, MPPAR = mean patch perimeter-area ratio, WCL = watercourse length, IWP = inland water body perimeter length.

Correlation		Spearman's *rho*	p value	*n*
1km	WCL, IWP	0.11	**<0.01**	809
5km	WCL, IWP	0.10	**<0.01**	802
10km	WCL, IWP	0.06	0.07	800
1km	PD, MPPAR	0.64	**<0.001**	809
5km	PD, MPPAR	0.53	**<0.001**	802
10km	PD, MPPAR	0.58	**<0.001**	800

Table S3.5: Pairwise contrasts between different levels of *system* in the PD system LMM (Table 2, Model 1) for the 1, 5 and 10 km scales, with and without Tukey-Kramer *p* value adjustment. Significant contrasts (*p*<0.05) are highlighted in bold.

Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
1km						
Arable - Forest	0.12	0.07	757.74	1.70	0.09	0.53
Arable - Grassland	-0.005	0.07	717.95	-0.07	0.95	1.00
Arable - Mosaic	0.02	0.07	704.52	0.30	0.76	1.00
Arable - Settlement	0.05	0.06	726.41	0.80	0.42	0.97
Arable - Wetland	**-0.16**	0.07	742.22	-2.47	**0.01**	0.13
Forest - Grassland	-0.13	0.08	746.44	-1.54	0.12	0.64
Forest - Mosaic	-0.10	0.07	741.66	-1.41	0.16	0.72
Forest - Settlement	-0.07	0.07	763.15	-0.99	0.32	0.92
Forest - Wetland	**-0.28**	0.07	780.61	-3.85	**<0.001**	**<0.01**
Grassland - Mosaic	0.02	0.08	703.63	0.32	0.75	1.00
Grassland - Settlement	0.06	0.07	718.64	0.77	0.44	0.97
Grassland - Wetland	**-0.16**	0.08	723.02	-2.10	**0.04**	0.29
Mosaic - Settlement	0.03	0.06	709.14	0.49	0.63	1.00
Mosaic - Wetland	**-0.18**	0.07	728.64	-2.69	**<0.01**	0.08
Settlement - Wetland	**-0.22**	0.06	746.65	-3.36	**<0.001**	**0.01**
5km						
Arable - Forest	0.06	0.06	770.34	1.06	0.29	0.83
Arable - Grassland	-0.002	0.06	685.78	-0.03	0.98	1.00
Arable - Settlement	-0.05	0.06	721.66	-0.93	0.35	0.89
Arable - Wetland	-0.14	0.08	745.25	-1.84	0.07	0.35
Forest - Grassland	-0.06	0.08	724.60	-0.82	0.41	0.92
Forest - Settlement	-0.12	0.06	758.50	-1.77	0.08	0.39
Forest - Wetland	**-0.20**	**0.09**	**771.00**	**-2.33**	**0.02**	0.14
Grassland - Settlement	-0.05	0.07	694.37	-0.69	0.49	0.96
Grassland - Wetland	-0.14	0.09	704.81	-1.62	0.11	0.49
Settlement - Wetland	-0.09	0.09	741.18	-1.03	0.30	0.84
10km						
Arable - Forest	-0.01	0.06	795.89	-0.10	0.92	1.00
Arable - Grassland	-0.01	0.06	672.00	-0.19	0.85	1.00
Arable - Settlement	**-0.13**	0.06	739.16	-2.07	**0.04**	0.23
Arable - Wetland	**-0.27**	0.09	740.46	-3.01	**<0.01**	**0.02**
Forest - Grassland	-0.01	0.08	727.39	-0.08	0.94	1.00
Forest - Settlement	-0.12	0.07	766.92	-1.81	0.07	0.37
Forest - Wetland	**-0.26**	0.10	765.09	-2.71	**<0.01**	0.05
Grassland - Settlement	-0.11	0.08	698.93	-1.47	0.14	0.58
Grassland - Wetland	**-0.26**	0.10	711.33	-2.63	**<0.01**	0.07
Settlement - Wetland	-0.14	0.10	742.72	-1.42	0.16	0.62

Table S3.6: Pairwise contrasts between different levels of *system* within each migratory group in the 1 km PD system LMM (Table 2, model 5), with and without Tukey-Kramer p value adjustment. Significant contrasts (p<0.05) are highlighted in bold.

1 km	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
Residents	**Arable Cropland - Forest**	**0.19**	0.07	892.09	2.58	**0.01**	0.10
	Arable Cropland - Grassland	0.09	0.08	849.34	1.20	0.23	0.84
	Arable Cropland - Mosaic	0.09	0.07	807.71	1.27	0.21	0.80
	Arable Cropland - Settlement	0.10	0.07	841.96	1.47	0.14	0.69
	Arable Cropland - Wetland	-0.06	0.07	918.48	-0.87	0.39	0.95
	Forest - Grassland	-0.10	0.09	873.73	-1.16	0.25	0.86
	Forest - Mosaic	-0.10	0.07	851.05	-1.40	0.16	0.73
	Forest - Settlement	-0.09	0.07	883.47	-1.28	0.20	0.80
	Forest - Wetland	**-0.25**	0.08	948.73	-3.23	**<0.01**	**0.02**
	Grassland - Mosaic	-0.01	0.08	810.27	-0.06	0.95	1.00
	Grassland - Settlement	0.01	0.08	838.10	0.07	0.95	1.00
	Grassland - Wetland	-0.15	0.08	882.65	-1.92	0.06	0.39
	Mosaic - Settlement	0.01	0.07	801.00	0.15	0.88	1.00
	Mosaic - Wetland	**-0.15**	0.07	869.13	-2.07	**0.04**	0.30
	Settlement - Wetland	**-0.16**	0.07	910.23	-2.34	**0.02**	0.18
Arid-zone Migrants	Arable Cropland - Forest	-0.06	0.13	5312.00	-0.49	0.62	1.00
	Arable Cropland - Grassland	-0.23	0.12	3963.02	-1.93	0.05	0.38
	Arable Cropland - Mosaic	-0.14	0.12	4756.15	-1.22	0.22	0.83
	Arable Cropland - Settlement	0.07	0.11	4648.23	0.67	0.50	0.98
	Arable Cropland - Wetland	**-0.24**	0.11	3864.32	-2.27	**0.02**	0.21
	Forest - Grassland	-0.17	0.14	4363.50	-1.24	0.22	0.82
	Forest - Mosaic	-0.08	0.13	5376.97	-0.60	0.55	0.99
	Forest - Settlement	0.14	0.13	5131.72	1.09	0.28	0.89
	Forest - Wetland	-0.18	0.13	4670.23	-1.40	0.16	0.72
	Grassland - Mosaic	0.09	0.12	3842.13	0.73	0.46	0.98
	Grassland - Settlement	**0.31**	0.12	3779.49	2.60	**0.01**	0.10
	Grassland - Wetland	-0.01	0.12	3266.39	-0.07	0.94	1.00
	Mosaic - Settlement	0.22	0.11	4771.56	1.92	0.06	0.39
	Mosaic - Wetland	-0.10	0.11	4019.04	-0.90	0.37	0.95
	Settlement - Wetland	**-0.32**	0.10	3989.92	-3.04	**<0.01**	**0.03**
Humid-zone Migrants	Arable Cropland - Forest	-0.03	0.10	2333.50	-0.36	0.72	1.00
	Arable Cropland - Grassland	**-0.20**	0.10	2147.05	-2.08	**0.04**	0.30
	Arable Cropland - Mosaic	-0.13	0.09	2190.49	-1.41	0.16	0.72
	Arable Cropland - Settlement	-0.09	0.09	2207.30	-0.99	0.32	0.92
	Arable Cropland - Wetland	**-0.42**	0.09	1996.30	-4.91	**<0.001**	**<0.001**
	Forest - Grassland	-0.17	0.11	2216.14	-1.56	0.12	0.62
	Forest - Mosaic	-0.09	0.10	2437.26	-0.93	0.35	0.94
	Forest - Settlement	-0.05	0.10	2412.05	-0.53	0.60	0.99
	Forest - Wetland	**-0.39**	0.10	2209.94	-3.96	**<0.001**	**0.001**
	Grassland - Mosaic	0.08	0.10	2131.60	0.76	0.45	0.97
	Grassland - Settlement	0.12	0.10	2184.71	1.20	0.23	0.83

	Grassland - Wetland	**-0.22**	0.10	1997.52	-2.19	**0.03**	0.24
	Mosaic - Settlement	0.04	0.09	2341.64	0.46	0.64	1.00
	Mosaic - Wetland	**-0.29**	0.09	2088.90	-3.27	**<0.01**	**0.01**
	Settlement - Wetland	**-0.34**	0.08	2146.57	-3.96	**<0.001**	**<0.01**

Table S3.7: Pairwise contrasts between different levels of *system* within each migratory group in the 5 km PD system LMM (Table 2, model 5), with and without Tukey-Kramer p value adjustment.

5 km	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
Residents	Arable Cropland - Forest	0.06	0.06	897.99	1.02	0.31	0.85
	Arable Cropland - Grassland	0.03	0.07	779.86	0.46	0.65	0.99
	Arable Cropland - Settlement	-0.02	0.06	823.02	-0.27	0.79	1.00
	Arable Cropland - Wetland	-0.10	0.08	923.32	-1.25	0.21	0.72
	Forest - Grassland	-0.03	0.08	813.47	-0.40	0.69	0.99
	Forest - Settlement	-0.08	0.07	880.73	-1.15	0.25	0.78
	Forest - Wetland	-0.16	0.09	932.58	-1.78	0.08	0.38
	Grassland - Settlement	-0.05	0.08	772.73	-0.60	0.55	0.98
	Grassland - Wetland	-0.13	0.09	856.43	-1.44	0.15	0.60
	Settlement - Wetland	-0.09	0.09	891.03	-0.95	0.34	0.88
Arid-zone Migrants	Arable Cropland - Forest	0.01	0.10	4970.72	0.08	0.94	1.00
	Arable Cropland - Grassland	-0.12	0.10	3330.27	-1.18	0.24	0.76
	Arable Cropland - Settlement	-0.09	0.09	3809.05	-0.94	0.35	0.88
	Arable Cropland - Wetland	-0.15	0.12	3189.60	-1.29	0.20	0.70
	Forest - Grassland	-0.12	0.12	3711.12	-1.00	0.32	0.85
	Forest - Settlement	-0.09	0.11	4793.25	-0.83	0.41	0.92
	Forest - Wetland	-0.16	0.14	3674.79	-1.14	0.25	0.78
	Grassland - Settlement	0.03	0.11	3062.34	0.26	0.80	1.00
	Grassland - Wetland	-0.03	0.13	2990.00	-0.25	0.80	1.00
	Settlement - Wetland	-0.06	0.13	3056.87	-0.49	0.63	0.99
Humid-zone Migrants	Arable Cropland - Forest	0.10	0.08	2173.82	1.25	0.21	0.72
	Arable Cropland - Grassland	-0.02	0.08	1948.91	-0.29	0.77	1.00
	Arable Cropland - Settlement	-0.14	0.08	2000.57	-1.91	0.06	0.31
	Arable Cropland - Wetland	**-0.22**	0.10	1989.92	-2.26	**0.02**	0.16
	Forest - Grassland	-0.12	0.10	1886.01	-1.22	0.22	0.74
	Forest - Settlement	**-0.24**	0.09	2223.42	-2.78	**<0.01**	**0.04**
	Forest - Wetland	**-0.32**	0.11	1957.90	-2.89	**<0.01**	**0.03**
	Grassland - Settlement	-0.12	0.10	1842.32	-1.23	0.22	0.73
	Grassland - Wetland	-0.20	0.11	1911.74	-1.78	0.08	0.39
	Settlement - Wetland	-0.08	0.11	1911.84	-0.74	0.46	0.95

Table S3.8: Pairwise contrasts between different levels of *system* within each migratory group in the 10 km PD system LMM (Table 2, model 5), with and without Tukey-Kramer p value adjustment.

10km	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
Residents	Arable Cropland - Forest	-0.01	0.06	925.01	-0.24	0.81	1.00
	Arable Cropland - Grassland	0.003	0.06	760.38	0.05	0.96	1.00
	Arable Cropland - Settlement	-0.07	0.06	850.60	-1.06	0.29	0.83
	Arable Cropland - Wetland	**-0.24**	0.10	944.69	-2.54	**0.01**	0.08
	Forest - Grassland	0.02	0.08	811.70	0.22	0.83	1.00
	Forest - Settlement	-0.05	0.07	900.22	-0.76	0.45	0.94
	Forest - Wetland	**-0.23**	0.10	952.92	-2.22	**0.03**	0.17
	Grassland - Settlement	-0.07	0.08	780.89	-0.88	0.38	0.91
	Grassland - Wetland	**-0.25**	0.10	889.59	-2.37	**0.02**	0.12
	Settlement - Wetland	-0.18	0.11	916.58	-1.65	0.10	0.46
Arid-zone Migrants	Arable Cropland - Forest	-0.01	0.10	5065.93	-0.10	0.92	1.00
	Arable Cropland - Grassland	-0.10	0.09	3327.08	-1.04	0.30	0.83
	Arable Cropland - Settlement	**-0.21**	0.10	3958.52	-2.14	**0.03**	0.20
	Arable Cropland - Wetland	-0.18	0.13	3115.42	-1.35	0.18	0.66
	Forest - Grassland	-0.09	0.12	3707.30	-0.72	0.47	0.95
	Forest - Settlement	-0.20	0.12	5120.24	-1.69	0.09	0.44
	Forest - Wetland	-0.17	0.15	3431.48	-1.14	0.25	0.78
	Grassland - Settlement	-0.11	0.12	3184.37	-0.95	0.34	0.88
	Grassland - Wetland	-0.08	0.14	2981.73	-0.56	0.58	0.98
	Settlement - Wetland	0.03	0.15	3023.32	0.21	0.83	1.00
Humid-zone Migrants	Arable Cropland - Forest	0.04	0.08	2181.23	0.51	0.61	0.99
	Arable Cropland - Grassland	0.01	0.08	2018.24	0.15	0.88	1.00
	Arable Cropland - Settlement	**-0.27**	0.08	2037.07	-3.38	**<0.001**	**<0.01**
	Arable Cropland - Wetland	**-0.35**	0.11	1926.49	-3.08	**<0.01**	**0.02**
	Forest - Grassland	-0.03	0.10	1881.64	-0.27	0.79	1.00
	Forest - Settlement	**-0.31**	0.09	2300.83	-3.44	**<0.001**	**<0.01**
	Forest - Wetland	**-0.39**	0.12	1873.43	-3.19	**<0.01**	**0.01**
	Grassland - Settlement	**-0.28**	0.10	1875.49	-2.79	**<0.01**	**0.04**
	Grassland - Wetland	**-0.36**	0.13	1908.53	-2.89	**<0.01**	**0.03**
	Settlement - Wetland	-0.08	0.13	1848.68	-0.65	0.51	0.97

Table S3.9: a) Mean standardised productivity across all bird species at European Constant Effort Sites within 10 km landscapes dominated by settlement systems, with differing *system* categories at the 1 km scale. These are marginal means (emmean) estimated using the *emmeans* package, plus the standard error (Std.Error), degrees of freedom (df) and lower and upper 95% Confidence Intervals (CI). b) Model output from a LMM examining the effect of 1 km system type on mean standardised productivity at sites within 10 km settlement landscapes. Settlement 1 km sites are the intercept.

a)

1km System	10km System	N sites	emmean	Std.Error	df	lower CI	upper CI
Settlement	Settlement	52	0.05	0.08	111.24	-0.11	0.22
Arable	Settlement	11	0.12	0.17	98.48	-0.23	0.46
Forest	Settlement	10	-0.08	0.18	90.44	-0.43	0.27
Grassland	Settlement	6	0.31	0.26	129.81	-0.20	0.83
Mosaic	Settlement	12	0.38	0.16	89.78	0.06	0.70
Wetland	Settlement	25	0.54	0.12	103.69	0.31	0.78

b)

1 km System	Estimate	Std.Error	df	t value	p value
(Intercept: Settlement)	0.05	0.08	111.00	0.62	0.54
Arable	0.06	0.19	97.00	0.34	0.74
Forest	-0.13	0.19	90.10	-0.70	0.49
Grassland	0.26	0.27	125.00	0.97	0.33
Mosaic	0.33	0.18	89.80	1.83	0.07
Wetland	**0.49**	0.14	99.60	3.51	**<0.001**

Table S3.10: a) Mean standardised productivity across all bird species European Constant Effort sites within 1 km landscapes dominated by wetlands and 10 km landscapes dominated by different *system* categories. These are marginal means (emmean) estimated using the *emmeans* package, plus the standard error (Std.Error), degrees of freedom (df) and lower and upper 95% Confidence Intervals (CI). b) Model output from a LMM examining the effect of 10 km system type on mean standardised productivity at sites within 1 km wetland landscapes. Settlement 10 km sites are the intercept.

a)

1km System	10km System	N sites	emmean	Std.Error	df	lower CI	upper CI
Wetland	Settlement	25	0.54	0.12	139.88	0.31	0.77
Wetland	Wetland	25	0.48	0.12	135.68	0.25	0.71
Wetland	Arable	63	0.08	0.07	137.69	-0.06	0.23
Wetland	Forest	21	0.06	0.14	165.63	-0.20	0.33
Wetland	Grassland	19	0.18	0.13	130.96	-0.08	0.44

b)

10 km System	Estimate	Std.Error	df	t value	p value
(Intercept: Settlement)	0.54	0.12	140	4.60	<0.001
Wetland	-0.07	0.17	136	-0.40	0.69
Arable	-0.46	0.14	138	-3.31	**<0.01**
Forest	-0.48	0.18	152	-2.68	**<0.01**
Grassland	-0.36	0.18	133	-2.03	**0.04**

Table S3.11 – Pairwise contrasts between different levels of *intensity* in the PD intensity LMM (Table 2, model 3) for the 1, 5 and 10 km scales, with and without Tukey-Kramer p value adjustment.

Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
1 km						
low - medium	0.07	0.05	583.28	1.39	0.17	0.35
low - high	0.03	0.06	586.49	0.60	0.55	0.82
high - medium	0.04	0.05	586.38	0.66	0.51	0.78
5 km						
low - medium	0.28	0.08	571.33	3.74	**<0.001**	**<0.001**
low - high	0.27	0.08	570.34	3.50	**<0.001**	**<0.01**
high - medium	0.01	0.04	671.51	0.33	0.74	0.94
10 km						
low - medium	0.15	0.08	569.5.0	1.94	0.05	0.13
low - high	0.22	0.08	572.03	2.72	**0.01**	**0.02**
high - medium	-0.07	0.04	684.88	-1.62	0.12	0.24

Table S3.12 – Pairwise contrasts between different levels of *intensity* within each migratory group in the 1 km PD intensity LMM (Table 2, model 7), with and without Tukey-Kramer p value adjustment.

1 km	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
	Residents						
	low - medium	0.05	0.05	675.04	0.92	0.36	0.63
	low – high	-0.001	0.06	679.50	-0.01	0.99	1.00
	high - medium	0.05	0.06	684.89	0.89	0.38	0.65
	Arid-zone Migrants						
	low - medium	0.05	0.09	3929.20	0.62	0.54	0.81
	low - high	-0.04	0.10	3758.37	-0.38	0.70	0.92
	high - medium	0.09	0.09	3791.14	1.00	0.32	0.58
	Humid-zone Migrants						
	low - medium	**0.16**	0.07	1892.80	2.25	**0.02**	0.06
	low - high	**0.20**	0.08	1869.74	2.59	**0.01**	**0.03**
	high - medium	-0.05	0.07	1885.19	-0.65	0.52	0.79

Table S3.13: Pairwise contrasts between different levels of *intensity* within each migratory group in the 5 km PD intensity LMM (Table 2, model 7), with and without Tukey-Kramer p value adjustment.

5 km	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
	Residents						
	low - medium	**0.25**	0.08	652.73	3.15	**<0.01**	**<0.01**
	low – high	**0.23**	0.08	652.86	2.83	**<0.01**	**0.01**
	high - medium	0.02	0.04	789.11	0.48	0.63	0.88
	Arid-zone Migrants						
	low - medium	**0.31**	0.13	3449.49	2.39	**0.02**	**0.04**
	low - high	0.22	0.13	3141.94	1.70	0.09	0.21
	high - medium	0.09	0.07	4242.73	1.24	0.21	0.43
	Humid-zone Migrants						
	low - medium	**0.38**	0.10	1771.20	3.68	**<0.001**	**<0.001**
	low - high	**0.43**	0.10	1686.13	4.11	**<0.0001**	**<0.001**
	high - medium	-0.05	0.06	2077.97	-0.82	0.413	0.69

Table S3.14: Pairwise contrasts between different levels of *intensity* within each migratory group in the 10 km PD intensity LMM (Table 2, model 7), with and without Tukey-Kramer p value adjustment.

10km	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
	Residents						
	low - medium	0.13	0.08	634.57	1.62	0.10	0.24
	low – high	**0.19**	0.08	634.34	2.28	**0.02**	0.06
	high - medium	-0.06	0.04	806.73	-1.33	0.19	0.38
	Arid-zone Migrants						
	low - medium	0.24	0.14	4253.68	1.70	0.09	0.20
	low - high	**0.32**	0.14	3836.76	2.21	**0.03**	0.07
	high - medium	-0.07	0.07	4238.88	-1.03	0.31	0.56
	Humid-zone Migrants						
	low - medium	0.18	0.11	2052.40	1.64	0.10	0.23
	low - high	**0.28**	0.11	1992.44	2.47	**0.01**	**0.04**
	high - medium	-0.10	0.06	2099.95	-1.73	0.08	0.20

Table S3.15: Pairwise contrasts between different levels of *intensity* within each migratory group in the 1 km PD grassland sites LMM, with and without Tukey-Kramer p value adjustment.

1 km Gras.	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
	Residents						
	low - medium	0.13	0.17	72.61	0.76	0.45	0.73
	low – high	0.11	0.20	75.05	0.56	0.58	0.84
	high - medium	0.02	0.18	71.49	0.12	0.91	0.99
	Arid-zone Migrants						
	low - medium	0.19	0.24	238.93	0.80	0.43	0.71
	low - high	0.35	0.25	189.33	1.40	0.16	0.34
	high - medium	-0.16	0.23	206.52	-0.70	0.49	0.77
	Humid-zone Migrants						
	low - medium	0.20	0.21	148.91	0.98	0.33	0.59
	low - high	**0.53**	0.23	135.15	2.33	**0.02**	0.06
	high - medium	-0.33	0.21	138.31	-1.56	0.12	0.27

Table S3.16: Pairwise contrasts between different levels of *intensity* within each migratory group in the 5 km PD grassland sites LMM, with and without Tukey-Kramer p value adjustment.

5 km Gras.	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
	Residents						
	low - medium	**0.44**	0.16	92.19	2.79	**<0.01**	**0.02**
	low – high	**0.42**	0.16	91.65	2.57	**0.01**	**0.03**
	high - medium	0.02	0.13	87.49	0.16	0.87	0.99
	Arid-zone Migrants						
	low - medium	**0.64**	0.23	379.45	2.78	**<0.01**	**0.02**
	low - high	**0.64**	0.22	304.46	2.86	**<0.01**	**0.01**
	high - medium	-0.003	0.19	419.03	-0.02	0.99	1.00
	Humid-zone Migrants						
	low - medium	**0.76**	0.20	258.34	3.71	**<0.001**	**<0.001**
	low - high	**1.02**	0.20	225.51	5.00	**<0.0001**	**<0.0001**
	high - medium	-0.27	0.16	240.78	-1.62	0.11	0.24

Table S3.17: Pairwise contrasts between different levels of *intensity* within each migratory group in the 10 km PD grassland sites LMM, with and without Tukey-Kramer p value adjustment.

10km Gras.	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
	Residents						
	low - medium	0.21	0.16	99.32	1.36	0.18	0.37
	low – high	0.18	0.17	98.64	1.08	0.28	0.53
	high - medium	0.03	0.12	101.13	0.25	0.80	0.97
	Arid-zone Migrants						
	low - medium	0.38	0.24	474.98	1.57	0.12	0.26
	low - high	0.41	0.24	376.54	1.70	0.09	0.21
	high - medium	-0.03	0.19	444.83	-0.17	0.86	0.98
	Humid-zone Migrants						
	low - medium	0.27	0.22	380.66	1.21	0.23	0.45
	low - high	**0.54**	0.23	313.04	2.39	**0.02**	0.05
	high - medium	-0.27	0.16	273.47	-1.70	0.09	0.21

Table S3.18: Pairwise contrasts between different levels of *intensity* within each migratory group in the 5 km PD arable cropland sites LMM, with and without Tukey-Kramer p value adjustment.

5 km Ara.	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
	Residents						
	low - medium	0.46	0.19	380.26	2.42	**0.02**	**0.04**
	low – high	0.45	0.19	372.77	2.38	**0.02**	0.05
	high - medium	0.01	0.07	336.69	0.09	0.92	1.00
	Arid-zone Migrants						
	low - medium	0.04	0.31	1936.72	0.12	0.91	0.99
	low - high	-0.11	0.31	1865.56	-0.37	0.71	0.93
	high - medium	0.15	0.11	1746.94	1.37	0.17	0.36
	Humid-zone Migrants						
	low - medium	0.24	0.23	824.88	1.06	0.29	0.54
	low - high	0.17	0.23	802.36	0.77	0.44	0.72
	high - medium	0.06	0.09	833.02	0.75	0.45	0.73

Table S3.19: Pairwise contrasts between different levels of *intensity* within each migratory group in the 1 km PD settlement sites LMM, with and without Tukey-Kramer p value adjustment.

1 km Sett.	Contrast	Estimate	Std.Error	df	t ratio	Non-adjusted *p*	Tukey-Kramer adjusted *p*
	Residents						
	low - medium	0.19	0.11	163.57	1.76	0.08	0.19
	low – high	0.22	0.13	168.82	1.71	0.09	0.20
	high - medium	-0.03	0.10	162.03	-0.28	0.78	0.96
	Arid-zone Migrants						
	low - medium	-0.18	0.19	976.50	-1.00	0.32	0.58
	low - high	**-0.55**	0.23	1140.08	-2.36	**0.02**	0.05
	high - medium	0.37	0.19	1180.88	1.89	0.06	0.14
	Humid-zone Migrants						
	low - medium	0.14	0.14	475.98	0.96	0.34	0.61
	low - high	0.20	0.18	601.73	1.11	0.27	0.51
	high - medium	-0.07	0.15	637.90	-0.43	0.67	0.90

Table S3.20: Model output for fixed effects in a LMM (Table 2, Model 1) examining the effect of 1 km scale *patch density* and *system* predictors on the mean standardised productivity for each bird species at each site, with p-values calculated by Satterthwaite's approximation (significant terms where $p<0.05$ indicated in **bold**). Additional 1 km continuous predictors *watercourse length, inland water perimeter* and *elevation* were fitted as orthogonal polynomial quadratic terms. Random effects of species (n = 88) and site (n = 809). Total n = 10111. Conditional $R^2 = 0.081$; Marginal $R^2 = 0.004$.

1 km	Estimate	Std.Error	df	t value	p value
Intercept (system = arable cropland)	0.08	0.05	676.00	1.65	0.10
poly(patch density, 2)1	0.17	2.02	739.00	0.08	0.93
poly(patch density, 2)2	-2.53	1.96	751.00	-1.29	0.20
system: forest	-0.12	0.07	758.00	-1.70	0.09
system: grassland	0.005	0.07	718.00	0.07	0.95
system: mosaic	-0.02	0.07	705.00	-0.30	0.76
system: settlement	-0.05	0.06	726.00	-0.81	0.42
system: wetland	**0.16**	0.07	742.00	2.47	**0.01**
poly(watercourse length 1km, 2)1	0.46	1.98	723.00	0.23	0.82
poly(watercourse length 1km, 2)2	-1.51	2.02	688.00	-0.75	0.46
poly(inland water perimeter 1km, 2)1	1.34	2.22	698.00	0.60	0.55
poly(inland water perimeter 1km, 2)2	-1.04	2.11	634.00	-0.50	0.62
poly(elevation, 2)1	-2.47	2.01	839.00	-1.23	0.22
poly(elevation, 2)2	0.23	1.88	795.00	0.12	0.90

Table S3.21: As Table S3.20, but with fixed effects of *mean patch perimeter-area ratio (MPPAR), system* and continuous predictors measured at the 1 km scale (Table 2, Model 2). N sites = 809, N species = 88, Total N = 10111. Conditional R^2 = 0.081; Marginal R^2 = 0.004.

1 km	Estimate	Std.Error	df	t value	p value
Intercept (system = arable cropland)	0.07	0.05	675.00	1.60	0.11
poly(MPPAR, 2)1	0.80	2.05	724.00	0.39	0.70
poly(MPPAR, 2)2	0.20	1.99	727.00	0.10	0.92
system: forest	-0.12	0.07	762.00	-1.73	0.08
system: grassland	0.01	0.07	719.00	0.08	0.94
system: mosaic	-0.01	0.07	707.00	-0.16	0.87
system: settlement	-0.05	0.06	729.00	-0.73	0.47
system: wetland	**0.16**	0.07	746.00	2.50	**0.01**
poly(watercourse length 1km, 2)1	0.31	1.98	726.00	0.16	0.87
poly(watercourse length 1km, 2)2	-1.48	2.03	688.00	-0.73	0.47
poly(inland water perimeter 1km, 2)1	1.75	2.23	699.00	0.78	0.44
poly(inland water perimeter 1km, 2)2	-1.03	2.11	635.00	-0.49	0.63
poly(elevation, 2)1	-2.53	2.03	846.00	-1.25	0.21
poly(elevation, 2)2	0.08	1.88	794.00	0.04	0.97

Table S3.22: As Table S3.20, but with fixed effects of *patch density, system,* and continuous predictors measured at the 5 km scale (Table 2, Model 1). N sites = 802, N species = 88, Total N = 10073. Conditional R^2 = 0.081; Marginal R^2 = 0.003.

5 km	Estimate	Std.Error	df	t value	p value
Intercept (system = arable cropland)	0.07	0.03	545.00	2.05	0.04
poly(patch density, 2)1	2.67	2.34	765.00	1.14	0.26
poly(patch density, 2)2	2.19	1.95	833.00	1.13	0.26
system: forest	-0.06	0.06	770.00	-1.06	0.29
system: grassland	0.002	0.06	686.00	0.03	0.98
system: settlement	0.05	0.06	722.00	0.93	0.36
system: wetland	0.14	0.08	745.00	1.84	0.07
poly(watercourse length 5km, 2)1	-3.12	2.01	731.00	-1.55	0.12
poly(watercourse length 5km, 2)2	-2.52	1.99	765.00	-1.27	0.21
poly(inland water perimeter 5km, 2)1	2.61	2.14	722.00	1.22	0.22
poly(inland water perimeter 5km, 2)2	-2.45	1.98	834.00	-1.24	0.22
poly(elevation, 2)1	-1.77	2.17	824.00	-0.81	0.42
poly(elevation, 2)2	0.37	1.93	803.00	0.19	0.85

Table S3.23: As Table S3.20, but with fixed effects of *mean patch perimeter-area ratio (MPPAR), system* and continuous predictors measured at the 5 km scale (Table 2, Model 2). N sites = 802, N species = 88, Total N = 10073. Conditional R^2 = 0.081; Marginal R^2 = 0.003.

5 km	Estimate	Std.Error	df	t value	p value
(Intercept)	0.07	0.03	535.00	1.97	0.05
poly(MPPAR, 2)1	4.13	2.33	771.00	1.77	0.08
poly(MPPAR, 2)2	2.61	2.04	693.00	1.28	0.20
system: forest	-0.06	0.06	777.00	-1.13	0.26
system: grassland	0.01	0.06	680.00	0.12	0.91
system: settlement	0.07	0.05	723.00	1.38	0.17
system: wetland	0.14	0.08	744.00	1.75	0.08
poly(watercourse length 5km, 2)1	-3.81	2.04	732.00	-1.87	0.06
poly(watercourse length 5km, 2)2	-2.47	1.98	760.00	-1.25	0.21
poly(inland water perimeter 5km, 2)1	3.28	2.15	721.00	1.53	0.13
poly(inland water perimeter 5km, 2)2	-2.79	1.99	833.00	-1.40	0.16
poly(elevation, 2)1	-2.81	2.26	845.00	-1.25	0.21
poly(elevation, 2)2	0.53	1.93	797.00	0.28	0.78

Table S3.24: As Table S3.20, but with fixed effects of *patch density, system,* and continuous predictors measured at the 10 km scale (Table 2, Model 1). N sites = 800, N species = 88, Total N = 10062. Conditional R^2 = 0.08; Marginal R^2 = 0.004.

10 km	Estimate	Std.Error	df	t value	p value
(Intercept)	0.03	0.03	514.00	1.09	0.27
poly(patch density, 2)1	2.85	2.49	777.00	1.14	0.25
poly(patch density, 2)2	0.19	1.99	775.00	0.09	0.93
system: forest	0.01	0.06	796.00	0.10	0.92
system: grassland	0.01	0.06	672.00	0.19	0.85
system: settlement	**0.13**	0.06	739.00	2.07	**0.04**
system: wetland	**0.27**	0.09	740.00	3.01	**0.003**
poly(watercourse length 10km, 2)1	-4.09	2.05	758.00	-1.99	0.05
poly(watercourse length 10km, 2)2	-2.05	1.98	803.00	-1.03	0.30
poly(inland water perimeter 10km, 2)1	-0.55	2.11	764.00	-0.26	0.80
poly(inland water perimeter 10km, 2)2	**-4.70**	1.90	1000.00	-2.47	**0.01**
poly(elevation, 2)1	-2.13	2.22	826.00	-0.96	0.34
poly(elevation, 2)2	1.16	1.94	817.00	0.60	0.55

Table S3.25: As Table S3.20, but with fixed effects of *mean patch perimeter-area ratio (MPPAR), system* and continuous predictors measured at the 10 km scale (Table 2, Model 2). N sites = 800, N species = 88, Total N = 10062. Conditional R^2 = 0.08; Marginal R^2 = 0.004.

10 km	Estimate	Std.Error	df	t value	p value
(Intercept)	0.03	0.03	497.00	1.03	0.30
poly(MPPAR, 2)1	3.27	2.43	798.00	1.34	0.18
poly(MPPAR, 2)2	1.71	2.06	728.00	0.83	0.41
system: forest	0.01	0.06	797.00	0.19	0.85
system: grassland	0.01	0.06	670.00	0.14	0.89
system: settlement	**0.15**	0.06	737.00	2.59	**0.01**
system: wetland	**0.26**	0.09	740.00	2.87	**<0.01**
poly(watercourse length 10km, 2)1	**-4.92**	2.11	767.00	-2.33	**0.02**
poly(watercourse length 10km, 2)2	-2.26	2.00	807.00	-1.13	0.26
poly(inland water perimeter 10km, 2)1	0.22	2.14	762.00	0.10	0.92
poly(inland water perimeter 10km, 2)2	**-4.89**	1.91	999.00	-2.56	**0.01**
poly(elevation, 2)1	-2.58	2.28	849.00	-1.13	0.26
poly(elevation, 2)2	0.97	1.93	811.00	0.50	0.62

Table S3.26: Model output for fixed effects in a LMM (Table 2, Model 5) examining the effect of 1 km scale *patch density*, *system* and *migratory status* predictors on the mean standardised productivity for each bird species at each site, with p values calculated by Satterthwaite's approximation (significant terms where p<0.05 indicated in **bold**). Additional 1 km continuous predictors *watercourse length, inland water perimeter* and *elevation* were fitted as orthogonal polynomial quadratic terms. Interactions (*) between *migratory status* and *system, watercourse length* and *inland water perimeter*. Random effects of species (n = 88) and site (n = 809). Total N = 10111. Conditional R^2 = 0.084; Marginal R^2 = 0.006.

