Optimising habitat creation for woodland birds: the relative importance of local *vs* landscape scales

Robin C. Whytock

March 2018

Thesis submitted for the degree of Doctor of Philosophy

Biological and Environmental Sciences, School of Natural Sciences

The University of Stirling

Declaration

I hereby declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others.

…………………………………………………………………….

Robin C. Whytock

SUMMARY

Global land-use change and industrialisation has driven biodiversity declines and impaired ecosystem functioning. Recently, there have been large-scale efforts to not only halt habitat loss but create and restore habitat on formerly managed (e.g. agricultural) land. However, although the effects of habitat loss and fragmentation on biodiversity are well understood, our understanding of how biodiversity responds to habitat created in a patchy configuration is not. In particular, little is known about the relative importance of local (e.g. patch size) *vs* landscape scales (e.g. amount of habitat in the landscape) for restoring biodiversity in created habitat. Here, a long-term, large-scale natural experiment (the Woodland Creation and Ecological Networks project) was used to understand how bird species, communities and behaviour respond to woodland created in a patchy configuration on post-agricultural land. I used a combination of direct and indirect survey methods to quantify bird diversity, abundance and vocal behaviour in post-agricultural woodlands of known age in Great Britain. I show that secondary woodlands favour generalist species and older patches contain more individuals and species due to their vegetation structure. In relative terms, local-scale factors such as patch size made the greatest contribution to bird diversity and abundance. Colonisation events drive community assembly in new habitat, and I found that large-scale (km^2) habitat patterns were more important than patch-level factors during colonisation of breeding territories by a long distance migrant bird (Willow Warbler *Phylloscopus trochilus*). Land management practices surrounding a habitat patch can also affect its perceived quality and relative attractiveness to potential colonisers. Using the Eurasian Wren *Troglodytes troglodytes* as a model species, I found that high proportions of agricultural land at woodland edges caused an increase in perceived predation risk. In conclusion, I suggest that post-agricultural woodlands rapidly provide valuable habitat for generalist woodland birds. Local, patch-level factors (area, vegetation structure) also appear relatively more important than landscape factors for woodland bird communities. Land-managers seeking to maximise the benefits of woodland creation for birds should thus focus on creating large patches with a diverse vegetation structure.

ACKNOWLEDGEMENTS

Many people describe their PhD experience as highly isolating. I am happy to say that I did not share this experience. Rather, I have had great companionship from family, friends, colleagues and supervisors throughout my 3.5 years as a PhD student, and I would not have made it without their tremendous support.

First, I am extremely grateful to Kirsty Park who has been an inspirational supervisor and incredible mentor. Thank you for your critical feedback and eye for scientific rigour. Likewise, Elisa Fuentes-Montemayor, Kevin Watts, Phil McGowan and Nicholas Macgregor have all been highly supportive and inspiring co-supervisors and collaborators, and I hope we can work together again in future.

My wife, Baru and sons Jason and Arrey deserve a special thank you. I have spent the last 7.5 years in full-time education and on many occasions have had to prioritise studying over family. Despite this they have remained patient and supportive through good and bad. I am forever grateful and promise to make up for lost time.

I would like to say a huge thankyou to my mum Hazel, brother Rory, sister's Heather and Polly, dad Andy, second mum Sally, second dad Dmytro, sister in-law Daisy and nephew Rowan, who were all there for me during the highs and lows of the past 3.5 years. Also, a huge thankyou to Zarah Pattison, Chris Pollard, Rachael Cooper-Bohannon, Rebecca Barclay, Andy Carroll, Pauline Pantoja, Mark Wilson, Nils Bunnefeld, Tom Jones, Dan Davis, Tom Scullion, Roland Digby, Nigel Willby and James and Bethan Christie for long coffee breaks, extended phone calls and general friendship throughout.

I received substantial assistance with data collection from many people both in the field and in the lab. In particular I would like to thank Patanjaly Andrade, Ruth Howe, Emma Gesquière, Julia Kovacs, Lefora Williams, Eilidh Call, Jennifer Mann, Hannah Easdon, Rory Whytock and Paul French for their contributions.

Dozens of people have passed through my small office since I first arrived in 2014. Thanks to everyone who has put up with my constant fidgeting, distracting conversation, terrible jokes, (occasional) grouching and disgraceful desk-space, but most of all thanks for being great company.

I would also like to thank everyone involved in the IAPETUS Doctoral Training Partnership, and Forest Research for supporting my CASE studentship. Sam Lattaway of the National Forest Company kindly provided additional financial support towards my work on bioacoustic technology. Thanks also to everyone who has been involved with the Woodland Creation and Ecological networks project, past and present.

Finally, I have thoroughly enjoyed being part of Stirling University's Department of Biological and Environmental Sciences for the past 7.5 years during my undergraduate degree and now PhD. There are too many people to list here, so I would like to thank everyone in the department for their help, advice and companionship during that time.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

LIST OF APPENDICES

CHAPTER 1

GENERAL INTRODUCTION

LAND-USE CHANGE AND ITS IMPACT ON THE NATURAL ENVIRONMENT

The industrial revolution of the 1700s triggered dramatic changes in land management practices that transformed the Earth's ecosystems and biophysical functioning (Figure 1.1) (Lambin 2001). Formerly natural landscapes were converted to agricultural land, and cleared to be exploited for oil, minerals and timber. Remaining natural habitat became fragmented (i.e. broken into smaller pieces) and embedded in a patchwork or 'matrix' of managed land-cover. For many societies, large-scale industrialisation and land-use change paved the way to improved food production and security, better health, universal access to education and increased life expectancy. However, industrialisation also came at the expense of the natural environment and its biodiversity, which in turn affected those communities who rely on natural resources for their livelihoods. The continued exploitation of globally limited resources also poses a threat to future societies, who will be shouldered with the challenge of coping with and repairing the environmental damage caused by our current and past actions.

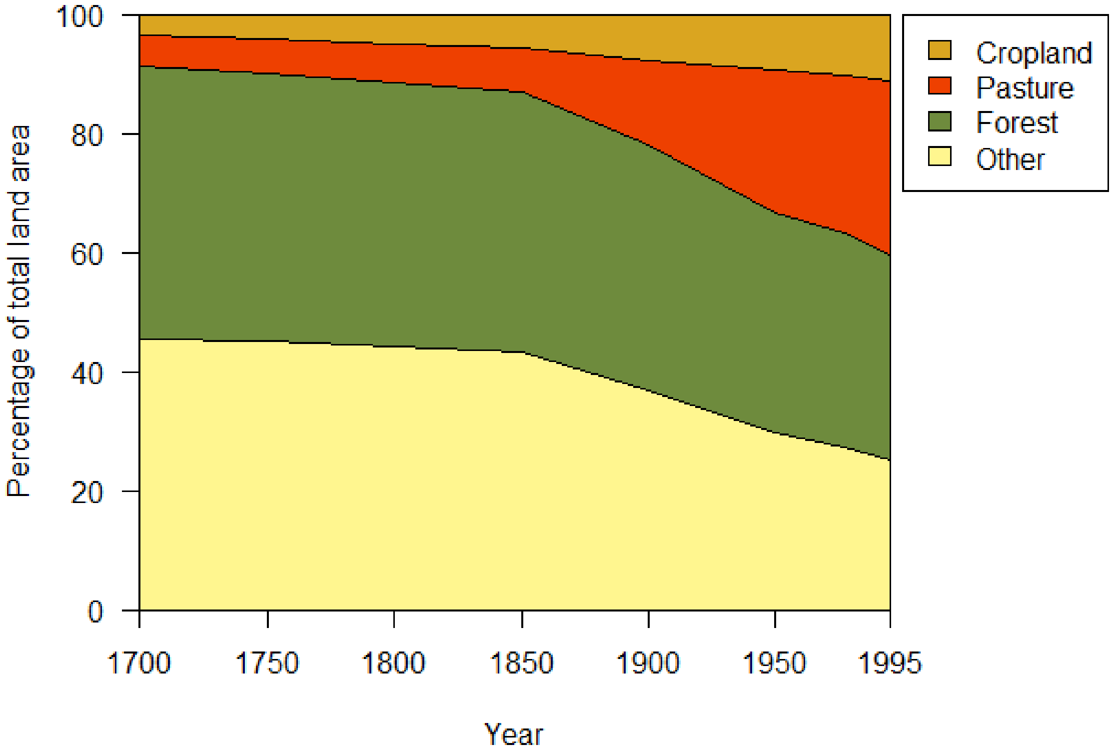


Figure 1.1 Estimated global land-use change from 1700 to 1995. Adapted from Figure 1 in Lambin et al. (2001).

Perhaps the most damaging consequence of land-use change has been the fragmentation and loss of natural habitats, which threatens the earth's animal and plant diversity (Haddad et al. 2015; Maxwell et al. 2016). Habitat loss can also impact on environmental processes, for example contributing to greenhouse gas emissions or causing landslides and exacerbating floods (e.g. García-Ruiz et al. 2017). For biodiversity (the diversity of species and their genes), habitat fragmentation affects how individuals move through the landscape during dispersal and colonisation (Hanski 1994), which disrupts gene flow between previously connected populations. This can cause local and global extinctions of sensitive species and can impair ecosystem resilience to future change, such as a warming climate (Oliver et al. 2015).

By the 1970s there was increasing interest in combining biogeography and metapopulation theories with conservation planning (MacArthur & Wilson 1967; Diamond 1975) to understand how changes in the spatial arrangement (i.e. configuration) and amount (i.e. composition) of natural habitat alters ecosystems (Simberloff & Abele 1976). Early work focused on understanding patterns of biodiversity responses to habitat loss due to fragmentation, with the aim of informing the size, shape and location of protected areas (Diamond 1975). Later, attention moved to understanding the ecological processes that cause spatial and temporal patterns of biodiversity change (e.g. Tewksbury et al. 2008; Thompson 2007). More recently, there has been a focus on disentangling the impact of habitat loss and fragmentation on ecosystem function (e.g. the Stability of Altered Forest Ecosystems Experiment). However, given the extent of historic losses in many regions, it is increasingly acknowledged that we must also seek to understand how habitat creation on formerly managed (e.g. agricultural) land can be optimised to benefit biodiversity using the limited resources available for conservation (Dolman 2012; Humphrey et al. 2015; Watts et al. 2016).

Habitat creation vs habitat loss

Until recently, actions to restore or *create* habitat on formerly managed land have typically been informed by lessons learned from studying biodiversity responses to habitat *loss* (i.e. fragmentation) (Humphrey et al. 2015). The rationale for this has been that biodiversity declines can theoretically be reversed by creating and replicating habitat patterns that minimise biodiversity declines following habitat loss. However, biodiversity responses to habitat loss and habitat creation are not necessarily reciprocal. The reasons for this are two-fold. Firstly, biodiversity declines due to habitat loss occur because the *pre-existing* ecological community is *disassembled* over time, whereas biodiversity is expected to increase following habitat creation because a *new* community *assembles* over time. Secondly, most assessments of biodiversity responses to habitat loss are made over relatively short timescales (Haddad et al. 2015), which can be misleading because species with slow life histories can persist long after the surrounding landscape has been fragmented. Often, such remnant populations will eventually become extinct following large-scale land-use change, but there is a delayed response or ‘extinction debt’ to be paid at a later date (Tilman et al. 1994; Kuussaari et al. 2009), sometimes centuries after the initial disturbance. Thus, some species can, at least initially, appear immune to the effects of habitat fragmentation or loss, and this might lead us to conclude that such species are tolerant of fragmented landscapes in general. However, in the case of new habitat created in a patchy configuration, there can be a substantial time lag between habitat creation, resource development in a patch and eventual colonisation, the length of which will depend on interactions between a species’ life history traits such as dispersal ability and the composition or configuration of the surrounding landscape. This time lag occurs in the opposite direction to an extinction debt, and is known as a ‘colonisation (or ‘immigration’) credit’ (Jackson & Sax 2010). Such ecological time lags present a significant challenge to understanding how best to create and configure new habitat at large spatial scales (Kuusaari et al. 2009; Jackson & Sax 2010).

Forest loss and its impacts on biodiversity

Except for Polar Regions, almost all terrestrial environments have been affected by land-use change, but temperate regions have experienced some of greatest and most prolonged losses of natural habitat (Haddad et al. 2015). Temperate forest, for example, declined substantially following large-scale timber exploitation (e.g. for ship building and sea defences) and clearance for cropland and pasture. Forests support more biodiversity than any other terrestrial habitat and provide significant social, economic and environmental benefits (Moseley et al. 2015; García-Ruiz et al. 2017), and habitat loss and fragmentation pose the greatest threat to global forest biodiversity (Haddad et al. 2015; Maxwell et al. 2016).

Following a decline of approximately 29% since the 1700s, global forest cover now stands at 30.8% of the Earth's land surface (Food and Agriculture Organisation 2017) and remaining forest is highly fragmented (Haddad et al. 2015). There is significant regional variation in the scale of deforestation, however. In Great Britain, forest cover (Plate 1) currently stands at approximately 13%. This comprises approximately 5% native broadleaf forest or 'woodland' and 8% commercial plantations, which are typically coniferous and non-native (e.g. monocultures of Sitka spruce *Picea sitchnesis*). Although forest loss in Great Britain lies at the extreme end of the spectrum of loss, similar patterns have occurred in other temperate regions (Haddad et al. 2015).

Plate 1.1 Example of an immature (*c.*20 years old) broadleaf woodland (right) in an agricultural landscape in Great Britain (overlooking the village of Bo'ness) with surrounding scattered trees, arable fields and hedgerows.

Population trends of forest-dependent species also show significant regional variation (Figure 1.2). In Europe, the common forest bird index (standardised population trends) declined by 5% between 1980 and 2015 (Figure 1.2a), but in the United Kingdom the similar woodland bird index declined by 23% between 1970 and 2015 (Figure 1.2b).

Despite these declines, however, both indices have stabilised in the past decade, with continuing declines of obligate forest specialists such as Lesser-spotted woodpecker *Dendrocopos minor* being offset by increasing numbers of more generalist, facultative forest species such as Blackcap *Sylvia atricapilla* (Balmer et al. 2013). For other taxa, such as woodland mammals, invertebrates, plants and reptiles, the picture is less clear. This is in-part due to insufficient long-term population trend data and also because other taxa (particularly mammals) are less diverse than birds, making it difficult to quantify general, community-level trends.

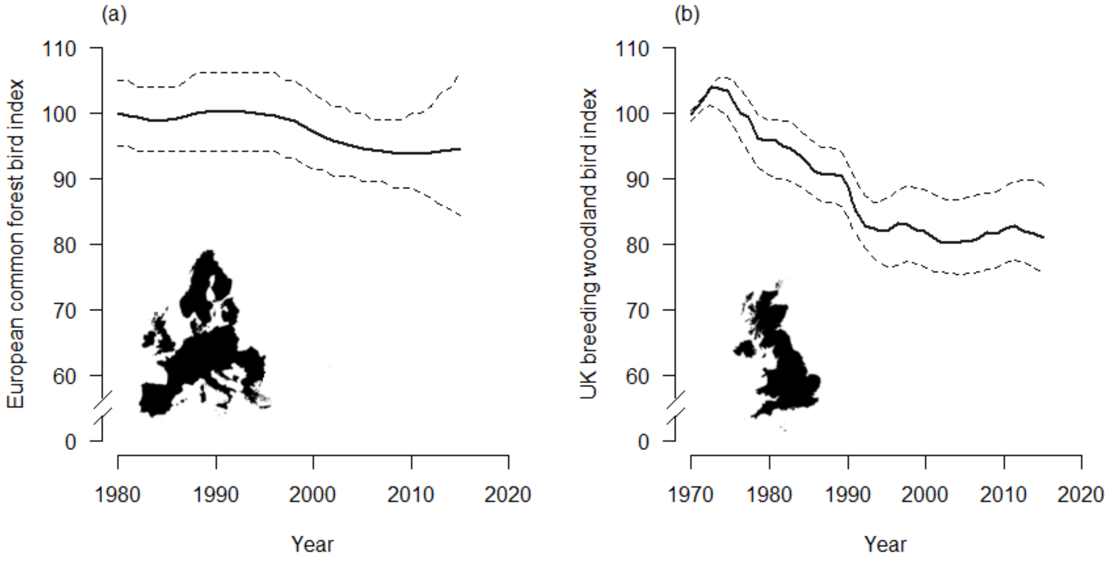


Figure 1.2 Estimated forest/woodland bird population trends in Europe (a: 34 species; source EBCC/BirdLife/RSPB/CSO) and the United Kingdom (b: 37 species; source BTO/RSPB). Black lines show smoothed indices and dashed lines are 95% confidence intervals. Inset maps are © EuroGeographics for the administrative boundaries.

Conserving forest biodiversity

Landscape-scale biodiversity conservation combines efforts to protect existing natural habitats with those aimed at restoring and creating new habitat. Habitat creation is often focused on increasing the size of existing sites or improving ‘connectivity’ between remnant natural patches, with a particular focus on ancient woodland in Great Britain (Lawton 2010). Ancient woodland is defined as a stand that has existed on historic maps since 1600 AD in England and Wales, or 1750 AD in Scotland. Although these dates are used for practical purposes (map availability), many ancient woodlands are probably much older and likely became established soon after the last glacial period *c.*12,000 years ago.

Ancient woodland in good condition is often said to be ‘irreplaceable’, but secondary woodland can also have substantial value for biodiversity. Theory predicts that natural communities will re-establish over time given a sufficient source of colonists. However, for many taxa it remains unknown if communities will ever resemble those found in ancient habitat, and one of the most important unanswered questions in landscape conservation is how long will it take for communities to re-establish after habitat creation? This is a difficult question to answer because community assembly in most habitats occurs over decades or centuries. Thus, it is rarely possible to observe community assembly over time using experimental approaches because the observation time required exceeds the lifetime of most ecological studies, and certainly exceeds the lifespan of most ecologists.

To address this problem, it is possible to use ‘natural’ or ‘mensurative’ approaches (McGarigal & Cushman 2002; Lindenmayer 2009; Watts et al. 2016). These methods seek to strike a balance between the rigidity of controlled experiments, which are often limited in scale, and the often weakly controlled nature of observational studies (Haddad et al. 2015). One of the main benefits of a carefully designed natural experiment is that it can encompass much larger scales than highly controlled experimental designs (Haddad et al. 2015). For example, the Metatron is a relatively large, well-controlled, enclosed experiment designed to simulate a ‘metaecosystem’ (Stokstad 2012). This state-of-the-art facility can be used to study how changes in landscape configuration affect dispersal under a warming climate, for example. However, although the Metatron is large relative to other true experiments, it remains relatively small (10s of m^2) in a landscape context, which limits the taxa that can be studied. Furthermore, the enclosed design leads to boundary effects that are likely to influence disperser movement in ways that could be difficult to extrapolate to natural environments (Stokstad 2012). These limitations reinforce the need for natural experiments.

There are now several well-known natural experiments designed to understand how individuals, populations and communities respond to large-scale changes in habitat configuration or composition under near-natural or natural conditions. These include the Savannah River Site Corridor Experiment, USA (Haddad 1999), the Biological Dynamics of Forest Fragments Project, Brazil (Laurance et al. 2011), the Stability of Altered Forest Ecosystems Experiment in Malaysian Borneo (Ewers et al. 2011), and the Nanangroe Natural Experiment, Australia (Lindenmayer et al. 2001). These vary in scale from hundreds of m^2 to km^2, and in scope from studying the specific effects of corridor creation on dispersal behaviour to understanding whole ecosystem responses to large-scale habitat loss. Experiments like these have provided valuable insights into the effects of habitat fragmentation on biodiversity from individual to community levels, but they all share on main limitation that limits their usefulness for studying habitat *creation* - they are all relatively young. Thus, they can only give limited insights into the long-term temporal responses of biodiversity to habitat fragmentation and creation, and for many taxa with slow life histories they cannot be used to understand how long it will take for communities to become re-established in new habitat.

These limitations are being addressed by a new type of natural experiment that uses historic habitat creation to inform future restoration efforts, such as the Woodland Creation and Ecological Networks (WrEN) project (Watts et al. 2016). The WrEN project is a collaboration between the University of Stirling and Forest Research, which receives ongoing support and input from the National Forest Company, the Woodland Trust, the Department for the Environment, Food and Rural Affairs, Natural England and other stakeholders. This diversity of stakeholders from the public and private sectors has driven the WrEN project's research agenda; to understand how habitat creation can be optimised to benefit biodiversity, and to disentangle the relative importance of local and landscape scales for biodiversity in fragmented secondary habitats (i.e. woodland). The WrEN project uses a patch-based approach and exploits detailed historical maps in Great Britain to estimate woodland creation dates over the past 160 years (Watts et al. 2016) (n = 101 woods; Figure 1.3). To date, the WrEN project has recorded a total of over 1100 species, including bats, small terrestrial mammals, birds, ground and aerial invertebrates, vascular plants, lichens and bryophytes, and has over 150 measures of local and landscape-scale characteristics for each patch and its surrounding landscape. This unique dataset offers a wealth of opportunities for disentangling the relative importance of spatial and temporal scales for biodiversity in habitats created in a patchy configuration.

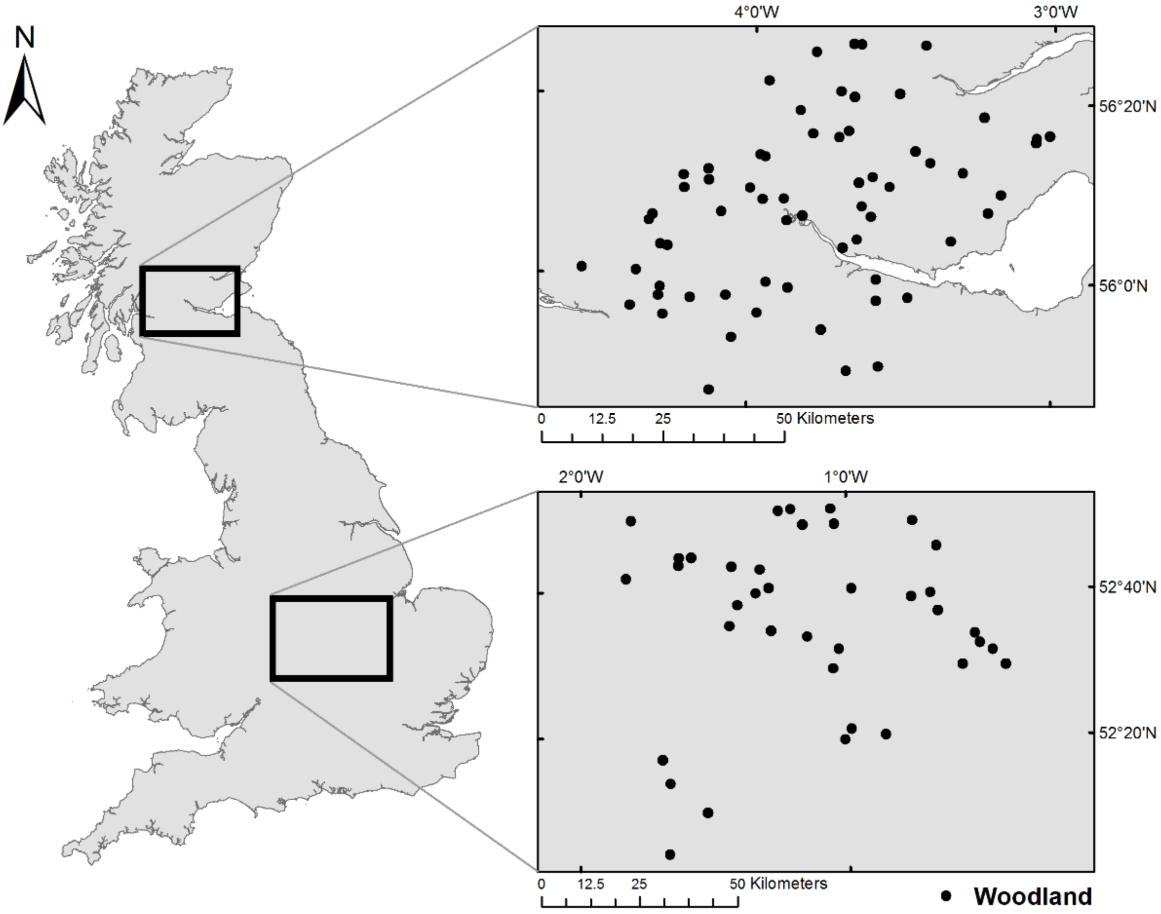


Figure 1.3 Map of Great Britain showing the two study areas in Scotland and England with approximate locations of the study woodlands (*n* = 101).

Woodland birds

Although the negative effects of habitat loss and fragmentation on biodiversity are pervasive, studies of forest birds (individual species and communities) underpin much of the evidence base (Humphrey et al. 2015). Forest birds are an ideal taxon for studying the impacts of land-use change because they are diverse, show interspecific variation in how they respond to patterns of land-use at local and landscape scales, and are relatively easy to detect and identify in the field. As for other taxa, most studies have focused on species, community or behavioural responses to habitat *loss* and *fragmentation* (Dolman 2007; Dolman 2012). There are multiple lines of evidence to suggest that patch size is the most important predictor of woodland/forest bird species richness and occupancy (Bayard & Elphick 2010; Dolman 2012), both in remnant fragments and in new patches. However, the process or processes that drive this pattern have been unclear (Dolman 2012). Do larger patches have more structural heterogeneity (e.g. tree-fall gaps) and therefore higher niche availability than smaller patches? Does interspecific competition limit the number of territories a patch can support? Do patches act as ‘nets’ that capture individuals from the available species pool in proportion to their area, and thus larger patches have higher abundance and diversity due to probability alone? Or, does patch size and shape affect predation pressure and reproductive output? The strength of support for these potential mechanisms is varied (Dolman 2012) and it has been argued that species or community responses to landscape configuration or composition are likely to vary between geographical regions (Villard 2002; Bayard & Elphick 2010). If this is true, then making general recommendations for habitat creation is likely to be extremely challenging (Dolman 2012).

Pattern vs process

Species or community responses to habitat configuration and composition are both temporally and spatially hierarchical (Dolman 2012). In forests, successional processes play an important temporal role in shaping bird communities. Generalist species that prefer more open canopies and dense vegetation with a low canopy height are the first to colonise young stands. These are then forced to move to patch edges when the canopy begins to close. Then, facultative forest species begin to colonise as trees mature and the vegetation structure begins to diversify. Finally, obligate forest species that require a closed canopy, open understorey and mature trees colonise when the shrub layer is lost following full canopy closure. Thus, a forest or woodland patch is expected to comprise a nested subset of these three broad groups (generalists, facultative and obligate species) depending on its age (Dolman et al. 2007).

The spatial scales that determine the suitability of a forest for bird species and communities are also nested (Dolman et al. 2007; Dolman 2012). At very fine scales (m^2), the vegetation structure is important for nest-site location. Then, the vegetation structure and management (i.e. grazing pressure, coppicing) of the woodland at the territory scale (10s – 100s of m^2) influences resource availability (food, roosting sites), and vegetation structure can also be linked to predation risk (e.g. Whittingham & Evans 2004; Bellamy et al. 2017). In a fragmented landscape, there is also substantial evidence (but mainly from North America) that the type of land-use at the patch edge (e.g. within 10s of m) can affect nest predation risk (Thompson 2007). At larger scales (100s to 1000s m^2), patterns of land-use can affect colonisation rates, dispersal processes and predation pressure. For example, when there is more habitat in the landscape then there is a larger pool of potential colonists for the focal patch, and patch isolation or ‘connectedness’ can affect movement between patches (Hanski 1994; Bélisle 2005).

Disentangling which of the many temporal and spatial processes have the greatest relative importance for species and communities is a significant challenge, not least because they are often interconnected and highly co-linear. For example, older patches might have higher bird abundance and diversity (e.g. species richness), but is this due to the greater availability of time-dependent resources such as tree holes, or because older patches simply have more time to sample individuals from the available species pool (Figure 1.4)? Since patch age and vegetation structure are highly correlated in forest habitats, separating their independent effects analytically is often impossible and this problem has impeded progress in landscape ecology generally.

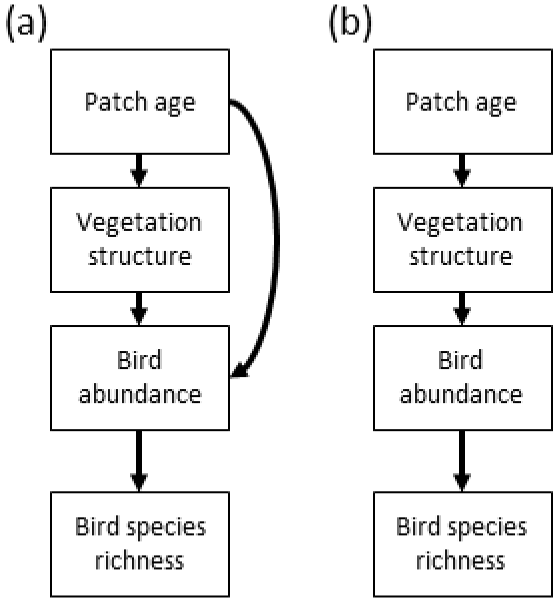


Figure 1.4 Alternate hypotheses illustrating two potential relationships between patch age and bird abundance and diversity (species richness). In (a), older patches have higher bird abundance and richness because (i) they have a greater chance of sampling individuals from the available species pool, and (ii) they have a more diverse vegetation structure. In (b), patch age has no direct relationship with bird diversity or abundance, but older patches have a more diverse vegetation structure and thus greater niche and resource availability, which can support higher bird abundance and diversity.

Methodological advances

Recent analytical developments have made it possible to address some of the common problems associated with analysing data that are correlated in time and space. One of the most useful statistical developments has been improved accessibility to a technique known as piecewise structural equation modelling (or confirmatory path analysis; Lefcheck 2016). This method can be used to examine the relative support for multiple alternate hypotheses and can account for direct and indirect causal relationships, correlations between both dependent and independent variables and data with non-normal error distributions (e.g. Poisson), which are common in ecology.

Large-scale ecological studies can also be limited by sample size in time and space, which affects statistical power. In many cases, there is a time-for-space trade-off (Haddad et al. 2012). Studies conducted over very large spatial scales (1000s of km^2) typically have low temporal resolution (e.g. annual visits to study sites) compared to those conducted over small scales (100s of m^2), which might be visited daily. Because of these trade-offs, there is a middle-ground that is poorly understood. For example, observed patterns of colonisation rates in a patch are predicted to be driven by movement behaviour, where higher physical connectivity (e.g. hedgerow availability) in a landscape means that individuals can move more freely between patches. However, because of the challenges associated with tracking individual movements at sufficiently large temporal and spatial scales, support for a direct link between patterns of physical landscape connectivity and movement behaviour in birds is actually very weak (Dolman 2012). The majority of evidence is based on observational inference or from ‘removal’ trials, which involve trapping, translocating and re-releasing individuals into landscapes with different habitat configurations to monitor their movement behaviour. The generalisability of this work to natural systems has been questioned, and there is a need to understand how large-scale habitat patterns influence behaviours linked to movement, such as colonisation rates. Technological developments, such as inexpensive, automated audio recorders, can help advance knowledge in this area.

AIMS AND OUTLINE

Here, I aim to address two primary questions that have limited our ability to optimise woodland creation for the benefit of biodiversity, focusing on bird communities in post-agricultural woodlands:

1. What is the relative importance of local (e.g. management practices) and landscape scales (e.g. habitat amount, configuration), and time (woodland age) for bird communities in woodland created on post-agricultural land?
2. What are the behavioural processes that could be driving patterns of species and community responses to woodland created in a patchy configuration?

I combine natural experiments with the latest analytical and technological tools to answer these questions. In Chapter 2, I examine bird community responses to habitat creation using structural equation modelling to disentangle the direct and indirect relationships between local and landscapes scales and woodland age for bird species richness and abundance. In Chapter 3, I develop a new, inexpensive, bioacoustic monitoring tool (the ‘Solo’ system) that can be used to remotely monitor environmental sounds, such as bird song, for long time periods. I then used the Solo system in Chapter 4 where I present a novel experimental design that can be used to detect daily bird colonisation events in naturally replicated woodland patches. This design allowed me to test if large scale habitat patterns act as cues for a long-distance migrant bird, the Willow Warbler *Phylloscopus sibilatrix,* during colonisation and settlement of breeding territories.

It has been suggested that predation pressure could drive community responses to local and landscape-scale habitat patterns. To address this question in Chapter 5, I tested if land-use surrounding a woodland patch affects perceived predation risk and causes a trade-off between alarm call behaviour and singing behaviour in the Wren *Troglodytes troglodytes*.

Thesis structure

Chapters 1 and 6 present a general introduction and discussion to the thesis topic and results, data chapters 2 – 5 are written in manuscript form. I have indicated if these are published, are under review or are in preparation to submit to a journal. Because chapters 2 – 5 have individual Discussion sections I have tried to avoid substantial repetition in Chapter 6 as far as possible. The thesis is written in the first person singular form, but much of the work would not have been possible without the contributions of my supervisors and other collaborators, whose contributions are detailed at the beginning of each chapter.

CHAPTER 2

BIRD COMMUNITY RESPONSES TO HABITAT CREATION IN A LONG-TERM, LARGE-SCALE NATURAL EXPERIMENT

An adapted version of this chapter has been published as:

Robin C. Whytock, Elisa Fuentes-Montemayor, Kevin Watts, Patanjaly Barbosa De Andrade, Rory T. Whytock, Paul French, Nicholas Macgregor and Kirsty J. Park. 2017. Bird community responses to habitat creation in a long-term, large-scale natural experiment. *Conservation Biology* DOI:10.1111/cobi.12983

Contributions: RCW, EF-M, KW, NM and KP co-designed the study. RW collected the data with assistance from RTW, PF and PBDA. RCW analysed the data and wrote the manuscript, and all co-authors commented on an earlier draft.

ABSTRACT

Ecosystem function and resilience are compromised when habitats become fragmented due to land-use change. This has led to national and international conservation strategies aimed at restoring habitat extent and improving functional connectivity (i.e. maintaining dispersal processes). However, biodiversity responses to landscape-scale habitat creation and the relative importance of spatial and temporal scales is poorly understood, and there is disagreement over which conservation strategies should be prioritised. I used 160 years of historic post agricultural woodland creation as a natural experiment to evaluate biodiversity responses to habitat creation in a landscape context. Birds were surveyed in 101 secondary, broadleaf woodlands aged 10 – 160 years with ≥ 80% canopy cover and 0 – 17% broadleaf woodland in the surrounding landscape (within 3000 m). I used piecewise structural equation modeling to examine the direct and indirect relationships between bird abundance and diversity, ecological continuity (patch age), patch characteristics, and landscape structure, and also quantified the relative conservation value of local and landscape scales for bird communities. Ecological continuity indirectly affected total bird abundance and species richness through its effects on stand structure, but ecological continuity had a weaker influence (effect size close to 0) on the abundance and diversity of species most closely associated with woodland habitats. This was probably because woodlands were rapidly colonised by woodland generalists in ≤ 10 years (minimum patch age) but were on average too young (median 50 years) to be colonised by woodland specialists. Local patch characteristics were relatively more important than landscape characteristics for bird communities. Based on my results, biodiversity responses to habitat creation depended on local-and landscape-scale factors that interacted across time and space. I suggest there is a need for further studies that focus on habitat creation in a landscape-context, and that knowledge gained from studies of habitat fragmentation and loss should be used to inform habitat creation with caution because they are not necessarily reciprocal.

INTRODUCTION

For landscapes to support biodiversity and ecosystem services in the long term they need to function as coherent "ecological networks" (Lawton et al. 2010; Humphrey et al. 2015). Conceptually, these comprise a spatial network of core habitats areas, corridors, stepping-stones, and buffer zones. In combination, these local and landscape elements are expected to contribute to ecosystem function by increasing the persistence and movement of species across fragmented landscapes (e.g. Opdam et al. 2006; Lawton et al. 2010; Humphrey et al. 2015).

Based on principles derived from island biogeography and conservation planning (MacArthur & Wilson 1967; Diamond 1975), there is increasing interest in applying the ecological network concept to landscape-scale conservation (e.g. Hoctor et al. 2000; Jongman et al. 2011; Watts et al. 2016). However, the value of this concept as a conservation tool has been contested (Boitani et al. 2007), and there is disagreement over which elements should be prioritised. For example, should the focus be on actions to restore functional connectivity by creating habitat corridors or on actions to increase habitat quality or extent (e.g. Hodgson et al. 2011; Fahrig 2013; Hanski 2015).

There are two main knowledge gaps that potentially impede efforts to design effective ecological networks. First, for most taxa, the relative ecological importance of local versus landscape-scale characteristics is poorly understood, which has led to uncertainty over where to prioritise resources (Dolman et al. 2007; Humphrey et al. 2015). Second, understanding of biodiversity responses to landscape configuration is underpinned by studies of habitat loss (e.g. Villard et al. 1999; Vergara & Armesto 2009; Gibson et al. 2013) and it is unclear if the ecological consequences of removing habitat (i.e. fragmentation) and the outcomes of habitat creation are reciprocal (Munro et al. 2007; Naaf & Kolk 2015; Watts et al. 2016).

Addressing these knowledge gaps has been challenging, not least because the time lag between habitat creation and biodiversity responses can be tens to hundreds of years, and many taxa respond to landscape configuration at kilometre scales or more (Boitani et al. 2007; Haddad et al. 2015; Watts et al. 2016). Processes occurring over such long periods and large spatial scales are difficult to replicate (Watts et al. 2016); thus, controlled experiments designed to test the effects of alternate conservation actions remain rare (Haddad 2012; Jenerette & Shen 2012; Legrand et al. 2012).

Recently, natural (or mensurative) experiments have advanced understanding of landscape-scale ecological processes and patterns (McGarigal & Cushman 2002;

Lindenmayer 2009; Watts et al. 2016). These seek to strike a balance between the rigidity of manipulative experiments and the relatively low control of observational studies (Watts et al. 2016). For example, Mortelliti and Lindenmayer (2015) used a longitudinal (16 years) natural experiment (Nanangroe, Australia) to evaluate the effects of landscape-scale matrix transformation on bird communities. They used a random stratified design to control for factors that could influence the bird community independent of the changing matrix. Thus, the effects of matrix change could be untangled from the effects of other local and landscape characteristics (Mortelliti & Lindenmayer 2015), and results showed that matrix transformation in the form of forestry plantations can influence bird turnover rates in remnant native woodland.