1 km	Estimate	Std.Error	df	t value	p value
Intercept (system = arable cropland; mig. status = humid)	-0.12	0.06	1040.00	-1.92	0.05
poly(patch density, 2)1	0.26	2.03	739.00	0.13	0.90
poly(patch density, 2)2	-2.41	1.97	752.00	-1.23	0.22
system: forest	0.03	0.10	2330.00	0.37	0.72
system: grassland	0.21	0.10	2150.00	2.08	0.04
system: mosaic	0.13	0.09	2190.00	1.41	0.16
system: settlement	0.09	0.09	2210.00	0.99	0.32
system: wetland	**0.42**	0.09	2000.00	4.91	**<0.0001**
mig. status: arid	0.03	0.08	819.00	0.35	0.73
mig. status: resident	**0.29**	0.05	573.00	5.26	**<0.0001**
poly(watercourse length 1km, 2)1	0.51	2.65	2170.00	0.19	0.85
poly(watercourse length 1km, 2)2	-3.44	2.71	2090.00	-1.27	0.21
poly(inland water perimeter 1km, 2)1	2.95	2.82	1760.00	1.05	0.30
poly(inland water perimeter 1km, 2)2	0.71	2.62	1480.00	0.27	0.79
poly(elevation, 2)1	-2.62	2.01	838.00	-1.30	0.19
poly(elevation, 2)2	0.25	1.88	794.00	0.13	0.90
system: forest*mig. status: arid	0.03	0.13	9300.00	0.22	0.83
system: grassland*mig. status: arid	0.03	0.12	9410.00	0.23	0.82
system: mosaic*mig. status: arid	0.02	0.12	9540.00	0.13	0.90
system: settlement*mig. status: arid	-0.16	0.11	9540.00	-1.42	0.16
system: wetland*mig. status: arid	-0.18	0.11	9430.00	-1.66	0.10
system: forest*mig. status: resident	**-0.23**	0.08	9720.00	-2.74	**0.01**
system: grassland*mig. status: resident	**-0.30**	0.08	9580.00	-3.54	**<0.001**
system: mosaic*mig. status: resident	**-0.22**	0.08	9650.00	-2.83	**<0.01**
system: settlement*mig. status: resident	**-0.18**	0.07	9680.00	-2.52	**0.01**
system: wetland*mig. status: resident	**-0.36**	0.07	9670.00	-4.90	**<0.0001**
mig. status: arid*poly(watercourse length 1km, 2)1	-6.11	3.31	9530.00	-1.84	0.07
mig. status: arid*poly(watercourse length 1km, 2)2	3.81	3.17	9450.00	1.20	0.23
mig. status: resident*poly(watercourse length 1km, 2)1	0.84	2.26	9640.00	0.37	0.71
mig. status: resident*poly(watercourse length 1km, 2)2	2.38	2.26	9550.00	1.05	0.29
mig. status: arid*poly(inland water perimeter 1km, 2)1	1.26	3.35	9370.00	0.38	0.71
mig. status: arid*poly(inland water perimeter 1km, 2)2	-2.10	2.80	9270.00	-0.75	0.45
mig. status: resident*poly(inland water perimeter 1km, 2)1	-2.46	2.33	9300.00	-1.06	0.29
mig. status: resident*poly(inland water perimeter 1km, 2)2	-2.58	2.04	9420.00	-1.26	0.21

Table S3.27: As Table S3.26, but with fixed effects of *mean patch perimeter-area ratio (MPPAR), system* and continuous predictors measured at the 1 km scale (Table 2, Model 6). N sites = 809, N species = 88, Total N = 10111. Conditional R^2 = 0.084; Marginal R^2 = 0.006.

1 km	Estimate	Std.Error	df	t value	p value
Intercept (system = arable cropland; mig. status = humid)	-0.12	0.06	1030.00	-2.00	0.05
poly(MPPAR, 2)1	0.82	2.06	724.00	0.40	0.69
poly(MPPAR, 2)2	0.34	1.99	727.00	0.17	0.86
system: forest	0.03	0.10	2370.00	0.36	0.72
system: grassland	**0.21**	0.10	2150.00	2.09	**0.04**
system: mosaic	0.14	0.09	2230.00	1.53	0.13
system: settlement	0.09	0.09	2270.00	1.08	0.28
system: wetland	**0.42**	0.09	2030.00	4.94	**<0.0001**
mig. status: arid	0.03	0.08	819.00	0.36	0.72
mig. status: resident	**0.29**	0.05	572.00	5.27	**<0.0001**
poly(watercourse length 1km, 2)1	0.38	2.65	2180.00	0.15	0.89
poly(watercourse length 1km, 2)2	-3.41	2.72	2080.00	-1.25	0.21
poly(inland water perimeter 1km, 2)1	3.37	2.83	1750.00	1.19	0.23
poly(inland water perimeter 1km, 2)2	0.72	2.62	1480.00	0.27	0.78
poly(elevation, 2)1	-2.68	2.03	845.00	-1.32	0.19
poly(elevation, 2)2	0.11	1.89	794.00	0.06	0.96
system: forest*mig. status: arid	0.03	0.13	9300.00	0.22	0.83
system: grassland*mig. status: arid	0.03	0.12	9410.00	0.23	0.82
system: mosaic*mig. status: arid	0.02	0.12	9540.00	0.13	0.90
system: settlement*mig. status: arid	-0.16	0.11	9540.00	-1.42	0.16
system: wetland*mig. status: arid	-0.18	0.11	9430.00	-1.67	0.10
system: forest*mig. status: resident	**-0.23**	0.08	9720.00	-2.74	**0.01**
system: grassland*mig. status: resident	**-0.30**	0.08	9580.00	-3.56	**<0.001**
system: mosaic*mig. status: resident	**-0.22**	0.08	9650.00	-2.85	**<0.01**
system: settlement*mig. status: resident	**-0.18**	0.07	9680.00	-2.53	**0.01**
system: wetland*mig. status: resident	**-0.36**	0.07	9670.00	-4.91	**<0.0001**
mig. status: arid*poly(watercourse length 1km, 2)1	-6.14	3.31	9530.00	-1.85	0.06
mig. status: arid*poly(watercourse length 1km, 2)2	3.84	3.17	9450.00	1.21	0.23
mig. status: resident*poly(watercourse length 1km, 2)1	0.82	2.26	9640.00	0.37	0.72
mig. status: resident*poly(watercourse length 1km, 2)2	2.37	2.26	9550.00	1.05	0.29
mig. status: arid*poly(inland water perimeter 1km, 2)1	1.25	3.35	9370.00	0.37	0.71
mig. status: arid*poly(inland water perimeter 1km, 2)2	-2.10	2.80	9270.00	-0.75	0.45
mig. status: resident*poly(inland water perimeter 1km, 2)1	-2.46	2.33	9300.00	-1.06	0.29
mig. status: resident*poly(inland water perimeter 1km, 2)2	-2.57	2.04	9420.00	-1.26	0.21

Table S3.28: As Table S3.26, but with fixed effects of *patch density, system* and continuous predictors measured at the 5 km scale (Table 2, Model 5). N sites = 802, N species = 88, Total N = 10073. Conditional R^2 = 0.083; Marginal R^2 = 0.004.

5 km	Estimate	Std.Error	df	t value	p value
Intercept (system = arable cropland; mig. status = humid)	0.01	0.05	357.00	0.13	0.90
poly(patch density, 2)1	2.44	2.35	767.00	1.04	0.30
poly(patch density, 2)2	2.17	1.95	834.00	1.11	0.27
system: forest	-0.10	0.08	2170.00	-1.25	0.21
system: grassland	0.02	0.08	1950.00	0.29	0.77
system: settlement	0.14	0.08	2000.00	1.91	0.06
system: wetland	**0.23**	**0.10**	**1990.00**	**2.26**	**0.02**
mig. status: arid	-0.06	0.06	210.00	-0.98	0.33
mig. status: resident	**0.11**	0.04	138.00	2.67	**0.01**
poly(watercourse length 5km, 2)1	**-7.96**	2.64	2030.00	-3.01	**<0.01**
poly(watercourse length 5km, 2)2	-0.24	2.60	2110.00	-0.09	0.93
poly(inland water perimeter 5km, 2)1	4.60	2.75	1880.00	1.67	0.10
poly(inland water perimeter 5km, 2)2	-1.58	2.50	2200.00	-0.63	0.53
poly(elevation, 2)1	-1.99	2.18	826.00	-0.91	0.36
poly(elevation, 2)2	0.19	1.94	804.00	0.10	0.92
system: forest*mig. status: arid	0.09	0.11	8710.00	0.85	0.40
system: grassland*mig. status: arid	0.09	0.10	9340.00	0.94	0.35
system: settlement*mig. status: arid	-0.06	0.09	9410.00	-0.62	0.54
system: wetland*mig. status: arid	-0.08	0.12	9490.00	-0.65	0.52
system: forest*mig. status: resident	0.03	0.07	8890.00	0.53	0.60
system: grassland*mig. status: resident	-0.05	0.07	9090.00	-0.81	0.42
system: settlement*mig. status: resident	**-0.13**	0.06	9520.00	-2.09	**0.04**
system: wetland*mig. status: resident	-0.12	0.08	9590.00	-1.45	0.15
mig. status: arid*poly(watercourse length 5km, 2)1	1.01	3.39	9380.00	0.30	0.77
mig. status: arid*poly(watercourse length 5km, 2)2	0.68	3.25	9500.00	0.21	0.83
mig. status: resident*poly(watercourse length 5km, 2)1	**7.23**	2.23	9130.00	3.24	**<0.01**
mig. status: resident*poly(watercourse length 5km, 2)2	-3.52	2.20	9640.00	-1.60	0.11
mig. status: arid*poly(inland water perimeter 5km, 2)1	-1.00	3.30	9190.00	-0.30	0.76
mig. status: arid*poly(inland water perimeter 5km, 2)2	-2.59	3.21	9450.00	-0.81	0.42
mig. status: resident*poly(inland water perimeter 5km, 2)1	-2.50	2.30	8880.00	-1.09	0.28
mig. status: resident*poly(inland water perimeter 5km, 2)2	-1.29	2.17	9440.00	-0.60	0.55

Table S3.29: As Table S3.26, but with fixed effects of *mean patch perimeter-area ratio (MPPAR), system* and continuous predictors measured at the 5 km scale (Table 2, Model 6). N sites = 802, N species = 88, Total N = 10073. Conditional R^2 = 0.083; Marginal R^2 = 0.004.

5 km	Estimate	Std.Error	df	t value	p value
Intercept (system = arable cropland; mig. status = humid)	<0.01	0.04	354.00	0.06	0.95
poly(MPPAR, 2)1	3.89	2.34	772.00	1.66	0.10
poly(MPPAR, 2)2	2.52	2.05	694.00	1.23	0.22
system: forest	-0.10	0.08	2260.00	-1.29	0.20
system: grassland	0.03	0.08	1950.00	0.37	0.71
system: settlement	**0.16**	0.07	2170.00	2.27	**0.02**
system: wetland	**0.22**	0.10	1980.00	2.19	**0.03**
mig. status: resident	**0.11**	0.04	139.00	2.69	**0.01**
mig. status: arid	-0.06	0.06	212.00	-0.96	0.34
poly(watercourse length 5km, 2)1	**-8.64**	2.66	2000.00	-3.25	**<0.01**
poly(watercourse length 5km, 2)2	-0.22	2.60	2120.00	-0.09	0.93
poly(inland water perimeter 5km, 2)1	5.25	2.76	1870.00	1.90	0.06
poly(inland water perimeter 5km, 2)2	-1.89	2.51	2190.00	-0.75	0.45
poly(elevation, 2)1	-2.99	2.27	846.00	-1.32	0.19
poly(elevation, 2)2	0.36	1.94	798.00	0.18	0.85
system: forest*mig. status: resident	0.03	0.07	8880.00	0.49	0.62
system: grassland*mig. status: resident	-0.05	0.07	9090.00	-0.80	0.42
system: settlement*mig. status: resident	**-0.13**	0.06	9530.00	-2.11	**0.03**
system: wetland*mig. status: resident	-0.12	0.08	9590.00	-1.44	0.15
system: forest*mig. status: arid	0.09	0.11	8720.00	0.86	0.39
system: grassland*mig. status: arid	0.09	0.10	9350.00	0.92	0.36
system: settlement*mig. status: arid	-0.06	0.09	9420.00	-0.64	0.52
system: wetland*mig. status: arid	-0.07	0.12	9490.00	-0.64	0.52
mig. status: resident*poly(watercourse length 5km, 2)1	**7.27**	2.23	9140.00	3.26	**<0.01**
mig. status: arid*poly(watercourse length 5km, 2)1	1.01	3.39	9390.00	0.30	0.77
mig. status: arid*poly(watercourse length 5km, 2)2	0.68	3.25	9500.00	0.21	0.84
mig. status: resident*poly(watercourse length 5km, 2)2	-3.45	2.20	9640.00	-1.57	0.12
mig. status: resident*poly(inland water perimeter 5km, 2)1	-2.55	2.30	8890.00	-1.11	0.27
mig. status: arid*poly(inland water perimeter 5km, 2)1	-1.02	3.30	9200.00	-0.31	0.76
mig. status: arid*poly(inland water perimeter 5km, 2)2	-2.59	3.21	9450.00	-0.81	0.42
mig. status: resident*poly(inland water perimeter 5km, 2)2	-1.30	2.17	9440.00	-0.60	0.55

Table S3.30: As Table S3.26, but with fixed effects of *patch density, system* and continuous predictors measured at the 10 km scale (Table 2, Model 5). N sites = 800, N species = 88, Total N = 10062. Conditional R^2 = 0.082; Marginal R^2 = 0.006.

10 km	Estimate	Std.Error	df	t value	p value
Intercept (system = arable cropland; mig. status = humid)	-0.02	0.04	297.00	-0.48	0.63
poly(patch density, 2)1	2.53	2.50	779.00	1.01	0.31
poly(patch density, 2)2	0.38	2.00	777.00	0.19	0.85
system: forest	-0.04	0.08	2180.00	-0.51	0.61
system: grassland	-0.01	0.08	2020.00	-0.15	0.88
system: settlement	**0.27**	0.08	2040.00	3.38	**<0.001**
system: wetland	**0.35**	0.11	1930.00	3.08	**<0.01**
mig. status: arid	-0.06	0.06	174.00	-1.07	0.29
mig. status: resident	0.09	0.04	117.00	2.43	0.02
poly(watercourse length 10km, 2)1	**-9.84**	2.72	2180.00	-3.61	**<0.001**
poly(watercourse length 10km, 2)2	2.11	2.70	2530.00	0.78	0.44
poly(inland water perimeter 10km, 2)1	-0.93	2.76	2110.00	-0.34	0.74
poly(inland water perimeter 10km, 2)2	**-5.16**	2.47	2970.00	-2.09	**0.04**
poly(elevation, 2)1	-2.21	2.23	829.00	-0.99	0.32
poly(elevation, 2)2	1.08	1.95	824.00	0.55	0.58
system: forest*mig. status: arid	0.05	0.10	9090.00	0.47	0.64
system: grassland*mig. status: arid	0.11	0.09	9310.00	1.16	0.24
system: settlement*mig. status: arid	-0.06	0.10	9450.00	-0.60	0.55
system: wetland*mig. status: arid	-0.17	0.13	9480.00	-1.30	0.19
system: forest*mig. status: resident	0.05	0.06	9120.00	0.84	0.40
system: grassland*mig. status: resident	0.01	0.07	8880.00	0.14	0.89
system: settlement*mig. status: resident	**-0.20**	0.07	9620.00	-3.10	**0.002**
system: wetland*mig. status: resident	-0.11	0.10	9640.00	-1.11	0.27
mig. status: arid*poly(watercourse length 10km, 2)1	1.20	3.50	8920.00	0.34	0.73
mig. status: arid*poly(watercourse length 10km, 2)2	-0.83	3.51	9530.00	-0.24	0.81
mig. status: resident*poly(watercourse length 10km, 2)1	**8.23**	2.32	8740.00	3.55	**<0.001**
mig. status: resident*poly(watercourse length 10km, 2)2	**-5.89**	2.35	9700.00	-2.51	**0.01**
mig. status: arid*poly(inland water perimeter 10km, 2)1	0.88	3.60	9240.00	0.25	0.81
mig. status: arid*poly(inland water perimeter 10km, 2)2	-5.66	3.64	9470.00	-1.56	0.12
mig. status: resident*poly(inland water perimeter 10km, 2)1	0.99	2.38	8980.00	0.42	0.68
mig. status: resident*poly(inland water perimeter 10km, 2)2	1.30	2.29	9370.00	0.57	0.57

Table S3.31: As Table S3.26, but with fixed effects of *mean patch perimeter-area ratio (MPPAR), system* and continuous predictors measured at the 10 km scale (Table 2, Model 6). N sites = 800, N species = 88, Total N = 10062. Conditional R^2 = 0.082; Marginal R^2 = 0.006.

10 km	Estimate	Std.Error	df	t value	p value
Intercept (system = arable cropland; mig. status = humid)	-0.02	0.04	291.00	-0.54	0.59
poly(MPPAR, 2)1	2.90	2.44	800.00	1.19	0.24
poly(MPPAR, 2)2	1.55	2.07	730.00	0.75	0.45
system: forest	-0.03	0.07	2310.00	-0.45	0.66
system: grassland	-0.01	0.08	1990.00	-0.18	0.86
system: settlement	**0.29**	0.08	2230.00	3.78	**<0.001**
system: wetland	**0.34**	0.11	1930.00	2.99	**<0.01**
mig. status: arid	-0.06	0.06	174.00	-1.06	0.29
mig. status: resident	**0.09**	0.04	117.00	2.44	**0.02**
poly(watercourse length 10km, 2)1	**-10.60**	2.77	2110.00	-3.83	**<0.001**
poly(watercourse length 10km, 2)2	1.95	2.71	2490.00	0.72	0.47
poly(inland water perimeter 10km, 2)1	-0.27	2.78	2070.00	-0.10	0.92
poly(inland water perimeter 10km, 2)2	**-5.35**	2.48	2950.00	-2.16	**0.03**
poly(elevation, 2)1	-2.63	2.29	852.00	-1.15	0.25
poly(elevation, 2)2	0.91	1.94	817.00	0.47	0.64
system: forest*mig. status: arid	0.05	0.10	9090.00	0.49	0.63
system: grassland*mig. status: arid	0.11	0.09	9310.00	1.15	0.25
system: settlement*mig. status: arid	-0.06	0.10	9450.00	-0.61	0.54
system: wetland*mig. status: arid	-0.17	0.13	9480.00	-1.30	0.19
system: forest*mig. status: resident	0.05	0.06	9110.00	0.80	0.42
system: grassland*mig. status: resident	0.01	0.07	8870.00	0.14	0.89
system: settlement*mig. status: resident	**-0.20**	0.07	9620.00	-3.11	**<0.01**
system: wetland*mig. status: resident	-0.11	0.10	9640.00	-1.11	0.27
mig. status: arid*poly(watercourse length 10km, 2)1	1.24	3.50	8920.00	0.35	0.72
mig. status: arid*poly(watercourse length 10km, 2)2	-0.85	3.51	9530.00	-0.24	0.81
mig. status: resident*poly(watercourse length 10km, 2)1	**8.22**	2.32	8740.00	3.55	**<0.001**
mig. status: resident*poly(watercourse length 10km, 2)2	**-5.90**	2.35	9700.00	-2.51	**0.01**
mig. status: arid*poly(inland water perimeter 10km, 2)1	0.86	3.60	9240.00	0.24	0.81
mig. status: arid*poly(inland water perimeter 10km, 2)2	-5.65	3.63	9470.00	-1.56	0.12
mig. status: resident*poly(inland water perimeter 10km, 2)1	0.98	2.38	8980.00	0.41	0.68
mig. status: resident*poly(inland water perimeter 10km, 2)2	1.31	2.29	9370.00	0.57	0.57

Table S3.32: Model output for fixed effects in a LMM (Table 2, Model 3) examining the effect of 1 km scale *patch density* and *intensity* predictors on the mean standardised productivity for each bird species at each site, with p values calculated by Satterthwaite's approximation (significant terms where $p<0.05$ indicated in **bold**). Additional 1 km continuous predictors *watercourse length, inland water perimeter* and *elevation* were fitted as orthogonal polynomial quadratic terms. All species. Excludes wetland sites. Random effects of species (n = 88) and site (n = 645). Total N = 8018. Conditional R^2 = 0.077; Marginal R^2 = 0.001.

1 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low)	0.08	0.04	482.00	2.00	0.05
poly(patch density, 2)1	-0.42	1.95	601.00	-0.22	0.83
poly(patch density, 2)2	-1.07	1.89	608.00	-0.56	0.57
intensity: high	-0.03	0.06	586.00	-0.60	0.55
intensity: medium	-0.07	0.05	583.00	-1.38	0.17
poly(watercourse length 1km, 2)1	0.85	1.90	588.00	0.45	0.65
poly(watercourse length 1km, 2)2	-3.18	1.90	602.00	-1.68	0.09
poly(inland water perimeter 1km, 2)1	2.00	1.97	578.00	1.01	0.31
poly(inland water perimeter 1km, 2)2	-0.32	1.91	582.00	-0.17	0.87
poly(elevation, 2)1	-3.08	1.95	664.00	-1.57	0.12
poly(elevation, 2)2	-0.34	1.82	637.00	-0.19	0.85

Table S3.33: As Table S3.32, but with fixed effects of *mean patch perimeter-area ratio (MPPAR), intensity* and continuous predictors measured at the 1 km scale (Table 2, Model 4). N species = 88, N sites = 645, Total N = 8018. Conditional R^2 = 0.077; Marginal R^2 = 0.001.

1 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low)	0.08	0.04	483.00	2.02	0.04
poly(MPPAR, 2)1	-0.42	1.99	583.00	-0.21	0.83
poly(MPPAR, 2)2	1.31	1.89	598.00	0.70	0.49
intensity: high	-0.04	0.06	587.00	-0.66	0.51
intensity: medium	-0.07	0.05	587.00	-1.39	0.17
poly(watercourse length 1km, 2)1	0.72	1.90	589.00	0.38	0.70
poly(watercourse length 1km, 2)2	-3.27	1.90	602.00	-1.72	0.09
poly(inland water perimeter 1km, 2)1	2.22	1.97	576.00	1.13	0.26
poly(inland water perimeter 1km, 2)2	-0.35	1.91	583.00	-0.18	0.86
poly(elevation, 2)1	-3.11	1.98	669.00	-1.57	0.12
poly(elevation, 2)2	-0.42	1.82	635.00	-0.23	0.82

Table S3.34: As Table S3.32, but with fixed effects of *patch density, intensity* and continuous predictors measured at the 5 km scale (Table 2, Model 3). N species = 88, N sites = 731, Total N = 9186. Conditional R^2 = 0.077; Marginal R^2 = 0.003.

5 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low)	0.31	0.08	43.50	4.09	<0.001
poly(patch density, 2)1	1.84	2.20	201.00	0.84	0.40
poly(patch density, 2)2	1.64	1.87	759.00	0.88	0.38
intensity: high	**-0.27**	0.08	570.00	-3.49	**<0.001**
intensity: medium	**-0.28**	0.08	571.00	-3.74	**<0.001**
poly(watercourse length 5km, 2)1	-3.62	1.96	673.00	-1.85	0.07
poly(watercourse length 5km, 2)2	-2.41	1.92	705.00	-1.25	0.21
poly(inland water perimeter 5km, 2)1	2.95	1.99	666.00	1.48	0.14
poly(inland water perimeter 5km, 2)2	-0.21	1.92	775.00	-0.11	0.91
poly(elevation, 2)1	**-4.58**	2.12	627.00	-2.16	**0.03**
poly(elevation, 2)2	0.22	1.87	741.00	0.12	0.91

Table S3.35: As Table S3.32, but with fixed effects of *mean patch perimeter-area ratio (MPPAR), intensity* and continuous predictors measured at the 5 km scale (Table 2, Model 4). N species = 88, N sites = 731, Total N = 9186. Conditional R^2 = 0.077; Marginal R^2 = 0.003.

5 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low)	0.28	0.07	673.00	3.96	<0.001
poly(MPPAR, 2)1	1.89	2.29	696.00	0.82	0.41
poly(MPPAR, 2)2	0.50	2.04	638.00	0.25	0.81
intensity: high	**-0.24**	0.08	667.00	-3.05	**<0.01**
intensity: medium	**-0.25**	0.08	679.00	-3.18	**<0.01**
poly(watercourse length 5km, 2)1	-3.82	1.98	677.00	-1.92	0.05
poly(watercourse length 5km, 2)2	-2.20	1.93	701.00	-1.14	0.25
poly(inland water perimeter 5km, 2)1	2.77	1.99	672.00	1.39	0.16
poly(inland water perimeter 5km, 2)2	-0.30	1.93	776.00	-0.16	0.88
poly(elevation, 2)1	**-5.64**	2.16	783.00	-2.61	**0.01**
poly(elevation, 2)2	0.44	1.88	737.00	0.23	0.82

Table S3.36: As Table S3.32, but with fixed effects of *patch density, intensity* and continuous predictors measured at the 10 km scale (Table 2, Model 3). N species = 88, N sites = 750, Total N = 9422. Conditional R^2 = 0.077; Marginal R^2 = 0.003.

10 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low)	0.24	0.08	38.70	2.99	0.005
poly(patch density, 2)1	1.47	2.32	129.00	0.63	0.53
poly(patch density, 2)2	0.49	1.92	719.00	0.25	0.80
intensity: high	**-0.22**	0.08	572.00	-2.72	**0.01**
intensity: medium	-0.15	0.08	569.00	-1.94	0.05
poly(watercourse length 10km, 2)1	**-5.99**	2.03	706.00	-2.94	**<0.01**
poly(watercourse length 10km, 2)2	-0.48	1.94	742.00	-0.25	0.80
poly(inland water perimeter 10km, 2)1	0.77	1.97	702.00	0.39	0.70
poly(inland water perimeter 10km, 2)2	-2.86	1.83	1050.00	-1.56	0.12
poly(elevation, 2)1	-3.71	2.21	723.00	-1.68	0.09
poly(elevation, 2)2	0.59	1.92	767.00	0.31	0.76

Table S3.37: As Table S3.32, but with fixed effects of *mean patch perimeter-area ratio (MPPAR), intensity* and continuous predictors measured at the 10 km scale (Table 2, Model 4). N species = 88, N sites = 750, Total N = 9422. Conditional R^2 = 0.077; Marginal R^2 = 0.003.

10 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low)	0.24	0.09	47.80	2.81	0.01
poly(MPPAR, 2)1	1.58	2.42	561.00	0.65	0.51
poly(MPPAR, 2)2	-0.22	2.15	677.00	-0.10	0.92
intensity: high	**-0.22**	0.09	635.00	-2.56	**0.01**
intensity: medium	-0.15	0.09	625.00	-1.79	0.07
poly(watercourse length 10km, 2)1	**-6.27**	2.08	718.00	-3.02	**<0.01**
poly(watercourse length 10km, 2)2	-0.31	1.95	744.00	-0.16	0.88
poly(inland water perimeter 10km, 2)1	0.87	1.99	691.00	0.44	0.66
poly(inland water perimeter 10km, 2)2	-2.88	1.84	1050.00	-1.57	0.12
poly(elevation, 2)1	-3.97	2.27	777.00	-1.75	0.08
poly(elevation, 2)2	0.58	1.91	757.00	0.31	0.76

Table S3.38: Model output for fixed effects in a LMM (Table 2, Model 7) examining the effect of 1 km scale *patch density*, *intensity* and *migratory status* predictors on the mean standardised productivity for each species at each site, with p values calculated by Satterthwaite's approximation (significant terms where p<0.05 indicated in **bold**). Additional 1 km continuous predictors *watercourse length, inland water perimeter* and *elevation* were fitted as orthogonal polynomial quadratic terms. Interactions (*) between *migratory status* and *intensity, watercourse length* and *inland water perimeter*. Wetland sites excluded. Random effects of species (n = 88) and site (n = 645). Total N = 8108. Conditional R^2 = 0.077; Marginal R^2 = 0.003.

1 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low; mig. status = humid)	0.08	0.06	390.00	1.47	0.14
poly(patch density, 2)1	-0.52	1.95	602.00	-0.27	0.79
poly(patch density, 2)2	-0.99	1.89	608.00	-0.53	0.60
intensity: high	**-0.20**	0.08	1870.00	-2.59	**0.01**
intensity: medium	**-0.16**	0.07	1890.00	-2.25	**0.02**
mig. status: arid	-0.09	0.08	286.00	-1.18	0.24
mig. status: resident	0.01	0.05	177.00	0.25	0.81
poly(watercourse length 1km, 2)1	0.03	2.64	1990.00	0.01	0.99
poly(watercourse length 1km, 2)2	-4.78	2.71	2250.00	-1.76	0.08
poly(inland water perimeter 1km, 2)1	2.42	2.58	1640.00	0.94	0.35
poly(inland water perimeter 1km, 2)2	0.06	2.51	1710.00	0.02	0.98
poly(elevation, 2)1	-3.07	1.96	663.00	-1.57	0.12
poly(elevation, 2)2	-0.28	1.82	637.00	-0.15	0.88
intensity: high*mig. status: arid	**0.24**	0.10	7650.00	2.35	**0.02**
intensity: medium*mig. status: arid	0.10	0.09	7660.00	1.10	0.27
intensity: high*mig. status: resident	**0.21**	0.07	7770.00	3.05	**<0.01**
intensity: medium*mig. status: resident	0.11	0.06	7770.00	1.81	0.07
mig. status: arid*poly(watercourse length 1km, 2)1	-3.88	3.47	7680.00	-1.12	0.26
mig. status: arid*poly(watercourse length 1km, 2)2	2.78	3.60	7690.00	0.77	0.44
mig. status: resident*poly(watercourse length 1km, 2)1	1.57	2.30	7780.00	0.69	0.49
mig. status: resident*poly(watercourse length 1km, 2)2	1.86	2.40	7730.00	0.78	0.44
mig. status: arid*poly(inland water perimeter 1km, 2)1	2.45	3.27	7430.00	0.75	0.45
mig. status: arid*poly(inland water perimeter 1km, 2)2	-0.27	3.29	7570.00	-0.08	0.94
mig. status: resident*poly(inland water perimeter 1km, 2)1	-0.97	2.20	7360.00	-0.44	0.66
mig. status: resident*poly(inland water perimeter 1km, 2)2	-0.60	2.18	7690.00	-0.28	0.78

Table S3.39: As Table S3.38, but with fixed effects of *mean patch perimeter-area ratio (MPPAR)*, *intensity* and continuous predictors measured at the 1 km scale (Table 2, Model 8). N sites = 731, N species = 88, Total N = 9186. Conditional $R^2 = 0.079$; Marginal $R^2 = 0.005$.

1 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low; mig. Status = humid)	0.08	0.06	389.00	1.48	0.14
poly(MPPAR, 2)1	-0.47	1.99	583.00	-0.24	0.81
poly(MPPAR, 2)2	1.39	1.89	599.00	0.73	0.46
intensity: high	**-0.21**	0.08	1900.00	-2.64	**0.01**
intensity: medium	**-0.16**	0.07	1910.00	-2.26	**0.02**
mig. status: arid	-0.09	0.08	286.00	-1.17	0.24
mig. status: resident	0.01	0.05	177.00	0.24	0.81
poly(watercourse length 1km, 2)1	-0.08	2.63	1990.00	-0.03	0.98
poly(watercourse length 1km, 2)2	-4.87	2.71	2240.00	-1.80	0.07
poly(inland water perimeter 1km, 2)1	2.65	2.58	1640.00	1.03	0.31
poly(inland water perimeter 1km, 2)2	0.03	2.51	1710.00	0.01	0.99
poly(elevation, 2)1	-3.11	1.98	668.00	-1.57	0.12
poly(elevation, 2)2	-0.35	1.83	635.00	-0.19	0.85
intensity: high*mig. status: arid	**0.24**	0.10	7650.00	2.35	**0.02**
intensity: medium*mig. status: arid	0.10	0.09	7660.00	1.11	0.27
intensity: high*mig. status: resident	**0.21**	0.07	7770.00	3.06	**<0.01**
intensity: medium*mig. status: resident	0.11	0.06	7770.00	1.82	0.07
mig. status: arid*poly(watercourse length 1km, 2)1	-3.89	3.47	7680.00	-1.12	0.26
mig. status: arid*poly(watercourse length 1km, 2)2	2.80	3.60	7690.00	0.78	0.44
mig. status: resident*poly(watercourse length 1km, 2)1	1.55	2.30	7780.00	0.68	0.50
mig. status: resident*poly(watercourse length 1km, 2)2	1.86	2.40	7740.00	0.78	0.44
mig. status: arid*poly(inland water perimeter 1km, 2)1	2.44	3.27	7430.00	0.75	0.46
mig. status: arid*poly(inland water perimeter 1km, 2)2	-0.27	3.29	7570.00	-0.08	0.94
mig. status: resident*poly(inland water perimeter 1km, 2)1	-0.98	2.20	7360.00	-0.45	0.66
mig. status: resident*poly(inland water perimeter 1km, 2)2	-0.60	2.18	7690.00	-0.28	0.78

Table S3.40: As Table S3.38, but with fixed effects of *patch density*, *intensity* and continuous predictors measured at the 5 km scale (Table 2, Model 7). N sites = 731, N species = 88, Total N = 9186. Conditional R^2 = 0.079; Marginal R^2 = 0.005.

5 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low; mig. Status = humid)	0.37	0.10	133.00	3.77	<0.001
poly(patch density, 2)1	1.74	2.20	190.00	0.79	0.43
poly(patch density, 2)2	1.69	1.88	757.00	0.90	0.37
intensity: high	**-0.43**	0.10	1690.00	-4.11	**<0.0001**
intensity: medium	**-0.38**	0.10	1770.00	-3.68	**<0.001**
mig. status: arid	-0.16	0.12	2270.00	-1.31	0.19
mig. status: resident	-0.07	0.08	1240.00	-0.86	0.39
poly(watercourse length 5km, 2)1	**-8.39**	2.62	2000.00	-3.20	**<0.01**
poly(watercourse length 5km, 2)2	0.14	2.56	2070.00	0.06	0.96
poly(inland water perimeter 5km, 2)1	4.42	2.60	1840.00	1.70	0.09
poly(inland water perimeter 5km, 2)2	-0.63	2.45	2240.00	-0.26	0.80
poly(elevation, 2)1	**-4.71**	2.12	617.00	-2.22	**0.03**
poly(elevation, 2)2	0.22	1.87	742.00	0.12	0.91
intensity: high*mig. status: arid	0.21	0.13	7610.00	1.58	0.11
intensity: medium*mig. status: arid	0.07	0.13	8110.00	0.53	0.60
intensity: high*mig. status: resident	**0.20**	0.09	7670.00	2.26	**0.02**
intensity: medium*mig. status: resident	0.13	0.09	8540.00	1.47	0.14
mig. status: arid*poly(watercourse length 5km, 2)1	-1.86	3.50	8620.00	-0.53	0.59
mig. status: resident*poly(watercourse length 5km, 2)1	**7.39**	2.27	8470.00	3.26	**<0.01**
mig. status: arid*poly(watercourse length 5km, 2)2	-0.61	3.29	8680.00	-0.19	0.85
mig. status: resident*poly(watercourse length 5km, 2)2	-3.96	2.21	8830.00	-1.79	0.07
mig. status: arid*poly(inland water perimeter 5km, 2)1	2.29	3.30	8390.00	0.70	0.49
mig. status: resident*poly(inland water perimeter 5km, 2)1	-2.38	2.22	8400.00	-1.07	0.29
mig. status: arid*poly(inland water perimeter 5km, 2)2	3.23	3.23	8690.00	1.00	0.32
mig. status: resident*poly(inland water perimeter 5km, 2)2	-0.04	2.20	8820.00	-0.02	0.99

Table S3.41: As Table S3.38, but with fixed effects of *mean patch perimeter-area ratio (MPPAR)*, *intensity* and continuous predictors measured at the 5 km scale (Table 2, Model 8). N sites = 731, N species = 88, Total N = 9186. Conditional R^2 = 0.079; Marginal R^2 = 0.005.