Responses of bird communities to landscape configuration have received widespread attention (e.g. Bennet et al. 2004; Vergara & Armesto 2009; Galitsky & Lawler 2015). This is in part because of the taxon's high diversity and because landscape attributes, such as patch isolation and matrix composition, can inhibit some species' movements despite their ability to fly and apparent high mobility (e.g. Bélisle et al. 2001). This paradox raises questions about the biological and ecological mechanisms that govern dispersal (Stevens et al. 2014). Forest birds are particularly vulnerable to landscape change, and many species have declined globally as a result of deforestation, which has wider implications for ecosystem function (Şekercioğlu et al. 2004).

Existing evidence, primarily from studies of habitat loss, suggests that for forest birds there should be a focus on maintaining or creating large forest patches, and patch area consistently predicts avian diversity, occupancy, and turnover rates (e.g. Dolman 2007; Bregman et al. 2014; Humphrey et al. 2015). Other factors such as vegetation structure, management practices (e.g. livestock grazing) and patch shape can also play an important role in determining diversity of forest birds (Martin & McIntyre, 2007; Munro et al. 2007). However, few studies (Vergara & Armesto, 2009; Galitsky & Lawler 2015) have simultaneously examined the relative influence of these factors across multiple spatial and temporal scales.

In addition to maintaining gene flow, migration and dispersal processes, functional ecological networks should satisfy the reproductive, feeding, resting, and sheltering requirements of multiple taxa. However, conservation actions that benefit one species can disadvantage another. For example, restoring contiguous forest on grazing pasture will benefit forest species but is likely to be detrimental to species associated with grassland. Furthermore, even within a land-cover type, individual species can have opposing responses to environmental factors and landscape configuration (Law et al. 2014; Galitsky & Lawler 2015). Finding a balance between the needs of multiple taxa therefore presents a challenge, and biodiversity metrics such as species richness may not capture the diverse needs of different groups or individual species. To find a middle ground, species can be grouped objectively according to shared ecological traits. For example, French and Picozzi (2002) used hierarchical clustering to group breeding birds based on their feeding, breeding, and resting habitat requirements and assessed the relationship between these clusters and large-scale patterns of land use.

I moved beyond investigating biodiversity responses to landscape fragmentation and habitat loss and evaluated, in a natural experiment, biodiversity responses to habitat creation in a landscape context. I surveyed bird abundance and diversity in 101 agricultural woodlands that appeared on historic maps in the last 10 – 160 years (Watts et al. 2016). I used structural equation models and tested for the existence of direct and indirect causal relationships between patch characteristics, ecological continuity, and landscape structure based on *a priori* expectations (Appendix 2.1), which allowed interactions that operate across temporal and spatial scales to be teased apart. I also compared the relative importance of local versus landscape-scale characteristics for the purposes of informing conservation and policy.

METHODS

Study area and site selection

A detailed description of the methods I used for site selection, as part of the Woodland Creation and Ecological Networks (WrEN) project, is in Watts et al. (2016). In summary, broadleaf, secondary woodland patches >0.5 ha with ≥80% canopy cover were identified in lowland agricultural areas in central Scotland and central England (Appendix 2.2) from the National Forest Inventory for Great Britain data set (Forestry Commission 2013). Potential sites were systematically selected based on multiple local- (e.g. size, age) and landscape- (e.g. amount and degree of connectivity of surrounding woodland) level selection criteria.

A total of 101 woodlands were surveyed for birds. Woodlands were 10 – 160 years old, 0.5 – 31.89 ha in area (reflecting the size distribution in the landscape), 0 – 17% broadleaf woodland cover in the surrounding landscape (within 3000 m), and 7 – 1573 m to the nearest broadleaf woodland. Detailed information and summary statistics for all local and landscape variables are in Appendix 2.3.

Bird surveys

Breeding birds were surveyed using a reduced version of the common bird census method (Marchant et al. 1990). Sites were visited in 2015 on three occasions, once in April, May, and June respectively. There was a minimum of seven days between surveys. Based on national bird census data, bird population trends for most species of interest did not fluctuate significantly from the average in 2015 (British Trust for Ornithology 2016), suggesting it was a representative year. Surveys began 30 minutes after sunrise and usually ended by 1100 (no later than 1130). Woodland patch geometry varied considerably. To account for this, survey effort was standardised to 10-minutes per hectare per visit, and observers approached all areas of the patch within a minimum distance of 50 m to increase the probability of detecting territorial birds. Repeat visits were made by the same observer and patches of <1 ha were surveyed for a minimum of 10 minutes per visit. Further details on the bird-survey methods are given in Appendix 2.4.

Corvids (other than Eurasian Jay [*Garrulus glandarius*]) and raptors were excluded due to their large territories and, for some species, low detectability (e.g. Eurasian Sparrowhawk [*Accipiter nisus*]). Species with a distribution that did not include both of my study areas in Scotland and England (e.g. Nightingale *Luscinia megarhynchos*) were also excluded (Appendix 2.4). I included resident and migrant species in the analyses, and species were assigned to one of five functional groups (see Results) based on the classifications given in Table 1 of French and Picozzi (2002), who used Euclidean distance and hierarchical clustering (Ward, 1963) to group British birds based on their feeding, breeding, and resting habitat requirements. Each species belongs to a single cluster. Nomenclature follows the British Ornithologists' Union (2013).

Patch characteristics and landscape data

Local patch characteristics (patch age, patch geometry, vegetation structure, management practices) and landscape metrics (landscape composition, landscape configuration) were recorded during field surveys in 2013, 2014, and 2015 or estimated from the U.K. Land Cover Map 2007 (Morton et al. 2011) and National Forest Inventory data set (Forestry Commission 2013) using ArcMap *v*10.2 (ESRI 2011).

Landscape composition was quantified by calculating the percent cover of broadleaf woodland, any woodland, semi-natural land cover (excluding woodland) and urban land cover surrounding the patch at eight nested scales (GIS buffers): 100, 250, 500, 1000, 1500, 2000, 2500, and 3000 m. I limited the maximum buffer size to 3000 m to ensure spatial independence between sites as far as possible, and this was also considered ecologically appropriate based on knowledge of woodland-bird dispersal distances (Paradis et al. 1998).

To quantify landscape configuration, I calculated a connectivity index for broadleaf woodland (broadleaf woodland connectivity) based on the incidence function model (Hanski 1994; Moilanen & Hanski 2001).

Modeling approach

My two main aims were to disentangle the direct and indirect relationships between bird diversity and abundance, local patch characteristics (i.e. metrics of ecological continuity, patch geometry, vegetation structure and management) and landscape metrics (habitat composition and configuration in the landscape) and to quantify the relative importance of local versus landscape scales. I therefore used piecewise structural equation models (SEMs) (Lefcheck 2016), a multivariate technique that can be used to test whether *a priori* hypothesised direct and indirect causal relationships between variables are supported by the observed data, and to compare relative effect sizes between variables. A global conceptual model (metamodel) (Figure 2.1) based on underlying theory and evidence was used to guide the construction of more narrow hypotheses for individual functional groups and total species richness (Appendix 2.1).

Before fitting SEMs, constituent generalised linear models (GLMs) were validated following Zuur et al. (2010). In some cases variables were log transformed to achieve a normal error distribution (Appendix 2.5). Bivariate relationships were explored graphically to identify potential nonlinear relationships. No multicollinearity was detected in constituent GLMs with a variance-inflation-factor threshold of < 5. Continuous predictor variables were mean centered and scaled by 1 SD, and binary predictor variables were transformed to have values of -1 and 1 so that their effect sizes were directly comparable with those of continuous predictors. For all landscape metrics I preselected the most appropriate buffer size for inclusion in the SEM by creating generalised linear models for each metric, scale, and response combination and retained only the scale with the lowest corrected Akaike information criterion (AICc).

During SEM validation, missing paths were evaluated and either added to the model if they were considered causal (these were few and are indicated in Appendix 2.5) or allowed to freely covary. Shipley’s test of directed separation (Fisher’s *C*) was used to evaluate global SEM fit, where values of $p > 0.05$ indicated the model was supported by the observed data (although alternative models may also be valid). Predictions from SEMs were made with non-focal predictors set at their median value. I used R statistical software (R Core Team, 2015) for all analyses.

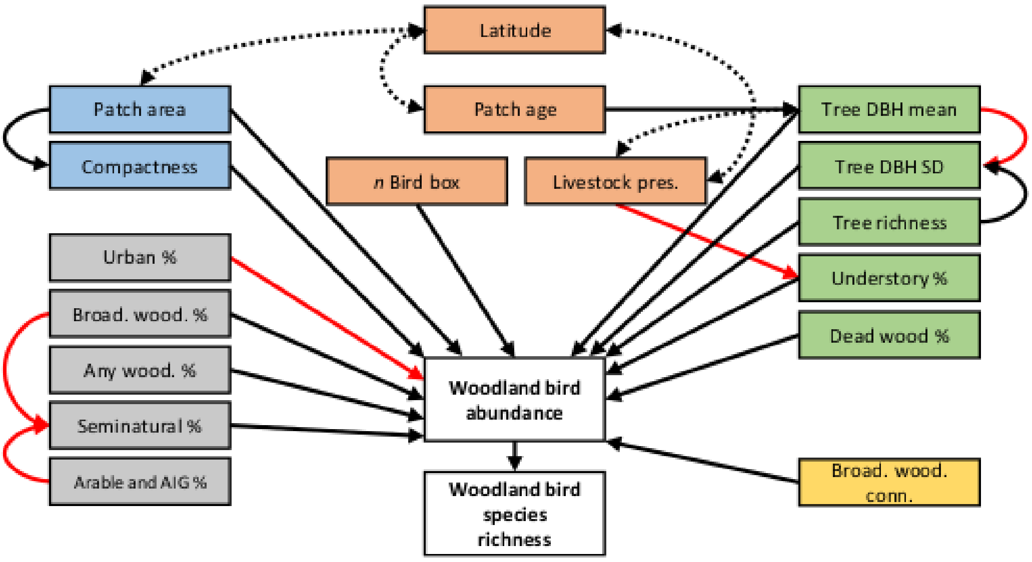


Figure 2.1 Metamodel used to guide structural equation model (SEM) construction illustrating general hypothesised direct and indirect relationships (Appendix 2.1) between response variables (bird abundance and bird species richness) and metrics of patch geometry, vegetation structure, management practices, landscape composition, and landscape configuration (dashed arrows, hypothesised correlated relationships [based on knowledge of my study sites] that do not have a causal explanation). Agriculturally improved grassland is abbreviated as AIG.

RESULTS

A total of 8,252 records of adult birds of 59 species were recorded. After applying selection criteria to exclude probable non-breeders and species with a restricted range, 7,791 records of adult birds (median = 59, range = 17 – 495 records per site) of 46 species (median = 13, range 5 – 26 species per site) were retained for analysis. The remaining species fell into five functional groups (Figure 2.2). Those in the open, mixed, or general wood and scrub group, such as Eurasian Wren (*Troglodytes troglodytes*) (96% of woodlands), Blue Tit (*Cyanistes caeruleus*) (90% of woodlands), and European Robin (*Erithacus rubecula*) (89% of woodlands) dominated. Chaffinch (*Fringilla coelebs*), a farmland seed eater, was detected in 98% of woodlands.

A complete analysis was conducted for each of the five functional groups. For brevity, only results for raw species richness and the two groups most strongly associated with woodland habitats (open, mixed, or general wood and scrub and broadleaf trees and hedgerows) are discussed in the main text, but all results are given in Appendix 2.5. These two functional groups are also likely to be the main conservation focus of woodland creation. Goodness-of-fit statistics for all SEMs are given in Appendix 2.5, and in all cases the final models reproduced the data well ($P > 0.05$).

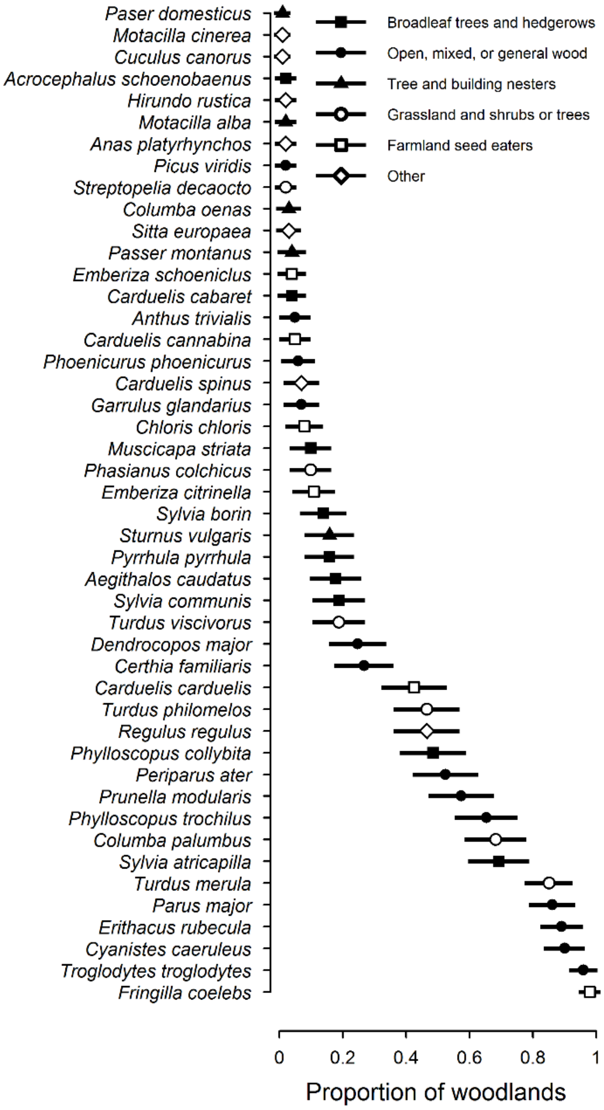


Figure 2.2 The proportion of woodlands in which each species was recorded as probably breeding (points and 95% confidence intervals, equation in Appendix 2.6). Functional groups are from French & Picozzi (2002) (see Methods).

Total species richness

As expected, there was a strong positive relationship between total bird abundance and total bird species richness (Figure 2.3a; Appendix 2.5). However, in contrast to expectations, abundance was not the only direct driver of species richness, and by evaluating missing paths I also identified significant direct relationships between species richness and local- (patch area) and landscape-scale (broadleaf woodland connectivity) variables (Figure 2.3a).

Confirming my expectations, mean tree diameter at breast height was larger in older patches, which in turn positively influenced total bird species richness. Other than patch area, only tree species richness directly affected total bird abundance at the local scale.

Broadleaf woodland connectivity at 250 m had a positive, direct effect on species richness, but no other landscape-scale metric strongly affected total bird abundance or richness (Figure 2.3a).

Broadleaf trees and hedgerows functional group

Only two of the nine species expected in the broadleaf trees and hedgerows group were recorded in ≥20% of woodlands (Figure 2.2), and two species with a geographic distribution that overlaps the two study areas were not detected, Wood Warbler (*Phylloscopus sibilatrix*) and Pied Flycatcher (*Ficedula hypoleuca*) (Balmer et al. 2013).

Unexpectedly, patch age and abundance of this group were not significantly related (Figure 2.3b; Appendix 2.5). After evaluating missing paths, there was a direct negative relationship between patch size and species richness (controlling for abundance), although the effect was relatively small and unlikely to be ecologically relevant.

Livestock presence in the woodland reduced the group’s relative abundance by approximately 61%, from an estimated mean of 5.41 (5.24 – 7.84 CI) to 2.12 (2.02 – 4.82 CI) adult birds recorded. In contrast to my original hypothesis, analysis of missing paths showed this effect was direct and not mediated by the negative effect of livestock presence on understorey cover.

Also contradicting expectations, high proportions of broadleaf woodland in the landscape reduced rather than increased relative abundance. This effect was equivalent to a 4% reduction in abundance per 1% increase in the amount of broadleaf woodland surrounding the patch at 1000 m, from an estimated mean of 7.52 records of adult birds

(6.3 – 11.53 CI) in woodlands with no surrounding broadleaf at 1000 m to 1.72 (1.32 – 5.56 CI) records with 20% broadleaf woodland at 1000 m.

Open, mixed, or general wood and scrub functional group

All 13 species expected in the open, mixed, or general wood and scrub group were detected: seven species in >40% of woodlands and nine in >20% of woodlands (Figure 2.2). Results from the SEM (Figure 2.3c; Appendix 2.5) were similar to the broadleaf trees and hedgerows group.

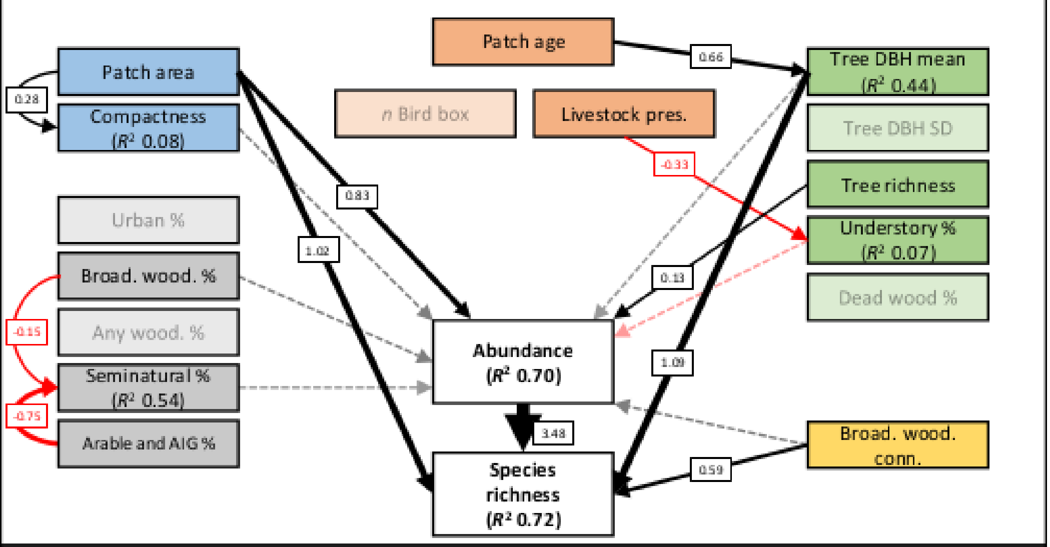
Ecological continuity had no detectable influence on abundance. Unexpectedly, after controlling for the positive area-abundance relationship, larger patches had lower species richness than smaller patches, although the effect was small relative to other variables. Livestock presence directly reduced relative abundance but not because of reduced understorey cover.

At the landscape-scale, there was a direct positive relationship between species richness and the amount of any woodland in the landscape at 500 m, but other landscape metrics were of relatively low importance.

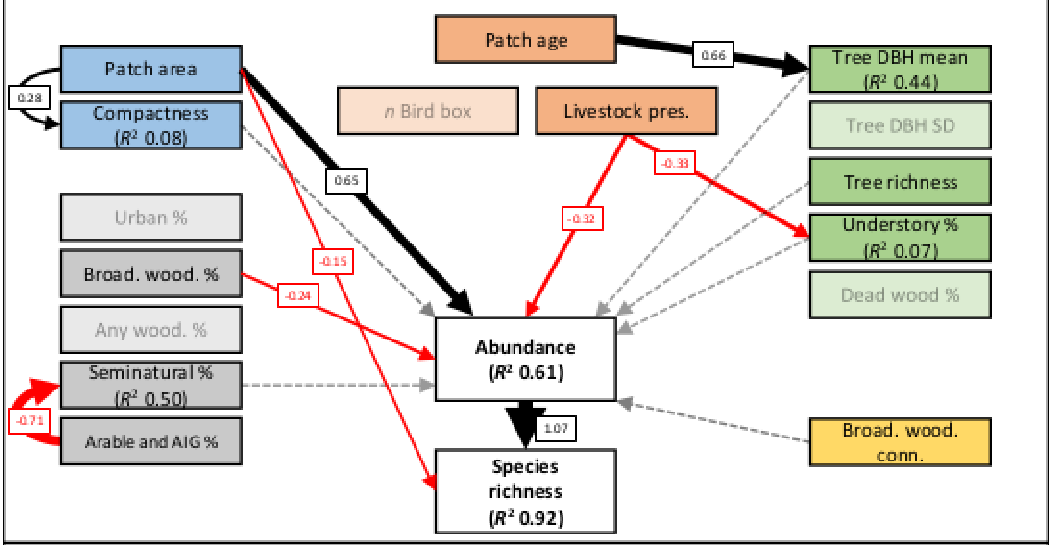
I also hypothesised that dead wood cover and the number of nest boxes in the woodland would have a positive effect on the relative abundance of this group, but I did not detect any significant relationships, and effect sizes for these predictors were small relative to other variables in the model.

⟶ **Figure 2.3** Structural equation model (SEM) path diagrams for (a) total bird species richness and (b, c) species richness and abundance of birds belonging to functional groups associated with woodland. Arrows and standardised effect sizes for significant variables indicate direction and relative magnitude of the relationship. Dashed arrows indicate nonsignificant relationships that were specified in the *a priori* model. Grey text indicates a variable in the metamodel that was not in the SEM (Appendix 2.5). Coefficients of determination (R^2) are shown for all response variables and goodness-of-fit statistics are in Appendix 2.5: Table 7. Agriculturally improved grassland is abbreviated as AIG.

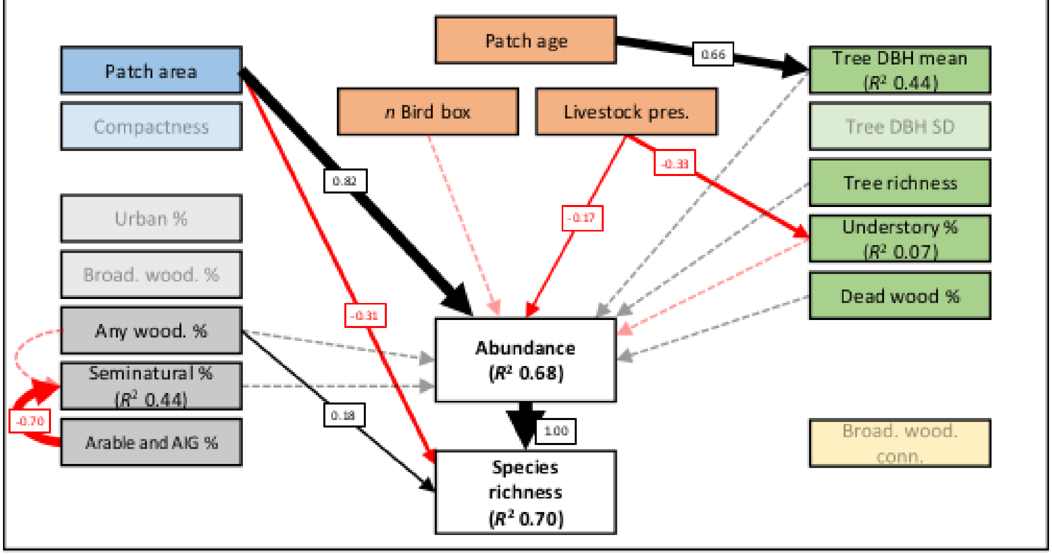
(a) Total species richness



(b) Broadleaf trees and hedgerows



(c) Open, mixed, or general wood and scrub



DISCUSSION

The strategic creation of ecological networks could mitigate the effects of past habitat loss and fragmentation by improving ecosystem function and resilience (Lawton et al. 2010; Humphrey et al. 2015). For most taxa there are likely to be substantial time lags between habitat creation and species' responses (e.g. patch colonisation), and it could take centuries for communities to fully re-establish. However, despite the theoretical importance of ecological continuity, its importance for biodiversity has rarely been measured at representative time scales, and its importance relative to other factors such as patch size is generally unknown (Munro et al. 2007; Humphrey et al. 2015). Here, ecological continuity (i.e. patch age) ranged from 10 to 160 years (median 50 years), and older woodlands with mature trees had higher total bird abundance and thus richness, supporting my hypothesis that older woodlands can support more individuals and species due to greater structural diversity.

Although ecological continuity was important for total species richness, it had little detectable influence on functional groups most closely associated with wooded habitats. Generalist woodland species in the open, mixed, or general wood and scrub group (*n* = 13 species) were found in a high proportion of study sites, and the lack of any strong direct or indirect relationships between patch age and this group's abundance or diversity suggests they can rapidly colonise post agricultural woodlands, probably in ≤10 years. This agrees with results of short-term studies (≤ 25 years) of bird community responses to woodland creation in Australia (Kavanagh et al. 2007; Law et al. 2014) and the Scottish uplands (Savory 2016). In contrast to generalist species, those in the more specialist broadleaf trees and hedgerows group were relatively scarce in my study sites. Although the reasons for this are unclear, I suggest that a combination of woodland age, size, and historic management practices inside the patch (e.g. livestock grazing) may have played a role in reducing woodland suitability for these species (Fuller et al. 2005; Dolman et al. 2007).

Several species of woodland birds have declined in the United Kingdom during the past 30 years, and others have increased, but reasons for these contrasting trends are unclear (Fuller et al. 2005). From 1995 to 2015, nine of the 13 species belonging to the open, mixed, or general wood and scrub group increased, three did not change significantly, and one declined (British Trust for Ornithology, 2016). During the same period, five species in the broadleaf trees and hedgerows group increased significantly, 22 did not change significantly, and two declined (British Trust for Ornithology, 2016). All three declining species and the two species missing from my study sites (Pied Flycatcher and Wood Warbler) are long distance migrants, and there is evidence that factors outside the breeding range are in part to blame for these declines (Vickery et al. 2014). For the remaining species that have increased or remained stable, some evidence suggests that population trends could be linked to higher overwinter survival rates due to a warming climate (Gregory et al. 2007). Based on my results, which show that post agricultural woodlands provide highly favourable habitat for generalist woodland birds, I further suggest that the recent expansion of broadleaf woodland cover in the United Kingdom during the past 30 years (Harmer et al. 2015) may have contributed to population increases or stability. Although speculative, this gives some grounds for optimism, and conservation policies aimed at increasing broadleaf woodland cover can potentially have rapid, positive effects on woodland biodiversity. Nonetheless, some declining species have not apparently benefited from expanding broadleaf woodland cover, and it is unclear just how long it will take for any benefits to be accrued.

Local, patch-level factors were generally more important than landscape characteristics. Patch area was consistently the most important predictor of bird abundance and thus species richness, which is a well-known relationship (Dolman 2012). However, the relative importance of patch area versus other important factors such as ecological continuity, management practices, vegetation structure, patch age, and landscape composition has been unclear. This knowledge gap has made it difficult for land managers and policy makers to identify which of the many possible local and landscape-scale actions should be prioritised during woodland creation. My results show that larger patches not only have higher abundance and thus species richness but also that this relationship is, in relative terms, almost twice as important as other local and landscape-scale metrics for bird communities in post agricultural woodlands. I propose that, as a simple rule of thumb, patches larger than 5 ha should be created where possible (Appendix 2.4) (Bellamy et al. 1996; Dolman et al. 2012) when the aim is to benefit generalist woodland bird communities, although much larger woodlands (i.e. > 30 ha) may be required to benefit woodland specialists (Dolman et al. 2012).

Secondary to patch area, livestock presence (an index of grazing pressure) within the woodland was consistently negative for the two functional groups of woodland birds, and the effect was strongest for the broadleaf trees and hedgerows group. I hypothesised that this negative relationship would be due to the effect of grazing on understorey cover, but my results did not support this, and I found that livestock directly reduced bird abundance. This could be because my measure of understorey cover did not reflect the structural needs of affected species or because disturbance from livestock has more of an effect than the structural impact of grazing. I suggest that both explanations are plausible, and further work is needed to disentangle their independent effects. Because livestock was present in approximately 18% of woodlands I studied (all in Scotland), reducing or removing grazing pressure could be an efficient way to increase woodland bird diversity in Great Britain. I also suggest that, where woodland exists for conservation purposes, livestock should be excluded unless grazing forms part of a well-defined conservation strategy (Pollock et al. 2005).

My results also showed some unexpected relationships. For example, abundance of the broadleaf trees and hedgerows group declined when there were higher proportions of broadleaf woodland cover in the surrounding landscape. My original hypothesis was based on the assumption that source populations would be larger in the presence of more woodland in the landscape and this would lead to higher abundance and richness in the focal patch. However, results instead suggest that when there is more broadleaf woodland in the landscape, this might draw individuals away from the relatively small isolated patches represented by my study sites. Perhaps the perceived quality (as captured by patch age and measures of vegetation structure and size) and thus attractiveness of a patch is therefore relative to the amount and quality of other patches in the landscape (Stier & Osenberg 2010), but further work is required to test this hypothesis, which I address in Chapter 4.

To achieve the best outcomes for biodiversity there is a need for evidence-based habitat creation, which may involve using knowledge gained from studies of habitat fragmentation (i.e. habitat loss) to inform habitat creation efforts. However, biodiversity responses to habitat fragmentation and biodiversity responses to habitat created in a patchy configuration are not necessarily reciprocal. This is because time-dependent resources will likely pre-exist in remnant patches after fragmentation of the surrounding landscape has occurred (e.g. ancient woodland fragments), but in new habitat patches there are likely to be time lags between resource development and subsequent colonisation. Thus, remnant patches might retain species associated with long periods of ecological continuity until the patch eventually pays an extinction debt (Tilman 1994), which could temporarily mask the importance of local and landscape-scale factors for colonisation. I therefore suggest that lessons learned from studies of habitat fragmentation should only be used to inform habitat creation with caution, and there is a need for further work that specifically examines biodiversity responses to habitat creation in a landscape context.

Results demonstrate that local and landscape-scale factors interact across time and space to determine the biodiversity outcomes of habitat creation; and factors at the local scale have relatively more effect on woodland bird communities than landscape characteristics. Policy makers and conservationists are often faced with the challenge of evaluating the outcomes of their actions, such as habitat creation. Although some taxa may respond rapidly to habitat creation (i.e. generalists), it could take centuries for specialist communities to fully re-establish. Thus, short-term assessments of biodiversity responses to conservation actions, such as the decadal time scales used to assess the conservation status of global biodiversity (e.g. Aichi biodiversity targets), could paint an overly pessimistic view of conservation actions. One must therefore be careful to acknowledge the existence of time lags between conservation actions and biodiversity responses when evaluating the efficacy of conservation efforts.

ACKNOWLEDGEMENTS

I thank landowners for granting access to woodlands. H. Crick, S. Baylis, and P. Bellamy kindly provided methodological advice. The work was part funded by the Natural Environment Research Council through the IAPETUS doctoral training partnership, and CASE funding was provided by Forest Research. Additional funding was provided by the National Forest Company, Department for Environment, Food and Rural Affairs and Natural England. I also thank A. Merenlender, H. Resit Akçakaya, and two anonymous reviewers for their helpful comments, which greatly improved an earlier version of the manuscript.

Appendix 2.1 Hypotheses underlying the metamodel

My primary response variables of interest were total bird species richness and relative abundance, and within functional group species richness and relative abundance. Species richness was calculated as the total number of breeding species recorded in a patch, and relative abundance was calculated as the pooled, total number of adult birds recorded from all three visits.

Preliminary graphical analyses suggested that, as expected, relative abundance and species-richness were positively correlated. As such, I hypothesised that local and landscape characteristics indirectly influence species richness through their direct effects on abundance. This was based on the assumption that species are sampled in proportion to their availability (i.e. abundance) in the local species pool. Thus, if a patch can support more individuals then the probability that a species is sampled from the local species pool is higher.

Ecological continuity (patch age, calculated from the date of planting; see Watts et al. 2016) can influence colonisation rates either by increasing colonisation probability over time, or by allowing time-dependent resources (such as tree cavities for hole-nesting birds) to develop in a patch (Vesk et al. 2008). Since birds are generally highly mobile it is likely that colonisation can occur rapidly, but only where there are sufficient patch-level resources. For example, cavity nesting birds might rapidly reach a woodland but fail to breed (i.e. colonies) due to a lack of mature trees and associated tree holes. Other potentially limiting resources include, for example, a lack of invertebrate prey species associated with mature, veteran trees (Davies et al. 2008). Older woodlands are also likely to have greater within-patch heterogeneity and thus greater niche diversity, for example as a result of canopy gaps created by tree falls. I therefore expected ecological continuity to indirectly influence bird abundance and diversity through its direct effects on stand structure (an index of resource/niche availability). This was accounted for in the model by including a direct path between patch age and tree DBH mean, which in turn was expected to directly influence stand heterogeneity (tree DBH standard deviation) and bird abundance.

Intensive grazing pressure in woodlands can reduce woodland bird abundance and diversity (Martin & McIntyre 2007), for example through changes in understorey structure. I therefore hypothesised that livestock presence (an index of grazing pressure) would indirectly influence abundance by reducing woodland understorey cover. Wild ungulates can also influence woodland bird communities through grazing pressure (Gill & Fuller 2007) but this was not assessed here since it is difficult to accurately quantify deer abundance/presence in such a large number of woodlands.

Evidence from similar studies suggests that there are positive log-linear and power-law relationships between patch size and bird species richness and abundance in woodland patches (Dolman et al. 2007). Here, continuing with my hypothesis that abundance drives species richness through sampling effects, I included only a direct path between patch area (log transformed) and abundance in my *a priori* model. An index of patch ‘compactness’ (see Appendix 2.3) was also included to account for potential edge effects (Dolman 2012). Larger patches were expected to be more compact, since several of the smaller patches were linear shelter belts, and I therefore also included a direct path between patch area and compactness.

Other patch-level metrics expected to be important included tree species richness and % dead wood cover, both of which can increase resource availability and niche diversity in a patch. Bird boxes were also common in many of the woodlands and I expected a positive relationship between their availability and the abundance of birds (within functional groups) that commonly nest in boxes.

At the landscape scale, I expected higher proportions of woodland in the landscape to act as a source for the focal patch, and thus expected a direct positive relationship between woodland amount (either broadleaf woodland or any woodland depending on the functional group of interest) in the landscape and bird abundance. Landscape configuration (broadleaf woodland connectivity) was expected to be important for obligate woodland species, which are less likely to cross non-wooded habitats during dispersal.

Agricultural activity in the landscape can have a negative impact on bird communities (Donald et al. 2006). Here, I hypothesised that the % cover of agriculture in the landscape would indirectly affect woodland bird communities by reducing the amount of semi-natural habitat surrounding the woodland, and thus reducing potential foraging habitat. Lastly, I predicted that the % of urban land cover in the landscape would directly reduce bird abundance, perhaps by limiting colonisation or reducing foraging opportunities.

Appendix 2.2 Map of the study sites

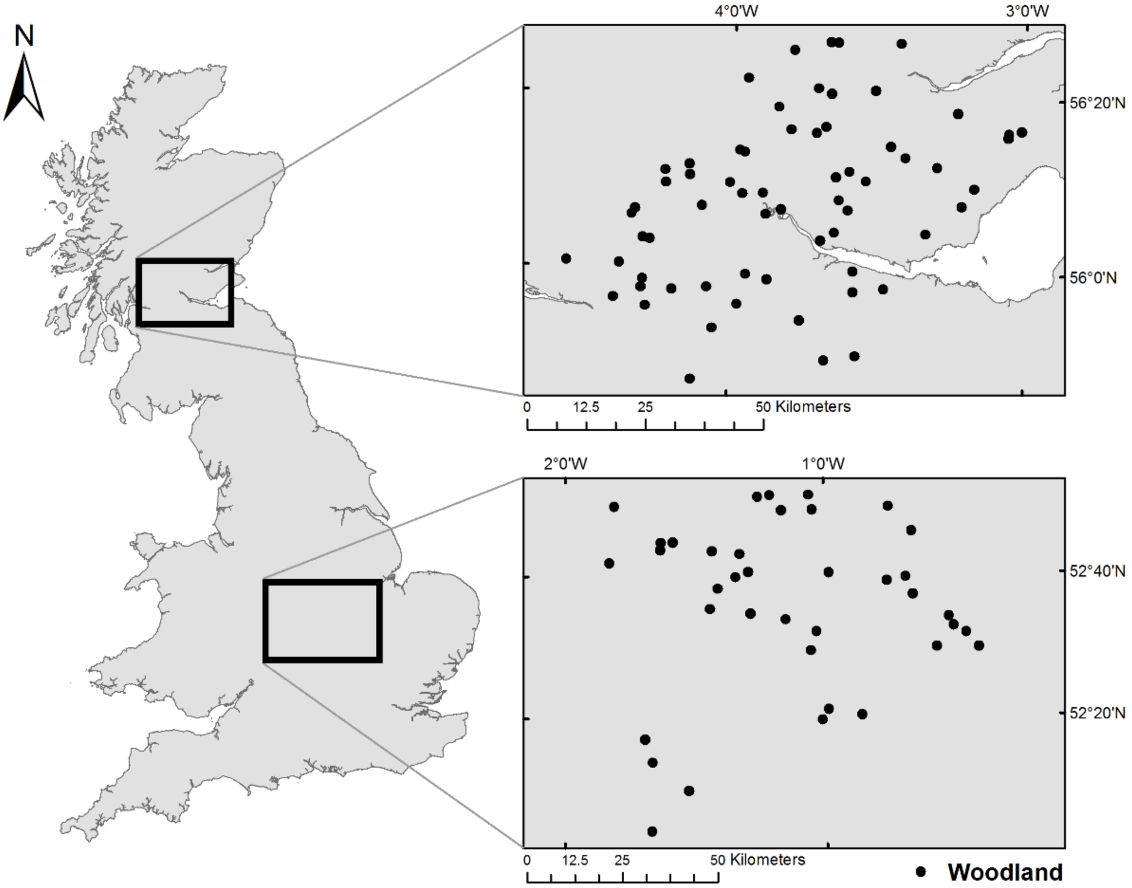


Figure 1. Map of Great Britain showing the two study areas in Scotland and England with approximate locations of the study woodlands.

Appendix 2.3 Descriptions and summary statistics for all variables

Table 1. Description and source of local and landscape metrics used in analyses. Summary statistics for all variables are given in Table 2.