5 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low; mig. Status = humid)	0.37	0.10	137.00	3.69	0.0003
poly(MPPAR, 2)1	2.17	2.33	629.00	0.93	0.35
poly(MPPAR, 2)2	0.50	2.03	636.00	0.24	0.81
intensity: high	**-0.43**	0.11	1720.00	-4.01	**<0.001**
intensity: medium	**-0.38**	0.11	1750.00	-3.57	**<0.001**
mig. status: arid	-0.16	0.12	2290.00	-1.32	0.19
mig. status: resident	-0.07	0.08	1250.00	-0.86	0.39
poly(watercourse length 5km, 2)1	**-8.72**	2.64	1980.00	-3.31	**0.001**
poly(watercourse length 5km, 2)2	0.30	2.56	2060.00	0.12	0.91
poly(inland water perimeter 5km, 2)1	4.68	2.60	1850.00	1.80	0.07
poly(inland water perimeter 5km, 2)2	-0.70	2.46	2230.00	-0.29	0.78
poly(elevation, 2)1	**-5.14**	2.20	717.00	-2.34	**0.02**
poly(elevation, 2)2	0.34	1.88	737.00	0.18	0.86
intensity: high*mig. status: arid	0.21	0.13	7610.00	1.59	0.11
intensity: medium*mig. status: arid	0.07	0.13	8120.00	0.53	0.59
intensity: high*mig. status: resident	**0.20**	0.09	7670.00	2.26	**0.02**
intensity: medium*mig. status: resident	0.13	0.09	8540.00	1.47	0.14
mig. status: arid*poly(watercourse length 5km, 2)1	-1.89	3.50	8620.00	-0.54	0.59
mig. status: arid*poly(watercourse length 5km, 2)2	-0.62	3.29	8680.00	-0.19	0.85
mig. status: resident*poly(watercourse length 5km, 2)1	**7.42**	2.27	8480.00	3.27	**0.001**
mig. status: resident*poly(watercourse length 5km, 2)2	-3.91	2.21	8830.00	-1.77	0.08
mig. status: arid*poly(inland water perimeter 5km, 2)1	2.31	3.30	8390.00	0.70	0.48
mig. status: arid*poly(inland water perimeter 5km, 2)2	3.24	3.23	8690.00	1.00	0.32
mig. status: resident*poly(inland water perimeter 5km, 2)1	-2.40	2.22	8410.00	-1.08	0.28
mig. status: resident*poly(inland water perimeter 5km, 2)2	-0.04	2.20	8820.00	-0.02	0.98

Table S3.42: As Table S3.38, but with fixed effects of *patch density*, *intensity* and continuous predictors measured at the 10 km scale (Table 2, Model 7). N sites = 750, N species = 88, Total N = 9422. Conditional R^2 = 0.078; Marginal R^2 = 0.004.

10 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low; mig. Status = humid)	0.23	0.11	139.00	2.12	0.04
poly(patch density, 2)1	1.16	2.32	121.00	0.50	0.62
poly(patch density, 2)2	0.72	1.92	719.00	0.38	0.71
intensity: high	**-0.28**	0.11	1990.00	-2.47	**0.01**
intensity: medium	-0.18	0.11	2050.00	-1.64	0.10
mig. status: arid	0.01	0.14	3250.00	0.04	0.97
mig. status: resident	0.01	0.09	1810.00	0.10	0.92
poly(watercourse length 10km, 2)1	**-11.40**	2.74	2170.00	-4.16	**<0.0001**
poly(watercourse length 10km, 2)2	3.74	2.65	2380.00	1.41	0.16
poly(inland water perimeter 10km, 2)1	0.08	2.60	2030.00	0.03	0.98
poly(inland water perimeter 10km, 2)2	-4.32	2.34	3200.00	-1.85	0.06
poly(elevation, 2)1	-3.73	2.22	720.00	-1.68	0.09
poly(elevation, 2)2	0.74	1.92	774.00	0.38	0.70
intensity: high*mig. status: arid	-0.03	0.15	7880.00	-0.23	0.82
intensity: medium*mig. status: arid	-0.06	0.15	8420.00	-0.41	0.68
intensity: high*mig. status: resident	0.09	0.10	7540.00	0.93	0.35
intensity: medium*mig. status: resident	0.05	0.10	8580.00	0.51	0.61
mig. status: arid*poly(watercourse length 10km, 2)1	-1.67	3.63	8630.00	-0.46	0.65
mig. status: arid*poly(watercourse length 10km, 2)2	1.54	3.53	8920.00	0.44	0.66
mig. status: resident*poly(watercourse length 10km, 2)1	**8.32**	2.37	8760.00	3.51	**<0.001**
mig. status: resident*poly(watercourse length 10km, 2)2	-6.45	2.31	9110.00	-2.79	0.01
mig. status: arid*poly(inland water perimeter 10km, 2)1	4.01	3.43	8740.00	1.17	0.24
mig. status: arid*poly(inland water perimeter 10km, 2)2	-3.60	3.62	9060.00	-1.00	0.32
mig. status: resident*poly(inland water perimeter 10km, 2)1	1.01	2.28	8840.00	0.44	0.66
mig. status: resident*poly(inland water perimeter 10km, 2)2	3.01	2.27	9100.00	1.32	0.19

Table S3.43: As Table S3.38, but with fixed effects of *mean patch perimeter-area ratio (MPPAR)*, *intensity* and continuous predictors measured at the 10 km scale (Table 2, Model 8). N sites = 750, N species = 88, Total N = 9422. Conditional $R^2 = 0.078$; Marginal $R^2 = 0.004$.

10 km	Estimate	Std.Error	df	t value	p value
Intercept (intensity = low; mig. Status = humid)	0.23	0.11	158.00	2.06	0.04
poly(MPPAR, 2)1	1.37	2.42	542.00	0.57	0.57
poly(MPPAR, 2)2	-0.17	2.16	680.00	-0.08	0.94
intensity: high	**-0.28**	0.12	1960.00	-2.39	**0.02**
intensity: medium	-0.18	0.12	1970.00	-1.58	0.12
mig. status: arid	0.01	0.14	3270.00	0.04	0.97
mig. status: resident	0.01	0.09	1810.00	0.10	0.92
poly(watercourse length 10km, 2)1	**-11.70**	2.76	2120.00	-4.22	**<0.0001**
poly(watercourse length 10km, 2)2	3.87	2.66	2340.00	1.46	0.15
poly(inland water perimeter 10km, 2)1	0.12	2.62	1950.00	0.05	0.96
poly(inland water perimeter 10km, 2)2	-4.32	2.34	3170.00	-1.84	0.07
poly(elevation, 2)1	-4.01	2.28	777.00	-1.76	0.08
poly(elevation, 2)2	0.76	1.92	763.00	0.40	0.69
intensity: high*mig. status: arid	-0.04	0.15	7870.00	-0.25	0.81
intensity: medium*mig. status: arid	-0.06	0.15	8410.00	-0.40	0.69
intensity: high*mig. status: resident	0.09	0.10	7520.00	0.92	0.36
intensity: medium*mig. status: resident	0.05	0.10	8560.00	0.53	0.60
mig. status: arid*poly(watercourse length 10km, 2)1	-1.64	3.64	8670.00	-0.45	0.65
mig. status: arid*poly(watercourse length 10km, 2)2	1.65	3.53	8920.00	0.47	0.64
mig. status: resident*poly(watercourse length 10km, 2)1	**8.35**	2.37	8770.00	3.53	**<0.001**
mig. status: resident*poly(watercourse length 10km, 2)2	**-6.39**	2.31	9110.00	-2.77	**0.01**
mig. status: arid*poly(inland water perimeter 10km, 2)1	4.10	3.44	8750.00	1.19	0.23
mig. status: arid*poly(inland water perimeter 10km, 2)2	-3.71	3.62	9060.00	-1.03	0.31
mig. status: resident*poly(inland water perimeter 10km, 2)1	1.00	2.28	8840.00	0.44	0.66
mig. status: resident*poly(inland water perimeter 10km, 2)2	2.99	2.27	9100.00	1.32	0.19

Chapter 4: Productivity of European Landbirds is Positively Associated with Flying Insect Abundance at Breeding Sites

A sticky trap at a Constant Effort Site in Hungary. © Aniko Benke

Abstract

Recent research has revealed considerable spatial variation in the productivity of landbirds across breeding sites in Europe, which is consistent across species and years. Most landbird species are insectivorous in the breeding season, and so one potential driver of this variation could be the abundance of insect prey. We conducted a high-resolution, large-scale Pan-European study using a network of citizen scientists to examine how insect abundance maps onto spatial variation in productivity. We also explore whether insect abundance varies with the composition of the surrounding landscape. Flying insect abundance was measured at 176 Constant Effort bird ringing sites across 10 countries in 2024 using sticky traps. This was related to mean productivity across bird species at each site (averaged across years 1998 to 2019), as well as the dominant land cover type and management intensity within 1 km. Mean productivity across bird species showed a positive relationship with the mean insect count per hour at study sites. This relationship was significant but showed a high degree of variation. Insect abundance did not vary significantly among land use types or management intensity categories. These findings highlight the importance of conserving and enhancing insect populations for supporting landbird populations in Europe. We were unable to identify any landscape features associated with insect abundance in this study, and so it's possible that local-scale factors are more important. Further work is needed to understand how site-level habitat affects insect abundance, in order to identify the conditions needed to maintain and enhance insect populations and the food webs that they support.

4.1. Introduction

Food availability plays a key role in driving bird population abundance (Newton, 2002) and can be successfully manipulated by conservation efforts to help declining populations recover (e.g. Siriwardena et al., 2007). Much emphasis has been placed on winter food availability and its impact on survival rates, but food limitation can also occur during the breeding season and negatively impact productivity (Mallord et al., 2007). Such impacts can occur via different mechanisms acting at multiple stages of the reproductive cycle (Martin, 1987). For example, if food is scarce, females may lay reduced clutch sizes (Sanz and Moreno, 1995), lower provisioning rates may cause nestling starvation or reduced body condition, with negative impacts on chick survival rates at the nestling and post-fledging stages (Grüebler et al., 2018; Jones et al., 2017), and parents may spend longer away from the nest searching for food, increasing the risk of hatching failure or nest predation (Brickle et al., 2000; Duncan Rastogi et al., 2006).

Several studies have demonstrated positive associations between insect abundance or biomass and bird abundance (Benton et al., 2002; Evans et al., 2024; Møller, 2019), as well as reproductive success (Martay et al., 2023; Seress et al., 2018; Shutt et al., 2018), while supplementation experiments have shown direct positive impacts of insect food provision on reproductive success (Peach et al., 2015). In addition, a recent meta-analysis demonstrated that, generally, increased insect food availability is associated with both greater reproductive success and chick body condition in insectivorous birds, suggesting that this is a common phenomenon across species and geographic areas (Grames et al., 2023). Widespread declines in insectivorous bird populations across continents have therefore been attributed to widely reported declines in insect populations (Bowler et al., 2019; Dirzo et al., 2014; Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019; Tallamy and Shriver, 2021; Wagner, 2020). Importantly, the impacts of these insect declines are not likely to be restricted to insectivorous species because most landbirds feed invertebrates to nestlings, regardless of adult diet (Cramp, 2006).

Previous work has identified substantial and consistent site-level spatial variation in productivity of landbirds at European breeding sites (see **Chapter 3**), which covaries between species remaining in Europe throughout the year and those migrating to sub-Saharan Africa (Morrison et al., 2021, 2022). It is currently unknown whether insect prey availability is related to this spatial variation in productivity (Pearce-Higgins and Morris, 2022). If insect abundance maps onto this variation, such that sites with poor bird productivity record lower insect abundance than high productivity sites, this raises the possibility of enhancing insect populations to help boost productivity rates of European landbirds. However, our capacity to do so depends on our ability to identify the conditions associated with high insect abundance. Land use change is considered one of the greatest drivers of insect declines (Sánchez-Bayo and Wyckhuys, 2019), and so landscape composition around sites may play an important role (Sinclair et al., 2025). For example, insect prey availability has been shown to be greater in semi-natural landscapes compared to urban environments (Seress et al., 2018) and agricultural landscapes (Garrett et al., 2022). There is also evidence for negative impacts of agricultural intensity on insect abundance (Benton et al., 2002), with one driving factor being the increased use of pesticides in more intensive areas. Several studies have shown reduced insect and bird abundance and/or productivity in areas with increased pesticide applications (Brickle et al., 2000; Hallmann et al., 2014; Hart et al., 2006; Morris et al., 2005). Furthermore, how far the benefits of increasing insect abundance could extend across the bird community depends on whether responses differ between species. For example, sub-Saharan migrants are more constrained in their timing of breeding compared to residents (Both and Visser, 2001; Hedenström, 2007; Knudsen et al., 2011), and so may be expected to show different responses to insect abundance. In addition, species that are more strongly insectivorous, including most migrants (Jiguet et al., 2007), may show stronger associations between productivity and insect abundance than species feeding on other resources, such as granivores.

Most studies examining relationships between bird productivity and insect prey availability have been conducted over small spatial extents and/or on a single species, but there are calls to examine these relationships across species at large scales (Grames et al., 2023; Martay et al., 2023). We conducted a Pan-European citizen science study which measured insect abundance at sites where standardised bird captures are used to provide annual estimates of productivity. Our study was both high-resolution; relating site-level insect abundance to long-term, site-level productivity, and large-scale; spanning countries across Europe. Our aims were three-fold: (1) to examine whether insect abundance maps onto spatial variation in cross-community bird productivity at sites in Europe, (2) to explore how this varies between resident and migratory bird communities, and across individual species, because differences may be masked at the community-level, and (3) to examine how insect abundance varies spatially and temporally within and across sites, and with the composition of the surrounding landscape.

4.2. Methods

Insect Abundance

We recruited citizen scientist volunteers taking part in the European Constant Effort Sites (EuroCES) programme, previously described in **Chapter 3,** to measure insect abundance on their sites during the 2024 CES season. A total of 176 sites from 10 CES schemes contributed insect data, covering a wide latitudinal and longitudinal range (Table 4.1, Figure 4.1). During every other CES ringing session, volunteers hung a single double-sided yellow sticky trap measuring 25 x 10 cm at approximately 1.5 – 2 m height, from a branch or other suitable vegetation in a random, fixed location within 10 m of the mist-net rides. Sticky traps are a simple, low-cost but effective method for monitoring (mostly flying) invertebrate abundance (Kent et al., 2019), which allowed us to maximise the number of sites collecting insect data. Volunteers were asked to record the date, start and end times of trap deployment (Table 4.2), and to return photographs of each side of the traps, which were then imported into Fiji image processing software

(Schindelin et al., 2012) and the total number of insects caught on each trap manually counted (plus any arachnids, grouped with insects for simplicity). The total insect count for each trap was divided by the number of hours the trap was deployed (median = 4 hours; Figure S4.1) to obtain a total insect count per hour for each trap. The total number of traps was 741 and the number of trapping occasions per site ranged between 2 and 7 (see Table 4.1 for scheme-specific information). Dates of trapping varied between sites but were evenly spread across the breeding season (Figure S4.2). It was not feasible to operate more than one trapping location per site, but a pilot study conducted in 2023 with six traps installed per site demonstrated significant within-site repeatability in insect counts recorded on traps deployed on the same day (Appendix 4.1). The insect trapping was conducted with approval from the University of East Anglia Research Ethics Committee (ETH2223-2236), and relevant local site permissions were sought before sampling took place.

Table 4.1: For each Constant Effort Sites scheme, the three-letter abbreviation used in subsequent figures, the total number of sites that contributed sticky trap insect data, the number of these sites with productivity data in at least three years between 1998 and 2019, and the range in number of trapping occasions at sites within that scheme.

Scheme	Code	Total Number of Sites	Number of Sites with Productivity Data	Number of Trap Occasions Per Site
Czechia	CZE	15	12	3 – 5
Denmark	DEN	7	5	3 – 6
Finland	FIN	15	9	4 – 7
France	FRA	52	20	2 – 5
Great Britain & Ireland	GBT	29	16	4 – 6
Hungary	HUN	13	11	2 – 4
Italy	ITA	12	12	4 – 6
Spain (Basque)	SPB	6	6	3
Spain (Catalonia)	SPC	24	23	3 – 4
Sweden	SWE	3	3	6 – 7

Table 4.2: Mean and standard deviation for the start time (HH:MM), end time (HH:MM) and total hours of deployment of sticky traps measuring insect abundance across 741 trapping occasions at 176 European Constant Effort Sites in 2024.

	Mean	Standard Deviation
Start Time	05:37	00:55
End Time	11:31	01:10
Trap Hours	5.90	0.95

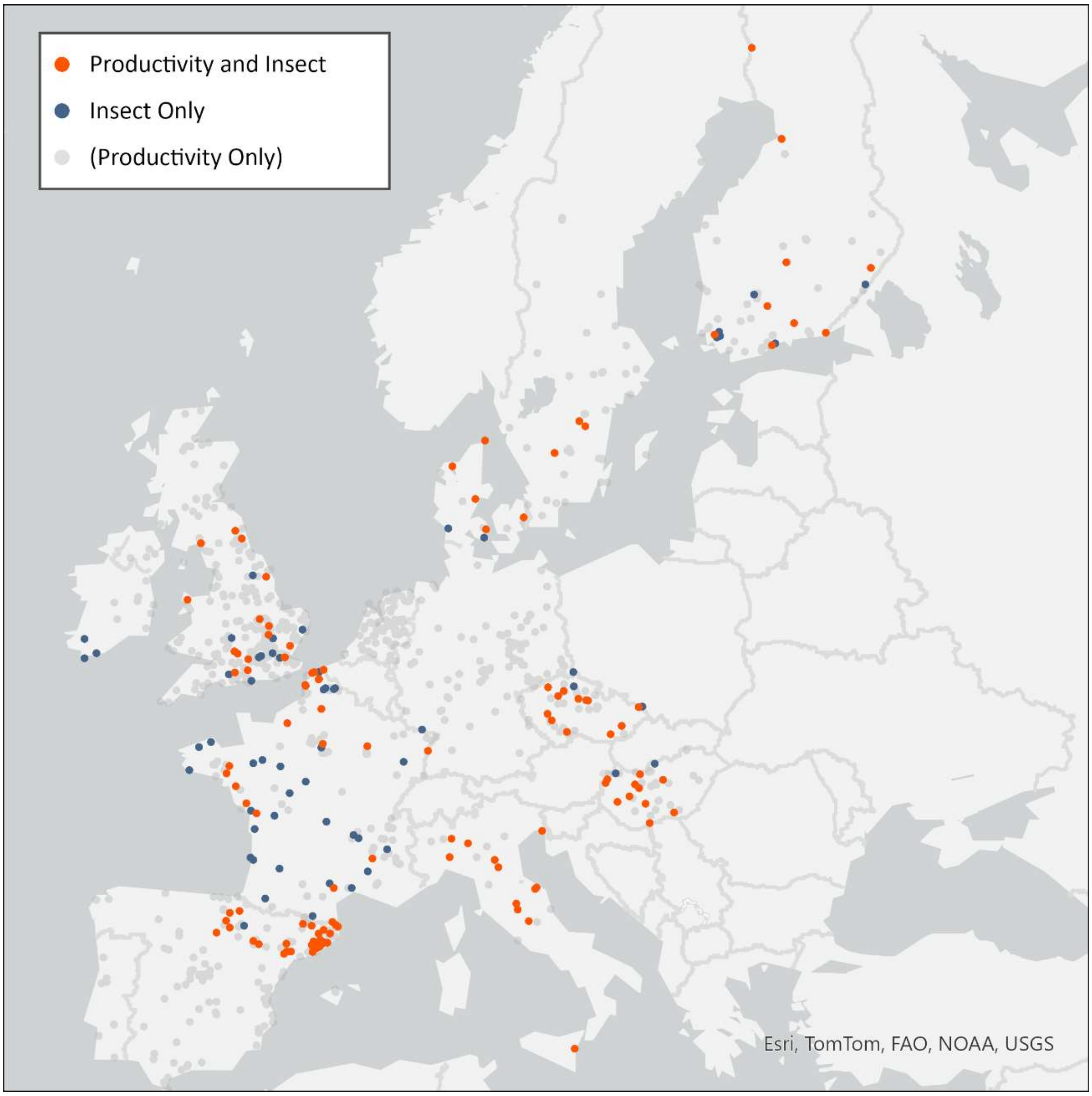


Figure 4.1: Constant Effort Sites (CES) which contributed data to this study. In orange are sites which contributed both insect abundance and mean landbird productivity data. Mean productivity could only be measured at sites with at least three years of productivity data between 1998 – 2019, and some CESs which monitored insect abundance did not meet this threshold and so did not contribute productivity data to this study (blue). In grey are all CESs in Europe active at any time during 1998 – 2019 (many no longer active and so could not contribute to this study).

Quantifying Site-level Mean Productivity

Productivity data were available for the years 1998 through to 2019, and were used to calculate a mean annual productivity value for each site, across years and species. As described in **Chapter 3**, the mean juvenile-adult ratio across years for each species at each site ('species-site mean') was estimated in a series of binomial generalised linear mixed models (GLMMs). We restricted the species list to passerines because the CES methodology most reliably measures productivity rates for these species, and excluded invasive non-native species, resulting in a final list of 80 species across our sample of sites (Table S4.1).

We then calculated the mean productivity across species at each site, employing a bootstrapping procedure to incorporate error associated with the individual species-site means. For each species at each site, 1000 estimates of across-year mean productivity were generated by randomly sampling from a normal distribution with a mean equal to the species-site mean estimate and standard deviation equal to the standard error around this estimate. To account for differences in species composition between sites, species-site estimates were standardised by subtracting the overall species mean across sites and dividing by the standard deviation (similarly to **Chapter 3**, but within each of the 1000 datasets here). This standardisation process was done within each scheme separately to avoid methodological differences biasing the productivity values. Subsequently, the 1000 standardised estimates were used to calculate the mean site-level productivity across species at each site and the standard deviation, which incorporates error around the species-site means.

Mean productivity was calculated across all species at a site, as well as across species classified into one of three migratory groups: (1) resident within Europe or short-distance migrant ("resident"), (2) long-distance migrant overwintering in the arid-zone of sub-Saharan Africa ("arid"), or (3) long-distance migrant overwintering in the more southerly humid-zone of sub-Saharan Africa ("humid"). We used the classifications from Morrison et al., (2021), resulting in 48 residents, 14 arid-zone migrants and 18 humid-zone migrants. The above process was carried out for *all* CE sites in each scheme to contextualise the mean productivity values on our sample of sites contributing insect data, and to increase the number of species included in our dataset (because standardisation is not possible if fewer than two sites record that species). The distributions of site-level mean productivity for the entire CES dataset and for our sample of sites were very similar, with medians of -0.07 and -0.08 respectively (Figure S4.3). The study sites can therefore be considered a random, representative sample of bird productivity on CE sites in Europe. Mean productivity could only be measured at sites with at least three years of productivity data between 1998 – 2019 (*n* = 117, Table 4.1; see **Chapter 3** Methods), which was not available for 59 of the 176 sites contributing insect data. These 59 sites were therefore excluded from analyses of productivity (see below).

For 13 of the 15 sites recording insect data in Finland, we also had concurrent productivity data from 2024 (the remaining two sites did not meet the minimum monitoring duration threshold for calculating productivity). This was within a wider dataset of 36 CE sites collecting productivity data in the 2024 season in Finland (Figure S4.4). Mean standardised productivity across 27 bird species was calculated following a very similar, but simplified procedure: 1) the juvenile-adult ratio was calculated for each species at each of the 36 sites, 2) values were standardised within each species across all 36 sites, and 3) the mean and standard deviation was calculated across species at each of the 13 sites with insect data.

Landscape Composition

As previously described in **Chapter 3**, we used the Land System typology from Dou et al., (2021) to characterise the landscape composition around sites using two categorical variables: system and intensity. First, each of the 176 CE sites contributing insect data was assigned the land system and sub-system category for the 1 km square in which it occurs. System was then simply defined by the land system category of that square (Table 4.3a), while intensity was defined by the management intensity level of the sub-system category (Table 4.3b; see Table S4.2 for sub-system groupings). Amongst the CE sites where insect data were collected, arable cropland landscapes were the most common and formed a greater proportion of sites surveyed compared to their proportion in the full EuroCES dataset (from **Chapter 3, Table 3.2a**), while grassland landscapes were under-represented. In addition, sites within low-intensity landscapes constituted nearly half of the sample of sites, which is a greater proportion compared to the full dataset (from **Chapter 3, Table 3.2b**). Meanwhile comparatively few sites were in high-intensity landscapes, which formed the greatest proportion in the full dataset.

Table 4.3: The number (#) and percentage (%) of Constant Effort Sites (CES) contributing insect data within 1 km scale landscapes dominated by each (a) system type, and (b) management intensity. The percentage of sites in the full EuroCES dataset represented by each category is also presented for comparison (taken from Chapter 3, Tables 3.2a and 3.2b).

a)	System	# sites	% sites	All CES % sites
	Arable Cropland	45	26	18
	Forest	32	18	14
	Grassland	7	4	11
	Mosaic	25	14	16
	Settlement	28	16	20
	Shrub	7	4	0
	Wetland	32	18	20

b)	Intensity	# sites	% sites	All CES % sites
	Low	82	47	34
	Medium	65	37	26
	High	29	16	40

Statistical Analysis

Productivity and Insect Abundance

i. All Species

To examine the association between productivity and insect abundance at sites across Europe, we ran a linear model using the *lm* function in the 'lme4' R package (Bates et al., 2015), with mean productivity across all species at each site as the response variable and the mean insect count per hour across traps at each site as a predictor variable (n = 117). The inverse of the standard deviation from the bootstrapped estimates of mean site-level productivity was used as a weighting variable to account for error around the individual species-site means. We accepted significance of the predictor variable if $p < 0.05$ in the model summary. We also ran the same model with an interaction term between mean insect count per hour and scheme to examine how the association between productivity and insect abundance varies across Europe. The *emtrends* function in the 'emmeans' package (Lenth et al., 2024) was used to extract the slope estimate and 95% confidence intervals for each scheme, accepting significance if the intervals did not include zero. In addition, to examine the relationship between concurrent productivity and insect abundance data in Finland, we ran a linear model with the mean standardised productivity at sites in 2024 as the response variable, and the mean insect count per hour as a predictor (n = 13; Figure S4.4).

ii. Migratory Groups and Individual Species

We then ran three separate models with the same main model structure as above, each with mean productivity across species in the different migratory groups (residents, arid-zone migrants and humid-zone migrants) as the response variable. Further, to examine how responses varied between individual species, standardised productivity values (taken from the binomial GLMMs mentioned previously) for species recorded on 5 or more sites (n = 52, see Table S4.1) were fitted as the response variable in a linear model, with mean insect count per hour and its interaction with species as predictor variables. The standard error from each of the species binomial GLMMs was used as a weighting variable. Slope estimates and 95% confidence intervals for the relationship between productivity and insect counts were extracted for each species from this model, again accepting significance if the intervals did not include zero.

Insect Abundance and Landscape Composition

To examine the effect of land system on insect counts, we ran a linear mixed model (LMM) using the *lmer* function in the 'lmerTest' package (Kuznetsova et al., 2017), with the log-transformed mean insect count per hour at a site as the response variable, the system category for each site as a categorical fixed effect, and scheme as a random intercept. We ran a similar model to examine the effect of management intensity on insect counts, with the intensity category for each site as a categorical fixed effect. System and intensity were fitted in separate models because wetland and shrub sites were always classified as "low intensity", so including the predictors in the same model would have confounded their effects. We assessed categorical predictor significance using term deletion and likelihood ratio tests, accepting significance if $p < 0.05$.

For all models, we inspected the distribution of residuals and checked for influential points using the 'performance' package (Lüdecke et al., 2021). All analyses were conducted in R 4.4.3. (R Core Team, 2025).

4.3. Results

Landbird Productivity and Insect Abundance

Across all sites, mean standardised productivity showed a weakly significant positive relationship with the mean insect count per hour recorded on sticky traps (Table 4.4). Sites with the lowest productivity values (<-0.3) only ever recorded fewer than 10 insects per hour on average, while sites recording more insects had mean productivity across the full range of values (Figure 4.2). The relationship between mean productivity and insect counts varied somewhat across schemes (Figures 4.3 and 4.4, Table S4.3). Finland was the only scheme to demonstrate a significant positive relationship, while none of the schemes demonstrated a negative slope. Within Finland, we also found a significant positive relationship between mean productivity recorded at sites in 2024 and the mean insect count per hour ($\beta = 0.05$, standard error = 0.02, $t = 2.42$, $p = 0.03$; Figure 4.5). In addition, mean productivity at Finnish sites with both the historic productivity (1998-2019) and 2024 productivity datasets ($n = 7$) was significantly positively correlated (Spearman's rho = 0.93, $S = 4$, $df = 5$, $p = 0.01$; Figure S4.5).

Table 4.4: Model output from a linear model with mean standardised productivity across all landbird species at a site as the response variable and mean insect count per hour recorded on sticky traps at that site in 2024 as a predictor variable, weighted by the inverse of the standard deviation of mean productivity. *N* sites = 117. (Model $R^2 = 0.04$).

	Estimate	Standard Error	t value	p value
Intercept	-0.15	0.06	-2.59	0.01
Mean Insect Count Per Hour	0.01	0.01	2.05	**0.04**

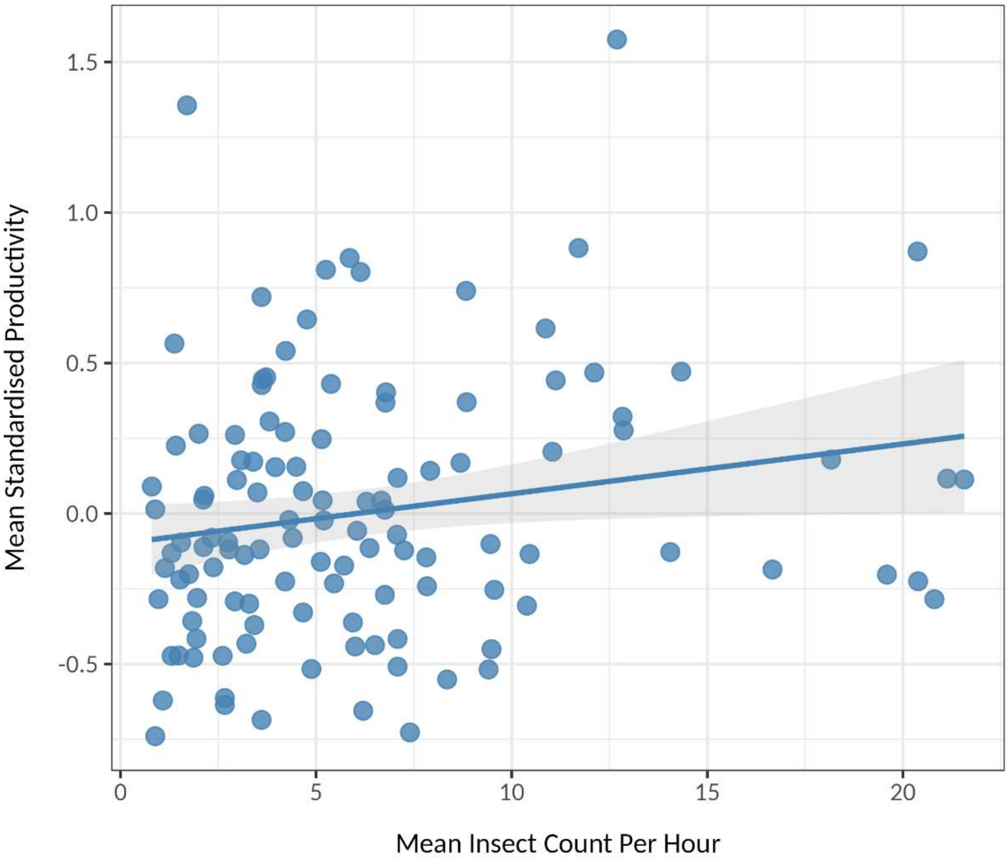


Figure 4.2: Relationship between the mean standardised productivity across 80 landbird species (1998 – 2019) and the mean insect count per hour recorded on sticky traps in 2024 at 117 Constant Effort Sites across Europe. Grey shading indicates 95% Confidence Intervals.

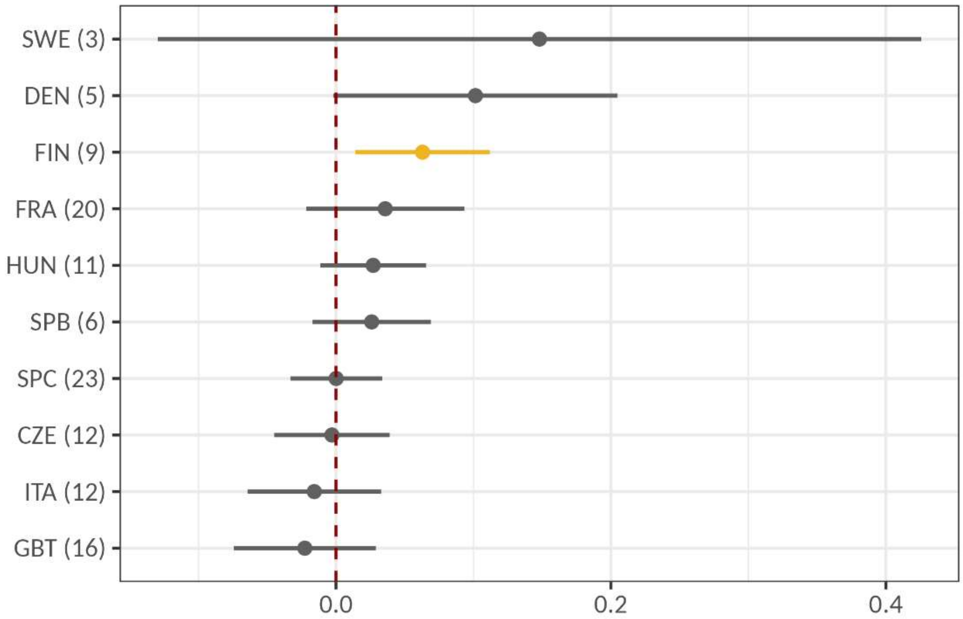


Figure 4.3: Slope estimates (points) and 95% Confidence Intervals (line intervals, CIs) from a linear model of mean standardised productivity across landbird species (1998 – 2019) at Constant Effort Sites (CES), fitted as a function of mean total insect count per hour recorded on sticky traps in 2024, and its interaction with CES scheme. Number of sites for each scheme is shown in brackets after the scheme code (see Table 4.1). Significant associations highlighted in orange (95% CIs do not overlap 0).

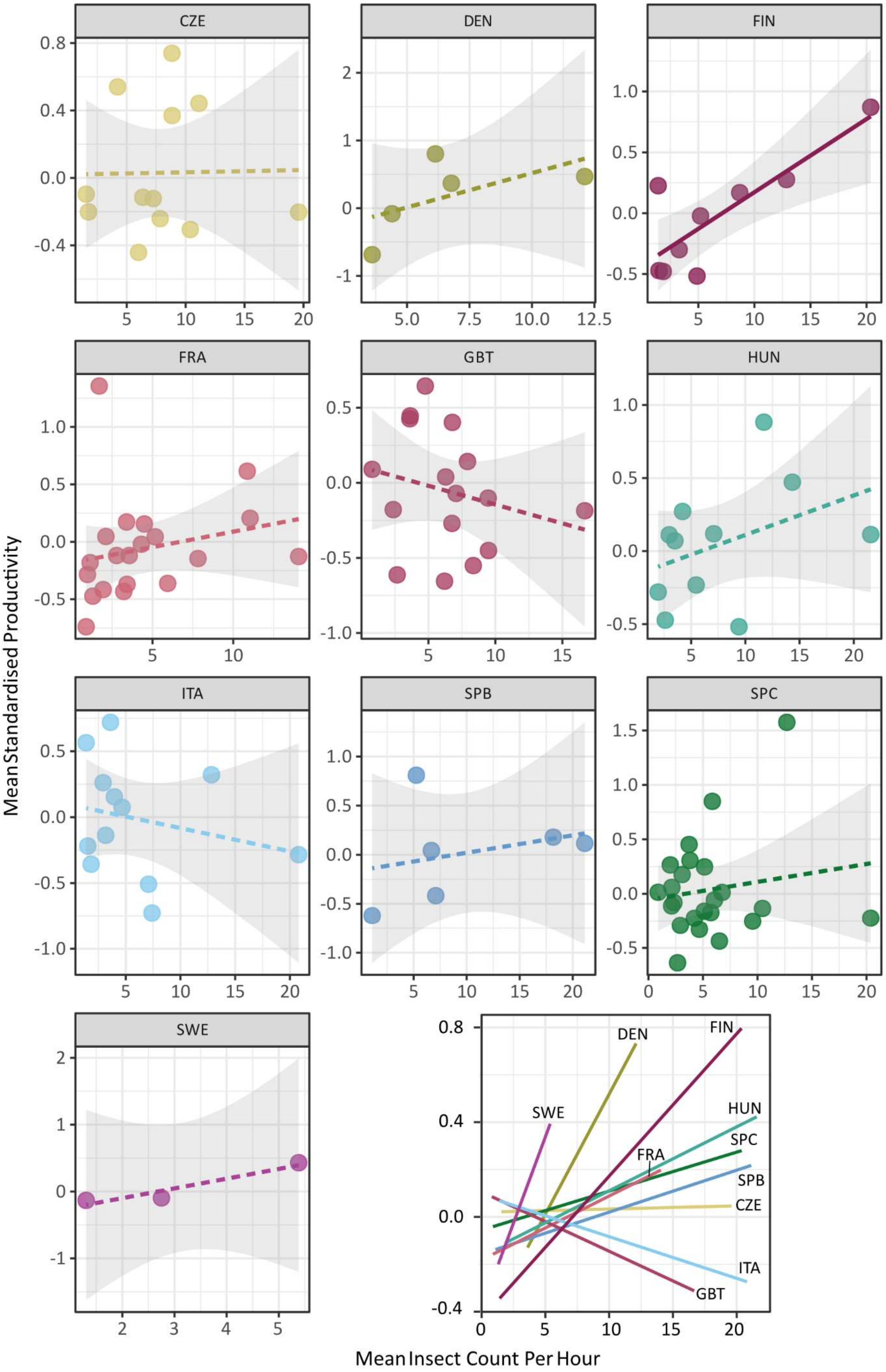


Figure 4.4: Relationship between the mean standardised productivity across landbird species (1998 – 2019) and the mean insect count per hour recorded on sticky traps in 2024 at Constant Effort Sites within different schemes. Grey shading indicates 95% Confidence Intervals. A combined plot shows fitted regression lines on the same scale.

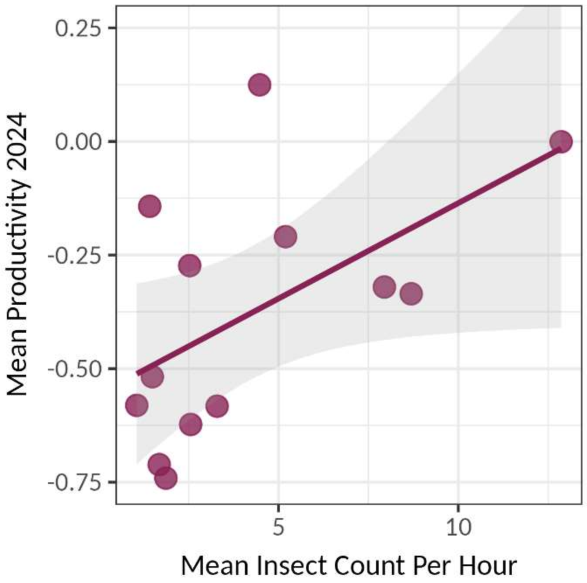


Figure 4.5: Relationship between the mean standardised productivity across 27 landbird species and the mean insect count per hour recorded on sticky traps in 2024 at 13 Constant Effort Sites in Finland. Grey shading indicates 95% Confidence Intervals.

The relationship between mean productivity and mean insect count per hour also varied between groups of landbirds with different migratory strategies. Mean productivity of species resident within Europe was significantly positively associated with mean insect count per hour, while mean productivity for arid-zone and humid-zone migrants was not significantly associated with insect counts (Table 4.5, Figure 4.6).

Table 4.5: Output from a linear model of mean standardised site-level productivity across a) 48 resident landbird species, b) 14 arid-zone migrants, and c) 18 humid-zone migrants, in relation to mean insect count per hour recorded on sticky traps at Constant Effort Sites across Europe, weighted by the inverse of the standard deviation of mean productivity. (Number of sites: a = 116, b = 81, c = 108; model R^2: a = 0.06, b = 0.01, c = 0.01).

a) *Residents*	Estimate	Standard Error	t value	p value
Intercept	-0.19	0.06	-3.11	<0.01
Mean Insect Count Per Hour	0.02	0.01	2.62	**0.01**
b) *Arid-zone migrants*	Estimate	Standard Error	t value	p value
Intercept	-0.26	0.13	-1.99	0.05
Mean Insect Count Per Hour	0.01	0.02	0.68	0.50
c) *Humid-zone migrants*	Estimate	Standard Error	t value	p value
Intercept	-0.14	0.09	-1.49	0.14
Mean Insect Count Per Hour	0.01	0.01	0.87	0.39

Overall, two species showed a significant positive relationship (slope 95% confidence intervals did not contain zero) between standardised productivity and mean insect count: one resident (Reed Bunting, REEBU; Figure 4.7) and one humid-zone migrant (Pied Flycatcher, PIEFL; Figure 4.8). None of the arid-zone species showed significant relationships (Figure 4.9). In addition, 23 out of the 32 resident species examined, 6 out of 11 humid-zone migrants examined and 5 out of 9 arid-zone migrants examined showed non-significant positive relationships (slope 95% confidence intervals contained zero; Table S4.4).

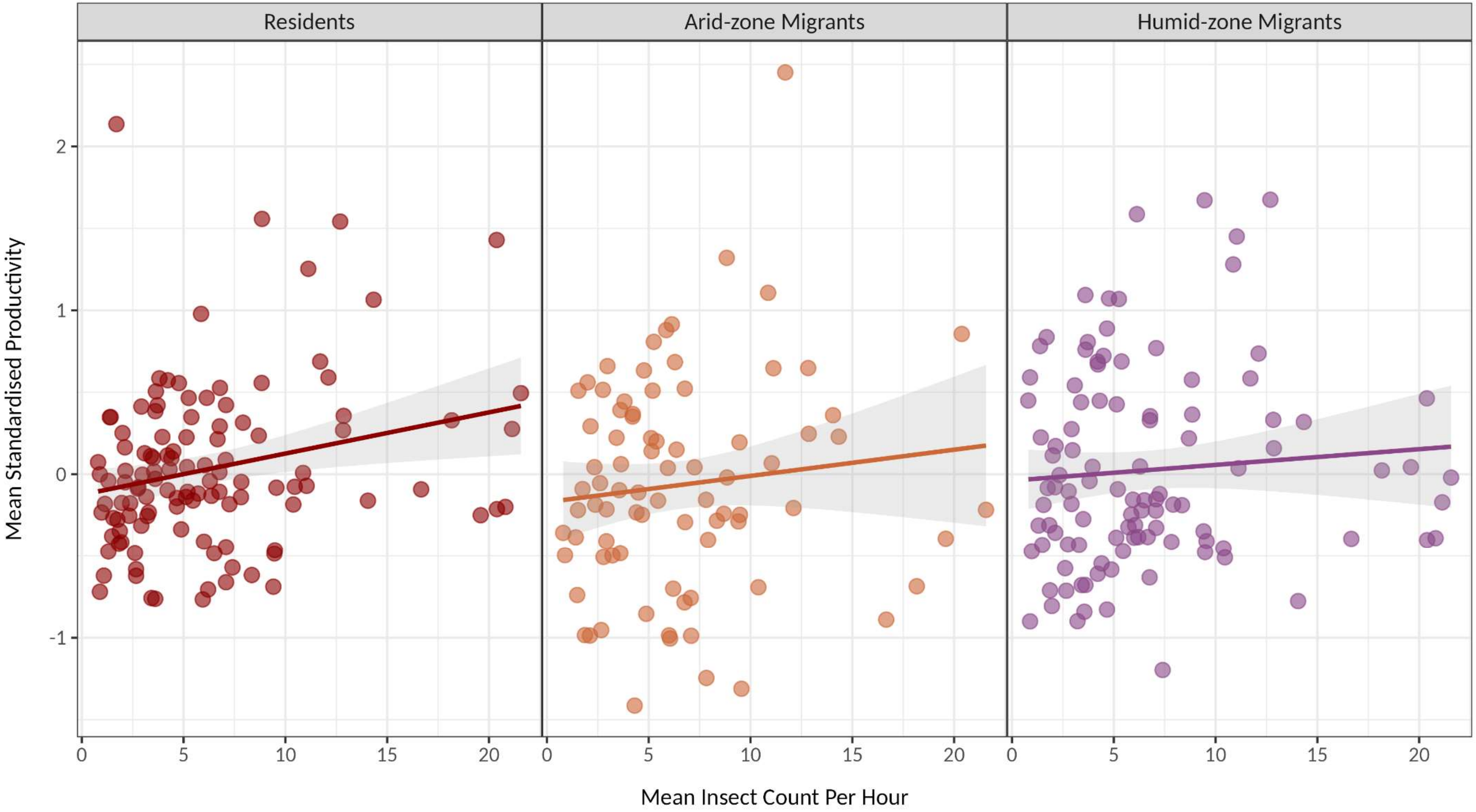


Figure 4.6: Relationship between the mean standardised productivity across 48 resident landbird species, 14 arid-zone migrants and 18 humid-zone migrants (1998 – 2019) and the mean insect count per hour recorded on sticky traps in 2024 at 116, 81, and 108 European Constant Effort Sites, respectively. Grey shading indicates 95% Confidence Intervals.

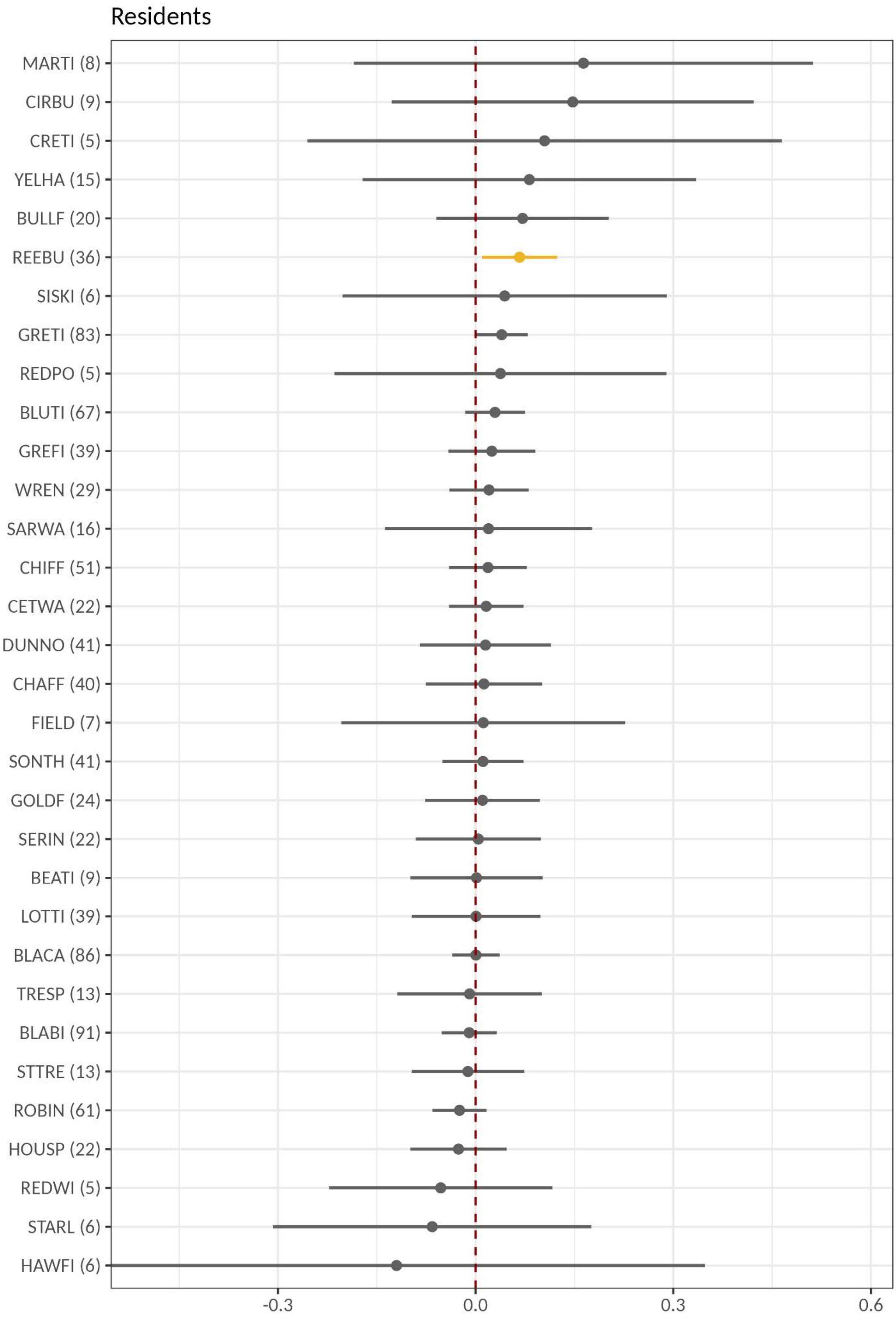


Figure 4.7: Slope estimates (points) and 95% Confidence Intervals (line intervals, CIs) from a linear model of mean standardised productivity (1998 – 2019) in relation to mean total insect count per hour recorded on sticky traps in 2024, and its interaction with species, for 32 landbird species that stay within Europe throughout the year. Number of sites for each species is shown in brackets after the 5 letter species code (see Table S4.1). Significant associations highlighted in orange (95% CIs do not overlap 0).

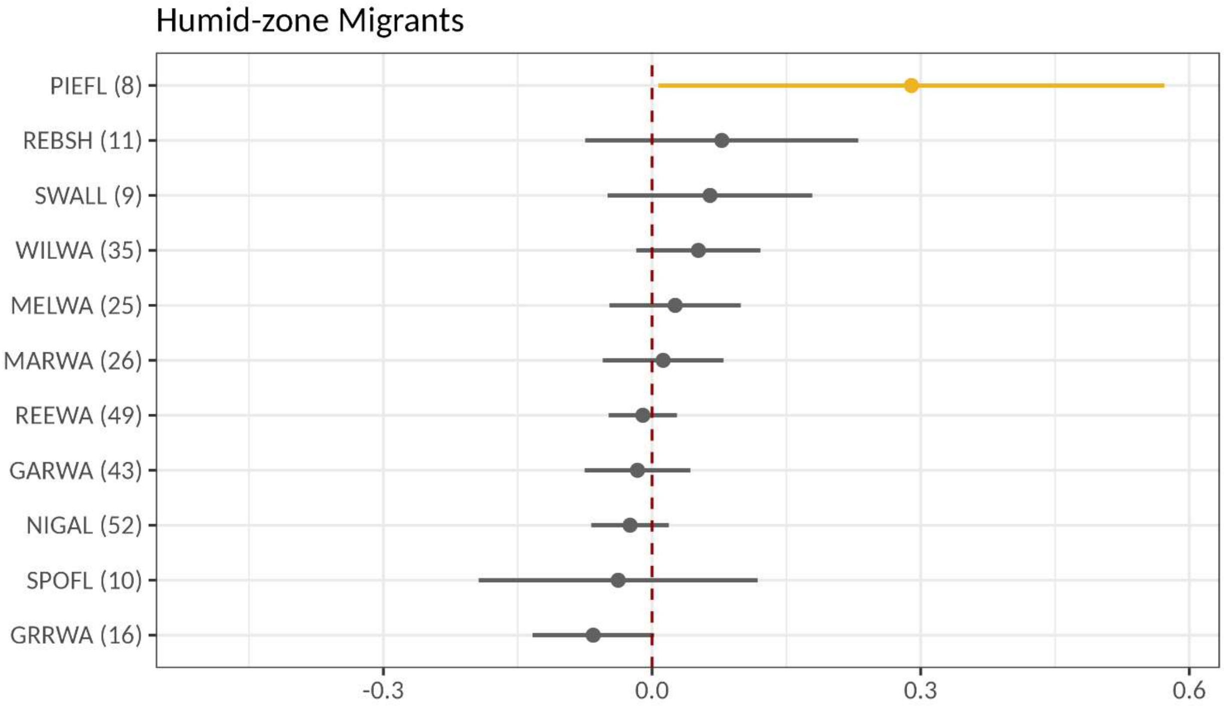


Figure 4.8: Slope estimates (points) and 95% Confidence Intervals (line intervals, CIs) from a linear model of mean standardised productivity (1998 – 2019) in relation to mean total insect count per hour recorded on sticky traps in 2024, and its interaction with species, for 11 humid-zone migrant landbird species. Number of sites for each species is shown in brackets after the 5 letter species code (see Table S4.1). Significant associations highlighted in orange (95% CIs do not overlap 0).

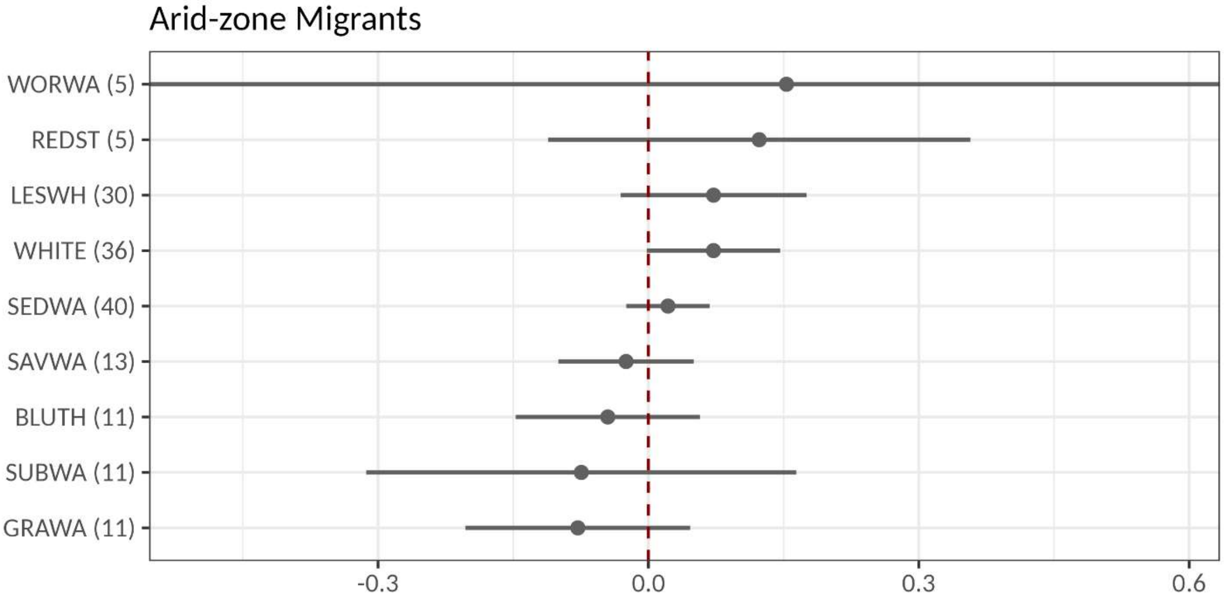


Figure 4.9: Slope estimates (points) and 95% Confidence Intervals (line intervals, CIs) from a linear model of mean standardised productivity (1998 – 2019) in relation to mean total insect count per hour recorded on sticky traps in 2024, and its interaction with species, for nine arid-zone migrant landbird species. Number of sites for each species is shown in brackets after the 5 letter species code (see Table S4.1). Significant associations highlighted in orange (95% CIs do not overlap 0).

Variation in Insect Counts

Within sites, insect counts varied across trapping occasions to differing degrees. The coefficient of variation (CV) of insect counts per hour for each site was significantly positively correlated with the mean insect count per hour (Pearson's cor = 0.17, *t* = 2.23, df = 174, *p* = 0.03), such that sites recording higher insect counts on average showed greater variation across trapping occasions. While sites with low mean insect counts showed consistently low counts, sites with high mean counts often had one or two very high counts, alongside medium and low counts (e.g. Figure 4.10; all schemes Figures S4.6 – S4.15). However, there were many sites with high mean counts that showed consistently high counts; hence the correlation between the CV and mean insect count was weak. Across schemes, there was no obvious phenological pattern to the temporal variation in insect counts over the trapping occasions, and so high and low counts could occur in any month throughout the sampling period (Figures S4.6 – S4.15).

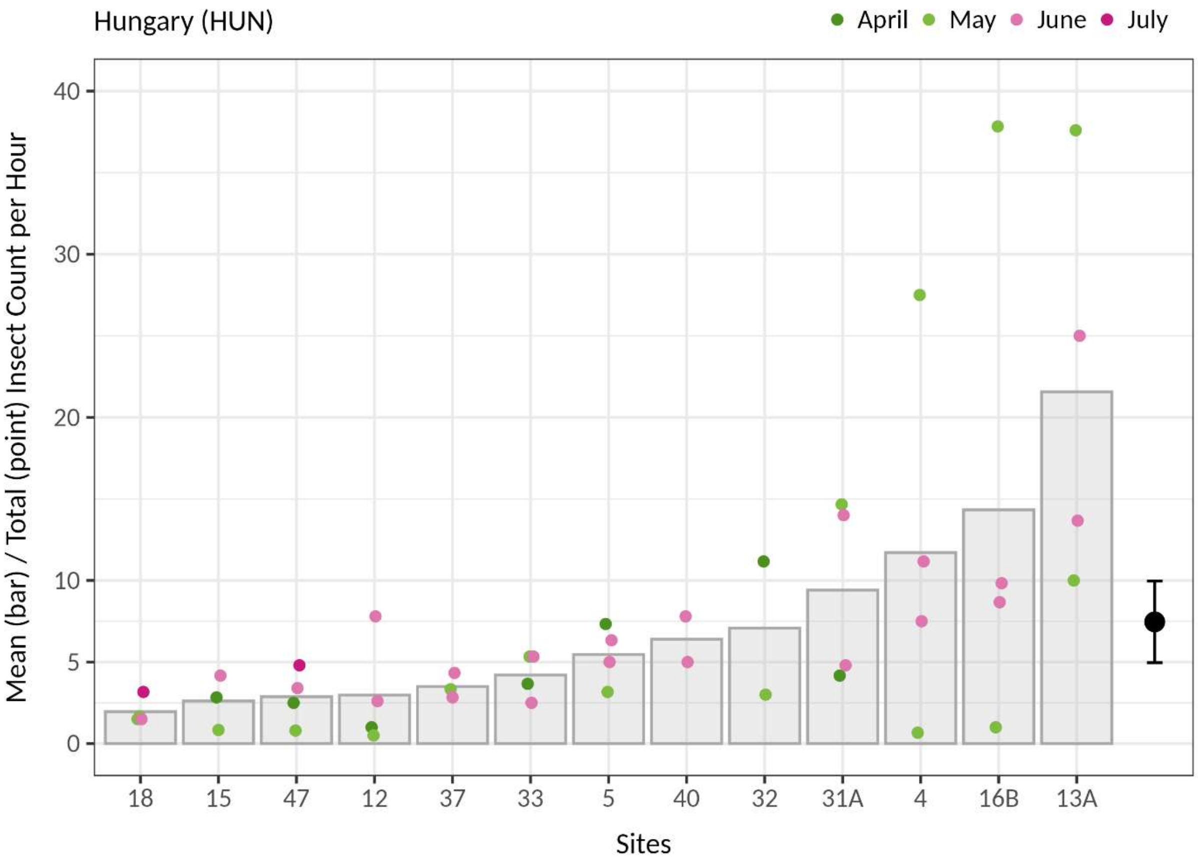


Figure 4.10: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 13 Constant Effort Sites in Hungary. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% Confidence Intervals) across all traps in Hungary is also shown in black.

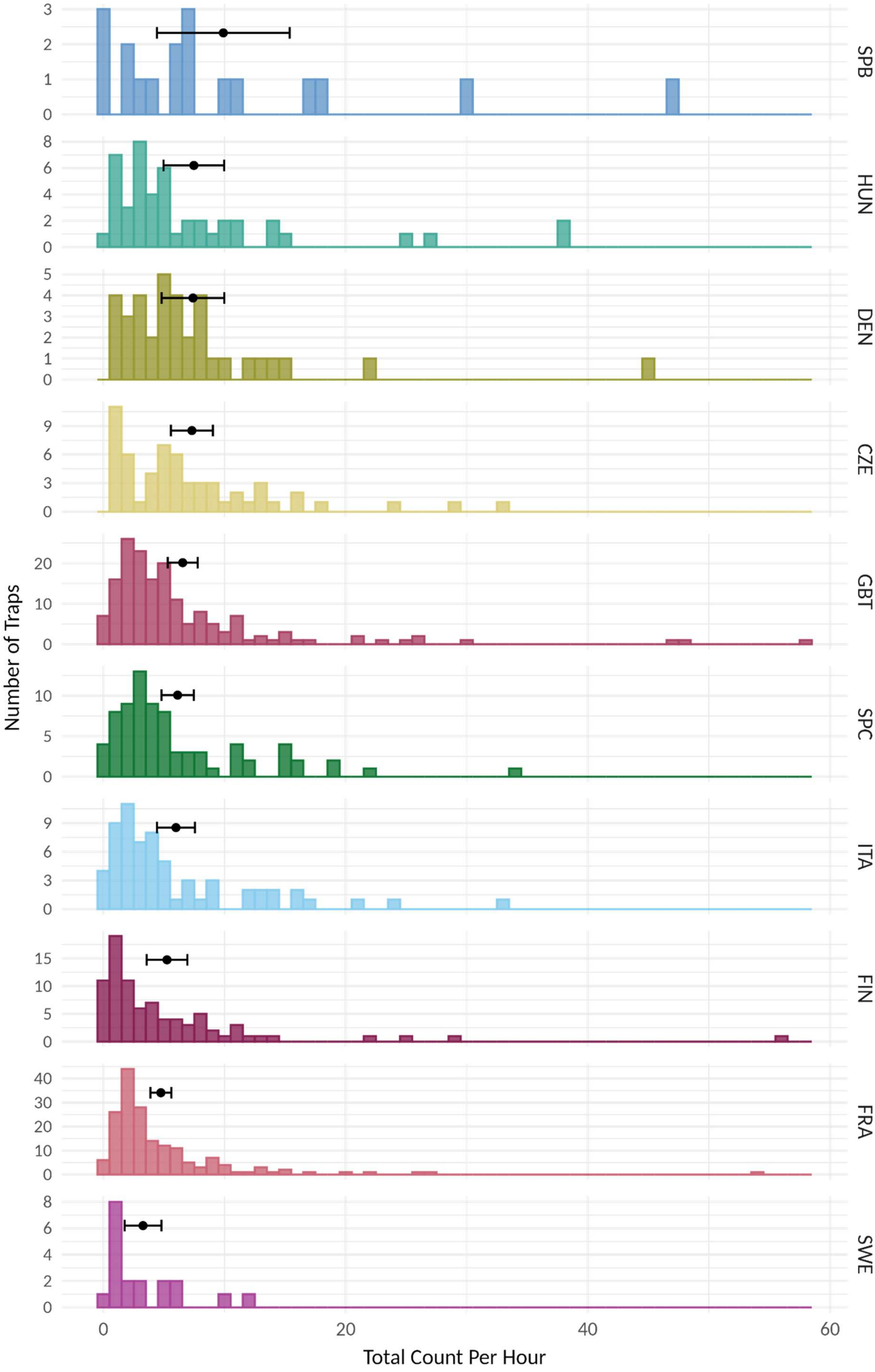


Figure 4.11: Frequency distributions of total insect count per hour across all sticky traps deployed in each Constant Effort Sites scheme in 2024. The mean (± 95% CIs) count per hour (point) across all traps is also shown for each scheme in black. Note the y-axis differs for each scheme.

We also detected broad-scale spatial variation between countries in insect counts, but there was no clear latitudinal structure to this (Figure 4.11). Mean insect count per hour across traps was highest in the Basque region of Spain, and lowest in Sweden. Both of these schemes had a limited sample size (six and three sites, respectively) and so insect counts may not be as representative as in the other schemes. For the intermediate schemes, the mean insect counts across traps were very similar, with the main differences being the frequency of high-count traps.

Landscape Characteristics and Insect Abundance

Mean insect count per hour did not significantly vary with the land system (LRT: $X^2 = 5.17$, df = 6, $p = 0.52$; Table 4.6, Figure 4.12) or land-use intensity (LRT: $X^2 = 2.90$, df = 2, $p = 0.23$; Table 4.7, Figure 4.13) within the 1 km landscape surrounding the site.

Table 4.6: Mean insect count per hour on sticky traps deployed at Constant Effort Sites within 1 km landscapes with different dominant land system categories. Estimated from a LMM with the log-transformed mean insect count per hour as the response variable, land system as a fixed effect and scheme as a random intercept, using the *emmeans* package. Estimates are provided on the response scale, and the 95% Confidence Levels (CL) are asymmetrical.

Land System	Emmean	Standard Error	df	Lower CL	Upper CL
Arable Cropland	4.91	0.60	55.33	3.83	6.28
Forest	3.89	0.57	57.69	2.89	5.22
Grassland	5.35	1.48	154.09	3.10	9.22
Mosaic	4.94	0.81	81.32	3.57	6.84
Settlement	4.08	0.63	87.58	3.00	5.56
Shrub	4.43	1.33	134.71	2.45	8.01
Wetland	5.62	0.81	72.97	4.22	7.49

Table 4.7: Mean insect count per hour on sticky traps deployed at Constant Effort Sites within 1 km landscapes with different dominant land-use intensities. Estimated from a LMM with the log-transformed mean insect count per hour as the response variable, land-use intensity as a fixed effect and scheme as a random intercept, using the *emmeans* package. Estimates are provided on the response scale, and the 95% Confidence Levels (CL) are asymmetrical.

Land-use Intensity	Emmean	Standard Error	df	Lower CL	Upper CL
Low	5.23	0.53	20.34	4.24	6.46
Medium	4.24	0.46	29.46	3.40	5.30
High	4.48	0.68	76.78	3.31	6.07

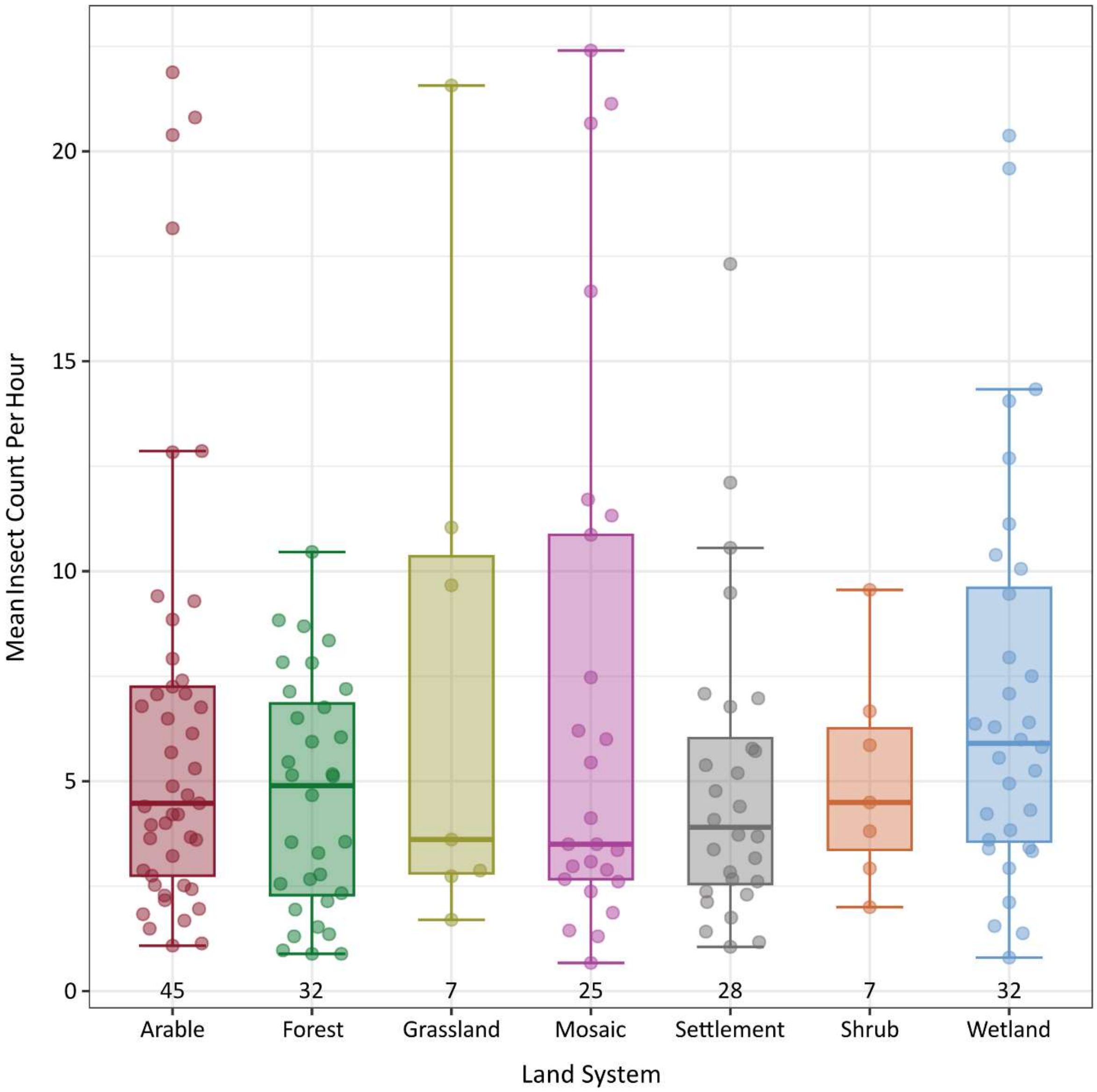


Figure 4.12: Boxplots of mean insect count per hour on sticky traps deployed in 2024 at Constant Effort Sites within 1 km landscapes dominated by different land system types. Each data point is a site and the number of sites in each land system category is provided at the base of each boxplot. Horizontal bars indicate medians, boxes indicate interquartile range, and whiskers indicate minimum and maximum values, with any outlying data points beyond those more than 1.5 times higher or lower than 1st and 3rd interquartile, respectively.