Variable	**Description**	**Source**
Management	***Edge habitat, patch age and management practices inside patch boundary***	
Patch age (years)	Time since appearance on historic maps	Ordnance Survey maps
n bird boxes	Counted on final bird survey	Field survey 2015
Livestock presence/absence	Sheep, cattle or horses inside patch	Field survey 2015
Vegetation structure	***Metrics describing habitat structure and heterogeneity inside the patch***	
Tree species richness	*n* tree species	Field survey 2013/14
Tree DBH[b] mean	Mean for patch	Field survey 2013/14
Tree DBH SD[c]	SD of patch mean	Field survey 2013/14
Understorey cover %	Mean for patch	Field survey 2013/14
Dead wood cover %	Mean for patch	Field survey 2013/14
Patch geometry	***2D patch size and shape***	
Patch area	ha	GIS NFI dataset
Shape index	Patch perimeter divided by perimeter of perfect circle with same area	GIS NFI dataset
Landscape	***Measures of landscape connectivity and matrix composition, each calculated at eight spatial scales[d]***	
Broadleaf woodland conn.	Index (incidence function model)	GIS NFI dataset
Any woodland %	Percent cover	GIS NFI dataset
BL %	Percent cover	GIS NFI dataset
Urban areas %	Percent cover	GIS LCM (2007) habitat codes 22 & 23

Variable	**Description**	**Source**
Arable / agriculturally improved grassland %	Percent cover	GIS LCM (2007) habitat codes 3 & 4
Semi-natural land cover %	Percent cover	GIS LCM (2007) habitat codes 5 – 14, 17 – 21

[a] Geographic Information System (GIS) data calculated using ArcMap *v*10.2 (ESRI 2011) and National Forest Inventory (Forestry Commission, 2013) and Land Cover Map 2007 data (Morton et al. 2011).

[b] Diameter at breast height

[c] Standard deviation

[d] Metric calculated in nested buffers at 100 m, 250 m, 500 m, 1000 m, 1500 m, 2000 m, 2500 m and 3000 m surrounding each woodland patch.

[e] Index based on Incidence Function Model (Hanski 1994; Moilanen & Hanski 2001; Moilanen & Nieminen 2002). The sum contribution from all surrounding woodland patches of each category was calculated based on their size and distance from the target patch (i.e. each of my study sites), assuming that 5% of dispersers would potentially reach each of the previously defined buffer sizes (i.e. 100, 250, 500, 1000, 1500, 2000, 2500 and 3000 m). Thus the contribution from each surrounding patch declines along a negative exponential dispersal function to the target patch.

Table 2. Summary statistics for predictor variables used in analyses, showing subsets of management, vegetation structure, patch geometry and landscape variables.

Variable	Scale	Mean	Median	SD	Min.	Max.	N obs. (factors)
Management							
Age (year)	Patch	68.28	50.00	47.26	10.00	160.00	-
n bird boxes	Patch	0.29	0.00	1.12	0.00	7.00	-
Livestock (yes)	Patch	-	-	-	-	-	21
Livestock (no)	Patch	-	-	-	-	-	80
Vegetation structure							
Tree species richness	Patch	4.45	4.00	2.29	1.00	13.00	-
Tree DBH mean	Patch	28.12	24.30	15.00	8.11	90.20	-
Tree DBH standard deviation	Patch	12.22	10.75	7.79	1.33	43.38	-
Understorey cover %	Patch	1.98	1.20	2.01	0.00	8.00	-
Dead wood cover %	Patch	1.76	1.80	0.63	0.00	3.00	-
Patch geometry							
Area	Patch	3.37	1.87	5.04	0.50	31.89	-
Shape index	Patch	1.60	1.44	0.47	1.12	3.17	-
Landscape							
Any woodland %	100 m GIS buffer	0.05	0.00	0.09	0.00	0.52	-
Any woodland %	250 m GIS buffer	0.07	0.04	0.09	0.00	0.53	-
Any woodland %	500 m GIS buffer	0.10	0.06	0.09	0.00	0.47	-
Any woodland %	1000 m GIS buffer	0.13	0.11	0.10	0.00	0.43	-
Any woodland %	1500 m GIS buffer	0.13	0.12	0.09	0.00	0.42	-

Variable	Scale	Mean	Median	SD	Min.	Max.	N obs. (factors)
Any woodland %	2000 m GIS buffer	0.13	0.13	0.09	0.01	0.37	-
Any woodland %	2500 m GIS buffer	0.13	0.13	0.09	0.01	0.37	-
Any woodland %	3000 m GIS buffer	0.13	0.12	0.08	0.01	0.35	-
Broadleaf woodland %	100 m GIS buffer	0.02	0.00	0.04	0.00	0.21	-
Broadleaf woodland %	250 m GIS buffer	0.03	0.02	0.04	0.00	0.21	-
Broadleaf woodland %	500 m GIS buffer	0.05	0.04	0.05	0.00	0.25	-
Broadleaf woodland %	1000 m GIS buffer	0.06	0.05	0.05	0.00	0.22	-
Broadleaf woodland %	1500 m GIS buffer	0.06	0.05	0.04	0.00	0.18	-
Broadleaf woodland %	2000 m GIS buffer	0.06	0.05	0.04	0.01	0.18	-
Broadleaf woodland %	2500 m GIS buffer	0.06	0.04	0.04	0.00	0.17	-
Broadleaf woodland %	3000 m GIS buffer	0.05	0.04	0.04	0.00	0.17	-
Broadleaf woodland connectivity	100 m GIS buffer	8643.05	348.07	25904.61	0.00	190035.08	-
Broadleaf woodland connectivity	250 m GIS buffer	21717.34	6511.39	39893.08	0.00	222386.70	-
Broadleaf woodland connectivity	500 m GIS buffer	49557.79	26431.09	63434.33	0.00	321256.86	-
Broadleaf woodland connectivity	1000 m GIS buffer	120934.83	85210.94	120224.75	740.21	672950.41	-
Broadleaf woodland connectivity	1500 m GIS buffer	211126.08	168084.60	178144.69	6388.44	1039764.24	-
Broadleaf woodland connectivity	2000 m GIS buffer	319189.01	249295.42	238279.40	21565.77	1405338.56	-
Broadleaf woodland connectivity	2500 m GIS buffer	444288.34	350377.67	302396.37	49482.91	1791266.07	-
Broadleaf woodland connectivity	3000 m GIS buffer	586000.65	469856.74	370738.26	89612.11	2202040.28	-
Urban %	100 m GIS buffer	0.02	0.00	0.05	0.00	0.24	-
Urban %	250 m GIS buffer	0.02	0.00	0.05	0.00	0.30	-
Urban %	500 m GIS buffer	0.03	0.00	0.06	0.00	0.36	-

Variable	Scale	Mean	Median	SD	Min.	Max.	N obs. (factors)
Urban %	1000 m GIS buffer	0.04	0.01	0.07	0.00	0.33	-
Urban %	1500 m GIS buffer	0.05	0.02	0.08	0.00	0.36	-
Urban %	2000 m GIS buffer	0.06	0.02	0.08	0.00	0.37	-
Urban %	2500 m GIS buffer	0.06	0.02	0.08	0.00	0.34	-
Urban %	3000 m GIS buffer	0.06	0.02	0.07	0.00	0.35	-
Arable/agriculturally improved grassland %	100 m GIS buffer	0.80	0.85	0.23	0.00	1.00	-
Arable/agriculturally improved grassland %	250 m GIS buffer	0.79	0.84	0.20	0.00	1.00	-
Arable/agriculturally improved grassland %	500 m GIS buffer	0.75	0.78	0.20	0.00	1.00	-
Arable/agriculturally improved grassland %	1000 m GIS buffer	0.69	0.75	0.20	0.07	0.99	-
Arable/agriculturally improved grassland %	1500 m GIS buffer	0.66	0.70	0.21	0.09	0.96	-
Arable/agriculturally improved grassland %	2000 m GIS buffer	0.63	0.65	0.23	0.03	0.95	-
Arable/agriculturally improved grassland %	2500 m GIS buffer	0.60	0.60	0.23	0.02	0.94	-
Arable/agriculturally improved grassland %	3000 m GIS buffer	0.58	0.60	0.25	0.03	0.93	-
Semi-natural land cover %	100 m GIS buffer	0.17	0.08	0.22	0.00	1.00	-
Semi-natural land cover %	250 m GIS buffer	0.17	0.12	0.19	0.00	1.00	-
Semi-natural land cover %	500 m GIS buffer	0.19	0.12	0.19	0.00	1.00	-
Semi-natural land cover %	1000 m GIS buffer	0.22	0.16	0.19	0.00	0.93	-
Semi-natural land cover %	1500 m GIS buffer	0.23	0.17	0.18	0.00	0.80	-
Semi-natural land cover %	2000 m GIS buffer	0.23	0.19	0.18	0.01	0.73	-
Semi-natural land cover %	2500 m GIS buffer	0.23	0.19	0.18	0.02	0.74	-
Semi-natural land cover %	3000 m GIS buffer	0.23	0.19	0.18	0.02	0.75	-

.

Appendix 2.4 Additional details of the bird-survey methods

All hand-drawn bird registrations from field maps were digitised into Geographic Information System (GIS) format using ArcMap *v*10.2. (ESRI 2011). Records of individuals flying over the patch or observed outside of the patch boundary were excluded from analyses. Species were considered present (i.e. probably breeding) if territorial behaviour (song, alarm call, mating, nest building, active nest, male and female pair) was observed on at least one visit, or if the species was detected during two of the three surveys. Since survey effort and the criteria used to determine breeding status were less stringent than similar studies (e.g. > 3 visits with territory mapping), I validated results by comparing an observed *vs* expected species-area curve for a subset of woodland species (n = 17 species) that were also surveyed by Bellamy et al. (1996). I found no significant difference (Figure 1), suggesting the methodology was robust.

Records of Nightingale *Luscinia megarhynchos* (n = 1 site), Lesser Whitethroat *Sylvia curruca* (n = 3 sites), and Marsh Tit *Poecile palustris* (n = 5 sites) were excluded due to their restricted geographical range and historic absence from the Scottish study area (Balmer et al. 2013). Nuthatch *Sitta europaea* (n = 3 sites) was excluded from functional group analysis because it was a rare breeding species in Scotland at the time of assessment by French and Picozzi (2002), who did not therefore assign it to any group. Grey Wagtail *Motacilla cinerea*, Cuckoo *Cuculus canorus*, Siskin *Spinus*, Goldcrest *Regulus*, Swallow *Hirundo rustica* and Mallard *Anas platyrhynchos* were also excluded from functional group analyses due to the low number of individuals and species in their respective groups.

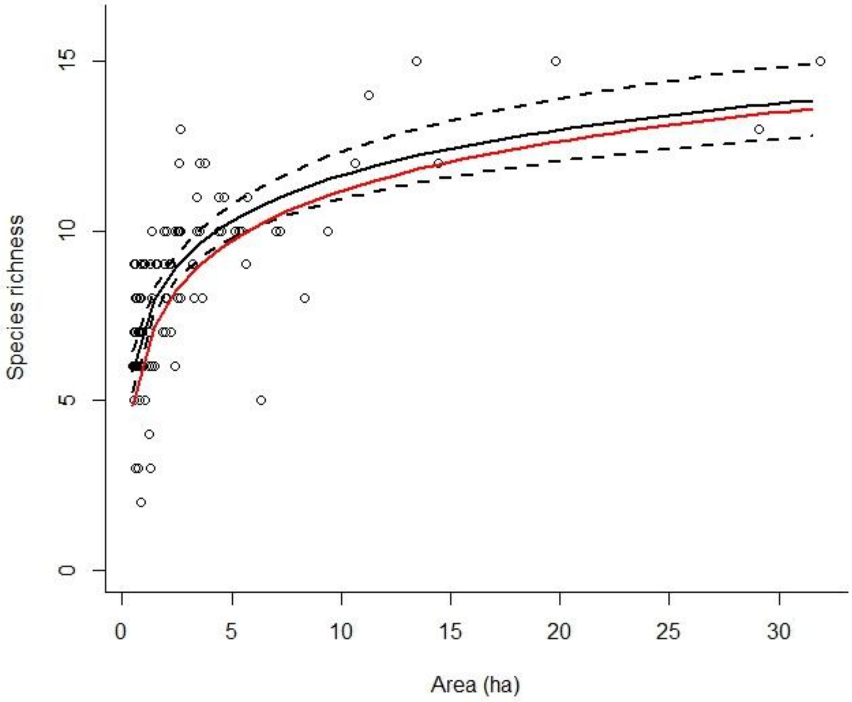


Figure 1. Observed species area curve (black line ±95% CI) from a linear regression model with raw species richness as the response and log(area) as a fixed effect, *vs* expected number of species (red line) based on formula given in Bellamy et al. (1996). Points show raw data from this study. The following subset of species ($n = 17$) were used for direct comparison: Blackbird *Turdus merula,* Bullfinch *Pyrrhula pyrrhula,* Blue tit *Cyanistes caeruleus,* Chaffinch *Fringilla coelebs,* Coal tit *Periparus ater,* Dunnock *Prunella modularis,* Green woodpecker *Picus viridis,* Goldcrest *Regulus regulus,* Great spotted woodpecker *Dendrocopos major,* Great tit *Parus major,* Jay *Garrulus glandrius,* Long-tailed tit *Aegithalos caudatus,* European nuthatch *Sitta europaea,* Robin *Erithacus rubecula,* Song thrush *Turdus philomelos,* Treecreeper *Certhia familiaris,* Wren *Troglodytes troglodytes.*

Appendix 2.5 Structural equation model results

Table 1. Full piecewise structural equation model (SEM) for total species richness. The hypothesised beta sign shows the expected, *a priori* relationship between pairs of variables as well missing paths that were considered likely to be causative. All significant and non-significant predictors are shown. Pairs of variables with correlated errors (i.e. those not considered causative but which had a significant correlation) are denoted ~~. For variables measured at multiple scales (see Appendix 2.3), the 'best' scale was selected using AICc prior to constructing the SEM (see main text). Goodness of fit statistics for the model are given in Table 7.

Response	**Predictor**	**Hypothesised Beta sign**	**Observed Beta**	**SE**	***p***	***R***^{2}
Raw richness	Log(abundance)	+	3.482	0.463	< 0.001	0.72
	Log(tree DBH mean)	Missing path in *a priori* model	1.091	0.305	0.001	
	Broadleaf conn. 250 m	Missing path in *a priori* model	0.591	0.275	0.035	
	Log(area)	Missing path in *a priori* model	1.017	0.486	0.039	
Understorey cover	Livestock y/n	-	-0.329	0.119	0.007	0.07
Semi-nat. % 100 m	Arable / AIG % 100 m	-	-0.748	0.070	< 0.001	0.54
	Broadleaf % 100 m	-	-0.147	0.070	0.038	
Shape index	Log(area)	+	0.282	0.096	0.004	0.08
Log(tree DBH mean)	Age	+	0.660	0.076	< 0.001	0.44
Log(abundance)	Log(area)	+	0.831	0.069	< 0.001	0.70
	Tree richness	+	0.131	0.060	0.031	
	Semi-nat. % 100 m	+	0.091	0.058	0.124	
	Understorey cover	+	-0.082	0.063	0.197	
	Shape index	+	0.063	0.063	0.321	
	Broadleaf conn. 250 m	+	0.058	0.066	0.383	
	Broadleaf % 100 m	+	0.026	0.065	0.693	
	Log(tree DBH mean)	+	0.018	0.066	0.784	
~~ Tree richness	~~ Shape index	NA	0.247	NA	0.006	
~~ Understorey cover	~~ Log(area)	NA	0.298	NA	0.001	
~~ Understorey cover	~~ Northing	NA	-0.473	NA	1.000	
~~ Log(abundance)	~~ Northing	NA	0.330	NA	< 0.001	
~~ Log(tree DBH mean)	~~ Log(area)	NA	-0.278	NA	0.998	

Table 2. Full piecewise structural equation model (SEM) for the broadleaf trees and hedgerows functional group. The hypothesised beta sign shows the expected, *a priori* relationship between pairs of variables as well missing paths that were considered likely to be causative. All significant and non-significant predictors are shown. Pairs of variables with correlated errors (i.e. those not considered causative but which had a significant correlation) are denoted ~~. For variables measured at multiple scales (Appendix 2.3), the 'best' scale was selected using AICc prior to constructing the SEM (see main text). Goodness of fit statistics for the model are given in Table 7.

Response	**Predictor**	**Hypothesised Beta sign**	**Observed Beta**	**SE**	***p***	***R*²**
Log(richness)	Log(abundance)	+	1.066	0.040	< 0.001	0.92
	Log(area)	Missing path in *a priori* model	-0.154	0.040	< 0.001	
Understorey cover	Livestock y/n	-	-0.329	0.119	0.007	0.07
Log(tree DBH mean)	Age	+	0.660	0.076	< 0.001	0.44
Shape index	Log(area)	+	0.282	0.096	0.004	0.08
Semi-nat. % 3000 m	Arable / AIG % 3000 m	-	-0.710	0.071	< 0.001	0.50
Log(abundance)	Log(area)	+	0.645	0.081	< 0.001	0.61
	Livestock y/n	Missing path in *a priori* model	-0.315	0.100	0.002	
	Broadleaf % 1000 m	+	-0.238	0.097	0.016	
	Broadleaf conn. 3000 m	+	0.160	0.095	0.097	
	Understorey cover	+	0.087	0.073	0.240	
	Semi-nat. % 3000 m	+	0.088	0.077	0.254	
	Log(tree DBH mean)	+	0.081	0.077	0.295	
	Shape index	+	0.036	0.074	0.624	
	Tree richness	+	0.012	0.072	0.871	
~~ Log(tree DBH mean)	~~ Livestock y/n	NA	0.129	NA	0.099	
~~ Log(tree DBH mean)	~~ Log(area)	NA	-0.278	NA	0.998	
~~ Semi-nat. % 3000 m	~~ Livestock y/n	NA	0.285	NA	0.002	
~~ Semi-nat. % 3000 m	~~ Broadleaf conn. 3000 m	NA	-0.248	NA	0.994	
~~ Log(area)	~~ Arable / AIG % 3000 m	NA	0.436	NA	< 0.001	
~~ Log(area)	~~ Northing	NA	-0.651	NA	1.000	
~~ Understorey cover	~~ Arable / AIG % 3000 m	NA	0.347	NA	< 0.001	
~~ Understorey cover	~~ Log(area)	NA	0.298	NA	0.001	
~~ Tree richness	~~ Northing	NA	0.157	NA	0.059	
~~ Tree richness	~~ Arable / AIG % 3000 m	NA	-0.155	NA	0.939	
~~ Shape index	~~ Tree richness	NA	0.267	NA	0.004	

Table 3. Full piecewise structural equation model (SEM) for the open, mixed, or general wood and scrub functional group. The hypothesised beta sign shows the expected, *a priori* relationship between pairs of variables as well missing paths that were considered likely to be causative. All significant and non-significant predictors are shown. Pairs of variables with correlated errors (i.e. those not considered causative but which had a significant correlation) are denoted ~~. For variables measured at multiple scales (Appendix 2.3), the 'best' scale was selected using AICc prior to constructing the SEM (see main text). Goodness of fit statistics for the model are given in Table 7.

Response	**Predictor**	**Hypothesised Beta**	**Observed Beta**	**SE**	***p***	***R*²**
Log(richness)	Log(abundance)	+	0.998	0.093	< 0.001	0.70
	Log(area)	Missing path in *a priori* model	-0.306	0.091	0.001	
	Any woodland % 500 m	Missing path in *a priori* model	0.176	0.057	0.003	
Understorey cover	Livestock y/n	-	-0.329	0.119	0.007	0.07
Semi-nat. % 100 m	Arable / AIG % 250 m	-	-0.702	0.084	< 0.001	0.44
	Any woodland % 500 m	Missing path in *a priori* model	-0.093	0.084	0.270	
Log(tree DBH mean)	Age	+	0.660	0.076	< 0.001	0.44
Log(abundance)	Log(area)	+	0.820	0.076	< 0.001	0.68
	Livestock y/n	-	-0.173	0.082	0.039	
	Any woodland % 500 m	+	0.125	0.064	0.053	
	Tree richness	+	0.091	0.062	0.145	
	Understorey cover	+	-0.086	0.066	0.195	
	Semi-nat. % 100 m	+	0.070	0.064	0.276	
	Cumulative woody debris	+	0.057	0.063	0.371	
	N bird box	+	-0.041	0.064	0.524	
	Log(tree DBH mean)	-	0.042	0.071	0.551	
~~ Abundance	~~ Northing	NA	0.455	NA	< 0.001	
~~ Log(area)	~~ N bird box	NA	0.263	NA	0.004	
~~ Log(area)	~~ Any woodland % 500 m	NA	0.071	NA	0.239	
~~ Log(area)	~~ Cumulative woody debris	NA	-0.281	NA	0.998	
~~ Log(area)	~~ Northing	NA	-0.651	NA	1.000	
~~ Understorey cover	~~ Log(area)	NA	0.298	NA	0.001	
~~ Understorey cover	~~ Northing	NA	-0.473	NA	1.000	
~~ Log(tree DBH mean)	~~ Livestock y/n	NA	0.129	NA	0.099	
~~ Log(tree DBH mean)	~~ Log(area)	NA	-0.278	NA	0.998	

Table 4. Full piecewise structural equation model (SEM) for the tree and building nesters functional group. The hypothesised beta sign shows the expected, *a priori* relationship between pairs of variables as well missing paths that were considered likely to be causative. All significant and non-significant predictors are shown. Pairs of variables with correlated errors (i.e. those not considered causative but which had a significant correlation) are denoted ~~. For variables measured at multiple scales (Appendix 2.3), the 'best' scale was selected using AICc prior to constructing the SEM (see main text). Goodness of fit statistics for the model are given in Table 7.

Response	**Predictor**	**Hypothesised Beta sign**	**Observed Beta**	**SE**	***p***	***R*²**
Log(richness)	Log(abundance)	+	0.865	0.039	< 0.001	0.88
	Livestock y/n	Missing path in *a priori* model	0.170	0.048	0.001	
Understorey cover	Livestock y/n	-	-0.329	0.119	0.007	0.07
Semi-nat. % 1000 m	Arable / AIG % 1500 m	-	-0.722	0.072	< 0.001	0.50
	Urban % 2000 m	Missing path in *a priori* model	-0.178	0.072	0.016	
Log(tree DBH mean)	Age	+	0.660	0.076	< 0.001	0.44
Log(abundance)	Urban % 2000 m	+	0.300	0.083	0.001	0.39
	Livestock y/n	+	0.432	0.122	0.001	
	Log(area)	+	0.213	0.096	0.029	
	Semi-nat. % 1000 m	+	0.175	0.094	0.065	
	Understorey cover	-	-0.148	0.090	0.104	
	Log(tree DBH mean)	-	0.119	0.094	0.207	
	Tree richness	+	0.004	0.084	0.958	
~~ Understorey cover	~~ Arable / AIG % 1500 m	NA	0.304	NA	0.001	
~~ Understorey cover	~~ Log(area)	NA	0.298	NA	0.001	
~~ Understorey cover	~~ Northing	NA	-0.473	NA	1.000	
~~ Livestock y/n	~~ Arable / AIG % 1500 m	NA	-0.440	NA	1.000	
~~ Semi-nat. % 1000 m	~~ Livestock y/n	NA	0.226	NA	0.012	
~~ Semi-nat. % 1000 m	~~ Age	NA	-0.212	NA	0.983	
~~ Log(tree DBH mean)	~~ Log(area)	NA	-0.278	NA	0.998	

Table 5. Full piecewise structural equation model (SEM) for the farmland seed eater functional group. The hypothesised beta sign shows the expected, *a priori* relationship between pairs of variables as well missing paths that were considered likely to be causative. All significant and non-significant predictors are shown. Pairs of variables with correlated errors (i.e. those not considered causative but which had a significant correlation) are denoted ~~. For variables measured at multiple scales (Appendix 2.3), the 'best' scale was selected using AICc prior to constructing the SEM (see main text). Goodness of fit statistics for the model are given in Table 7.

Response	**Predictor/s**	**Hypothesised Beta sign**	**Observed Beta**	**SE**	***p***	***R*²**
Log(richness)	Log(abundance)	+	0.730	0.072	< 0.001	0.53
	Age	Missing path in *a priori* model	-0.265	0.093	0.006	
	Semi-nat. % 1500 m	Missing path in *a priori* model	-0.184	0.073	0.013	
	Log(tree DBH mean)	Missing path in *a priori* model	0.157	0.094	0.100	
Semi-nat. % 1500 m	Arable / AIG % 2500 m	-	-0.668	0.075	< 0.001	0.45
Log(tree DBH mean)	Age	+	0.660	0.076	< 0.001	0.44
Log(abundance)	Log(area)	+	0.550	0.104	< 0.001	0.30
	Arable / AIG % 2500 m	Missing path in *a priori* model	-0.475	0.125	< 0.001	
	Urban % 100 m	+	-0.109	0.089	0.225	
	Log(tree DBH mean)	-	0.084	0.098	0.391	
	Semi-nat. % 1500 m	+	-0.031	0.117	0.790	
	Tree richness	-	-0.006	0.087	0.949	
~~ Log(tree DBH mean)	~~ Log(area)	NA	-0.278	NA	0.998	
~~ Abundance	~~ Northing	NA	0.489	NA	< 0.001	

Table 6. Full piecewise structural equation model (SEM) for the grassland and shrubs or trees functional group. The hypothesised beta sign shows the expected, *a priori* relationship between pairs of variables as well missing paths that were considered likely to be causative. All significant and non-significant predictors are shown. Pairs of variables with correlated errors (i.e. those not considered causative but which had a significant correlation) are denoted ~~. For variables measured at multiple scales (Appendix 2.3), the 'best' scale was selected using AICc prior to constructing the SEM (see main text). Goodness of fit statistics for the model are given in Table 7.

Response	**Predictor**	**Hypothesised Beta sign**	**Observed Beta**	**SE**	***p***	***R^2***
Log(richness)	Log(abundance)	+	0.717	0.058	< 0.001	0.68
	Livestock y/n	Missing path in *a priori* model	-0.214	0.074	0.005	
Understorey cover	Livestock y/n	-	-0.329	0.119	0.007	0.07
Semi-nat. % 3000 m	Arable / AIG % 3000 m	-	-0.737	0.072	< 0.001	0.52
	BL.1500	Missing path in *a priori* model	-0.117	0.072	0.106	
Tree DBH SD	Age	+	0.647	0.076	< 0.001	0.44
	Tree richness	+	0.243	0.076	0.002	
Shape index	Log(area)	+	0.282	0.096	0.004	0.08
Log(abundance)	Log(area)	+	0.669	0.099	< 0.001	0.47
	Broadleaf conn. 2500 m	-	-0.238	0.086	0.007	
	Semi-nat. % 3000 m	+	-0.303	0.116	0.011	
	Tree richness	+	0.197	0.082	0.018	
	Arable / AIG % 3000 m	-	-0.300	0.133	0.026	
	Understorey cover	-	-0.029	0.089	0.745	
	Tree DBH SD	+	0.013	0.092	0.889	
~~ Semi-nat. % 3000 m	~~ Livestock y/n	NA	0.313	NA	0.001	
~~ Log(area)	~~ Arable / AIG % 3000 m	NA	0.436	NA	< 0.001	
~~ Log(area)	~~ Northing	NA	-0.651	NA	1.000	
~~ Understorey cover	~~ Arable / AIG % 3000 m	NA	0.347	NA	< 0.001	
~~ Understorey cover	~~ Log(area)	NA	0.298	NA	0.001	
~~ Understorey cover	~~ Northing	NA	-0.473	NA	1.000	
~~ Shape index	~~ Tree richness	NA	0.267	NA	0.004	
~~ Abundance	~~ Northing	NA	0.069	NA	0.245	
~~ Tree DBH SD	~~ Log(area)	NA	-0.305	NA	0.999	

Table 7. Goodness of fit statistics for all piecewise structural equation models

Group	**Fisher's *C***	**df**	***p***	**AICc**	***K***	***n***
Raw species richness	57.06	56	0.435	114.034	22	101
Tree and building nesters	40.96	44	0.603	101.298	23	101
Farmland seed eaters	34.98	26	0.112	85.48	20	101
Grassland and shrubs, trees	63.26	74	0.809	137.972	27	101
Broadleaf trees and hedgerows	71.53	70	0.427	146.242	27	101
Open, mixed and general wood and scrub	56.02	62	0.690	126.993	26	101

Appendix 2.6 Formula for calculating 95% confidence intervals in Figure 2.2

$$\hat{p} \pm 1.96\left(\sqrt{\frac{\hat{p}(1-\hat{p})}{n}}\right)$$

Where n is the sample size and $\hat{p}$ is the sample proportion.

CHAPTER 3

SOLO: AN OPEN SOURCE, CUSTOMISABLE AND INEXPENSIVE AUDIO RECORDER FOR BIOACOUSTIC RESEARCH

An adapted version of this chapter has been published as:

Robin C. Whytock and James Christie. 2017. Solo: an open source, customisable and inexpensive audio recorder for bioacoustic research. *Methods in Ecology and Evolution* **8:**308-312.

Contributions: RCW and JC co-designed the Solo system. JC created the Solo software. RCW conducted field testing and wrote the manuscript, with comments on an earlier draft from JC.

ABSTRACT

Audio recorders are widely used in terrestrial and marine ecology, and are essential for studying many cryptic or elusive taxa. Although several commercial systems are available they are often expensive and are rarely user-serviceable or easily customised. Here, I present the Solo audio recorder. Units are constructed from the Raspberry Pi single board computer and run easy-to-install and freely available software. I provide an example configuration costing £167 (£83 excluding suggested memory card and battery), which records audible sound continuously for approximately 40 days. I also provide a video tutorial showing hardware assembly and documentation is available via a supporting website. The Solo recorder has been extensively field tested in temperate and tropical regions, with over 50,000 hours of audio collected to date. This highly customisable and inexpensive system could greatly increase the scale and ease of conducting bioacoustic studies.

INTRODUCTION

Bioacoustics has improved our understanding of evolution, taxonomy, wildlife conservation and animal physiology (Blumstein et al. 2011). Many birds (Aves) and invertebrates produce territorial song, bats (Chiroptera: Microchiroptera) use ultrasound to detect prey, and elephants *Loxodonta* sp. use infrasound to communicate. Calls and songs are often unique to a species, and in many instances convey the biological, behavioural and ecological characteristics of the source. Acoustic recordings can therefore reveal a wealth of information about individuals, populations and the environment.

Outside the laboratory, ecological sounds are typically recorded using remotely operated or handheld devices (Efford et al. 2009; Bardeli et al. 2010; Blumstein et al. 2011; Marques et al. 2013; Cerquiera & Aide 2016). Automated systems that record continuously or in response to acoustic triggers have become increasingly popular, and can be deployed in isolation or complex spatial arrays (e.g. Mennill et al. 2012). These are suitable for a variety of ecological applications ranging from simple species presence/absence surveys to tracking acoustically active animals in three-dimensional space, and identifying individuals from their unique vocalisations. Such systems are indispensable for studying cryptic taxa such as bats, and for detecting elusive, nocturnal or rare species. However, although deploying small numbers of commercially available recording units (e.g. Wildlife Acoustics' Song Meter) can be affordable (Mennill et al. 2012), deploying large numbers (e.g. for landscape-scale studies) can be costly. Relatively inexpensive systems based on tablet computers have become available more recently (Aide et al. 2013; Cerquiera & Aide 2016). However, the core components of these systems are rarely user-serviceable and they often contain unnecessary hardware and software that becomes redundant when used for bioacoustic research.

Inexpensive single board computers have become widely available in the past decade. For example, the Raspberry Pi single board computer (*c.* £20 at time of writing), which was originally developed as an educational tool, has been adapted for a broad variety of applications. These and similar devices, such as the BeagleBone Black development board consume minimal power and use high-specification hardware relative to their small size and low cost. Furthermore, they are operated using freely distributed and readily available open source, Unix-based operating systems, and can be powered by any DC battery, such as USB charging devices or vehicle batteries. These features make single board computers like the Raspberry Pi highly customisable, and they have many potential applications in ecology.

Here, I introduce the Solo audio recorder. The system records audible sound up to 22.05 kHz for long periods (> one month) without user intervention, and can also record audio up to a Nyquist frequency of 96 kHz (i.e. sampling rate of 192 kHz). The Solo is straightforward to build and operate, and is constructed from inexpensive hardware and freely available software. Solos have proven to be robust during extensive field testing in temperate and tropical environments, and users can customise the software or hardware configuration to suit research needs.

SYSTEM OVERVIEW

Solos (Plate 3.1) are operated using custom-written software and the current version is available online from https://solo-system.github.io/. The core system comprises a Raspberry Pi single board computer (Farnell element14, Leeds, UK), PiFace clock module (OpenLX SP Ltd, London, UK) and Cirrus Logic audio card (Cirrus Logic, Austin, Texas, USA; CLAC). Although other suitable single-board computers are available, I chose the Raspberry Pi as the foundation of the Solo, since it was the first single-board computer to be generally available, it was rapidly successful and the software is now widely supported and debugged. It also supports the CLAC high definition audio card, which has a sampling rate of up to 192 kHz.

The Solo is compatible with a wide range of external microphones, and accepts microSD cards and any 5 V power supply (Box 3.1). Using the default software configuration, the Solo records audio continuously at a sampling rate of 16 kHz (8 kHz Nyquist) in .wav format (saved as individual ten minute, time stamped sections) until the power supply is removed or the memory card reaches storage capacity. However, the audio file section length, time zone, sampling rate and microphone gain can be configured to suit research requirements. Source code is also available via the supporting website for advanced users who wish to customise the software.

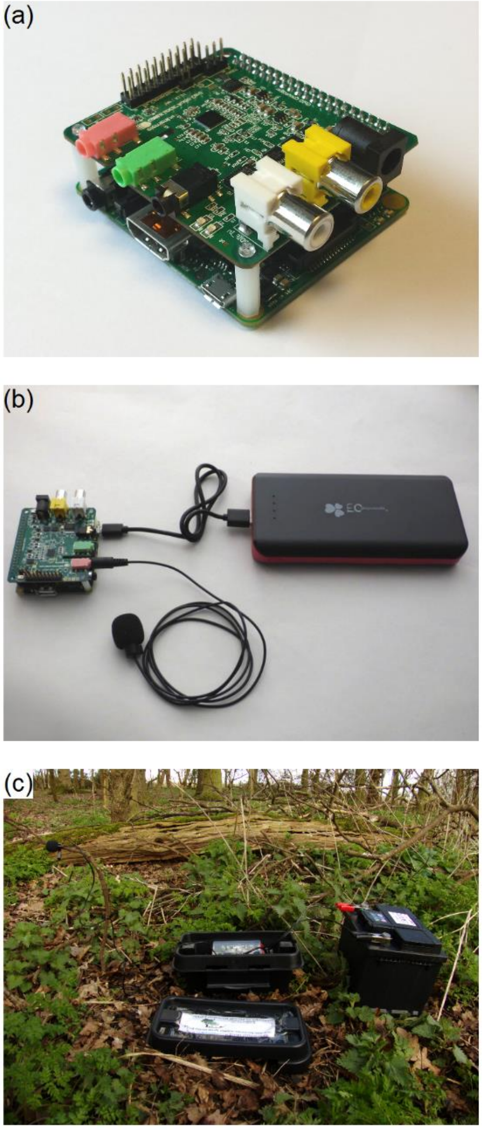


Plate 3.1 Illustrative examples of assembled Solo recorders; (a) Raspberry Pi A+ and CLAC, (b) Raspberry Pi A+ and CLAC with attached EM172 microphone and USB travel charger as a power supply, (c) example configuration (see text) deployed in a woodland (driBox lid removed to show contents).

Box 3.1: Hardware requirements

Raspberry Pi (essential): The following Raspberry Pi models have been tested: A+, B+, 2B, 3B, Pi Zero (the last model requires soldering). The Raspberry Pi A+ was used during all field testing because it has the lowest power consumption.

Cirrus Logic audio card (optional): Provides a high-fidelity (up to 192 kHz sampling rate) interface between the Raspberry Pi and an external microphone. The CLAC also has an internal stereo microphone, but this is difficult to weatherproof and an external microphone is recommended for field deployment.

External microphone/s (optional): The CLAC supports an external microphone (mono or stereo pair) with a 3.5 mm jack input (converters are widely available, e.g. from XLR to 3.5 mm jack). 2 – 3V of plug-in-power can be supplied to the microphone via the CLAC if required.

PiFace clock module (optional): Used to store the date and time of recordings and is powered by a button cell battery (CR1220). It must be set up prior to deployment using a network connection (see https://solo-system.github.io/).

Power: Any 5 V power supply (micro-USB) providing a minimum of 700 mA is suitable, such as a USB travel charger or 12 V car battery with a 5 V converter and micro-USB adapter. A mains supply can also be used if available. Using a Raspberry Pi A+, the units consume approximately 0.35 W during operation.

Memory: The Raspberry Pi accepts a single microSD card of any size. The Solo software image requires approximately 1.5 GB of memory space and the remainder is used to store audio data. Table 3.1 shows estimated storage requirements for various sampling rate and memory card size combinations.

Table 3.1 Approximate storage capacity (hours in .wav format) of different microSD memory card sizes and sampling rate combinations when recording on a single channel. These values should be halved when recording in stereo.

	8 GB	**16 GB**	**32 GB**	**64 GB**	**128 GB**	**256 GB**
8 kHz	112	251	529	1085	2196	4418
16 kHz	56	125	263	524	1098	2209
44.1 kHz	20	45	96	196	398	801
192 kHz	4	10	22	45	91	184

FIELD TESTING

Audible sound

Approximately 52,381 hours of audible sound have been recorded to date by 40 Solos using a variety of hardware and software configurations. Five systems (*n* = 600 hours recorded) were deployed in the Ebo forest, southwest Cameroon during the wet season in 2015, where annual rainfall is approximately 3,500 mm. A further ten systems (*n* = 10,383 hours recorded) were deployed between February and June 2015 in Central Scotland and Central England as part of a pilot study of long-eared owl *Asio otus* and tawny owl *Strix aluco* ecology in association with the British Trust for Ornithology. Finally, approximately 41,398 hours of audio (*n* = 35 systems) were recorded in 2015 and 2016 in Central Scotland and Central England as part of the Woodland Creation and Ecological Networks (WrEN) project (Watts et al. 2016). Four spectrograms of bird song recorded using the example configuration presented here are shown in Figure 3.1.