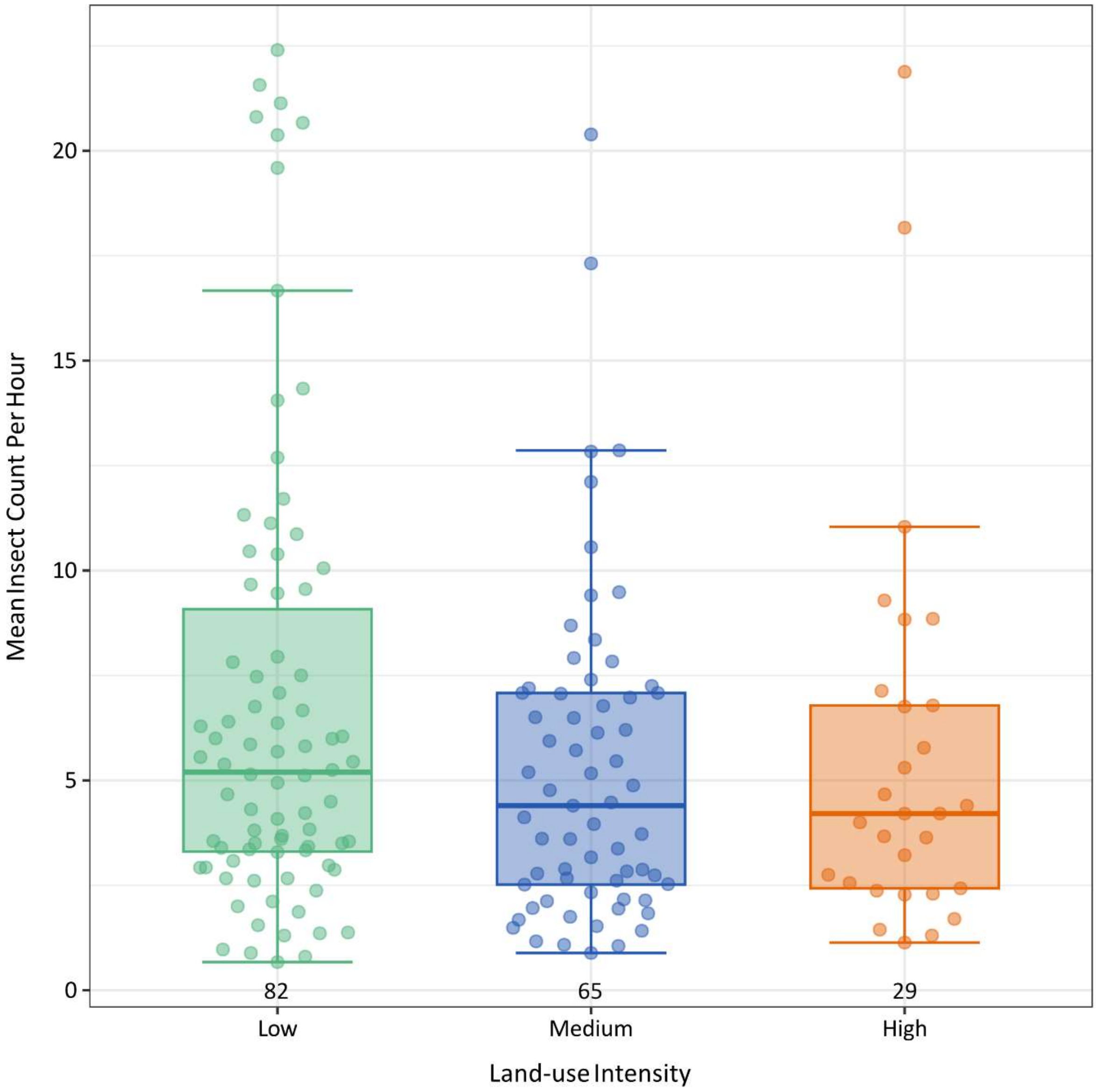


Figure 4.13: Boxplots of mean insect count per hour on sticky traps deployed in 2024 at Constant Effort Sites within 1 km landscapes dominated by different land-use intensities. Each data point is a site and the number of sites in each land-use intensity is provided at the base of each boxplot. Horizontal bars indicate medians, boxes indicate interquartile range, and whiskers indicate minimum and maximum values, with any outlying data points beyond those more than 1.5 times higher or lower than 1st and 3rd interquartile, respectively.

4.4. Discussion

With the help of a network of citizen scientists, we conducted a Pan-European study of site-level bird productivity and flying insect abundance, that was both large-scale and high-resolution. We found a positive relationship between insect abundance measured in 2024 and mean productivity across species and years at CE sites in Europe, with sites recording higher insect abundance tending to be those with higher mean productivity. For Finland, we also found a positive relationship between insect abundance and concurrent mean productivity measured at sites in 2024, suggesting that the relationship between insects and productivity is consistent across years. We further show that sites with low mean insect counts invariably recorded low counts across the breeding season, while sites with high mean insect counts recorded more variable counts, but these were still generally higher than those at ‘poor’ sites. We did not find that the observed spatial variation in insect abundance was related to the dominant land system or land-use intensity in the landscape surrounding sites.

The overall relationship between insect abundance and productivity was relatively weak: while high insect abundance was not observed at the lowest productivity sites, not all sites with high productivity recorded high insect abundance. Our capacity to detect associations between insects and productivity was likely influenced by whether sampling captured periods of high insect activity at the more variable ‘good’ sites, and so we may have missed high insect count peaks at some high productivity sites. Insect emergences can be localised in space as well as time, and so the lack of spatial replication of trapping within sites is likely to have introduced some random noise into the measurement of insect abundance and limited the representation of the wider site, especially given the short time period of each trapping occasion. Furthermore, while productivity varies relatively little between years (Morrison et al., 2021), insect numbers can vary considerably due to weather conditions (Duchenne and Fontaine, 2024; Fourcade et al., 2017), and so the strength of the relationship between productivity and insect abundance could also vary between years. Therefore, the single-year snapshot of insect data collected in this study could have weakened the observed relationship, and further years of data would be valuable to improve our understanding.

The observed patterns could also suggest that additional factors may play a role in driving productivity in conjunction with food availability. For example, it is possible that the poorest productivity sites have a combination of low insect food and other limiting conditions, such as high nest predation rates, while some sites are able to achieve relatively high productivity despite a lack of food if these other conditions are favourable (Zanette et al., 2003). Importantly, greater insect food availability allows some sites to achieve higher productivity despite other limiting factors. For example, increased food may allow parents to increase reproductive investment and raise larger or multiple broods (O’Brien and Dawson, 2013; Ruffino et al., 2014), potentially counteracting negative impacts of higher predation rates on productivity. In addition, an increase in food abundance may reduce the time parents spend away from the nest foraging, therefore increasing time available for nest guarding and thus reducing the probability of nest predation (Duncan Rastogi et al., 2006).

The association between insect abundance and productivity varied across the individual schemes. Despite having a relatively small number of sites, the most robust association between insect abundance and productivity was observed in Finland. It is unclear why insect abundance did not map onto spatial variation in productivity in the other schemes with larger samples of sites, not appearing to relate to the magnitude or variability of insect counts recorded in these schemes compared to Finland. A possible explanation could be the comparatively high latitude of the Finnish sites, if insect abundance is more strongly limiting for productivity at more northerly latitudes where the breeding season is shorter, while other factors, such as the availability of nesting sites or predation rates (Newton and Brockie, 1998), may be more important elsewhere. In addition, productivity values at lower latitude sites may be less representative of site-level productivity than at higher latitudes, because captures of transient migratory juveniles at the end of the CES season are more likely as they move their way down through Europe, potentially weakening the observed relationship with local insect abundance.

Regardless of the exact mechanisms driving the patterns observed, these findings suggest that managing sites to increase insect prey availability could help boost productivity rates of European landbirds. However, the success of these efforts may vary between species, because there was some variation in the association between insect abundance and productivity across the species community. Mean productivity across resident species was significantly associated with insect abundance, but we did not detect the same overall relationship in migratory species. This may result from the increased timing constraints on the breeding period of migratory species compared to residents (Both and Visser, 2001; Hedenström, 2007; Knudsen et al., 2011), making them less able to take advantage of the peaks in insect abundance at good-quality breeding sites for maximising reproductive success.

However, we did find that one humid-zone migrant, the European Pied Flycatcher (*Ficedula hypoleuca*), showed a significant positive relationship between insect abundance and productivity. This may reflect the fact that the diet of this species is mainly composed of flying insects (Cramp, 2006), which made up the majority of insects caught by sticky traps, although, the productivity of another flycatcher species (Spotted Flycatcher, *Muscicapa striata*) did not show a similar positive response. The only other species showing a significant positive relationship was the Reed Bunting (*Emberiza schoeniclus*), which do feed insects to nestlings, but it is not clear why this species and not others would show this relationship. There was a large degree of uncertainty around many of the individual species' relationships, likely a result of limited sample sizes and considerable noise in the insect data, limiting our power to detect these effects. It is possible that the two significant species relationships resulted from chance alone, due to the large number of species (n = 52) considered in the model relative to the number of data points (n = 117). It is therefore difficult to draw any species-specific conclusions pertaining to diet or other characteristics. The fact that many of the species considered here primarily feed on ground- or soil-dwelling invertebrates, which are not sampled by sticky traps, is likely to have weakened the overall relationship between insect abundance and mean productivity, depending on the extent to which abundances of different invertebrates are correlated. Future work could sample additional invertebrate groups to determine relationships with productivity, for example pitfall traps (e.g. Ndithia et al., 2017) or caterpillar frass traps (e.g. Smith et al., 2011), but these sampling techniques would require additional processing by participants, which would likely limit the scale over which this could be implemented.

Our capacity to manage insect prey availability to boost productivity rates ultimately depends on our ability to identify the conditions associated with high insect abundance. We did not find that insect abundance varied with the land system or land-use intensity in the local landscapes surrounding sites. This contrasts with several other studies demonstrating reduced insect abundance or biomass with increased urbanisation (De Wolf et al ., 2025; Piano et al., 2020; Svenningsen et al., 2022; Uhler et al., 2021). While our sample of sites covered a range of habitats, very few were located in high-intensity urban environments (three sites), and the immediate habitat in which insects were sampled at these sites still consisted of semi-natural vegetation suitable for catching birds. In fact, most of our sites were in low-intensity landscapes across the land system types, so we may have lacked the power to detect variation along a land-use intensity gradient. In addition, while the effects of urbanisation have been consistently shown, responses of insect populations to agricultural intensity have been relatively mixed (Benton et al., 2002; Svenningsen et al., 2022), and so our groupings of intensity categories across systems may have been too simplistic to pick up more complex effects of specific land-use types. In addition, with a single trapping location per site, the insect abundance may not have been fully representative of the wider site and surrounding landscape, therefore limiting our ability to detect the effects of larger-scale processes associated with the landscape variables explored.

It is also possible that our measurement of insect abundance and not biomass could have hidden responses in the insect community. For example, a study on Diptera found negative impacts of increased agricultural intensification on biomass but not abundance, which the authors hypothesised to result from community turnover towards smaller-bodied species (Powell et al., 2024). Newly published research identifies different responses in small- and large-bodied insects to agricultural intensity at different scales; small (<4 mm) insect abundance was best explained by factors operating at the field level, whereas that of larger insects (>4 mm) was best explained by soil type and landscape characteristics (Jansma et al., 2025). Most of the insects we trapped were smaller than 5 mm (84% insects on subsample of 619 traps), which in combination with these findings, may explain why we did not detect landscape effects.

Information on site-level habitat characteristics was not available for this study but may be an important driver of variation in insect abundance across our sites, and warrants further investigation, especially where this can directly inform management. For example, within-field level variation in herbaceous vegetation structure produced by different mowing practices has been shown to influence insect abundance, which increases with structural diversity (Crist et al., 2006). In addition, sward structure in grasslands can also influence prey accessibility for foraging insectivores (Kleijn et al., 2010; Vickery et al., 2001). Meanwhile, a factor that might be important in more urban settings is the pervasiveness of non-native plants, which cannot support large populations of native herbivorous insects (Tallamy and Shriver, 2021), thereby reducing prey availability for insectivores, with negative consequences for their reproductive success (Narango et al., 2018). Future work should look to explore the effects of local-scale drivers of insect populations at breeding sites and identify management actions which could support and enhance both insects and landbirds.

Conclusions

We show that sticky traps can be an effective method of collecting high resolution insect abundance data at large-scales that is representative of trophic interactions. Given the various sources of noise in the insect abundance data, it is compelling that we detected a positive relationship with bird productivity, and so insect abundance does seem to be a good metric for quantifying the quality of breeding sites. These findings suggest that insect declines across Europe (Pilotto et al., 2020) may be detrimental to productivity rates in landbirds, but also that managing insect prey availability could be a route to help boost those rates. We don’t yet know what is driving this variation in insect abundance, and so further work is needed to explore effects of site-level characteristics. We suggest that if local factors are more important than landscape factors for insect abundance, there is a possibility for any landscape to host sites with high or low insect abundance, providing wide opportunities to increase insect prey availability through site-level management to boost bird productivity.

References

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Benton, T.G., Bryant, D.M., Cole, L., Crick, H.Q.P., 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology 39, 673–687. https://doi.org/10.1046/j.1365-2664.2002.00745.x

Both, C., Visser, M.E., 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411, 296–298. https://doi.org/10.1038/35077063

Bowler, D.E., Heldbjerg, H., Fox, A.D., Jong, M. de, Böhning-Gaese, K., 2019. Long-term declines of European insectivorous bird populations and potential causes. Conservation Biology 33, 1120–1130. https://doi.org/10.1111/cobi.13307

Brickle, N.W., Harper, D.G.C., Aebischer, N.J., Cockayne, S.H., 2000. Effects of agricultural intensification on the breeding success of corn buntings Miliaria calandra. Journal of Applied Ecology 37, 742–755. https://doi.org/10.1046/j.1365-2664.2000.00542.x

Cramp, S., 2006. The birds of the western Palearctic interactive. Oxford University Press and BirdGuides, Oxford, U.K.

Crist, T.O., Pradhan-Devare, S.V., Summerville, K.S., 2006. Spatial variation in insect community and species responses to habitat loss and plant community composition. Oecologia 147, 510–521. https://doi.org/10.1007/s00442-005-0275-1

De Wolf, K., Verstraelen, N., Rommel, H., Vantieghem, P., Vanthournout, B., Bonte, D., 2025. Urbanization imposes declines in flying insect biomass through the loss of large-bodied species. Insect Conservation and Diversity 18, 1175–1183. https://doi.org/10.1111/icad.12859

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401–406. https://doi.org/10.1126/science.1251817

Dou, Y., Cosentino, F., Malek, Z., Maiorano, L., Thuiller, W., Verburg, P.H., 2021. A new European land systems representation accounting for landscape characteristics. Landscape Ecol 36, 2215–2234. https://doi.org/10.1007/s10980-021-01227-5

Duchenne, F., Fontaine, C., 2024. Weather explains inter-annual variability, but not the temporal decline, in insect biomass. Insect Conservation and Diversity 17, 932–937. https://doi.org/10.1111/icad.12769

Duncan Rastogi, A., Zanette, L., Clinchy, M., 2006. Food availability affects diurnal nest predation and adult antipredator behaviour in song sparrows, *Melospiza melodia*. Animal Behaviour 72, 933–940. https://doi.org/10.1016/j.anbehav.2006.03.006

Evans, L.C., Burgess, M.D., Potts, S.G., Kunin, W.E., Oliver, T.H., 2024. Population links between an insectivorous bird and moths disentangled through national-scale monitoring data. Ecology Letters 27, e14362. https://doi.org/10.1111/ele.14362

Fourcade, Y., Ranius, T., Öckinger, E., 2017. Temperature drives abundance fluctuations, but spatial dynamics is constrained by landscape configuration: Implications for climate-driven range shift in a butterfly. Journal of Animal Ecology 86, 1339–1351. https://doi.org/10.1111/1365-2656.12740

Garrett, D.R., Pelletier, F., Garant, D., Bélisle, M., 2022. Combined influence of food availability and agricultural intensification on a declining aerial insectivore. Ecological Monographs 92, e1518. https://doi.org/10.1002/ecm.1518

Grames, E.M., Montgomery, G.A., Youngflesh, C., Tingley, M.W., Elphick, C.S., 2023. The effect of insect food availability on songbird reproductive success and chick body condition: Evidence from a systematic review and meta-analysis. Ecology Letters n/a, 1–16. https://doi.org/10.1111/ele.14178

Grüebler, M.U., Müller, M., Michel, V.T., Perrig, M., Keil, H., Naef-Daenzer, B., Korner-Nievergelt, F., 2018. Brood provisioning and reproductive benefits in relation to habitat quality: a food supplementation experiment. Animal Behaviour 141, 45–55. https://doi.org/10.1016/j.anbehav.2018.05.009

Hallmann, C.A., Foppen, R.P.B., van Turnhout, C.A.M., de Kroon, H., Jongejans, E., 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature 511, 341–343. https://doi.org/10.1038/nature13531

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., De Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12, e0185809. https://doi.org/10.1371/journal.pone.0185809

Hart, J.D., Milsom, T.P., Fisher, G., Wilkins, V., Moreby, S.J., Murray, A.W.A., Robertson, P.A., 2006. The Relationship between Yellowhammer Breeding Performance, Arthropod Abundance and Insecticide Applications on Arable Farmland. Journal of Applied Ecology 43, 81–91.

Hedenström, A., 2007. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Philosophical Transactions of the Royal Society B: Biological Sciences 363, 287–299. https://doi.org/10.1098/rstb.2007.2140

Jansma, A.P., Hoekstra, N.J., van den Broek, B., de Kroon, H., van Eekeren, N., 2025. Linking key performance indicators to insect abundance in agricultural grasslands: Effects of plant diversity, farming intensity, soil type and landscape characteristics. NJAS: Impact in Agricultural and Life Sciences 97, 2529234. https://doi.org/10.1080/27685241.2025.2529234

Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S.E., Couvet, D., 2007. Climate envelope, life history traits and the resilience of birds facing global change. Global Change Biology 13, 1672–1684. https://doi.org/10.1111/j.1365-2486.2007.01386.x

Jones, T.M., Ward, M.P., Benson, T.J., Brawn, J.D., 2017. Variation in nestling body condition and wing development predict cause-specific mortality in fledgling dickcissels. Journal of Avian Biology 48, 439–447. https://doi.org/10.1111/jav.01143

Kent, C.M., Peele, A.M., Sherry, T.W., 2019. Comparing four simple, inexpensive methods for sampling forest arthropod communities. Journal of Field Ornithology 90, 57–69. https://doi.org/10.1111/jofo.12278

Kleijn, D., Schekkerman, H., Dimmers, W.J., Van Kats, R.J.M., Melman, D., Teunissen, W.A., 2010. Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits Limosa l. limosa in the Netherlands. Ibis 152, 475–486. https://doi.org/10.1111/j.1474-919X.2010.01025.x

Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W.J., Bach, L.A., Coppack, T., Ergon, T., Gienapp, P., Gill, J.A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P.P., Møller, A.P., Nilsson, A.L.K., Péron, G., Ranta, E., Rubolini, D., Sparks, T.H., Spina, F., Studds, C.E., Sæther, S.A., Tryjanowski, P., Stenseth, N.Chr., 2011. Challenging claims in the study of migratory birds and climate change. Biological Reviews 86, 928–946. https://doi.org/10.1111/j.1469-185X.2011.00179.x

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82, 1–26. https://doi.org/10.18637/jss.v082.i13

Lenth, R.V., Banfai, B., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Piaskowski, J., Riebl, H., Singmann, H., 2024. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software 6, 3139. https://doi.org/10.21105/joss.03139

Mallord, J.W., Dolman, P.M., Brown, A., Sutherland, W.J., 2007. Quantifying density dependence in a bird population using human disturbance. Oecologia 153, 49–56. https://doi.org/10.1007/s00442-007-0716-0

Martay, B., Leech, D.I., Shortall, C.R., Bell, J.R., Thackeray, S.J., Hemming, D.L., Pearce-Higgins, J.W., 2023. Aerial insect biomass, but not phenological mismatch, is associated with chick survival of an insectivorous bird. Ibis 165, 790–807. https://doi.org/10.1111/ibi.13190

Martin, T.E., 1987. Food as a Limit on Breeding Birds: A Life-History Perspective. Annual Review of Ecology and Systematics 18, 453–487.

Møller, A.P., 2019. Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. Ecology and Evolution 9, 6581–6587. https://doi.org/10.1002/ece3.5236

Morris, A.J., Wilson, J.D., Whittingham, M.J., Bradbury, R.B., 2005. Indirect effects of pesticides on breeding yellowhammer (*Emberiza citrinella*). Agriculture, Ecosystems & Environment 106, 1–16. https://doi.org/10.1016/j.agee.2004.07.016

Morrison, C.A., Butler, S.J., Clark, J.A., Arizaga, J., Baltà, O., Cepák, J., Nebot, A.L., Piha, M., Thorup, K., Wenninger, T., Robinson, R.A., Gill, J.A., 2022. Demographic variation in space and time: implications for conservation targeting. Royal Society Open Science 9, 211671. https://doi.org/10.1098/rsos.211671

Morrison, C.A., Butler, S.J., Robinson, R.A., Clark, J.A., Arizaga, J., Aunins, A., Baltà, O., Cepák, J., Chodkiewicz, T., Escandell, V., Foppen, R.P.B., Gregory, R.D., Husby, M., Jiguet, F., Kålås, J.A., Lehikoinen, A., Lindström, Å., Moshøj, C.M., Nagy, K., Nebot, A.L., Piha, M., Reif, J., Sattler, T., Škorpilová, J., Szép, T., Teufelbauer, N., Thorup, K., van Turnhout, C., Wenninger, T., Gill, J.A., 2021. Covariation in population trends and demography reveals targets for conservation action. Proceedings of the Royal Society B: Biological Sciences 288, 20202955. https://doi.org/10.1098/rspb.2020.2955

Narango, D.L., Tallamy, D.W., Marra, P.P., 2018. Nonnative plants reduce population growth of an insectivorous bird. Proc. Natl. Acad. Sci. U.S.A. 115, 11549–11554. https://doi.org/10.1073/pnas.1809259115

Nash, L.N., Zorzetti, L.W., Antiqueira, P.A.P., Carbone, C., Romero, G.Q., Kratina, P., 2023. Latitudinal patterns of aquatic insect emergence driven by climate. Global Ecology and Biogeography 32, 1323–1335. https://doi.org/10.1111/geb.13700

Ndithia, H.K., Matson, K.D., Versteegh, M.A., Muchai, M., Tieleman, B.I., 2017. Year-round breeding equatorial Larks from three climatically-distinct populations do not use rainfall, temperature or invertebrate biomass to time reproduction. PLoS ONE 12, e0175275. https://doi.org/10.1371/journal.pone.0175275

Newton, I., 2002. The Role of Food in Limiting Bird Numbers. Ardea 38–90, 11–30. https://doi.org/10.5253/arde.v68.p11

Newton, I., Brockie, K., 1998. Population Limitation in Birds.

O'Brien, E.L., Dawson, R.D., 2013. Experimental dissociation of individual quality, food and timing of breeding effects on double-brooding in a migratory songbird. Oecologia 172, 689–699. https://doi.org/10.1007/s00442-012-2544-0

Peach, W.J., Mallord, J.W., Ockendon, N., Orsman, C.J., Haines, W.G., 2015. Invertebrate prey availability limits reproductive success but not breeding population size in suburban House Sparrows Passer domesticus. Ibis 157, 601–613. https://doi.org/10.1111/ibi.12264

Pearce-Higgins, J.W., Morris, R.K.A., 2022. Declines in invertebrates and birds – could they be linked by climate change? Bird Study 69, 59–71. https://doi.org/10.1080/00063657.2022.2157373

Piano, E., Souffreau, C., Merckx, T., Baardsen, L.F., Backeljau, T., Bonte, D., Brans, K.I., Cours, M., Dahirel, M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J.M.T., Fontaneto, D., Gianuca, A.T., Govaert, L., Hanashiro, F.T.T., Higuti, J., Lens, L., Martens, K., Matheve, H., Matthysen, E., Pinseel, E., Sablon, R., Schön, I., Stoks, R., Van Doninck, K., Van Dyck, H., Vanormelingen, P., Van Wichelen, J., Vyverman, W., De Meester, L., Hendrickx, F., 2020. Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. Global Change Biology 26, 1196–1211. https://doi.org/10.1111/gcb.14934

Pilotto, F., Kühn, I., Adrian, R., Alber, R., Alignier, A., Andrews, C., Bäck, J., Barbaro, L., Beaumont, D., Beenaerts, N., Benham, S., Boukal, D.S., Bretagnolle, V., Camatti, E., Canullo, R., Cardoso, P.G., Ens, B.J., Everaert, G., Evtimova, V., Feuchtmayr, H., García-González, R., Gómez García, D., Grandin, U., Gutowski, J.M., Hadar, L., Halada, L., Halassy, M., Hummel, H., Huttunen, K.-L., Jaroszewicz, B., Jensen, T.C., Kalivoda, H., Schmidt, I.K., Kröncke, I., Leinonen, R., Martinho, F., Meesenburg, H., Meyer, J., Minerbi, S., Monteith, D., Nikolov, B.P., Oro, D., Ozoliņš, D., Padedda, B.M., Pallett, D., Pansera, M., Pardal, M.Â., Petriccione, B., Pipan, T., Pöyry, J., Schäfer, S.M., Schaub, M., Schneider, S.C., Skuja, A., Soetaert, K., Spriņģe, G., Stanchev, R., Stockan, J.A., Stoll, S., Sundqvist, L., Thimonier, A., Van Hoey, G., Van Ryckegem, G., Visser, M.E., Vorhauser, S., Haase, P., 2020. Meta-analysis of multidecadal biodiversity trends in Europe. Nat Commun 11, 3486. https://doi.org/10.1038/s41467-020-17171-y

Powell, K.E., Garrett, D., Roy, D.B., Oliver, T.H., Larrivée, M., Bélisle, M., 2024. Complex temporal trends in biomass and abundance of Diptera communities driven by the impact of agricultural intensity. Insect Conservation and Diversity 17, 1072–1083. https://doi.org/10.1111/icad.12770

R Core Team, 2025. R: A Language and Environment for Statistical Computing.

Ruffino, L., Salo, P., Koivisto, E., Banks, P.B., Korpimäki, E., 2014. Reproductive responses of birds to experimental food supplementation: a meta-analysis. Front Zool 11, 1–13. https://doi.org/10.1186/s12983-014-0080-y

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Sanz, J.J., Moreno, J., 1995. Experimentally induced clutch size enlargements affect reproductive success in the Pied Flycatcher. Oecologia 103, 358–364. https://doi.org/10.1007/BF00328625

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D.J., Hartenstein, V., Eliceiri, K., Tomancak, P., Cardona, A., 2012. Fiji: an open-source platform for biological-image analysis. Nat Methods 9, 676–682. https://doi.org/10.1038/nmeth.2019

Seress, G., Hammer, T., Bókony, V., Vincze, E., Preiszner, B., Pipoly, I., Sinkovics, C., Evans, K.L., Liker, A., 2018. Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. Ecological Applications 28, 1143–1156. https://doi.org/10.1002/eap.1730

Shutt, J.D., Bolton, M., Cabello, I.B., Burgess, M.D., Phillimore, A.B., 2018. The effects of woodland habitat and biogeography on blue tit Cyanistes caeruleus territory occupancy and productivity along a 220 km transect. Ecography 41, 1967–1978. https://doi.org/10.1111/ecog.03573

Sinclair, J.S., Buchner, D., Gessner, M.O., Müller, J., Pauls, S.U., Stoll, S., Welti, E.A.R., Bässler, C., Buse, J., Dziock, F., Enss, J., Hörren, T., Künast, R., Li, Y., Marten, A., Morkel, C., Richter, R., Seibold, S., Sorg, M., Twietmeyer, S., Weis, D., Weisser, W., Wiggering, B., Wilmking, M., Zotz, G., Frenzel, M., Leese, F., Haase, P., 2025. Effects of land cover and protected areas on flying insect diversity. Conservation Biology 39, e14425. https://doi.org/10.1111/cobi.14425

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, 920–932. https://doi.org/10.1111/j.1365-2664.2007.01339.x

Smith, K.W., Smith, L., Charman, E., Briggs, K., Burgess, M., Dennis, C., Harding, M., Isherwood, C., Isherwood, I., Mallord, J., 2011. Large-scale variation in the temporal patterns of the frass fall of defoliating caterpillars in oak woodlands in Britain: implications for nesting woodland birds. Bird Study 58, 506–511. https://doi.org/10.1080/00063657.2011.616186

Svenningsen, C.S., Bowler, D.E., Hecker, S., Bladt, J., Grescho, V., van Dam, N.M., Dauber, J., Eichenberg, D., Ejrnæs, R., Fløjgaard, C., Frenzel, M., Frøslev, T.G., Hansen, A.J., Heilmann-Clausen, J., Huang, Y., Larsen, J.C., Menger, J., Nayan, N.L.B.M., Pedersen, L.B., Richter, A., Dunn, R.R., Tøttrup, A.P., Bonn, A., 2022. Flying insect biomass is negatively associated with urban cover in surrounding landscapes. Diversity and Distributions 28, 1242–1254. https://doi.org/10.1111/ddi.13532

Tallamy, D.W., Shriver, W.G., 2021. Are declines in insects and insectivorous birds related? Ornithological Applications 123, duaa059. https://doi.org/10.1093/ornithapp/duaa059

Uhler, J., Redlich, S., Zhang, J., Hothorn, T., Tobisch, C., Ewald, J., Thorn, S., Seibold, S., Mitesser, O., Morinière, J., Bozicevic, V., Benjamin, C.S., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Riebl, R., Rojas-Botero, S., Rummler, T., Uphus, L., Schmidt, S., Steffan-Dewenter, I., Müller, J., 2021. Relationship of insect biomass and richness with land use along a climate gradient. Nat Commun 12, 5946. https://doi.org/10.1038/s41467-021-26181-3

Vickery, J. a., Tallowin, J. r., Feber, R. e., Asteraki, E. j., Atkinson, P. w., Fuller, R. j., Brown, V. k., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology 38, 647–664. https://doi.org/10.1046/j.1365-2664.2001.00626.x

Wagner, D.L., 2020. Insect Declines in the Anthropocene. Annual Review of Entomology 65, 457–480. https://doi.org/10.1146/annurev-ento-011019-025151

Zanette, L., Smith, J.N.M., Oort, H.V., Clinchy, M., 2003. Synergistic effects of food and predators on annual reproductive success in song sparrows. Proc. R. Soc. Lond. B 270, 799–803. https://doi.org/10.1098/rspb.2002.2311

Chapter 4 Supplementary Material

Table S4.1: 80 landbird species for which average productivity across sampling years falling between 1998 – 2019 was measured at Constant Effort Sites (CESs) in Europe. Listed for each is their migratory status, number of sites for which average productivity was measured, and, if greater than five sites, five-letter species code used in species plots.

English name	Latin name	Migratory Status	# Sites	Code
Eurasian Blackbird	*Turdus merula*	Resident	91	BLABI
Eurasian Blackcap	*Sylvia atricapilla*	Resident	86	BLACA
Great Tit	*Parus major*	Resident	83	GRETI
Eurasian Blue Tit	*Cyanistes caeruleus*	Resident	67	BLUTI
European Robin	*Erithacus rubecula*	Resident	61	ROBIN
Common Nightingale	*Luscinia megarhynchos*	Humid	52	NIGAL
Common Chiffchaff	*Phylloscopus collybita*	Resident	51	CHIFF
Eurasian Reed Warbler	*Acrocephalus scirpaceus*	Humid	49	REEWA
Garden Warbler	*Sylvia borin*	Humid	43	GARWA
Dunnock	*Prunella modularis*	Resident	41	DUNNO
Song Thrush	*Turdus philomelos*	Resident	41	SONTH
Common Chaffinch	*Fringilla coelebs*	Resident	40	CHAFF
Sedge Warbler	*Acrocephalus schoenobaenus*	Arid	40	SEDWA
European Greenfinch	*Chloris chloris*	Resident	39	GREFI
Long-tailed Tit	*Aegithalos caudatus*	Resident	39	LOTTI
Whitethroat	*Curruca communis*	Arid	36	WHITE
Reed Bunting	*Emberiza schoeniclus*	Resident	36	REEBU
Willow Warbler	*Phylloscopus trochilus*	Humid	35	WILWA
Lesser Whitethroat	*Curruca curruca*	Arid	30	LESWH
Eurasian Wren	*Troglodytes troglodytes*	Resident	29	WREN
Marsh Warbler	*Acrocephalus palustris*	Humid	26	MARWA
Melodious Warbler	*Hippolais polyglotta*	Humid	25	MELWA
European Goldfinch	*Carduelis carduelis*	Resident	24	GOLDF
Cetti's Warbler	*Cettia cetti*	Resident	22	CETWA
House Sparrow	*Passer domesticus*	Resident	22	HOUSP
European Serin	*Serinus serinus*	Resident	22	SERIN
Eurasian Bullfinch	*Pyrrhula pyrrhula*	Resident	20	BULLF
Great Reed Warbler	*Acrocephalus arundinaceus*	Humid	16	GRRWA
Sardinian Warbler	*Curruca melanocephala*	Resident	16	SARWA
Yellowhammer	*Emberiza citrinella*	Resident	15	YELHA
Eurasian Tree Sparrow	*Passer montanus*	Resident	13	TRESP
Savi's Warbler	*Locustella luscinioides*	Arid	13	SAVWA

Short-toed Treecreeper	*Certhia brachydactyla*	Resident	13	STTRE
Red-backed Shrike	*Lanius collurio*	Humid	11	REBSH
Bluethroat	*Luscinia svecica*	Arid	11	BLUTH
Grasshopper-Warbler	*Locustella naevia*	Arid	11	GRAWA
Subalpine Warbler	*Curruca cantillans/iberiae/subalpina*	Arid	11	SUBWA
Spotted Flycatcher	*Muscicapa striata*	Humid	10	SPOFL
Barn Swallow	*Hirundo rustica*	Humid	9	SWALL
Bearded Reedling	*Panurus biarmicus*	Resident	9	BEATI
Cirl Bunting	*Emberiza cirlus*	Resident	9	CIRBU
Marsh Tit	*Poecile palustris*	Resident	8	MARTI
European Pied Flycatcher	*Ficedula hypoleuca*	Humid	8	PIEFL
Fieldfare	*Turdus pilaris*	Resident	7	FIELD
European Starling	*Sturnus vulgaris*	Resident	6	STARL
Eurasian Siskin	*Spinus spinus*	Resident	6	SISKI
Hawfinch	*Coccothraustes coccothraustes*	Resident	6	HAWFI
Redpoll	*Acanthis flammea/cabaret*	Resident	5	REDPO
Common Redstart	*Phoenicurus phoenicurus*	Arid	5	REDST
Crested Tit	*Lophophanes cristatus*	Resident	5	CRETI
Redwing	*Turdus iliacus*	Resident	5	REDWI
Western Orphean Warbler	*Curruca hortensis*	Arid	5	WORWA
Barred Warbler	*Curruca nisoria*	Arid	4	
Eurasian Penduline-Tit	*Remiz pendulinus*	Resident	4	
Moustached Warbler	*Acrocephalus melanopogon*	Resident	4	
Bonelli's Warbler	*Phylloscopus bonelli/orientalis*	Arid	4	
Common Firecrest	*Regulus ignicapilla*	Resident	4	
Woodchat Shrike	*Lanius senator*	Arid	4	
Eurasian Linnet	*Linaria cannabina*	Resident	3	
White Wagtail	*Motacilla alba*	Resident	3	
Thrush Nightingale	*Luscinia luscinia*	Humid	3	
Whinchat	*Saxicola rubetra*	Humid	3	
Tree Pipit	*Anthus trivialis*	Humid	2	
Willow Tit	*Poecile montanus*	Resident	2	
Coal Tit	*Periparus ater*	Resident	2	
Eurasian Nuthatch	*Sitta europaea*	Resident	2	
Gray Wagtail	*Motacilla cinerea*	Resident	2	
European Stonechat	*Saxicola rubicola*	Resident	2	
Rock Bunting	*Emberiza cia*	Resident	2	
Bank Swallow	*Riparia riparia*	Arid	2	

Western Yellow Wagtail	*Motacilla flava*	Arid	1	
Black Redstart	*Phoenicurus ochruros*	Resident	1	
Mistle Thrush	*Turdus viscivorus*	Resident	1	
River Warbler	*Locustella fluviatilis*	Humid	1	
Icterine Warbler	*Hippolais icterina*	Humid	1	
Goldcrest	*Regulus regulus*	Resident	1	
Collared Flycatcher	*Ficedula albicollis*	Humid	1	
Eurasian Golden Oriole	*Oriolus oriolus*	Humid	1	
Citril Finch	*Carduelis citrinella*	Resident	1	
Red Crossbill	*Loxia curvirostra*	Resident	1	

Table S4.2: The number of Constant Effort Sites in 1 km landscapes dominated by different land sub-systems from the Dou et al., (2021) classification, and the higher-level system and intensity groupings used in this study.

System	Sub-system	Intensity	Number of sites
arable cropland	low-intensity cropland	low	2
arable cropland	medium-intensity cropland	medium	24
arable cropland	high-intensity cropland	high	19
forest	low-intensity forest	low	14
forest	medium-intensity forest	medium	14
forest	high-intensity forest	high	4
grassland	low-intensity grassland	low	3
grassland	medium-intensity grassland	medium	2
grassland	high-intensity grassland	high	2
mosaic	forest/shrubs and cropland mosaics	low	10
mosaic	forest/shrubs and grassland mosaics	low	6
mosaic	forest/shrubs and mixed agriculture mosaics	low	4
mosaic	low-intensity agricultural mosaics	low	1
mosaic	medium-intensity agricultural mosaics	medium	3
mosaic	high-intensity agricultural mosaics	high	1
settlement	low-intensity settlement	low	3
settlement	medium-intensity settlement	medium	22
settlement	high-intensity settlement	high	3
wetland	water body	low	8
wetland	wetland	low	24
shrub	shrub	low	6
shrub	extensive perm-crops	low	1

Table S4.3: For each Constant Effort Sites (CES) scheme, the estimated slope value, standard error, degrees of freedom (df) and 95% Confidence Intervals from a linear model with mean standardised productivity (1998 – 2019) across 80 landbird species at 117 CESs as the response variable, and the interaction between mean insect count per hour on sticky traps deployed in 2024 and CES scheme as a predictor, weighted by the inverse of the standard deviation of mean productivity. Estimated using the *emtrends* function from the 'emmeans' package.

CES Scheme	Slope	Standard Error	df	95% Confidence Intervals	Number of sites
CZE	-0.003	0.02	97	-0.04 – 0.04	12
DEN	0.10	0.05	97	-0.002 – 0.20	5
SPB	0.03	0.02	97	-0.02 – 0.07	6
SPC	0.0001	0.02	97	-0.03 – 0.03	23
FRA	0.04	0.03	97	-0.02 – 0.09	20
GBT	-0.02	0.03	97	-0.07 – 0.03	16
HUN	0.03	0.02	97	-0.01 – 0.07	11
ITA	-0.02	0.02	97	-0.06 – 0.03	12
FIN	0.06	0.02	97	0.01- 0.11	9
SWE	0.15	0.14	97	-0.13 – 0.43	3

Table S4.4: For each species, the estimated slope value, standard error, degrees of freedom (df) and upper and lower 95% confidence intervals (CI) from a linear model with mean standardised productivity across 52 landbird species at 117 Constant Effort Sites as the response variable, and the interaction between mean insect count per hour on sticky traps deployed in 2024 and species as a predictor, weighted by the inverse of the standard deviation of mean productivity. Estimated using the *emtrends* function from the 'emmeans' package.

Species Code	Slope	Standard Error	df	Lower CI	Upper CI
SWALL	0.06	0.06	1279	-0.05	0.18
WREN	0.02	0.03	1279	-0.04	0.08
DUNNO	0.01	0.05	1279	-0.08	0.11
ROBIN	-0.02	0.02	1279	-0.07	0.02
NIGAL	-0.02	0.02	1279	-0.07	0.02
BLUTH	-0.05	0.05	1279	-0.15	0.06
REDST	0.12	0.12	1279	-0.11	0.36
BLABI	-0.01	0.02	1279	-0.05	0.03
FIELD	0.01	0.11	1279	-0.20	0.23
SONTH	0.01	0.03	1279	-0.05	0.07
REDWI	-0.05	0.09	1279	-0.22	0.12
CETWA	0.02	0.03	1279	-0.04	0.07
GRAWA	-0.08	0.06	1279	-0.20	0.05
SAVWA	-0.02	0.04	1279	-0.10	0.05

SEDWA	0.02	0.02	1279	-0.02	0.07
MARWA	0.01	0.03	1279	-0.06	0.08
REEWA	-0.01	0.02	1279	-0.05	0.03
GRRWA	-0.07	0.03	1279	-0.13	0.00
MELWA	0.03	0.04	1279	-0.05	0.10
SUBWA	-0.07	0.12	1279	-0.31	0.16
SARWA	0.02	0.08	1279	-0.14	0.18
WORWA	0.15	0.42	1279	-0.66	0.97
LESWH	0.07	0.05	1279	-0.03	0.18
WHITE	0.07	0.04	1279	-0.002	0.15
GARWA	-0.02	0.03	1279	-0.08	0.04
BLACA	0.0004	0.02	1279	-0.04	0.04
CHIFF	0.02	0.03	1279	-0.04	0.08
WILWA	0.05	0.04	1279	-0.02	0.12
SPOFL	-0.04	0.08	1279	-0.19	0.12
PIEFL	0.29	0.14	1279	0.01	0.57
BEATI	0.001	0.05	1279	-0.10	0.10
LOTTI	0.001	0.05	1279	-0.10	0.10
MARTI	0.16	0.18	1279	-0.18	0.51
CRETI	0.10	0.18	1279	-0.26	0.46
BLUTI	0.03	0.02	1279	-0.02	0.07
GRETI	0.04	0.02	1279	-0.0001	0.08
STTRE	-0.01	0.04	1279	-0.10	0.07
REBSH	0.08	0.08	1279	-0.07	0.23
STARL	-0.07	0.12	1279	-0.31	0.18
HOUSP	-0.03	0.04	1279	-0.10	0.05
TRESP	-0.01	0.06	1279	-0.12	0.10
CHAFF	0.01	0.05	1279	-0.08	0.10
SERIN	0.004	0.05	1279	-0.09	0.10
GREFI	0.02	0.03	1279	-0.04	0.09
GOLDF	0.01	0.04	1279	-0.08	0.10
SISKI	0.04	0.13	1279	-0.20	0.29
REDPO	0.04	0.13	1279	-0.21	0.29
BULLF	0.07	0.07	1279	-0.06	0.20
HAWFI	-0.12	0.24	1279	-0.59	0.35
YELHA	0.08	0.13	1279	-0.17	0.33
CIRBU	0.15	0.14	1279	-0.13	0.42
REEBU	0.07	0.03	1279	0.01	0.12

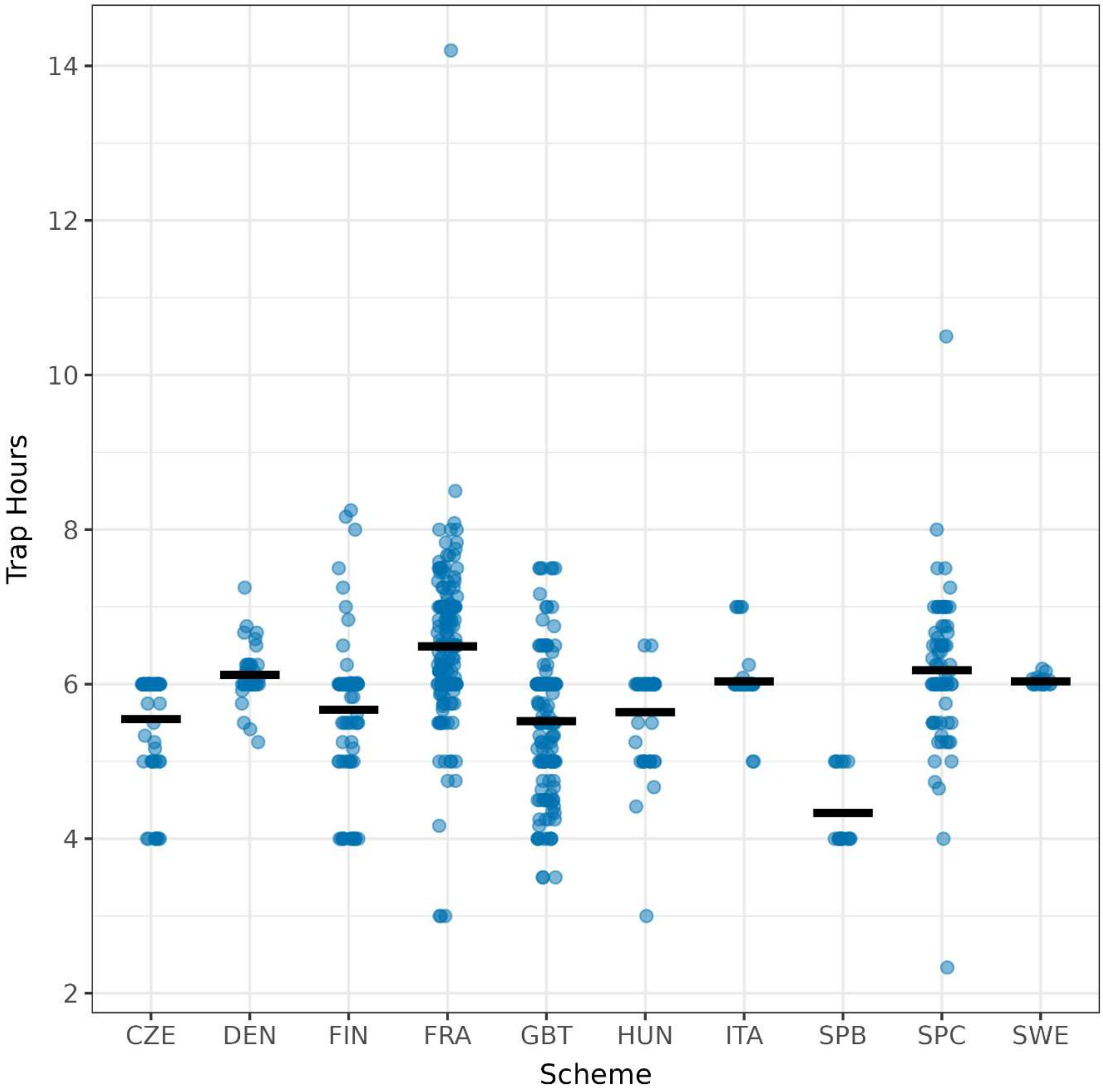


Figure S4.1: Number of hours each sticky trap was operational for (points) and the mean number of hours across traps deployed in 2024 (bar), plotted by each Constant Effort Sites scheme. Total number traps = 741.

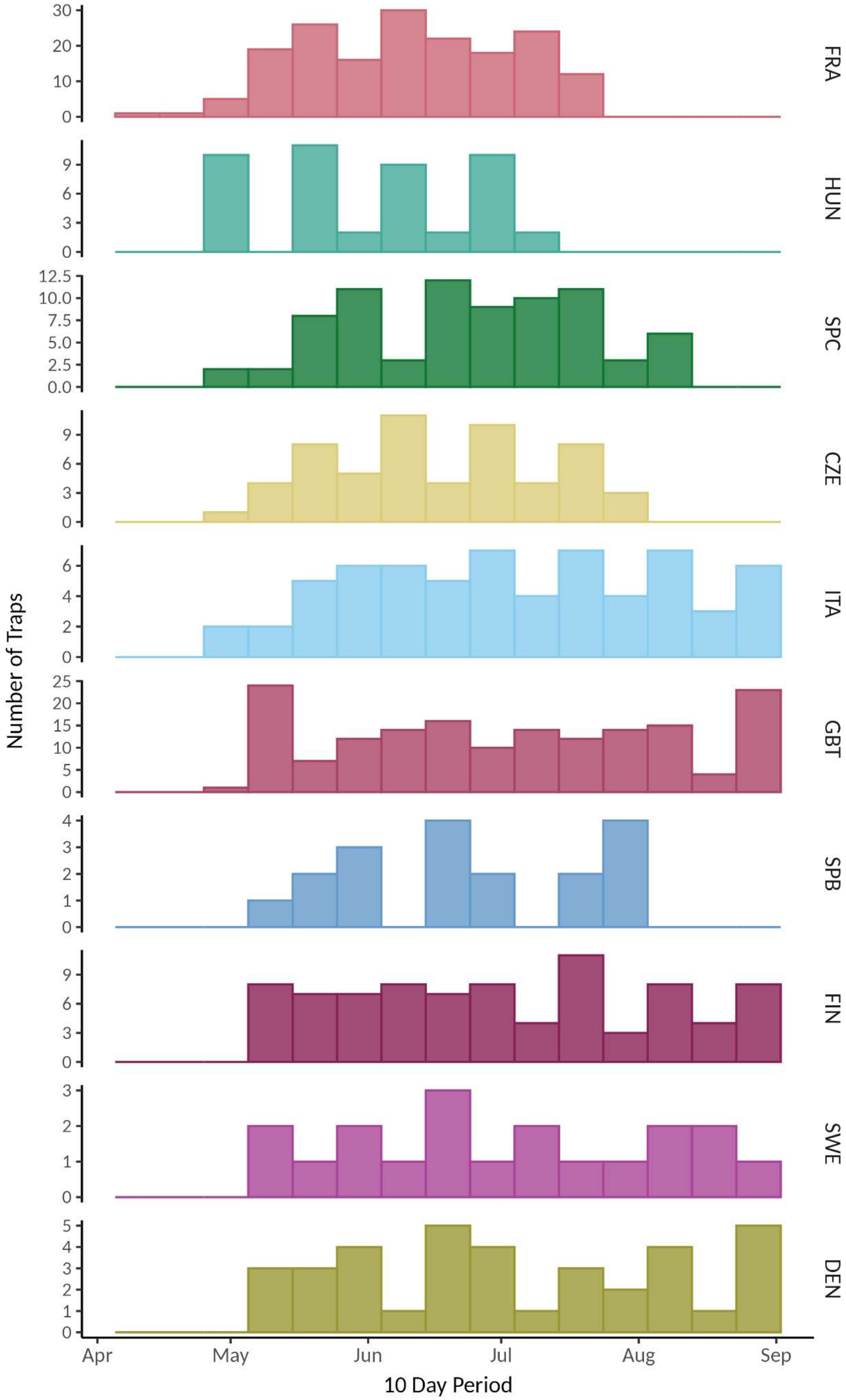


Figure S4.2: Frequency distributions of sticky trapping occasions in 2024 by Julian date, grouped into 10-day periods, for each Constant Effort Sites scheme.

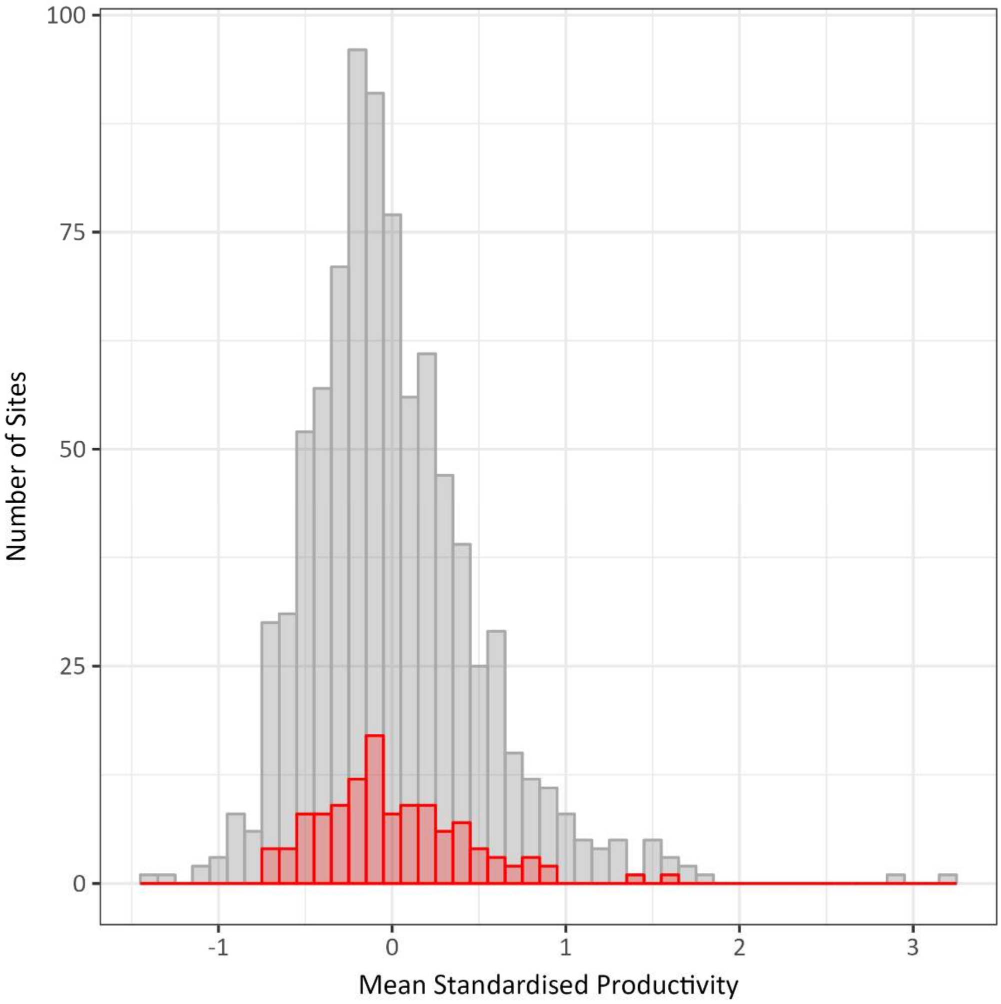


Figure S4.3: Distributions of site-level mean standardised landbird productivity (1998 – 2019) amongst all Constant Effort Sites (CESs) in participating schemes (grey) and all CESs in our study sample (red).

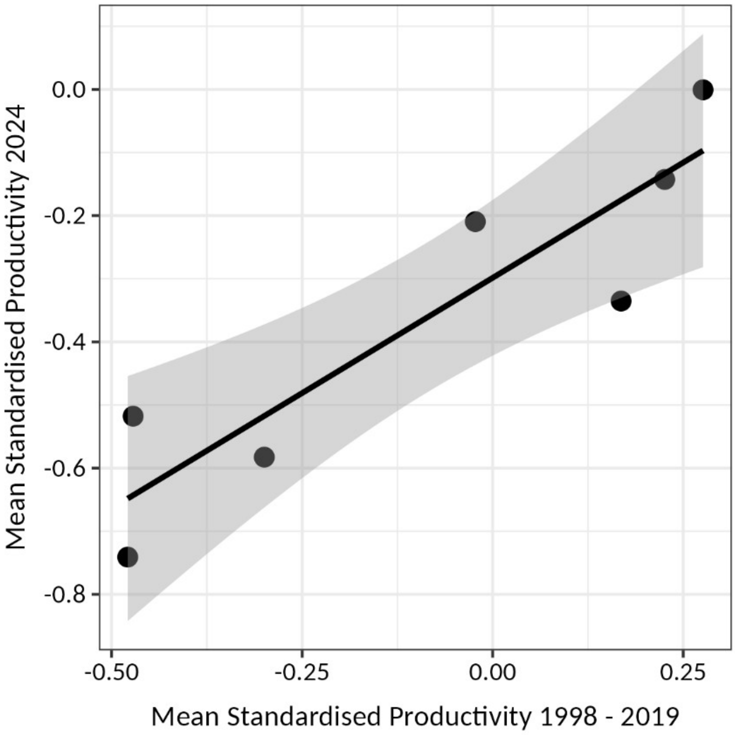


Figure S4.5: Mean standardised productivity across 27 landbird species, calculated in 1998 – 2019 and 2024 at Constant Effort Sites in Finland contributing insect data in 2024 (*n* = 7).

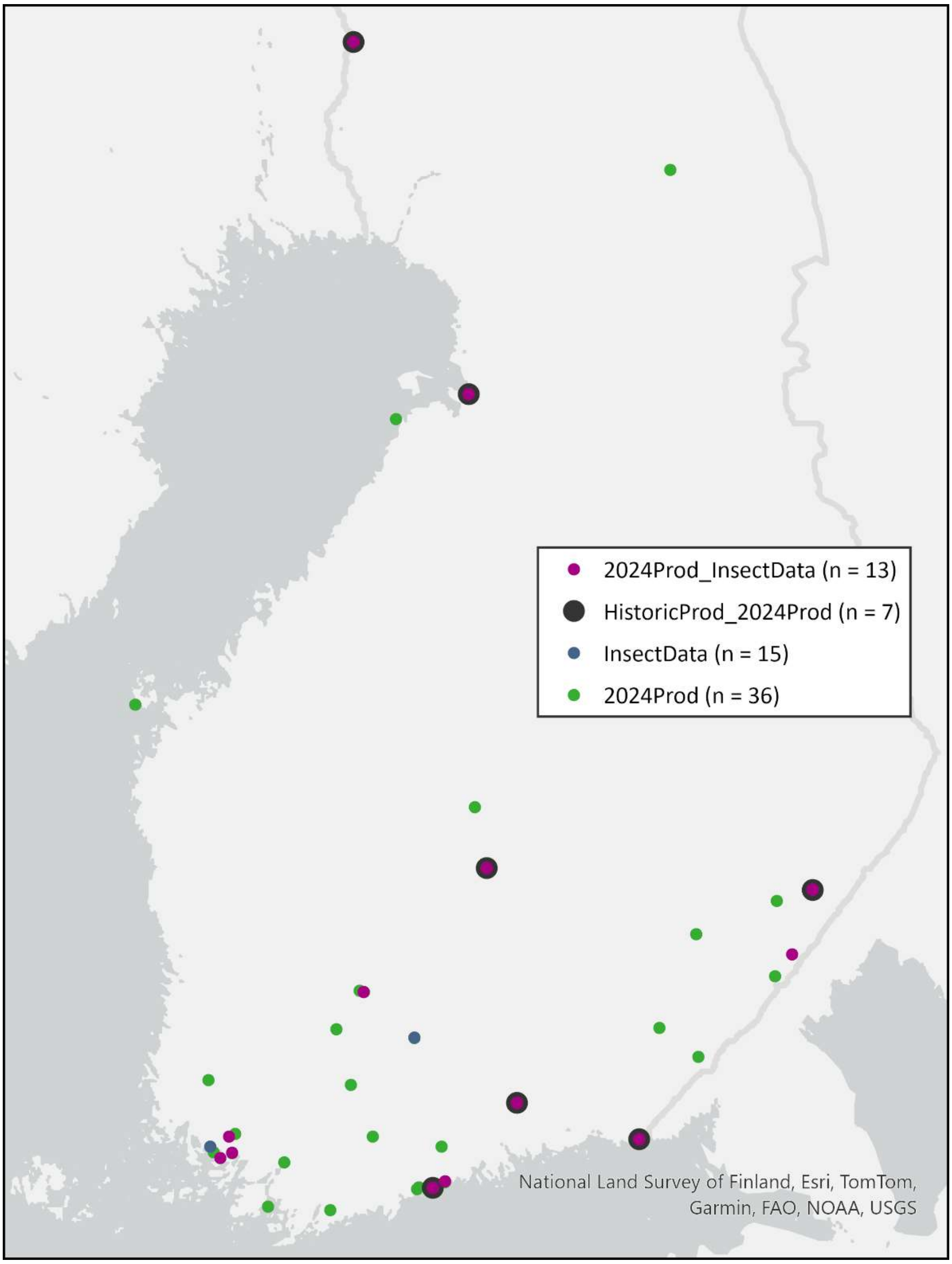


Figure S4.4: Locations of Constant Effort Sites in Finland used for different aspects of the analysis. Shown are all sites collecting 2024 landbird productivity data (2024Prod, *n* = 36), all sites collecting insect data (InsectData, *n* = 15) and sites for which both 2024 productivity and insect data were available (2024Prod_InsectData, *n* = 13). Sites with productivity data for both the period 1998 – 2019 and 2024 are also shown (HistoricProd_2024Prod, *n* = 7). Each site is only represented with one symbol.

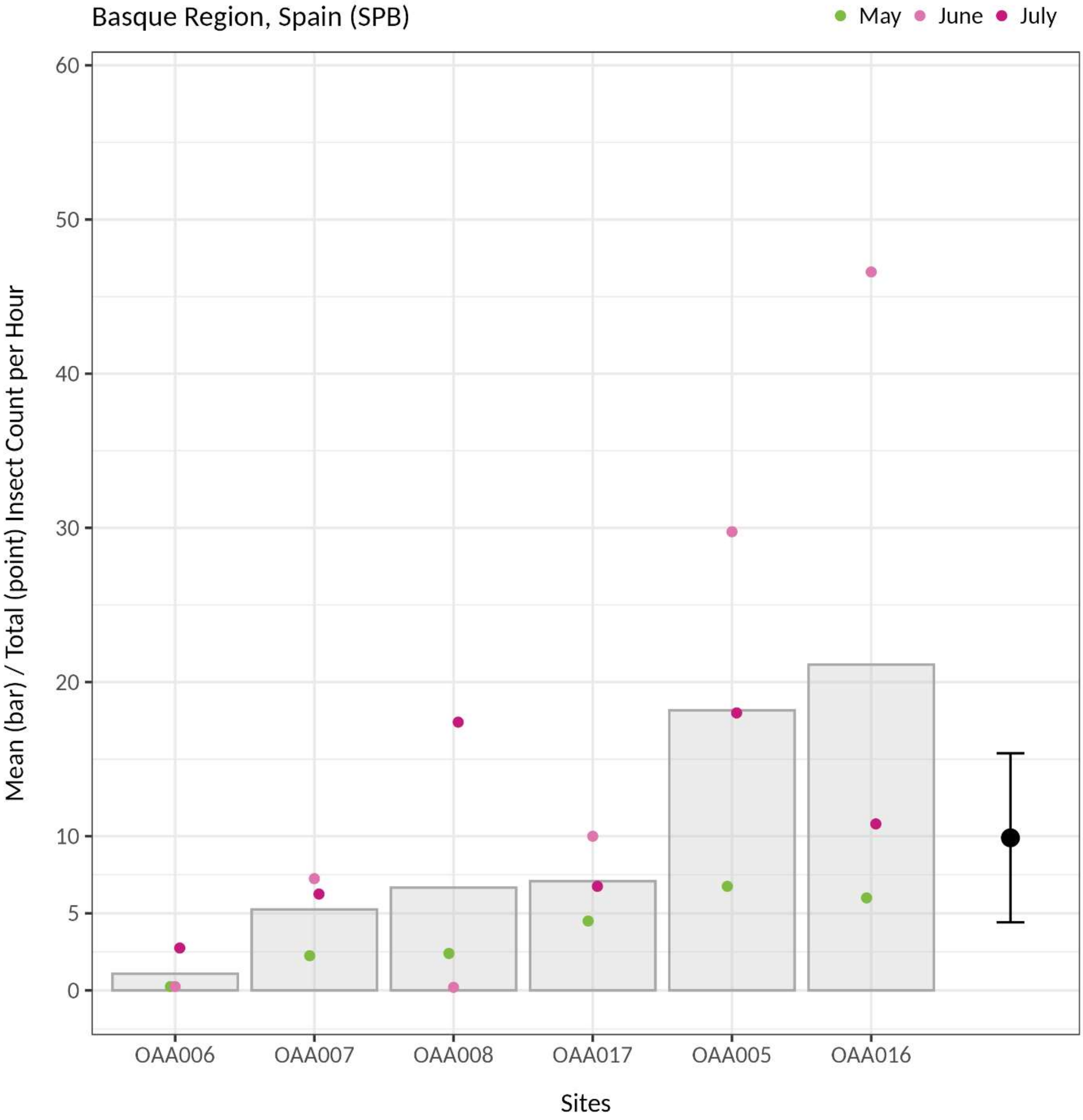


Figure S4.6: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 6 Constant Effort Sites in the Basque region of Spain. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% Confidence Intervals) across all traps in the Basque region is also shown in black.

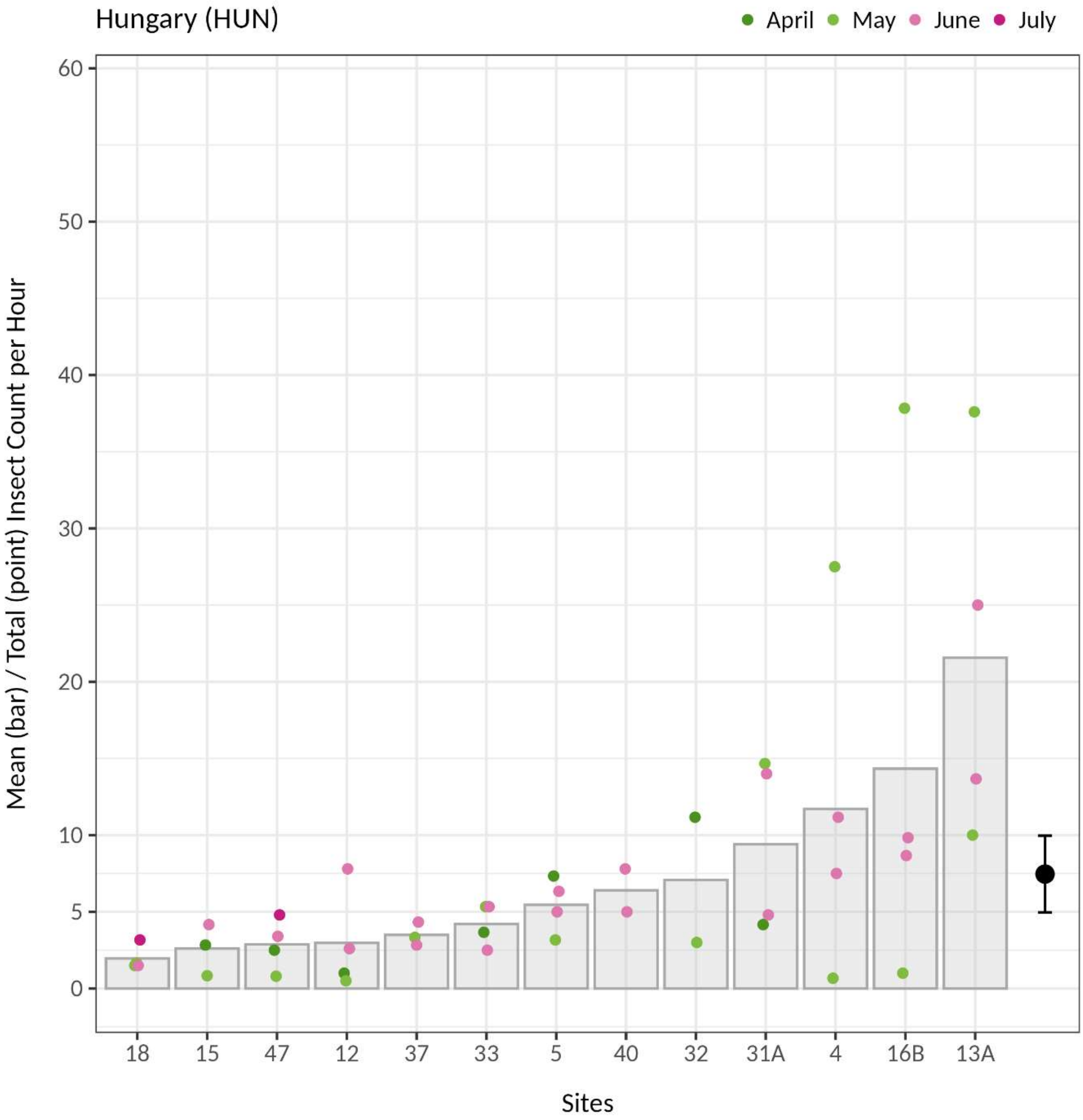


Figure S4.7: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 13 Constant Effort Sites in Hungary. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% Confidence Intervals) across all traps in Hungary is also shown.