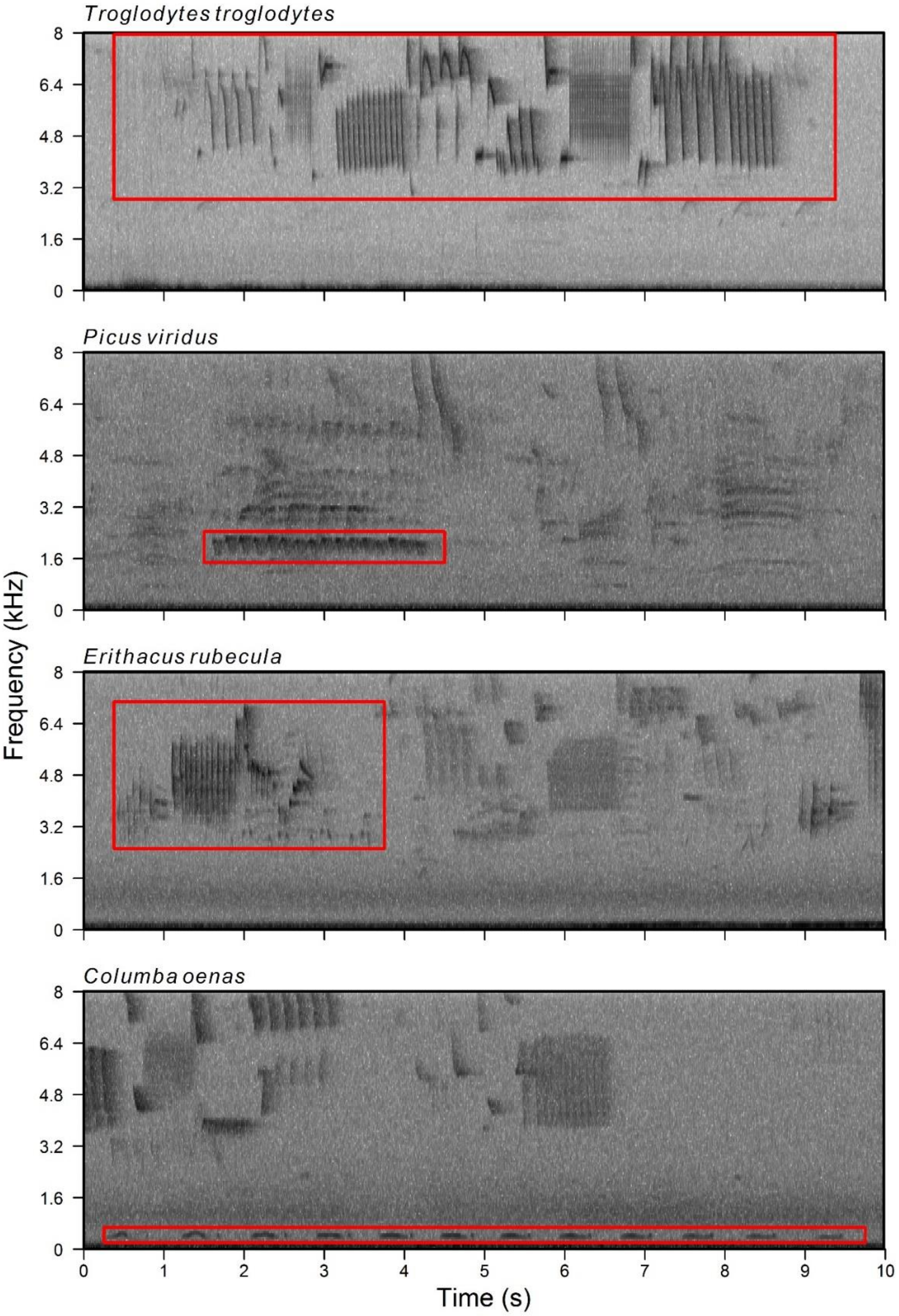


Figure 3.1 Spectrograms of four bird songs recorded using the example Solo configuration (Hanning window length = 256). The Solo was deployed in the middle of a small (*c*.1 ha) broadleaved woodland in Central Scotland. No post processing was performed.

Ultrasound

The ultrasound capabilities of the Solo have not been tested extensively, nonetheless there is considerable scope for development given the maximum sampling rate of 192 kHz. During a small scale field test in Central Scotland (*n* = 240 hours from five systems), foraging calls of soprano pipistrelle *Pipistrellus pygmaeus* were recorded (Figure 3.2). This was achieved using the example hardware configuration given below and setting the sampling rate to 192 kHz. The Solo was positioned on the ground beneath a known roost, and bats emerged and foraged approximately 3 - 4 m above the microphone.

There is considerable scope for developing the ultrasound capabilities of the Solo. We recommend that anyone interested in recording ultrasound should experiment with alternative microphones, such as the Knowles FG series (Knowles, Itasca, Illinois, USA).

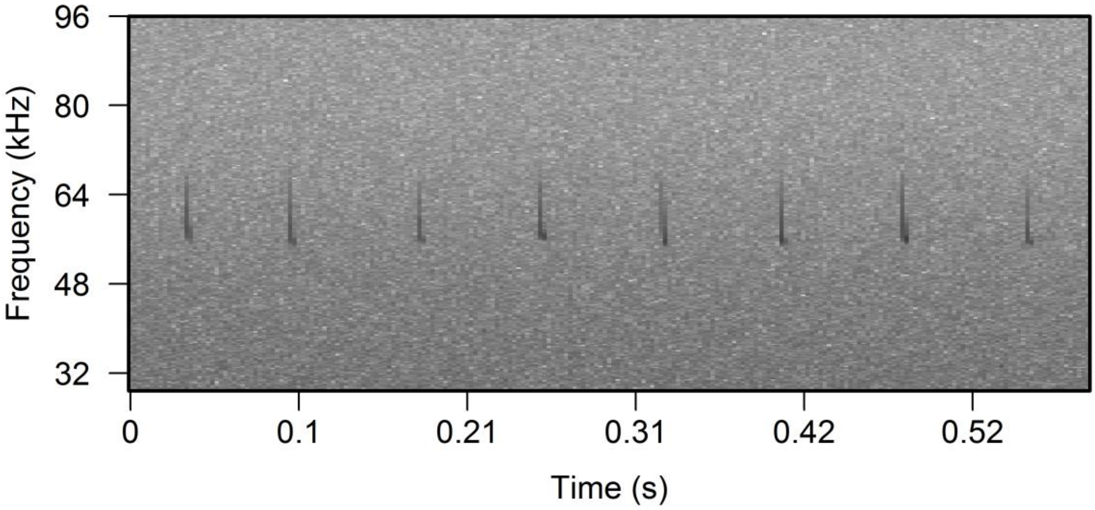


Figure 3.2 Spectrogram showing foraging calls of a soprano pipistrelle (Hanning window length = 1024). No post processing was performed.

EXAMPLE HARDWARE CONFIGURATION

The example hardware configuration (Table 3.2) described here was designed to record breeding woodland birds in temperate broadleaved woodland as part of the WrEN project, and it was found to be the most cost-effective configuration relative to battery life and audio quality. Using the default software settings, this configuration will record at a sampling rate of 16 kHz continuously (i.e. 24/7) for approximately 40 days during deployment (mean = 39.8, SE = 0.9 days, *n* = 24 systems with available data). See the supporting website https://solo-system.github.io/ and video tutorial https://youtu.be/2Fq05JlEKjw for a full description of how to build, operate and customise a Solo recorder.

Table 3.2 Components used to build the example Solo hardware configuration, approximate cost and manufacturer details. Suggested websites for purchasing non-generic components are also given.

Component	**Cost (£)**	**Model**	**Manufacturer**	**Website**
Raspberry Pi	15	Model A+ (lowest power consumption available)	Farnell element14, Leeds, UK	http://uk.farnell.com
Cirrus Logic Audio Card	24	One model	Cirrus Logic, Austin, Texas, USA	http://uk.farnell.com
PiFace clock	9	Clock module with dedicated button-cell battery (CR1220)	OpenLX SP Ltd, London, UK	http://uk.farnell.com
128 GB microSD memory card	40	SanDisk Ultra SDXC class 10	SanDisk, Milpitas, California, USA	-
Car battery	44	063XD: 12 V, 50 Ah	generic	-
Battery terminal clamp	2	12 V car battery terminal clip	generic	-
12 V to 5 V converter	9	DC-DC 12V To 5V converter module with USB adapter 15 W 3 A	generic	-
Microphone	15	Clippy EM172 model FC049	Primo Microphones, Inc. Mckinney, Texas, USA	http://micbooster.com/
Plastic electronics enclosure	1	Business card box	generic	
DRiBOX	8	FL-1859-200	DRiBOX, Black River Falls, Wisconsin, USA	http://dri-box.com/
Total cost	**£167**			

Data retrieval

Using the default configuration, audio is stored in a folder-per-day hierarchy as 10 minute sections. The data are stored on a dedicated partition on the microSD card and are accessed by using a computer and SD card reader. Free software may be required by non-Linux users to access the partition (see supporting website).

DISCUSSION

The Solo is a reliable, inexpensive, highly customisable audio recorder that can operate in remote locations for long time periods without user intervention. Example applications include landscape-scale studies (e.g. Watts et al. 2016) where dozens of systems might be required to achieve sufficient sample sizes, or deployment in situations where there is a high risk of the device being destroyed (e.g. by vandalism). Citizen science data are also increasingly used in ecological and conservation research (e.g. Newson et al. 2015; Kobori et al. 2016), and the Solo could increase participation in large-scale bioacoustic studies where the expense of commercial systems potentially limits participation.

Another advantage of the Solo over several existing systems is that it is predominantly built from open source hardware and software, and it can accept a wide variety of off-the-shelf microphones and power supplies. These features not only future-proof the system, but also make it user-serviceable, thus encouraging modification and development by the end user to suit specific research needs. Although commercial systems are likely to remain popular with those who require the additional benefits of warranties, customer services and out-of-the-box usability, the Solo recorder offers unprecedented flexibility at a fraction of the cost, which itself is likely to reduce over time given price trends in technology.

Directions for future development

At present, the Solo does not have a scheduling function, which would allow audio to be recorded only during predetermined time periods rather than continuously. In some audio recorders this can increase battery life. However, the Raspberry Pi does not have an efficient low-power mode, and a scheduling function would not therefore reduce power consumption significantly. Nonetheless, scheduling would improve storage capacity, which is of particular concern when recording at high sampling rates. In particular, scheduling is likely to be essential for recording taxa that are only active during short periods of the day and emit ultrasound, such as many bats and invertebrates. Furthermore, advanced scheduling could be used to improve the scope of field studies. For example, sampling rates could be changed according to prescheduled times, perhaps recording audible sound during daylight and ultrasound at night.

Audio is currently recorded in raw uncompressed .wav format, which requires approximately double the storage space of a compressed lossless format such as .flac, and future versions of the Solo software image could offer users a range of audio format options to address this. Furthermore, although the Solo can be operated for long time periods unattended, the user must collect the data and refresh the battery periodically, which may be difficult in some circumstances. Other systems are capable of wirelessly transmitting data to a base station (e.g. Aide et al. 2013), which addresses this problem. These capabilities could also be implemented in future Solo versions.

Finally, the processing power and potential functionality of the Raspberry Pi is underused by the Solo system in its current form, and the Raspberry Pi has the capacity to support many other features not discussed here. Examples include the addition of acoustic triggers that only record sounds above a specified amplitude, on-board data processing (e.g. species detection), a digital display, wireless communication in the field (e.g. with a smart phone or tablet) and the addition of peripherals (e.g. temperature loggers).

The Solo is an open source, customisable and inexpensive system for collecting high definition, long-term audio data. It has several advantages over comparable systems, and its introduction here (1) makes high-quality equipment accessible to those with limited resources, (2) improves the feasibility of conducting bioacoustic research across representative spatiotemporal scales, and (3) has the potential to advance the field of bioacoustics through the development of novel hardware and software configurations, leading to improved data collection.

ACKNOWLEDGEMENTS

Field trials in the UK were made possible by financial support and collaboration from the Natural Environment Research Council, the IAPETUS Doctoral Training Partnership, Forest Research, the British Trust for Ornithology, the Sound Approach, the National Forest Company and the Woodland Creation and Ecological Networks research project. Field trials in Cameroon were conducted in collaboration with the Zoological Society of San Diego’s Ebo Forest Research Project and the Wildlife Conservation Society. I would like to thank two anonymous reviewers for their comments on an earlier version of the manuscript.

CHAPTER 4

CONTEXT-DEPENDENT COLONISATION OF TERRESTRIAL HABITAT “ISLANDS” BY A LONG-DISTANCE MIGRANT BIRD

An adapted version of this chapter has been submitted for publication and is in review:

Robin C. Whytock, Elisa Fuentes-Montemayor, Kevin Watts, Nicholas Macgregor, Lefora Williams and Kirsty J. Park. *Submitted*. Context-dependent colonisation of terrestrial habitat “islands” by a long-distance migrant bird. Submitted to *Proceedings of the Royal Society B: Biological Sciences*

Contributions: RCW conceived the study with input from EF-M, KW, NM and KJP. RW collected the data with assistance from LW. RCW analysed the data and wrote the manuscript, and all co-authors commented on an earlier draft.

ABSTRACT

Global land-use change threatens species and ecosystems by affecting the movement behaviour of individuals and populations when landscapes become fragmented. Landscape context and fine-scale habitat characteristics can affect how individuals perceive patch quality during colonisation. However, although the effects of landscape context on colonisation behaviour has been investigated in aquatic environments, it has rarely been studied in terrestrial environments or at large spatial scales. I used a “natural” experiment to assess how landscape context influenced patch colonisation rates in a large-scale (*c.*7000 km^2) terrestrial system where colonisers (Willow Warbler *Phylloscopus trochilus* L.) are capable of rapid, long-distance (> 100 km / day) movements. Bioacoustic recorders were used to detect first colonisation dates in 23 spatially independent habitat patches in Scotland and England. I compared support for eight competing hypotheses that tested how first colonisation dates were affected by both local- and landscape-scale factors, such as the amount of bird song in a patch and the amount or configuration of habitat in the landscape (i.e. landscape context). Based on similar studies in aquatic environments, my general prediction was that landscape context would be a stronger predictor of arrival dates in isolated habitat patches than local, patch level factors. Results supported this expectation, and showed that first colonisation of focal patches was up to 5 days later in landscapes with high habitat availability, supporting the “propagule redirection” hypothesis. Alternative explanations, such as the diversity of bird song in a patch on the first song date had minimal support. Results suggest that large-scale habitat patterns can affect the timing of key events during the migrant bird breeding cycle. More broadly, I suggest that colonisation processes observed in fragmented aquatic environments can in some circumstances be extended to large-scale terrestrial environments.

INTRODUCTION

Understanding how landscape-scale habitat patterns influence colonisation dynamics in fragmented landscapes is an important theme in ecology and conservation (Haddad et al. 2015; Resetarits & Silberbush 2016). Theories of landscape connectivity broadly predict that during dispersal and colonisation the importance of habitat composition and configuration is related to a species' mobility and degree of habitat specialism (e.g. Taylor et al. 1993; Bélisle 2005). Colonisation can also be context-dependent, where colonisers select habitat patches based on the relative availability or quality of alternative habitat in the landscape (Resetarits 2005; Stier & Osenberg, 2010; Resetarits & Silberbush 2016). For many taxa, our understanding of how landscape-scale habitat patterns influence colonisation dynamics is limited to relatively coarse temporal scales (annual colonisation/extinction patterns; e.g. Bennet et al. 2004; Mortelliti & Lindenmayer 2015) and this can mask fine-scale behavioural processes that are important during initial colonisation of a breeding territory (Bélisle 2005). This knowledge gap is especially true for highly mobile, terrestrial species that are capable of rapid, kilometre-scale movements.

Evidence from aquatic islands provides some of the strongest support for context-dependent colonisation. In experimental coral landscapes, the number of colonisers is higher when focal patches have no adjacent patches, supporting the "propagule redirection" hypothesis (*sensu* Jones 1997; Stier & Osenberg 2010). Thus, colonisation rates are lower when isolated patches have more habitat in the surrounding landscape because colonists are redirected away from the focal patch. In the opposite direction, the "field of dreams" hypothesis predicts that "if you build it, they will come" and thus colonisation rates are expected to be proportional to habitat amount, which leads to higher colonisation rates in larger patches (Palmer et al. 1997; Stier & Osenberg 2010). Perceived patch quality can also be context-dependent; for example, predator presence in one patch can reduce the perceived quality of neighbouring patches in the local landscape (Resetarits & Binckley 2009; Resetarits & Silberbush 2016; Bohenek et al. 2017).

In terrestrial environments, the effects of landscape context on species turnover and community assembly are well-studied, but less is known about the influence of landscape context on colonisation *behaviour* (Bélisle 2005). The reasons for this knowledge gap are two-fold: (i) it is often difficult to precisely detect colonisation events and their timing, despite technological advances such as global positioning system (GPS) tracking, and (ii) it is difficult to conduct studies over sufficiently large spatial scales to ensure habitat patches are well replicated and spatially independent (i.e. colonisers should not move between focal patches).

Birds are among the most well-studied taxa in landscape ecology but although landscape configuration plays an important role in shaping bird communities the link between pattern and process is poorly understood (Bélisle 2005). Homing experiments show that displaced Ovenbirds *Seiurus aurocapilla* return faster to established territories when forest cover in the landscape is high (Bélisle & Desrochers 2001; Desrochers et al. 2011), suggesting that the amount of available habitat in the landscape is likely to be important during colonisation and habitat selection. Gap-crossing experiments have also been used to quantify how individuals cross non-habitat and indicate that forest species prefer to move through forest and forest edge rather than cross non-forest areas (Bélisle & Desrochers 2002; Robertson & Radford, 2009; Desrochers et al. 2011). Although this work has provided valuable insights into the movement behaviour of birds, such experiments have been criticised for being unrealistic (Powell & Stouffer 2015) and any link between experimental movement behaviour (e.g. during translocations) and natural colonisation behaviour remains speculative. Furthermore, there is usually a significant trade-off between spatial and temporal resolutions, where studies at large spatial scales tend to have low temporal resolution (e.g. monthly or yearly assessments of patch occupancy), and studies with high temporal resolution (daily counts of birds or translocation experiments) are usually limited to relatively small spatial scales. To meaningfully assess how landscape-scale habitat patterns influence habitat selection and colonisation behaviour in highly mobile taxa such as birds there is a need to achieve both high spatial and temporal resolutions (Bélisle 2005).