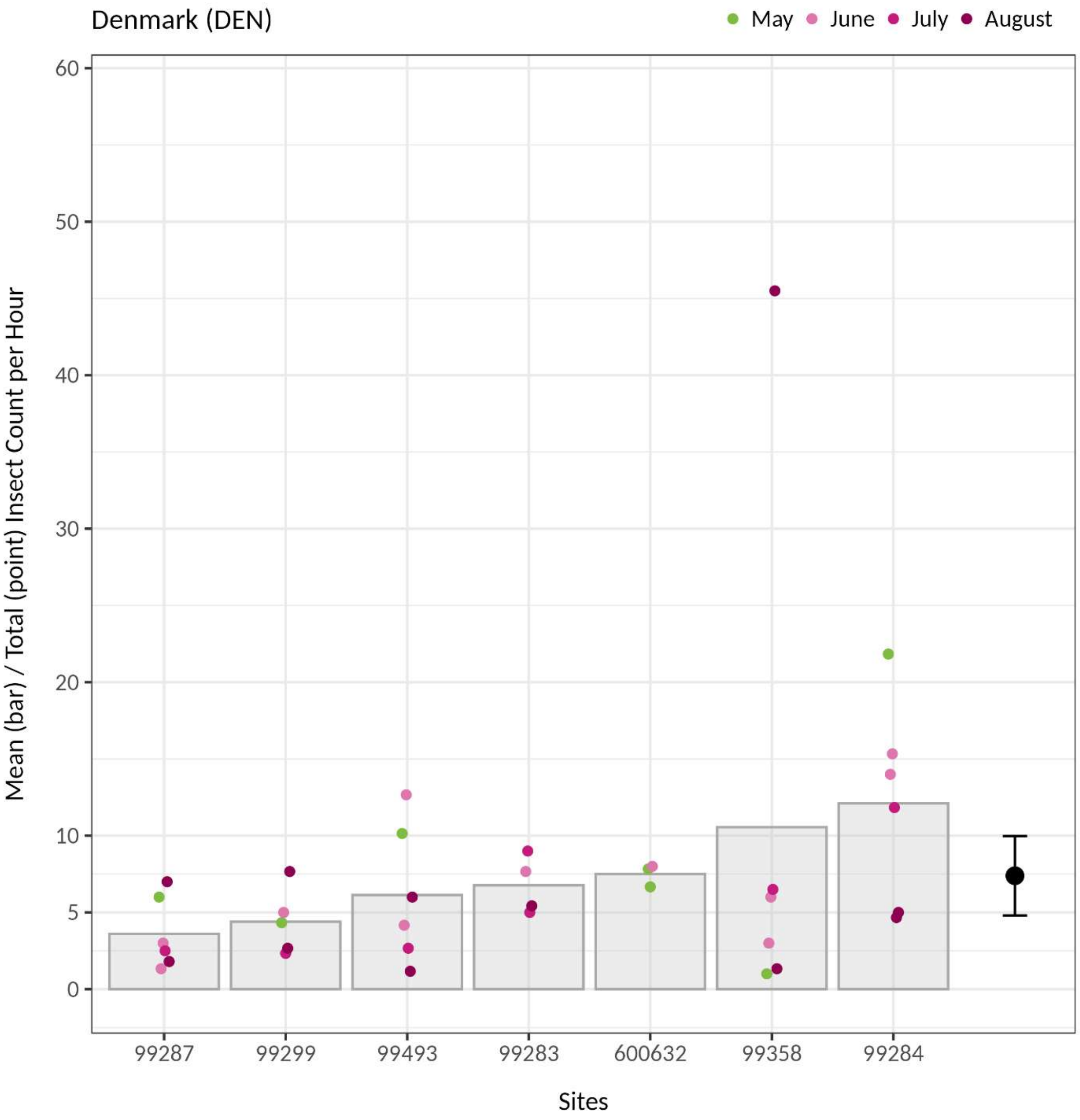


Figure S4.8: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 7 Constant Effort Sites in Denmark. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% Confidence Intervals) across all traps in Denmark is also shown in black.

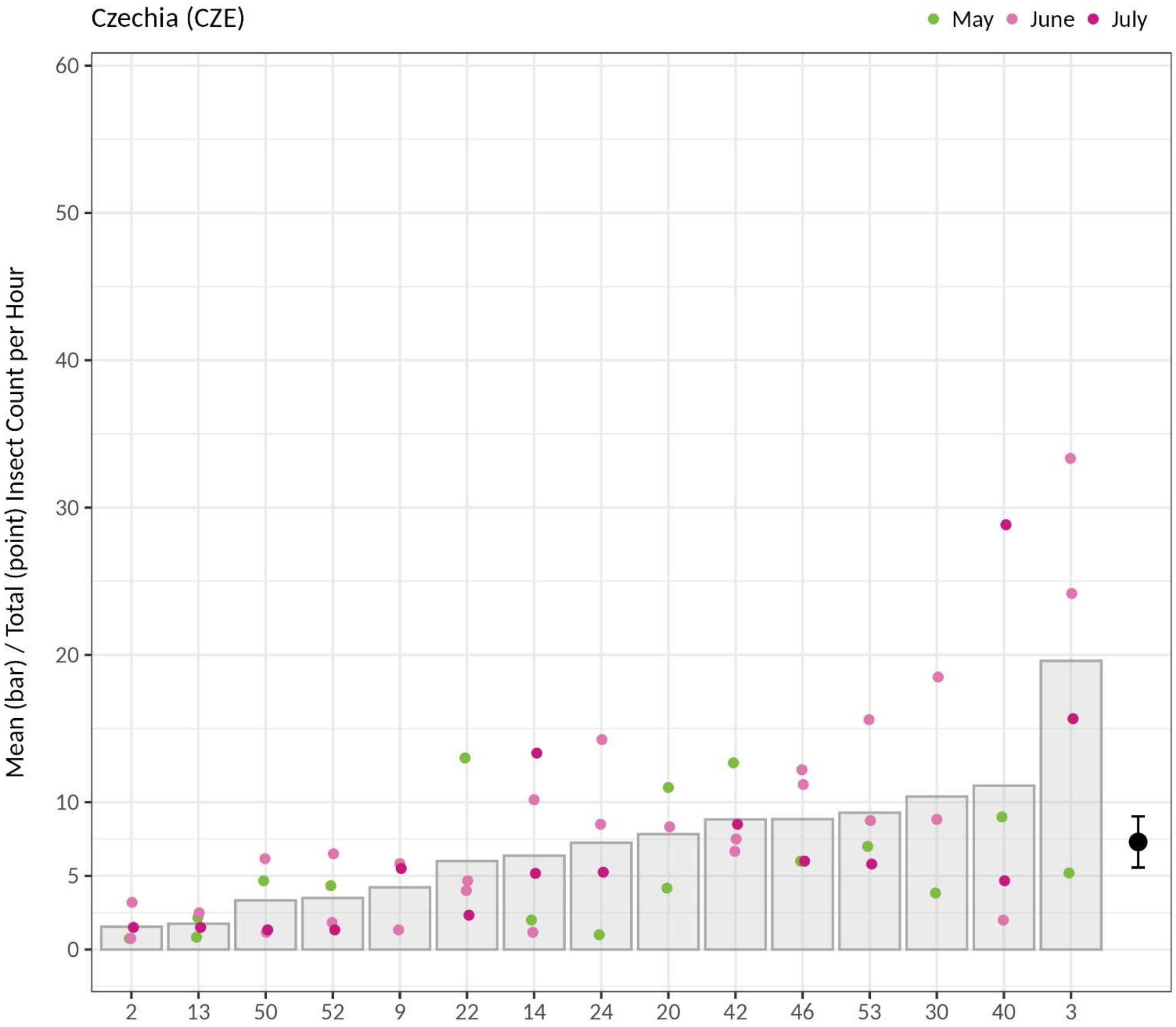


Figure S4.9: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 15 Constant Effort Sites in Czechia. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% Confidence Intervals) across all traps in Czechia is also shown in black.

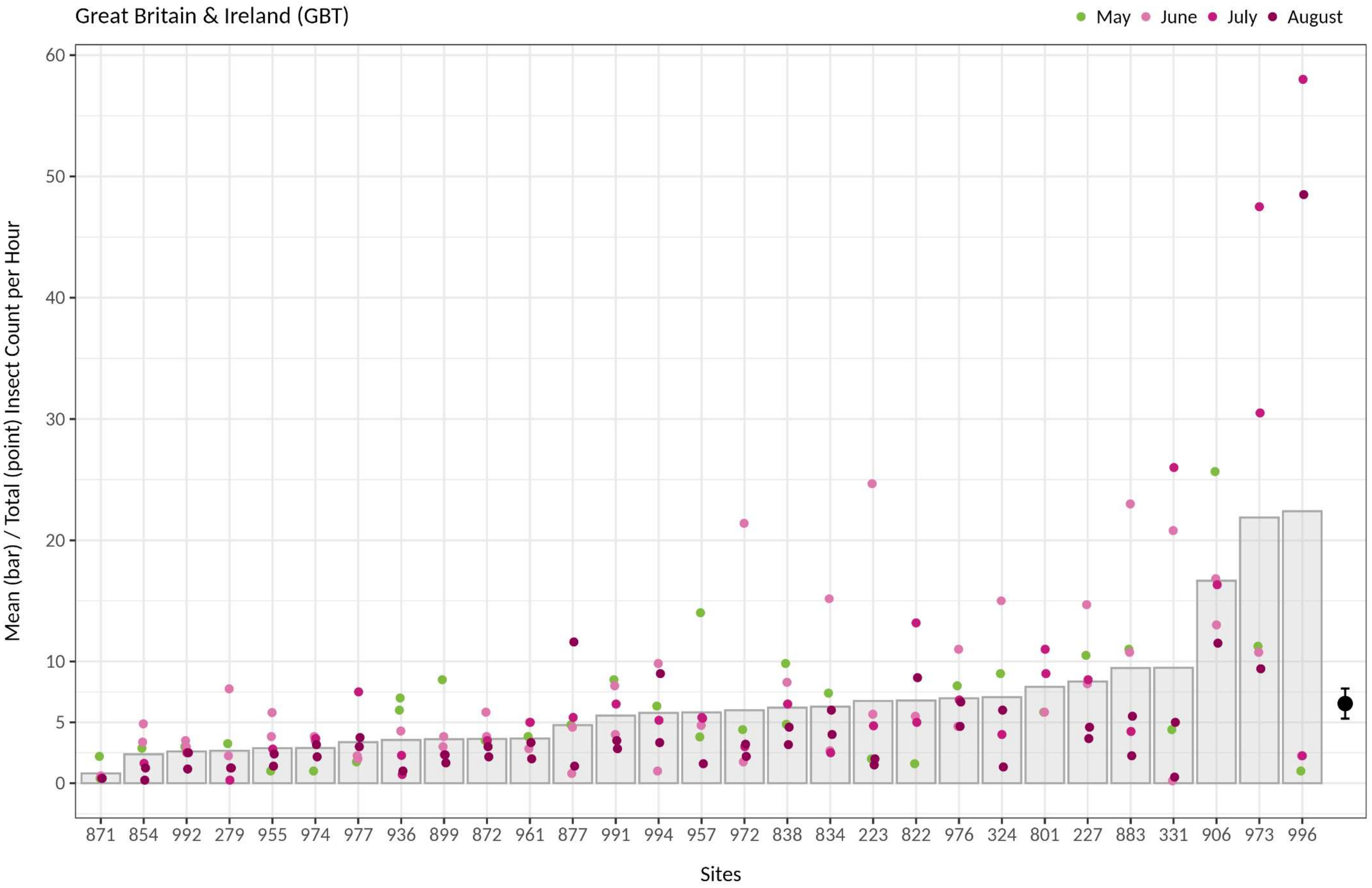


Figure S4.10: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 29 Constant Effort Sites in Great Britain & Ireland. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% Confidence Intervals) across all traps in Great Britain & Ireland is also shown in black.

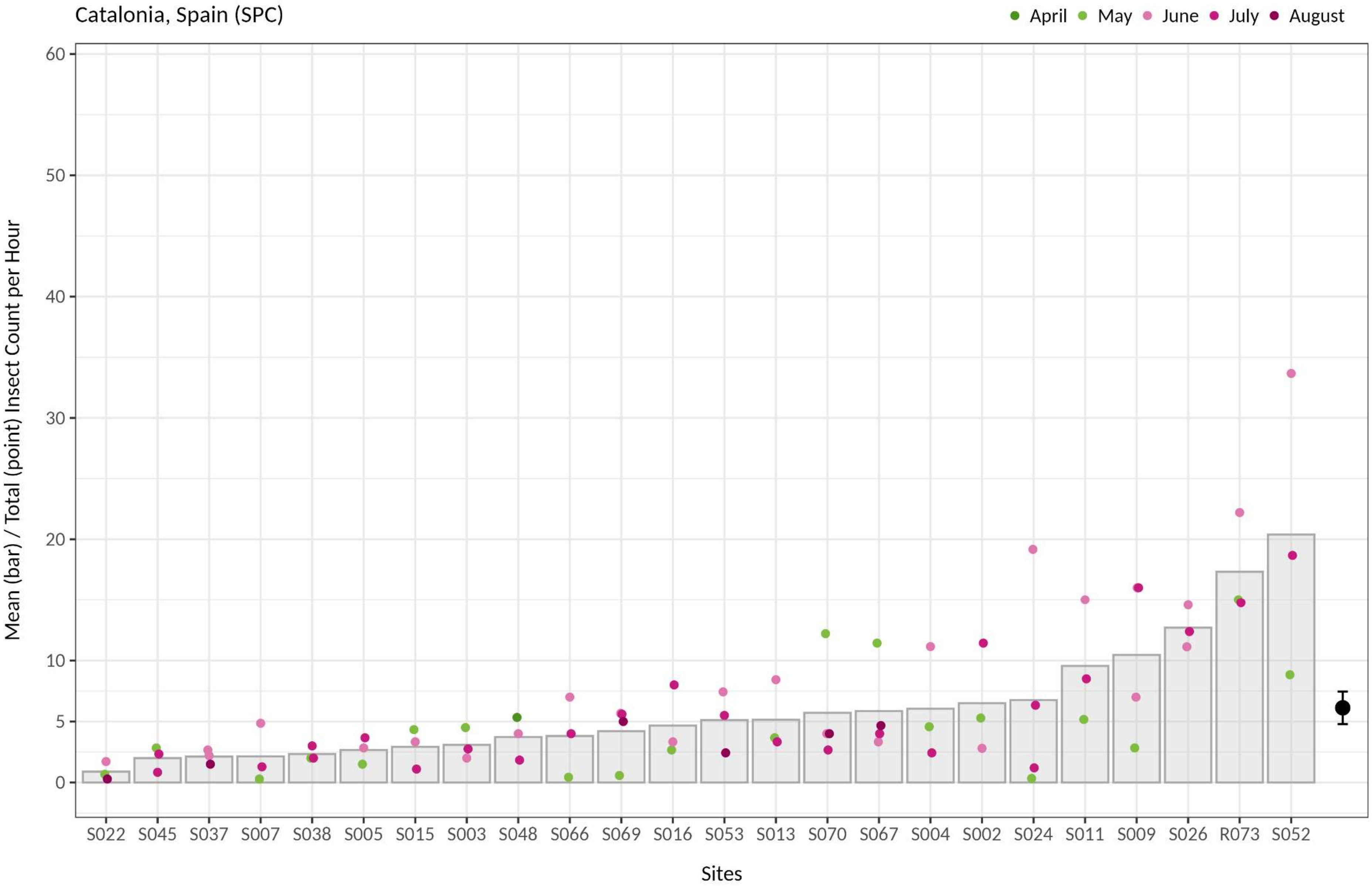


Figure S4.11: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 24 Constant Effort Sites in the Catalonia region of Spain. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% Confidence Intervals) across all traps in Catalonia is also shown in black.

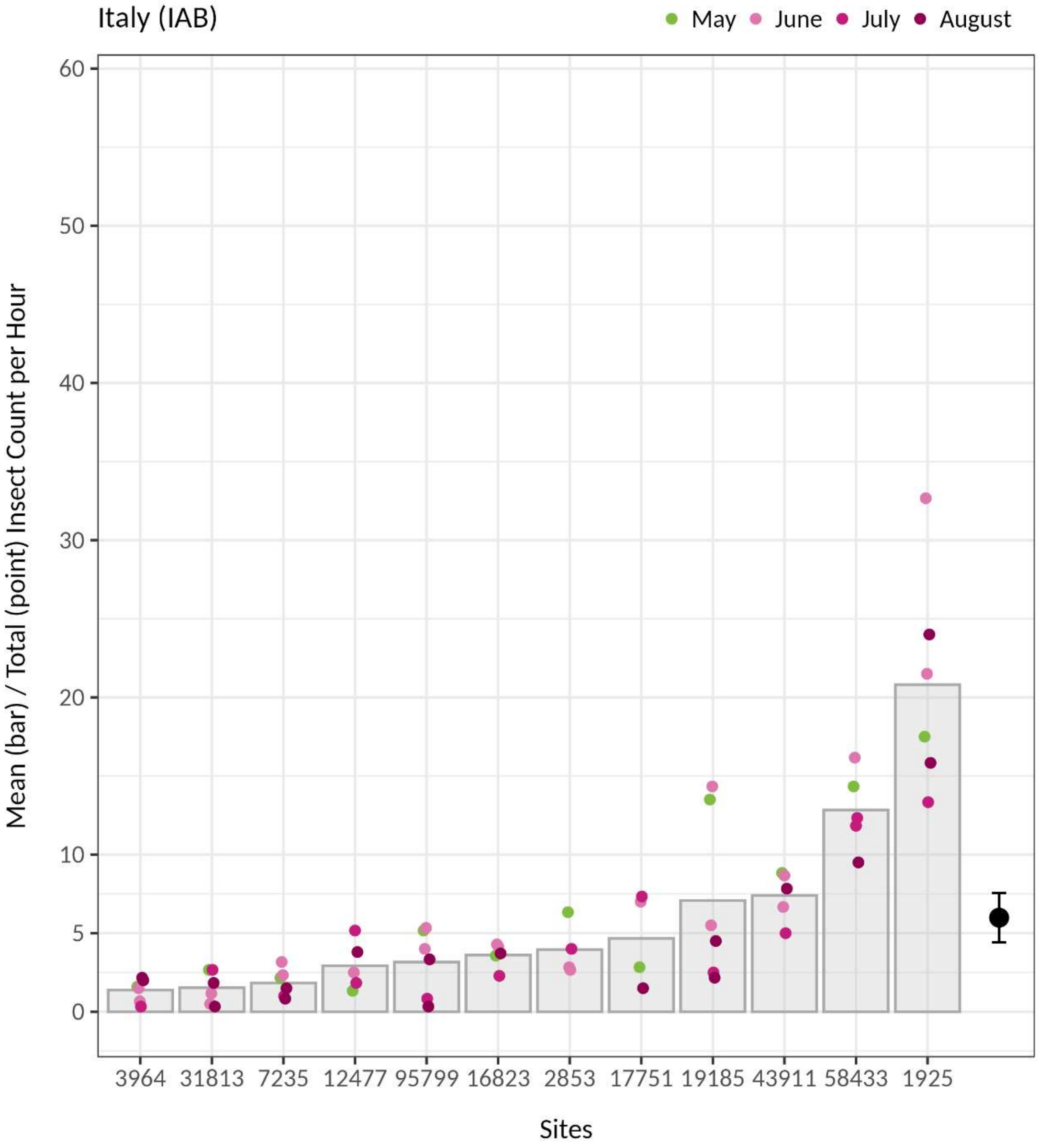


Figure S4.12: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 12 Constant Effort Sites in Italy. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% Confidence Intervals) across all traps in Italy is also shown in black.

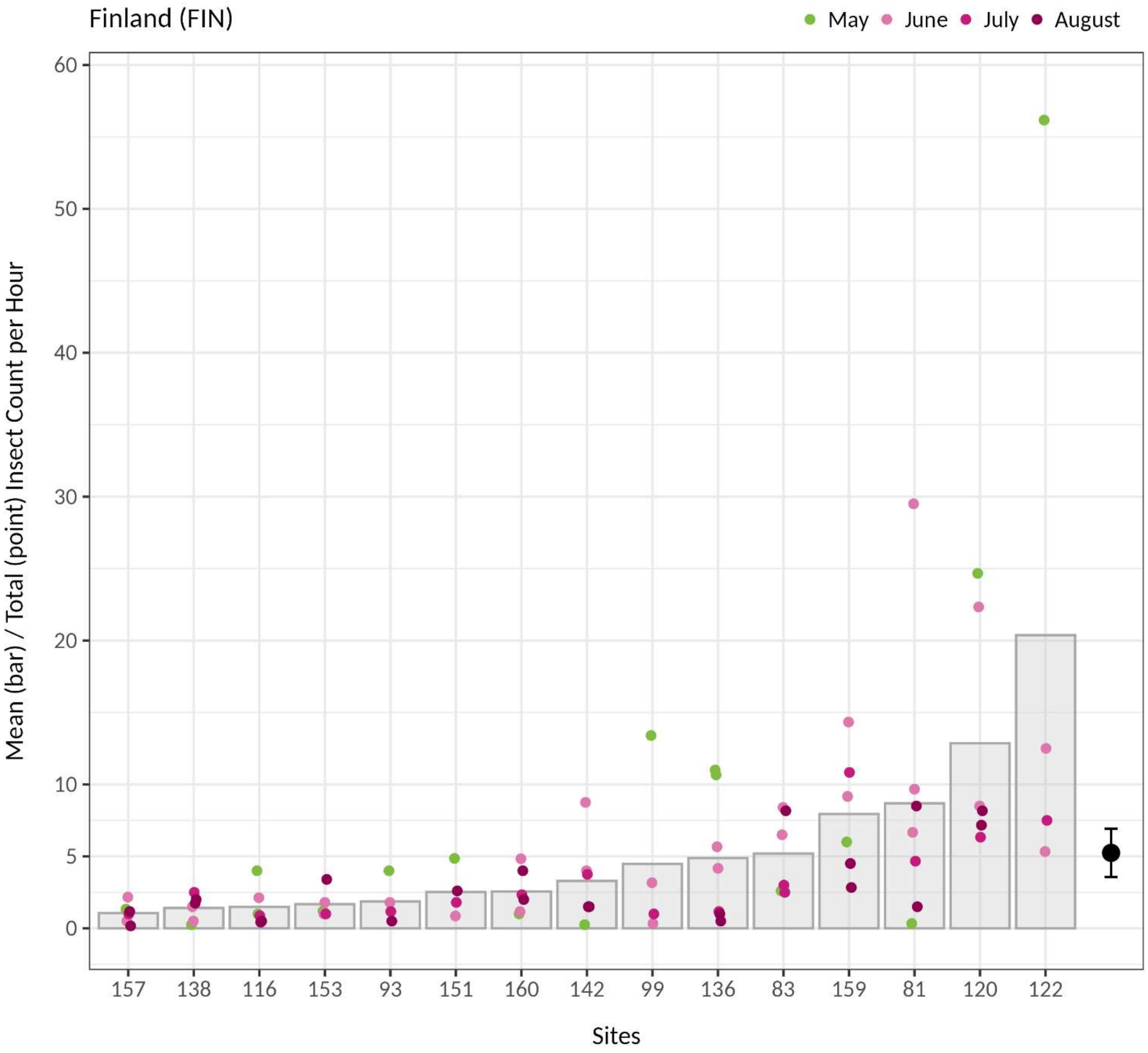


Figure S4.13: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 15 Constant Effort Sites in Finland. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% Confidence Intervals) across all traps in Finland is also shown in black.

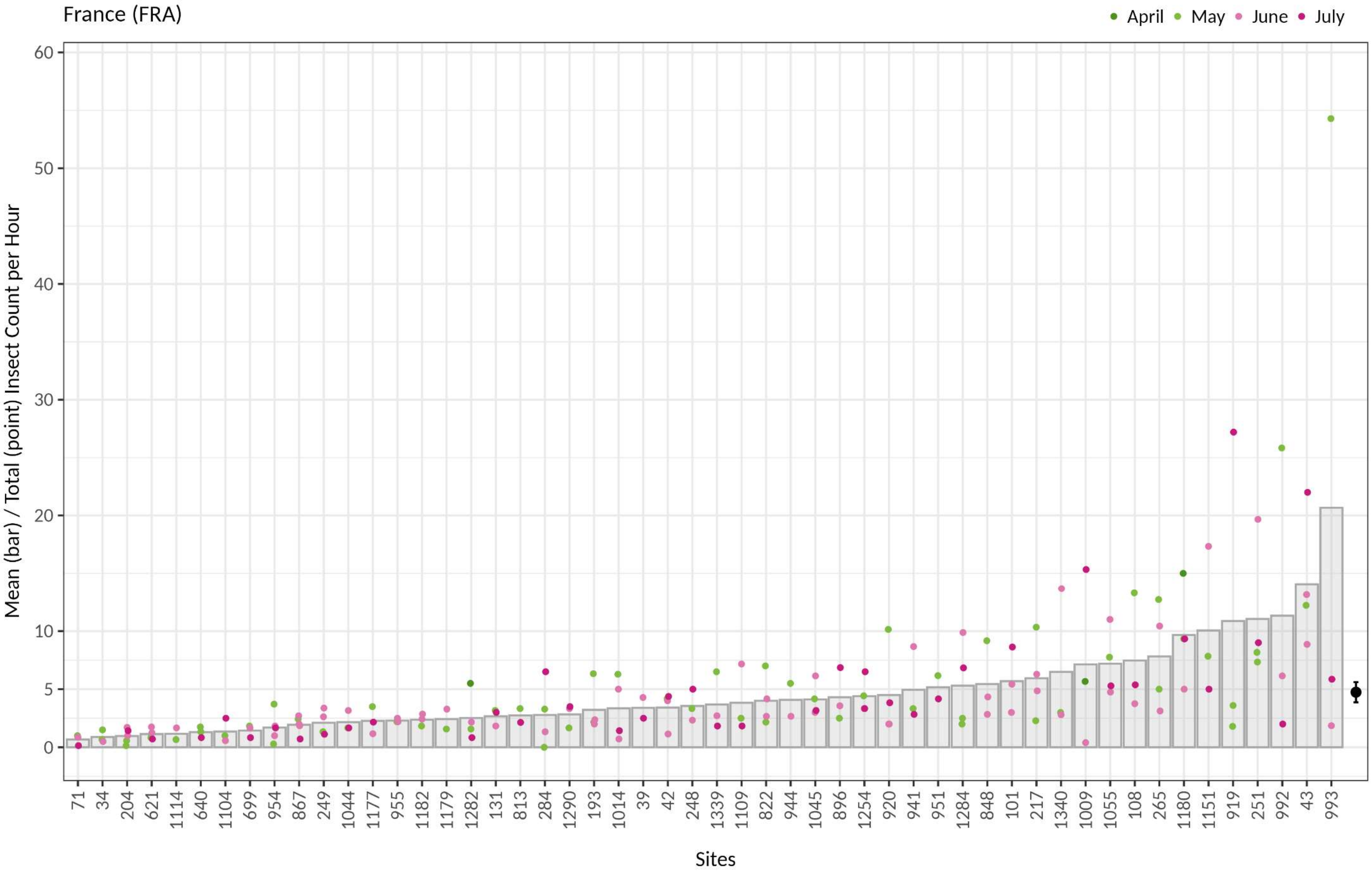


Figure S4.14: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 52 Constant Effort Sites in France. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% Confidence Intervals) across all traps in France is also shown in black.

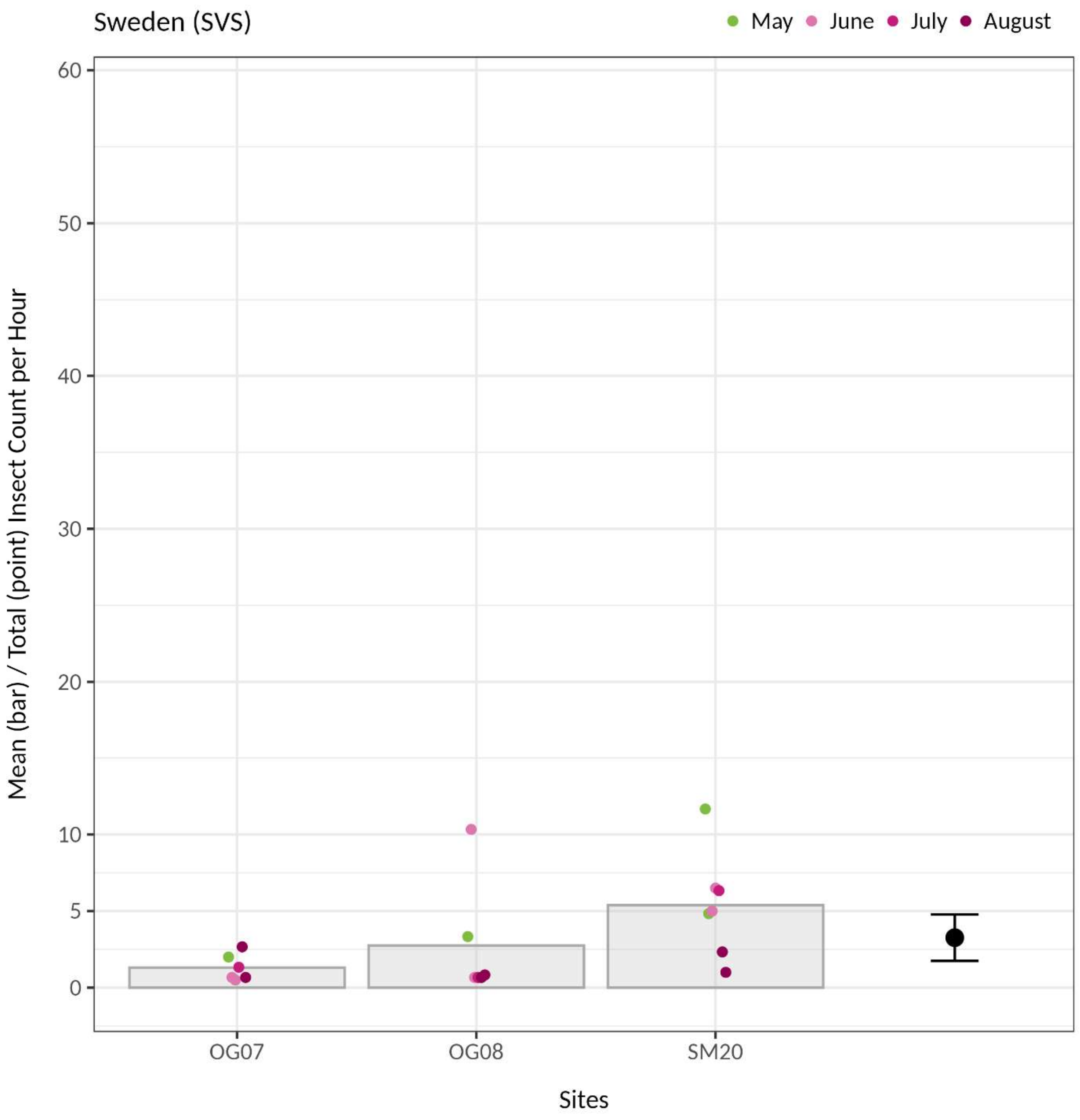


Figure S4.15: Total insect count per hour on each sticky trap (points), as well as the mean insect count per hour across traps for each site (bar), deployed at 3 Constant Effort Sites in Sweden. Points are coloured by the month in which the trap was deployed in 2024. The overall mean (±95% CIs) across all traps in Sweden is also shown in black.

Appendix 4.1.

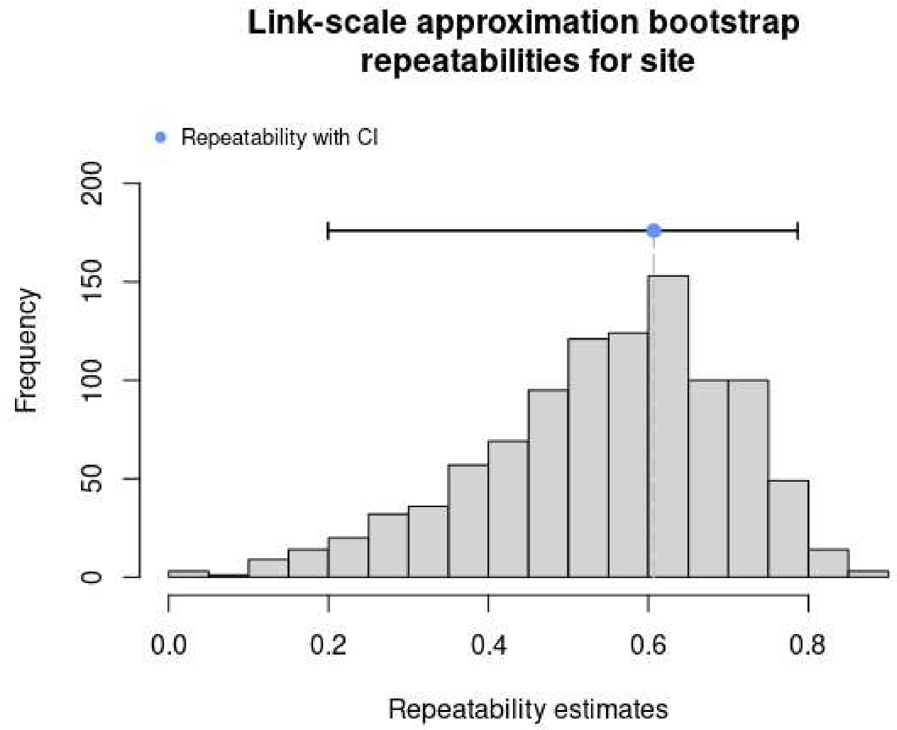
In 2023, we conducted a pilot study in the UK to investigate the suitability of sticky traps for measuring insect abundance at Constant Effort bird ringing sites, and whether this was related to average bird productivity at these sites. Full details of this pilot study are provided in **Section 1.5 of Chapter 1**, with the primary focus here being the repeatability of insect abundance measurements within sites. In summary, 12 scrub-dominated sites from the British Trust for Ornithology's Constant Effort Sites scheme were selected within central England, and were each visited on two separate occasions in 2023: once during the nesting period in June (n = 10 sites), and once during the post-fledging period in July/August (n = 12 sites). Visits to the different sites were made as close together as possible on days with warm, dry weather. To measure the relative abundance of flying or foliage-dwelling insects (plus arachnids, grouped with insects for simplicity), 6 yellow sticky traps were deployed throughout the mist net rides for approximately 8 hours (~08:00 – 16:00), placed in the same locations on both visits. All insects > 1 mm caught on the traps were subsequently counted.

The repeatability of insect counts recorded on traps on the same day within sites was measured using the *rptPoisson* function from the 'rptR' package in R (Stoffel et al., 2017). Total invertebrate counts on traps were modelled in a Poisson generalised linear mixed model (GLMM) with a log-link function and site fitted as a random effect, separately for each visit period. 1000 rounds of parametric bootstrapping were run to estimate the standard error and 95 % confidence intervals for the repeatability estimates. Likelihood ratio tests (LRT) were then run to determine whether these repeatability estimates were significantly different from 0. The agreement repeatability estimates represent the ratio of variance among groups (i.e. sites) to the total variance in the insect counts (Stoffel et al., 2017). In the June visits, 61% of the observed variation in total insect counts on traps was explained by differences between sites, with this repeatability estimate significantly greater than 0 (Table A4.1, Figure A4.1.1a). In the July/August visits, the repeatability estimate was lower but still significantly greater than 0 (Table A4.1, Figure A4.1.1b), with 47% of the observed variation in insect counts explained by differences between sites. This demonstrates that, for the most part, the between-site variation in insect counts was greater than the within-site variation, but there was also some random noise in insect counts within sites (Figures A4.1.2a-b).

Table A4.1. Repeatability estimates (R) of total insect counts recorded across sticky traps deployed on the same day within sites during June (10 sites) and July/August (12 sites) visits in 2023. Calculated as agreement repeatabilities with the 'rptR' package (Stoffel et al., 2017), using two Poisson GLMMs with a log-link function and site as a random effect, subjected to 1000 rounds of parametric bootstrapping to estimate the Standard Error and 95% Confidence Intervals. A likelihood ratio test (LRT) was run on each to determine whether the R estimate is significantly different from 0.

Visit	n	R	Standard Error	95% Confidence Intervals	LRT p value
June	60	0.61	0.15	0.20 – 0.79	<0.0001
July/August	72	0.47	0.14	0.12 – 0.68	<0.0001

a)



b)

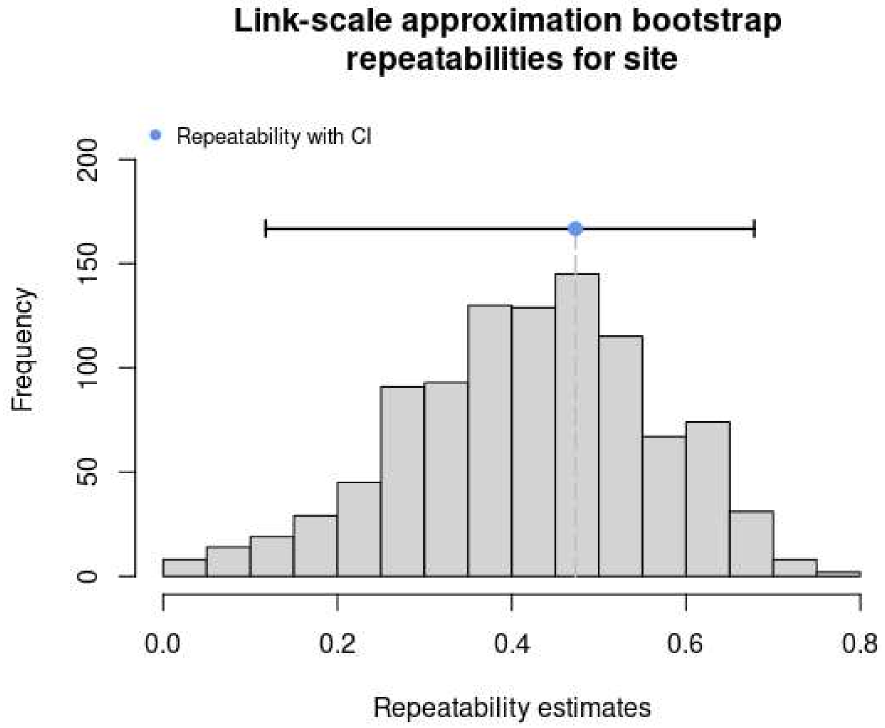


Figure A4.1.1: Repeatability estimates (blue point) of total insect counts recorded across sticky traps deployed on the same day within sites during a) June (10 sites) and b) July/August (12 sites) visits in 2023, with 95% confidence intervals (CI) and a histogram from 1000 bootstrap estimates. Estimates are agreement repeatabilities calculated with the ‘rptR’ package (Stoffel et al., 2017), using two Poisson GLMMs with a log-link function and site as a random effect.

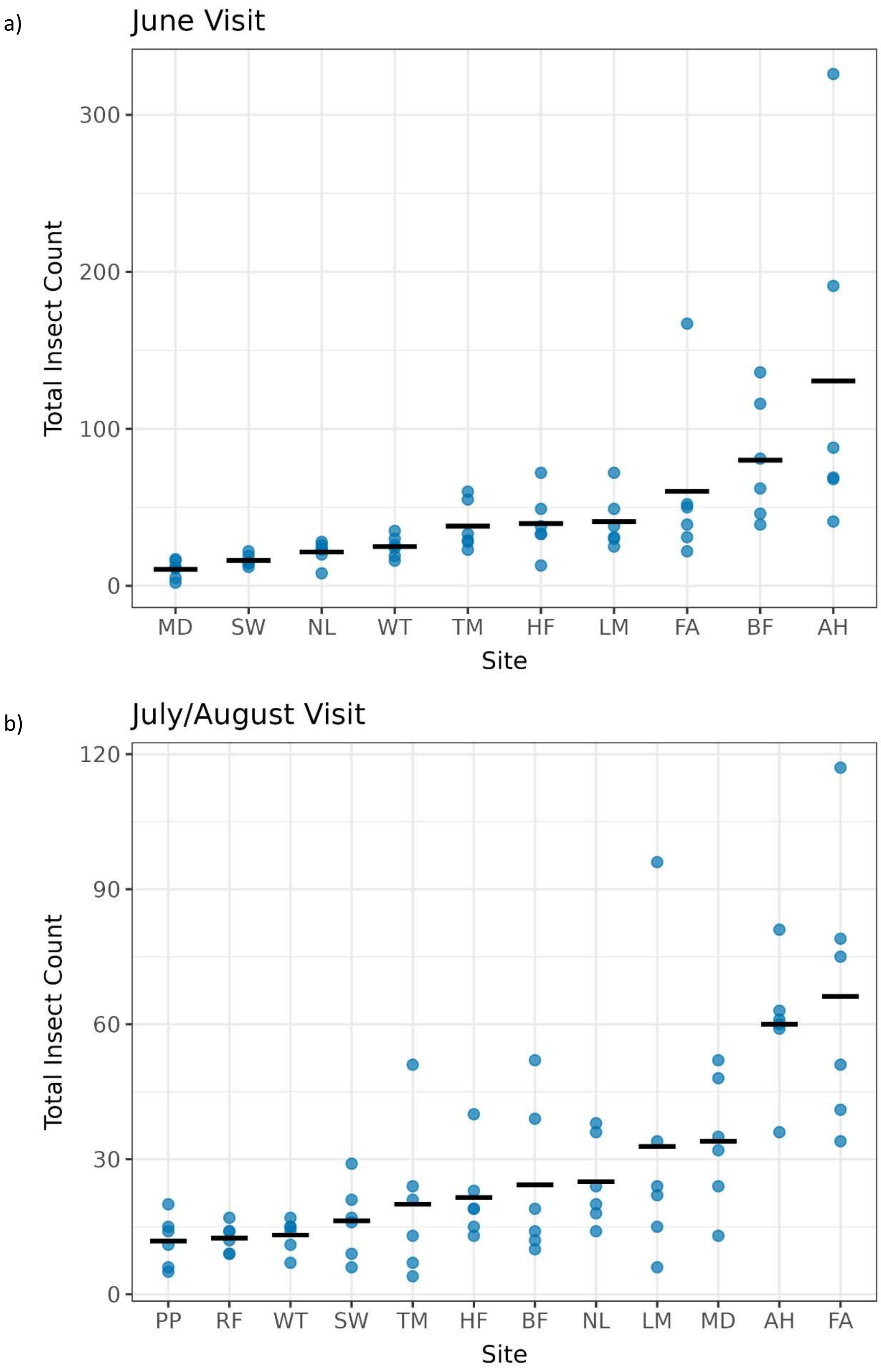


Figure A.4.1.2: Total insect counts on 6 sticky traps deployed on the same day at each site during a) June (10 sites), and b) July/August (12 sites) visits in 2023 (blue points). The mean insect count across the traps for each site during each visit is also shown (black dash). Site name abbreviations are given on the x-axis to allow comparison between a) and b).

References:

Stoffel, M.A., Nakagawa, S., Schielzeth, H., 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods in Ecology and Evolution 8, 1639–1644. https://doi.org/10.1111/2041-210X.12797

Chapter 5: General Conclusions

© Chas Holt

5.1. Synthesis of Results

Exploring spatiotemporal variation in demography can provide vital insights into the environmental drivers of population dynamics and effective and efficient conservation action. In **Chapter 2**, I reviewed the spatiotemporal structure of avian demographic research, and found that most studies have taken place over small spatial scales and annual timescales. While this captures local, short-term effects well, we may be less able to detect the impacts of changes operating over much larger spatial scales and longer timescales, such as land-use or climate change. To further understand the extent of this knowledge gap, it will be important to determine the degree to which local-scale studies can capture large-scale processes. As demonstrated in subsequent chapters, many of the practical barriers to studying demography at large scales can be overcome with collaborative research projects and data collection by citizen scientists.

In **Chapter 3**, I used a long-term, continent-wide bird ringing dataset to show that spatial variation in the productivity of European landbirds is at least partly driven by characteristics of the landscape surrounding breeding sites. Sites within landscapes locally dominated by wetlands and, at larger-scales, low-intensity land-uses are more frequently associated with higher productivity across the bird community. Whilst these results help inform landscape-level conservation actions which could benefit both resident and migratory bird populations across Europe, it is important to recognise that a large proportion of the spatial variation in productivity was left unexplained by the landscape-level variables explored. This suggests that local-scale processes, such as site-level habitat characteristics, and/or additional landscape factors to those examined here may also be important determinants of productivity.

In **Chapter 4**, I recruited citizen scientists across 10 European countries to explore insect prey availability as a mechanism behind the associations between landscape composition and productivity found in Chapter 3. The data on flying insect abundance they collected revealed an overall positive association between insect abundance and cross-community bird productivity at sites, although there was a high degree of variation around this relationship. Interestingly, sites with the lowest productivity always recorded low insect counts, whereas not all sites with high productivity recorded high insect counts. Therefore, while insect prey availability does seem to be a key factor influencing spatial variation in landbird productivity, additional factors, such as nesting habitat availability or predation, may also play an important role. Insect abundance was not related to land-use type or management intensity, and so we did not find evidence that it was driving the high productivity at sites within wetland and low-intensity landscapes. This contrast in responses of insects and birds may reflect the fact that the insect data was highly localised to a single location in the site, while the productivity data was representative of a larger area because of the greater vagility of birds. Although data was not available on site-level habitat for this study, local characteristics are likely important for insect abundance, and are considered in more detail further below.

The large-scale and community-wide scope of the work presented in Chapters 3 and 4 meant that the analyses performed were relatively coarse, which was reflected in the high degree of variation around the patterns observed. The findings outlined above could therefore be seen as relatively conservative, which suggests that the underlying relationships between productivity and landscape structure, and productivity and insect abundance may be much stronger than presented here. This also highlights how challenging it is to identify and mitigate drivers of population dynamics in communities of widespread but declining species, especially because of the potential interactive effects of local and landscape-scale processes. Studies which combine data on drivers at multiple scales can help tease apart these varying processes acting on populations, but this can prove difficult with limited resources.

Comparisons of species with different migratory strategies can also be revealing for understanding drivers of population dynamics (Morrison et al., 2013). Residents and migrants might be expected to show different demographic responses to factors on breeding grounds, because residents experience these conditions all year round, while migrants experience a wide range of conditions across their migratory routes (Vickery et al., 2014). Contrary to this, I found that relationships between productivity and landscape features were largely consistent between species with different migratory strategies (Chapter 3), which is in agreement with previous work identifying co-variation in site-level population trends and productivity of residents and migrants (Morrison et al., 2021). The findings presented here further suggest that migratory species' productivity is strongly driven by impacts of conditions at breeding grounds. However, unlike resident species' productivity, migrant productivity did not show a significant relationship with insect abundance at sites. This could result from the lower sample size associated with many migratory species, which may have reduced our power to detect this relatively weak effect, or it could suggest that insect food availability might not be as important for driving variation in migrant productivity as it is in residents. This, in combination with the lack of landscape effects on insect abundance, may suggest that the high productivity in wetland and low-intensity grassland landscapes detected across residents and migrants is driven by mechanisms other than insect prey availability, or a combination of processes that differ between these species groups. For example, productivity of long-distance migrants in grassland habitats has been shown to be strongly affected by nest predation rates (Pärt, 2001; Rime et al., 2025). Effective conservation action is best informed by an understanding of mechanistic processes, and so future work should look to examine how spatial variation in landbird productivity is related to nest predation rates, and if this is associated with landscape characteristics. For example, the British Trust for Ornithology's Nest Record Scheme monitors nest success rates and, where possible, reasons for nest failure, including predation (Crick et al., 2003). These nest predation rates could be spatially matched to CESs collecting productivity data and in turn related to the landscape variables explored in Chapter 3, to determine if nest predation rates are a possible mechanism for the landscape effects found.

5.2. Annual Variation in Insect Abundance

Annual variation in insect abundance may partly explain the weakness of the observed relationship with site-level productivity at the European scale (Chapter 4). Productivity was measured over several years at each site, and has been shown to be largely spatially consistent across those years (Morrison et al., 2022; Finland productivity data in Chapter 4). In comparison, insect abundance is known to vary considerably from year to year due to weather conditions (Duchenne and Fontaine, 2024; Fourcade et al., 2017), and so its association with bird productivity is also likely to vary in strength from one year to the next. Indeed, annual variation in insect abundance, and spatial variation in the degree of this annual variation, is also evident in some of the data I collected. As part of my research, six UK sites were sampled for insect abundance in 2023 (pilot study reported in Chapter 1) and 2024 (insect monitoring reported in Chapter 4), providing an opportunity to explore annual variation in insect abundance (Figure 5.1). Three sites had consistently high productivity values ('good'), and three sites had consistently low productivity values ('poor'). For three of the sites (two good and one poor), the mean insect count per hour was highly consistent between the two years, whereas the other three sites recorded greater mean insect counts in 2024 compared to 2023. These latter three sites also showed greater between-trap variation in insect counts in 2024, while the sites with consistent mean values showed similar levels of variation across the two years.

As the European-scale insect data was only collected in a single year, we currently have a limited picture of the extent of variation in this relationship between annual insect abundance and bird productivity, and our understanding could be much improved by replicating this data collection across multiple years. For example, a particularly valuable line of enquiry could be to compare spatial and temporal variation in insect abundance across sites and years, and determine if insect abundance shows similarly consistent spatial variation to that observed in productivity (Morrison et al., 2022). Furthermore, the small sample of sites with insect data from the two years revealed that some sites show a greater degree of annual variation in insect abundance compared to others. Within a wider sample, it may be possible to identify environmental characteristics associated with sites showing differing degrees of annual variation in insect abundance, which could inform management of insect populations, and advance our understanding of food limitation in birds.

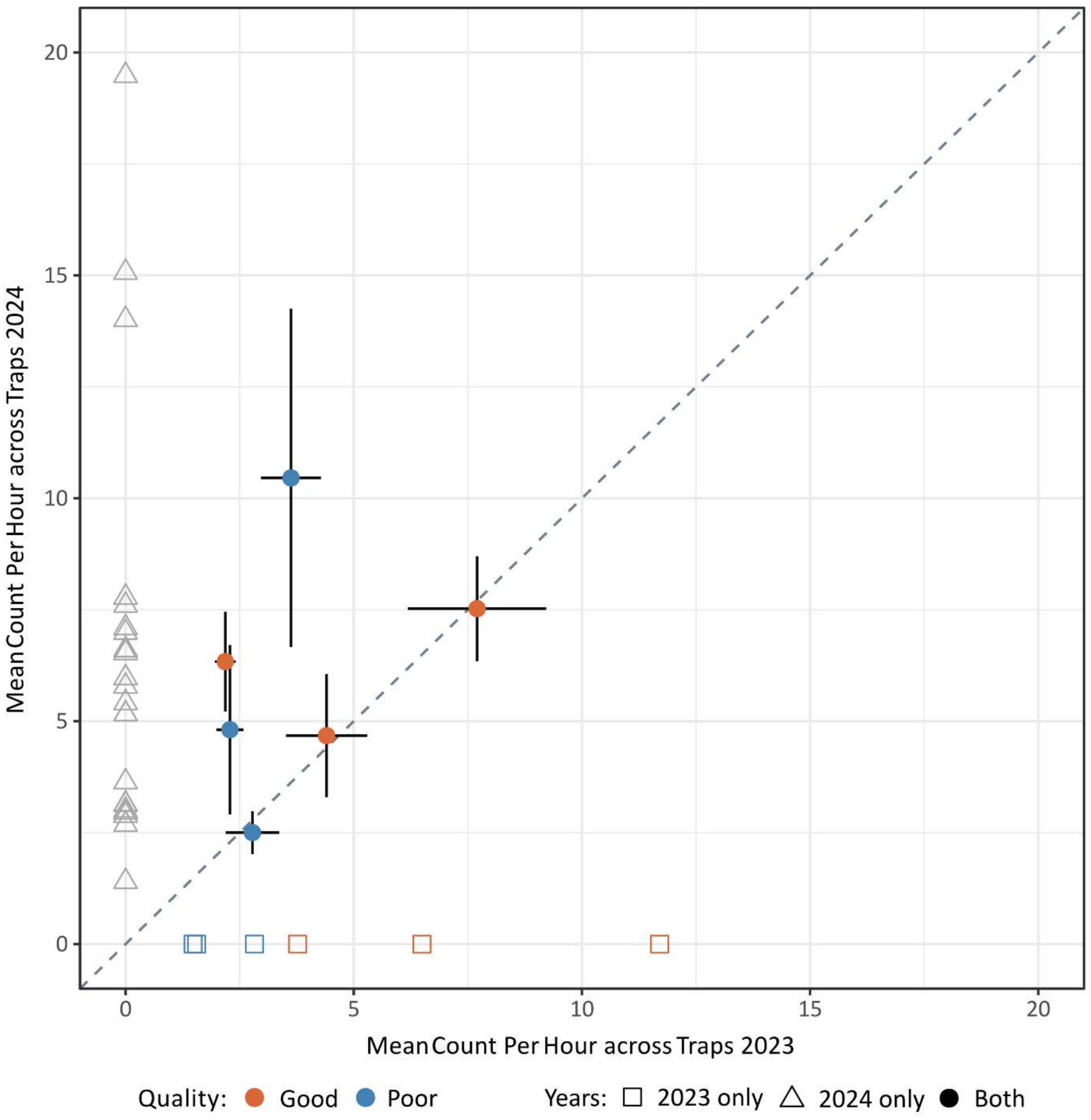


Figure 5.1: Mean insect count per hour on sticky traps at UK sites in 2023 and 2024. The 2023 pilot study sites were grouped into two quality categories: those with consistently high mean bird productivity (‘good’, orange) and those with consistently low mean bird productivity (‘poor’, blue). Circles were monitored in both years, and error bars represent the standard error in insect count per hour across traps at each site. Squares represent sites which were monitored in 2023 only, and triangles represent sites which were monitored in 2024 only. These 2024 sites were not categorised by quality because productivity data was not available for all sites.

One of the main challenges faced in the Europe-wide insect sampling study was the considerable time resources required for administrating the project and manually digitising insect counts from images of the traps, which prevented me from running the sampling again in 2025. A possible solution for a more time-efficient methodology in future years could be the use of machine-learning to digitise the insect counts, and potentially carry out coarse identification and size classification (e.g. Colares et al., 2025). Automation was explored as a possibility for the 2024 study, but the requirement for high quality, standardised images with uniform lighting posed a barrier. Successful automation can be achieved with relatively simple, inexpensive lighting setups and the use of smartphone cameras (Böckmann et al., 2021). However, to maximise the number of sites collecting insect data, we aimed to make the tasks required of volunteers as simple as possible, and so this additional need for equipment was beyond the scope of this study. Having already recruited volunteers, who now have one year of experience with deploying traps, it may be possible to increase the demand of the tasks and retain similar levels of participation. As well as standardised trap photography and automation, a further improvement to this study could include the sampling of multiple locations per site to improve the accuracy of site-level estimates of insect abundance, and to examine local-scale variation, especially if paired with data on local habitat conditions (see below). Furthermore, if Order-level identification was possible, it could be informative to explore different responses to terrestrial and aquatic insect abundance, because aquatic prey have been shown to be of higher quality and more strongly associated with productivity than terrestrial prey in insectivorous birds (Twining et al., 2018).

5.3. Implications for Conservation and Management

Based on the findings presented in this thesis, spatial variation in landbird productivity seems to be driven by a combination of large-scale processes associated with landscape composition, as well as local-scale processes, likely through effects on insect prey availability. A combination of landscape-level conservation strategies and local management actions are therefore needed to increase the number of high-quality breeding sites in Europe and help achieve recovery in landbird populations.

Landscape-level Conservation Strategies

Chapter 3 identified an urgent need to protect and restore wetland landscapes due to their association with high productivity sites. Nearly a quarter of Europe’s wetlands have been lost since 1700, as a result of drainage for agriculture, forestry and urban areas, as well as peatland extraction (Fluet-Chouinard et al., 2023), and so it is important that further loss is prevented by spatial prioritisation of wetlands for protected areas. Recent work in the UK demonstrated that protected areas which contain breeding sites with higher bird productivity rates are also associated with more positive population trends for several European species (Barnes et al., 2023), and so this could help prevent further reductions in landbird populations. However, wetlands are generally well-covered by the protected area network in Europe (Biodiversity Information System for Europe, 2025), and so gains through further protection may be limited. Actions outside of protected areas are likely to be of greater significance for bringing about population recovery in common and widespread species like the landbird species considered in this thesis (Burgess et al., 2019). For example, the results of Chapter 3 showed that sites within urban wetland landscapes can host just as high productivity for migratory species as those within large wetland landscapes. Urban wetlands are at high risk of degradation or destruction (Ward et al., 2010), but, as shown here, provide important habitat for many bird species, including non-aquatic species, as well as contributing a variety of ecosystem services (Morgan et al., 2025). These “urban blue spaces” therefore need to be given proper weight in urban planning that recognises their value, and managed appropriately to prevent pollution and vegetation encroachment.

In addition, landscapes dominated by low-intensity management were also shown to be beneficial for productivity, especially in grassland systems. Compared to high-intensity landscapes, less intensively-managed areas have a greater proportion of primary productivity remaining after human appropriation (Pellissier et al., 2017), reduced chemical inputs and higher habitat heterogeneity with greater retention of semi-natural features (Perkins et al., 2000; Vickery and Arlettaz, 2012). In grasslands, extensive management is typically characterised by low livestock density, reduced inorganic fertiliser and herbicide applications, as well as lower mowing frequency (Dou et al., 2021; Vickery et al., 2001). Extensive grasslands are one of the most threatened habitats in Europe due to intensification and abandonment (Klein et al., 2020; Shipley et al., 2024). Protection of semi-natural grasslands and traditional management practices will therefore be critical for maintaining high productivity sites, while the number of these sites could be increased through widespread restoration of extensively managed grassland landscapes.

Large-scale replication of the conditions associated with high productivity requires policy mechanisms which discourage intensification, and make extensive management and the removal of areas from production economically viable. Subsidies through flexible, regionally appropriate agri-environment schemes are a key method for achieving this (see Shipley et al., 2024), but the success of these schemes has been limited due to political and financial instability preventing the widespread uptake required for large-scale population recovery (Podruzsik & Fertő 2024). Newly emerging biodiversity credit schemes could help with delivering stable income for landowners to support de-intensification and therefore supplement these schemes (Manez & Clifton 2025), especially if organised into landscape recovery projects which facilitate coordinated conservation actions across large areas.

One of the challenges associated with large-scale land-use de-intensification is the need to strike a balance with food production and security. The “land-sharing” and “land-sparing” paradigms represent the two extremes of land-use strategies to balance the conservation of natural habitats with food production. Land-sharing strategies involve the co-existence of biodiversity and lower intensity agriculture across the entire landscape, while land-sparing approaches involve strictly separating smaller areas of high-intensity agricultural land from protected natural areas. The results of Chapter 3 indicated that, for the most part, productivity at sites within medium-intensity landscapes did not differ from that at sites within high-intensity landscapes, and so significant reductions in land-use intensity would be required to see increases in bird productivity and potential recovery of populations. This could be more achievable under land-sparing scenarios, rather than widespread but small reductions in land-use intensity seen under land-sharing. Previous research in the UK demonstrated that land-sparing scenarios were the most beneficial for bird populations, including extreme land-sparing scenarios with wetland restoration, and “three-compartment” sparing scenarios where areas of low-yield farmland were included alongside spared natural areas and high-yield arable land (Finch et al., 2021). The conservation recommendations made in this thesis could fit within these land-sparing scenarios, with the protection and restoration of wetlands and extensive grasslands within spared areas.

Informing Local Management Actions

The results of Chapter 4 highlight the importance of conserving and enhancing insect populations for supporting landbird populations in Europe. It is not yet clear what is driving the variation found in insect populations at sites, but the fact that landscape effects on insect abundance were not identified suggests that local factors are likely to be important. Further investigation is therefore needed to identify the site-level characteristics beneficial for insects, especially where this can directly inform management actions.

The focus on landscape structure in this thesis was partly a result of the availability of remotely sensed data for the vast area covered by the EuroCES dataset. This enabled me to identify factors driving spatial variation in productivity at a European scale, but the large degree of unexplained variation demonstrates that the limited resolution of this approach could have missed some key smaller-scale variables. For example, the hydrological data used in Chapter 3 are likely to have overlooked the presence of small water bodies in non-wetland landscapes. These are important sources of insects in farmland, especially when appropriately managed (Lewis-Phillips et al., 2020), with positive effects on insectivorous bird productivity (Berzins et al., 2022; McKellar et al., 2025). Fine-scale variation in vegetation structure is another potentially important variable that cannot be easily detected with remote-sensing, but has been shown to influence insect abundance, which increases with structural diversity (Crist et al., 2006), as well as prey accessibility for foraging insectivores (Kleijn et al., 2010; Vickery et al., 2001). A further consideration when working with remotely sensed data is that it typically represents a snapshot in time rather than recording changing conditions, such as local soil moisture levels, which are important for insect abundance (Carroll et al., 2011), with implications for birds foraging in these habitats (Poulin et al., 2002). Measurement of wetness throughout the season can provide insights into how local land management practices interact with weather conditions to influence habitat quality, but on-the-ground data is typically required.

Fine-scale data which can be used to explore local processes such as these often require intensive fieldwork and thus research projects collecting such data are typically small in extent (Klein et al., 2020). The citizen science study detailed in Chapter 4, and indeed the EuroCES scheme in general, provide great examples of where local-scale data collection can be replicated over large areas to expand the scope of research projects. Citizen science can be used to collect robust, reliable data if well-designed with trained volunteers (Brown and Williams, 2019). These studies need careful design to maximise the information collected for answering the research questions, while ensuring the methodology is manageable for participants to encourage as wide a participation as possible.

5.4. Conclusion

Collectively, the results presented in this thesis highlight the importance of considering spatial and temporal scales when interpreting patterns in demography and potential drivers, and informing conservation actions. Productivity-based conservation prioritisation requires not only protecting the best-quality breeding sites, but also replicating the associated conditions across large-scales. Key recommendations for future work are 1) further investigation of the mechanisms driving landscape composition effects on productivity, 2) continuation of the Europe-scale insect project in future years, with potential improvements to the methodology, and 3) exploration of the local-scale conditions which might be important drivers of insect abundance and productivity, and can inform management actions. The most significant takeaway from this thesis is the incredible value of collaborative research projects across institutes and citizen science to draw links between local-scale processes and large-scale patterns.

References

Barnes, A.E., Davies, J.G., Martay, B., Boersch-Supan, P.H., Harris, S.J., Noble, D.G., Pearce-Higgins, J.W., Robinson, R.A., 2023. Rare and declining bird species benefit most from designating protected areas for conservation in the UK. Nat Ecol Evol 7, 92–101. https://doi.org/10.1038/s41559-022-01927-4

Berzins, L.L., Morrissey, C.A., Howerter, D.W., Clark, R.G., 2022. Conserving wetlands in agroecosystems can sustain aerial insectivore productivity and survival. Can. J. Zool. 100, 617–629. https://doi.org/10.1139/cjz-2021-0204

Biodiversity Information System for Europe (2025) Protected Areas. Available at: https://biodiversity.europa.eu/europes-biodiversity/protected-areas (Accessed: 14 February 2026).

Böckmann, E., Pfaff, A., Schirrmann, M., Pflanz, M., 2021. Rapid and low-cost insect detection for analysing species trapped on yellow sticky traps. Sci Rep 11, 10419. https://doi.org/10.1038/s41598-021-89930-w

Brown, E.D., Williams, B.K., 2019. The potential for citizen science to produce reliable and useful information in ecology. Conservation Biology 33, 561–569. https://doi.org/10.1111/cobi.13223

Burgess, M., Gregory, R., Wilson, J., Gillings, S., Evans, A., Chisholm, K., Southern, A., Eaton, M., 2019. A new framework of spatial targeting for single-species conservation planning. Landscape Ecol 34, 2765–2778. https://doi.org/10.1007/s10980-019-00919-3

Carroll, M.J., Dennis, P., Pearce-Higgins, J.W., Thomas, C.D., 2011. Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. Global Change Biology 17, 2991–3001. https://doi.org/10.1111/j.1365-2486.2011.02416.x

Colares, L.F., Peres, C.A., Dambros, C.S., 2025. Life history induces markedly divergent insect responses to habitat loss. Journal of Animal Ecology n/a. https://doi.org/10.1111/1365-2656.70117

Crick, H.Q.P., Baillie, S.R., Leech, D.I., 2003. The UK Nest Record Scheme: its value for science and conservation. Bird Study 50, 254–270. https://doi.org/10.1080/00063650309461318

Crist, T.O., Pradhan-Devare, S.V., Summerville, K.S., 2006. Spatial variation in insect community and species responses to habitat loss and plant community composition. Oecologia 147, 510–521. https://doi.org/10.1007/s00442-005-0275-1

Dou, Y., Cosentino, F., Malek, Z., Maiorano, L., Thuiller, W., Verburg, P.H., 2021. A new European land systems representation accounting for landscape characteristics. Landscape Ecol 36, 2215–2234. https://doi.org/10.1007/s10980-021-01227-5

Duchenne, F., Fontaine, C., 2024. Weather explains inter-annual variability, but not the temporal decline, in insect biomass. Insect Conservation and Diversity 17, 932–937. https://doi.org/10.1111/icad.12769

Finch, T., Day, B.H., Massimino, D., Redhead, J.W., Field, R.H., Balmford, A., Green, R.E., Peach, W.J., 2021. Evaluating spatially explicit sharing-sparing scenarios for multiple environmental outcomes. Journal of Applied Ecology 58, 655–666. https://doi.org/10.1111/1365-2664.13785

Fluet-Chouinard, E., Stocker, B.D., Zhang, Z., Malhotra, A., Melton, J.R., Poulter, B., Kaplan, J.O., Goldewijk, K.K., Siebert, S., Minayeva, T., Hugelius, G., Joosten, H., Barthelmes, A., Prigent, C., Aires, F., Hoyt, A.M., Davidson, N., Finlayson, C.M., Lehner, B., Jackson, R.B., McIntyre, P.B., 2023. Extensive global wetland loss over the past three centuries. Nature 614, 281–286. https://doi.org/10.1038/s41586-022-05572-6

Fourcade, Y., Ranius, T., Öckinger, E., 2017. Temperature drives abundance fluctuations, but spatial dynamics is constrained by landscape configuration: Implications for climate-driven range shift in a butterfly. Journal of Animal Ecology 86, 1339–1351. https://doi.org/10.1111/1365-2656.12740

Kleijn, D., Schekkerman, H., Dimmers, W.J., Van Kats, R.J.M., Melman, D., Teunissen, W.A., 2010. Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits Limosa l. limosa in the Netherlands. Ibis 152, 475–486. https://doi.org/10.1111/j.1474-919X.2010.01025.x

Klein, N., Theux, C., Arlettaz, R., Jacot, A., Pradervand, J.-N., 2020. Modeling the effects of grassland management intensity on biodiversity. Ecology and Evolution 10, 13518–13529. https://doi.org/10.1002/ece3.6957

Lewis-Phillips, J., Brooks, S.J., Sayer, C.D., Patmore, I.R., Hilton, G.M., Harrison, A., Robson, H., Axmacher, J.C., 2020. Ponds as insect chimneys: Restoring overgrown farmland ponds benefits birds through elevated productivity of emerging aquatic insects. Biological Conservation 241, 108253. https://doi.org/10.1016/j.biocon.2019.108253

Manez, K.S., Clifton, J., 2025. Biodiversity credits: a new currency to support nature conservation? Oryx 59, 319–324. https://doi.org/10.1017/S0030605324001467

McKellar, A.E., Berzins, L.L., Morrissey, C.A., Michelson, C.I., Clark, R.G., 2025. The positive influence of wetlands on reproductive success and body mass in an aerial insectivore is more pronounced in intensively cropped agroecosystems. Ornithological Applications duaf051. https://doi.org/10.1093/ornithapp/duaf051

Morgan, M.C., Forster, R., Hopkins, C.R., Gómez, A., 2025. Just add water: Urban blue spaces increase avian richness and functional diversity. bioRxiv 2025.06.18.660350. https://doi.org/10.1101/2025.06.18.660350

Morrison, C.A., Butler, S.J., Clark, J.A., Arizaga, J., Baltà, O., Cepák, J., Nebot, A.L., Piha, M., Thorup, K., Wenninger, T., Robinson, R.A., Gill, J.A., 2022. Demographic variation in space and time: implications for conservation targeting. Royal Society Open Science 9, 211671. https://doi.org/10.1098/rsos.211671

Morrison, C.A., Butler, S.J., Robinson, R.A., Clark, J.A., Arizaga, J., Aunins, A., Baltà, O., Cepák, J., Chodkiewicz, T., Escandell, V., Foppen, R.P.B., Gregory, R.D., Husby, M., Jiguet, F., Kålås, J.A., Lehikoinen, A., Lindström, Å., Moshøj, C.M., Nagy, K., Nebot, A.L., Piha, M., Reif, J., Sattler, T., Škorpilová, J., Szép, T., Teufelbauer, N., Thorup, K., van Turnhout, C., Wenninger, T., Gill, J.A., 2021. Covariation in population trends and demography reveals targets for conservation action. Proceedings of the Royal Society B: Biological Sciences 288, 20202955. https://doi.org/10.1098/rspb.2020.2955

Morrison, C.A., Robinson, R.A., Clark, J.A., Risely, K., Gill, J.A., 2013. Recent population declines in Afro-Palaearctic migratory birds: the influence of breeding and non-breeding seasons. Diversity and Distributions 19, 1051–1058. https://doi.org/10.1111/ddi.12084

Pärt, T., 2001. The effects of territory quality on age-dependent reproductive performance in the northern wheatear, Oenanthe oenanthe. Animal Behaviour 62, 379–388. https://doi.org/10.1006/anbe.2001.1754

Pellissier, V., Mimet, A., Fontaine, C., Svenning, J.-C., Couvet, D., 2017. Relative importance of the land-use composition and intensity for the bird community composition in anthropogenic landscapes. Ecol. Evol. 7, 10513–10535. https://doi.org/10.1002/ece3.3534

Perkins, A.J., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Morris, A.J., Barnett, P.R., 2000. Habitat characteristics affecting use of lowland agricultural grassland by birds in winter. Biological Conservation 95, 279–294. https://doi.org/10.1016/S0006-3207(00)00042-2

Podruzsik, S., Fertő, I., 2024. Motivations for farmers' participation in agri-environmental scheme in the EU, literature review. Open Agriculture 9. https://doi.org/10.1515/opag-2022-0379

Poulin, B., Lefebvre, G., Mauchamp, A., 2002. Habitat requirements of passerines and reedbed management in southern France. Biological Conservation 107, 315–325. https://doi.org/10.1016/S0006-3207(02)00070-8

Rime, Y., Korner, P., Helm, B., Müller, T., Amrhein, V., Liechti, F., Meier, C.M., 2025. Drivers of nest site selection and breeding success in an Alpine ground-nesting songbird. J Ornithol 166, 357–370. https://doi.org/10.1007/s10336-024-02221-9

Shipley, J.R., Frei, E.R., Bergamini, A., Boch, S., Schulz, T., Ginzler, C., Barandun, M., Bebi, P., Bolliger, J., Bollmann, K., Delpouve, N., Gossner, M.M., Graham, C., Krumm, F., Marty, M., Pichon, N., Rigling, A., Rixen, C., 2024. Agricultural practices and biodiversity: Conservation policies for semi-natural grasslands in Europe. Current Biology 34, R753–R761. https://doi.org/10.1016/j.cub.2024.06.062

Twining, C.W., Shipley, J.R., Winkler, D.W., 2018. Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. Ecology Letters 21, 1812–1820. https://doi.org/10.1111/ele.13156

Vickery, J. a., Tallowin, J. r., Feber, R. e., Asteraki, E. j., Atkinson, P. w., Fuller, R. j., Brown, V. k., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology 38, 647–664. https://doi.org/10.1046/j.1365-2664.2001.00626.x

Vickery, J., Arlettaz, R., 2012. The importance of habitat heterogeneity at multiple scales for birds in European agricultural landscapes, in: Fuller, R.J. (Ed.), Birds and Habitat. Cambridge University Press, pp. 177–204. https://doi.org/10.1017/CBO9781139021654.009

Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J., Gregory, R.D., 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156, 1–22. https://doi.org/10.1111/ibi.12118

Ward, M.P., Semel, B., Herkert, J.R., 2010. Identifying the ecological causes of long-term declines of wetland-dependent birds in an urbanizing landscape. Biodivers Conserv 19, 3287–3300. https://doi.org/10.1007/s10531-010-9893-y