Entire populations of migratory birds move biannually between their breeding and wintering grounds. In spring in the northern hemisphere, males typically arrive on the breeding grounds before females and compete to secure the “best” territories (Part 1994), and changes in timing of arrival at the breeding grounds can have significant reproductive consequences due to phenological match or mismatch with resource availability (e.g. Arvidsson & Neergard 1991; Baker et al. 2004). Many migrant birds also show strong natal and breeding philopatry (e.g. Lawn 1994; Part 1994). Thus, the amount of available breeding habitat (i.e. territory availability) in a landscape will correlate with the number of individuals that return annually to breed in a given area. Combined with the varied landscapes over which migration and subsequent colonisation or re-colonisation of breeding territories occurs, this behaviour presents an ideal “natural experiment” to test the effects of local, patch -level factors (such as management practices) and landscape-scale habitat patterns (i.e. landscape context) on colonisation (Hollander et al. 2012). Furthermore, although landscape context can affect migrant bird fitness during stopover site selection during migration (Ktitorov et al. 2008), it remains unclear how landscape context influences initial colonisation of breeding territories. Bennet et al. (2004) found that migrant bird communities responded to regional gradients of land-use, but were unable to disentangle which factors were most important because of high multicollinearity between measures of land-cover. Despite a lack of empirical evidence, it is predicted that migrant birds will select landscapes with high habitat availability during initial colonisation (Bennet et al. 2004). Recent global declines of migratory birds are also poorly understood, and flyway-scale land-use change is implicated in population declines of some species (Vickery et al. 2014). Understanding how large-scale habitat patterns influence migratory bird colonisation behaviour is therefore a conservation priority.

Here, I used a natural experiment approach to test whether colonisation rates of terrestrial habitat "islands" are context-dependent when individuals are capable of rapid, large scale movements that are independent of habitat availability (i.e. direct, nocturnal migratory flights). I used inexpensive bioacoustic recorders to monitor migrant bird (Willow Warbler *Phylloscopus trochilus* L.) arrival (date of first male song) in focal patches distributed across large spatial scales. Habitat patches were spatially independent as far as possible and of similar size, but varied in the amount and configuration of habitat in the landscape (i.e. context). I explicitly tested three competing hypotheses that described how landscape context might affect colonisation rates landscape-selection", "redirection" and "relative patch size"; see Methods), and compared support for these with a further five hypotheses that accounted for patch "quality" and other non-landscape factors that are known to influence habitat selection in migratory birds, such as heterospecific attraction (Mönkkönen & Forsman 2002).

METHODS

Model species

To test whether colonisation rates of habitat islands depend on landscape context, the study system must satisfy six key assumptions: (i) the focal species must use habitats that can be easily characterised at coarse spatial scales (e.g. any wooded habitat in the landscape); (ii) territory densities must be proportional to habitat amount (this assumption is tested in Appendix 4.1: Figure 1); (iii) individuals must initially be absent from the patch; (iv) focal patches must provide suitable habitat for potential colonisers; (v) the timing of colonisation events must be detected with high precision and accuracy; and (vi) individuals must be capable of actively selecting patches (e.g. territorial bird *vs* wind dispersed invertebrate). To meet these criteria, I selected *P. trochilus*, a generalist woodland passerine bird that breeds in northern Eurasia (above approximately 41° N) and overwinters in sub-Saharan Africa (del Hoyo et al. 2017) as a model species.

In Great Britain, *P. trochilus* breeds in coniferous and broadleaf woodland and scrub, with an estimated 2.2 million territories across the island (Musgrove et al. 2013). Birds prefer woodland patches larger than 0.5 ha with intermediate canopy cover and vegetation ranging in height from roughly 3 to 6 m (Bellamy et al. 2009; Stostad & Menéndez 2014). Historical reporting rates show that *P. trochilus* begins to arrive in Great Britain in the last week of March and the population is fully installed by the end of April (BirdTrack 2017). Migration occurs mainly at night and birds travel at average speeds ranging from 40 to 85 km per day, but speeds of up to 218 km per day have been recorded (Southern 1938; Hedenström & Petterson 1987). Males arrive before females and are highly vocal when establishing territories, producing a loud, easily detected song that can be repeated up to six times or more per minute (Gil et al. 1999). Males of breeding age are highly philopatric, but adult interannual survival is relatively low at around 40% and thus individual turnover is high (Tiainen 1983; Lawn 1994). Once on the breeding grounds, males compete for the best territories, with higher quality territories occupied earlier in the season. Territory sizes range from approximately 0.2 - 0.3 ha (Foppen & Reijnen 1994; Hedlund 2015).

Habitat islands

Thirty-five post-agricultural broadleaf woodlands were selected to represent habitat islands from 107 woodlands used by the Woodland Creation and Ecological Networks (WrEN) research project (Appendix 4.2: Figure 1). The WrEN project (http://www.wren-project.com) comprises a large-scale natural experiment that aims to evaluate how landscape structure and patch characteristics influence biodiversity responses to habitat creation (Watts et al. 2016). Patch size is often a stronger predictor of bird species occurrence than other factors such as landscape configuration (Dolman et al. 2007; Chapter 2). Since my primary interest was the influence of landscape composition and configuration (i.e. context) on colonisation rates, I controlled for patch area by selecting small woodlands of similar size (0.5 - 2.6 ha), but which varied in the amount and configuration of suitable habitat in the surrounding landscape (c.f. Figure 7a in Fahrig 2013). Patches were previously surveyed in 2015 for breeding birds using standard census techniques (mapping over three visits; Chapter 2). The thirty-five woodlands consisted of twenty-three woods occupied by *P. trochilus* in 2015. To try and achieve a larger sample size, an additional 12 previously unoccupied woods that appeared to offer suitable habitat were also selected. The mean number of adult records (total mapped visual or aural registrations from three surveys) per occupied patch (n = 23) in 2015 was 3.48 ±1.26 95% CI, indicating that patches held one territory on average per survey. Patches were typically $\geq$ 3 km apart and were considered spatially independent because *P. trochilus* dispersal distances (i.e. distance between natal and breeding site) are typically < 1 km (Foppen & Reijnen 1994). Patch age (years since woodland establishment) ranged from 10 to 160 years (median 90 years), and age was correlated significantly with mean tree diameter at breast height (DBH) (r = 0.78, P < 0.001, n = 23 occupied patches).

Detecting colonisation

I used Solo audio recorders (Chapter 3) to record the first date of male *P. trochilus* song in each patch. Pilot tests were used to calibrate microphones so that songs could be detected at distances of approximately 50 m (Appendix 4.2: Figure 2), which is equivalent to a sampling area of 0.3 ha (i.e. one *P. trochilus* territory). It was therefore assumed that probability of detection was close to or equal to 1 within a focal patch, the unit of interest, and close to 0 for habitat in the surrounding landscape.

A single recorder was deployed in the centre of each woodland patch during the last week of March 2016 in advance of birds arriving and set to record audio continuously (24 hr, 7 days) until 1st May 2016. On the day of deployment, song playback was used to ensure that no territorial males were present in the study sites. *P. trochilus* song was broadcast using an .mp3 player and handheld speaker in 10 second bursts at 1-minute intervals for 3 minutes. No birds responded to song playback, indicating that patches were vacant when data collection commenced.

To identify the first song date in each woodland I used a sub-sampling approach. Three continuous 10-minute blocks of audio were randomly sampled from the three-hour period after sunrise per day of audio recording (i.e. 30 minutes of audio per day). I then manually examined audio spectrograms for *P. trochilus* song. After the first detection, I counted the number of calls in the sub-sampled audio for 14 consecutive days to ensure that the patch had been settled (i.e. colonised). Patches with no songs on two consecutive days of the 14 were considered not settled. To evaluate within-season turnover of individual males, I examined the relationship between song rates in a patch *n* days since the first song date, expecting the pattern to be consistent with Figure 4 in Arvidsson and Neergaard (1991) if there was no turnover (i.e. an initial steep rise in call rate followed by a plateau). I also compared first arrival dates with countrywide data from the British Trust for Ornithology to ensure that they were representative of those across Great Britain in 2016.

Hypotheses

The “propagule redirection” hypothesis (*sensu* Jones 1997; Stier & Osenberg 2010) predicts that when habitat availability in the landscape is low, focal patches will receive more colonists over time. This is based on the expectation that individuals sample randomly from the available habitat in a landscape. In the system used here, this would be indicated by earlier first song dates in more isolated patches because the probability of receiving an earlier colonist is higher per unit time (Figure 4.1a, solid line). In this case colonists are not a “propagule” *per se* but an adult male or first-year male of breeding age, and I therefore refer to this hypothesis as “redirection”.

Alternatively, if individuals are attracted to “landscape units” (i.e. not patches) that appear more favourable in general then focal patches might be colonised earlier when the amount of woodland in the landscape is higher. I call this the “landscape-selection” hypothesis, which would be consistent with the predictions made by Bennet et al. (2004). The expectation is that the initial cue to settlement is selection of landscapes with high habitat availability, with subsequent sorting into territories based on local, territory-level factors (e.g. food availably, vegetation structure etc). Thus, when the amount of habitat in the landscape is high, the expectation would be that the focal patch is colonised earlier than an equivalent patch with less habitat in the landscape (Figure 4.1a, dashed line). The direction of this predicted relationship, however, could also be caused by philopatry. Thus, landscapes with more habitat (and thus a higher number of potential territories) will receive more individuals returning to their previous breeding territories or close to their natal sites, which should lead to earlier colonisation of patches with more habitat in the surrounding landscape. The two mechanisms (i.e. landscape selection *vs* philopatry effects) are not mutually exclusive, however. It is therefore important to acknowledge that the study design used here cannot disentangle the independent effects of landscape selection *vs* philopatry where first song date is earlier in focal patches with more habitat in the landscape.

Larger patches have higher woodland bird abundance and occupancy (Dolman et al. 2007; Chapter 2). Individuals might therefore select patches based on their relative size in a landscape, with relatively large patches occupied earlier than relatively small patches. I therefore expected focal patches to be colonised earlier if they were large *relative* to nearby patches in the landscape, which I call the “relative patch size” hypothesis (Figure 4.1b).

In addition to the three competing hypotheses outlined above, I also considered the effect of distance to the nearest neighbouring patch (a simple measure of landscape connectivity) on colonisation rates. Based on my assumption that first colonisation occurs after nocturnal flights I hypothesised that it would have no effect (Figure 4.1c).

Measures of patch “quality” such as canopy cover, understory cover, tree DBH and tree diversity can be used to describe patch suitability for breeding *P. trochilus* (Bellamy et al. 2009; Stostad & Menéndez 2014). Since most of the patches were already known to be used by *P. trochilus* and generally similar in structure (i.e. broadleaf post-agricultural woodlands), and since I assumed that colonisation occurred rapidly at dawn after nocturnal flights, I predicted that patch-level factors would have no effect on colonisation rates (Figures 4.1d – 4.1g).

Manipulative experiments have demonstrated that migrant birds are attracted to the vocalisations of other woodland birds (heterospecific attraction) when choosing territories (Mönkkönen & Forsman 2002). To test for the existence of heterospecific attraction I calculated an index of acoustic complexity (which correlates with bird species richness) in the patch on the first song date, expecting that patches would be colonised earlier as soundscape complexity (i.e. bird song richness) increased (Figure 4.1h).

I attempted to control for patch size during site selection as far as possible, but since there was some small variation I tested for an effect, expecting no relationship between patch area and colonisation rates (not illustrated). Finally, the null model predicted that woodlands further north and east would be colonised later (not illustrated) based on knowledge of large-scale *P. trochilus* migration patterns in the UK (Southern 1938).

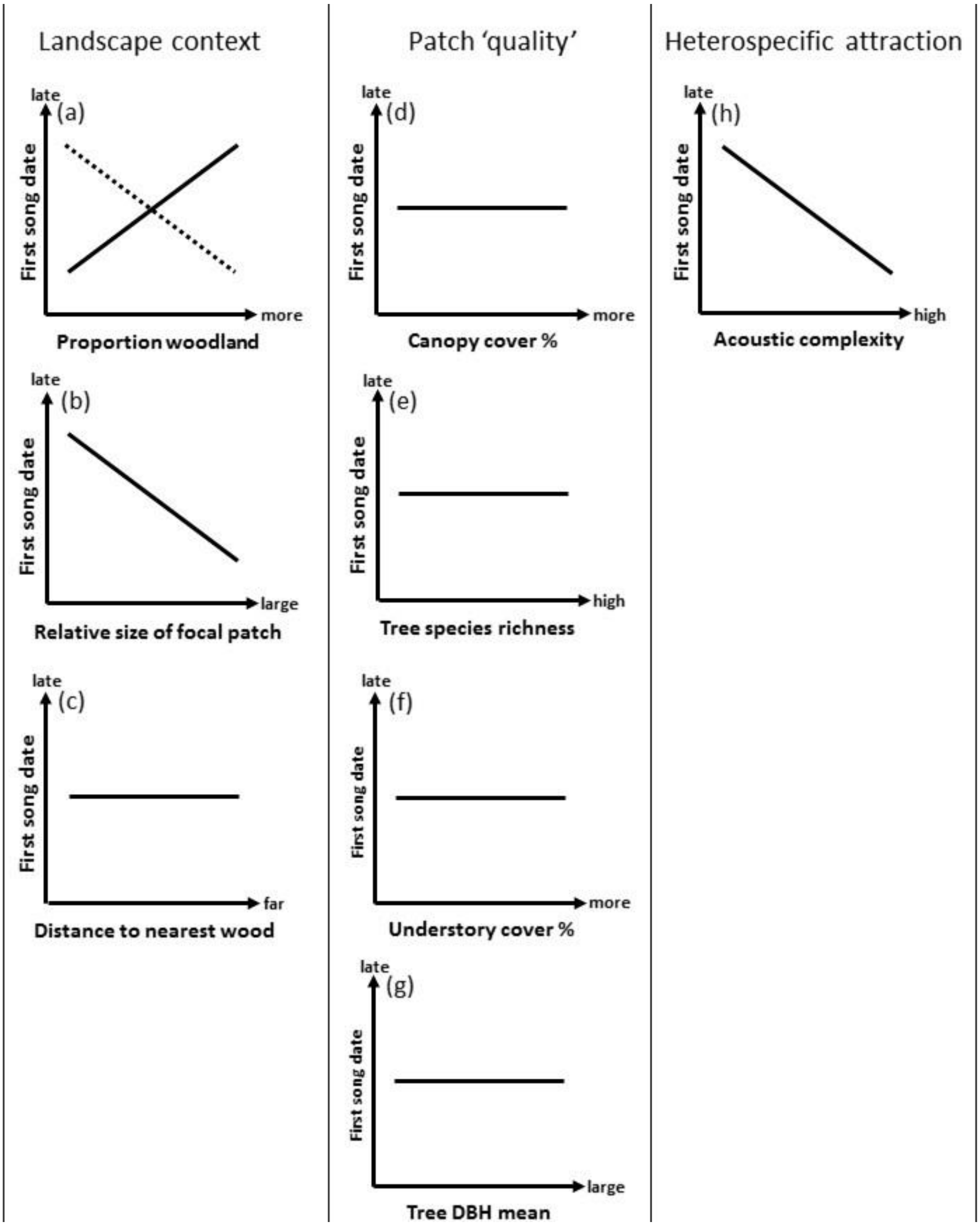


Figure 4.1 Hypothesised relationships between first *P. trochilus* song and variables describing landscape context (a - c), patch quality (d - g), and acoustic complexity in a patch (h) (see Methods). The dashed line in (a) represents the expected relationship for the "landscape-selection" hypothesis and the solid line in (a) the "redirection" hypothesis.

Predictor variables

Two variables were used to test my three primary hypotheses of interest. The amount of habitat (any woodland) in the landscape was used to test the “redirection” and “landscape-selection” hypotheses, and the ratio between the focal patch size and the median patch size of any woodland in the landscape was used to test the “relative patch size” hypothesis. Habitat amount and relative patch size were calculated from Forestry Commission (2013) spatial data at eight scales (nested buffers surrounding the patch; 100 m, 250 m, 500 m, 1000 m, 1500 m, 2000 m, 2500 m and 3000 m). I selected a single “scale of effect” (Fahrig 2013) for each landscape variable using univariate Poisson generalised linear models and corrected Akaike Information Criterion (AIC_c). Four variables were used to test the effects of vegetation structure on first arrival date, which were percent canopy cover, tree mean DBH, tree species richness and percent understory cover (obtained during field surveys; Appendix 4.3). Acoustic complexity was used to test the heterospecific attraction hypothesis and was calculated as the mean acoustic complexity index (Pieretti et al. 2011) for the 3 x 10-minute sub-sampled audio files from the first song date in a patch. To validate the index, I regressed the averaged acoustic complexity value against raw bird species richness per site (n = 23) in 2015, confirming that there was a positive relationship (Appendix 4.4: Figure 1). Patch size was calculated from Forestry Commission (2013) spatial data.

Modelling approach

Linear models were used to quantify the relative effects of each predictor on first *P. trochilus* song date. Geographical position (i.e. northing and easting) was expected to have the strongest effect on first song date, and the null model included northing and easting only as continuous predictors. Generalised linear models were fitted by maximum likelihood, and residual diagnostics suggested a Poisson error structure was more appropriate than a Gaussian error structure. To avoid overfitting the data (i.e. modeling the residual variation because the ratio between n and the number of parameters is too low), and because I was primarily interested in the relative magnitude of effects, separate models were constructed for each predictor of interest but in all models northing and easting were included as covariates.

Predictors were mean centred and scaled by one standard deviation to compare relative effect sizes (β). AIC_c was used to compare goodness of fit between each model and the null, and 95% confidence intervals for effect sizes were bootstrapped from 500 resamples of the data. Multicollinearity between predictors (i.e. northing, easting and the predictor of interest) was assessed using variance inflation factors (threshold < 5) and model validation followed Zuur et al. (2010). A correlation matrix for all predictors is in Appendix 4.5: Table 1 and results for the null model are given in Appendix 4.5: Table 2. R statistical software was used for the analysis (R Core Team, 2016).

RESULTS

Of the 35 woodland patches surveyed, *P. trochilus* were detected only in the 23 patches previously occupied in 2015, and these data were used in the analysis (Appendix 4.6: Figure 1). The median arrival date was the 16th of April (range 5th - 22nd April). Arrival dates were consistent with British Trust for Ornithology countrywide data in the same year (Appendix 4.6: Figure 2), indicating that results were representative. Although *P. trochilus* was detected in 23 woodlands it did not settle in five of them; however, since the hypotheses were structured in a way that focused on first song date and not subsequent probability of settlement, I retained all 23 sites in the analyses. In patches that were settled, song rates increased over time after the first detection before reaching a plateau, and the shape of the relationship was generally consistent with those observed by Arvidsson and Neergaard (1991) (Appendix 4.6: Figure 1). In several instances males may have been replaced, however (e.g. Appendix 4.6: Figures 1f and 1g).

After accounting for geographic location, the first song was detected significantly earlier in patches with low amounts of woodland in the surrounding landscape at 2 km compared to those patches with high amounts of woodland (Table 4.1; Figures 4.2 and 4.3). The effect size was relatively large (Table 4.1) and first song date was delayed by approximately 5 days as woodland amount in a 2 km buffer increased from 5 – 30%. The positive direction of this effect was consistent with the “redirection” hypothesis (Figure 4.1a), and the variance explained (36%) was 11 – 12% higher than alternative models (Table 4.1).

Contradicting expectations, there was no evidence to suggest that the relative size of the focal patch compared to other patches in the landscape affected colonisation rates. Distance to the nearest woodland, patch size and vegetation structure inside the patch also had no detectable effects on first colonisation, as expected. Counter to expectations, I found no support for heterospecific attraction.

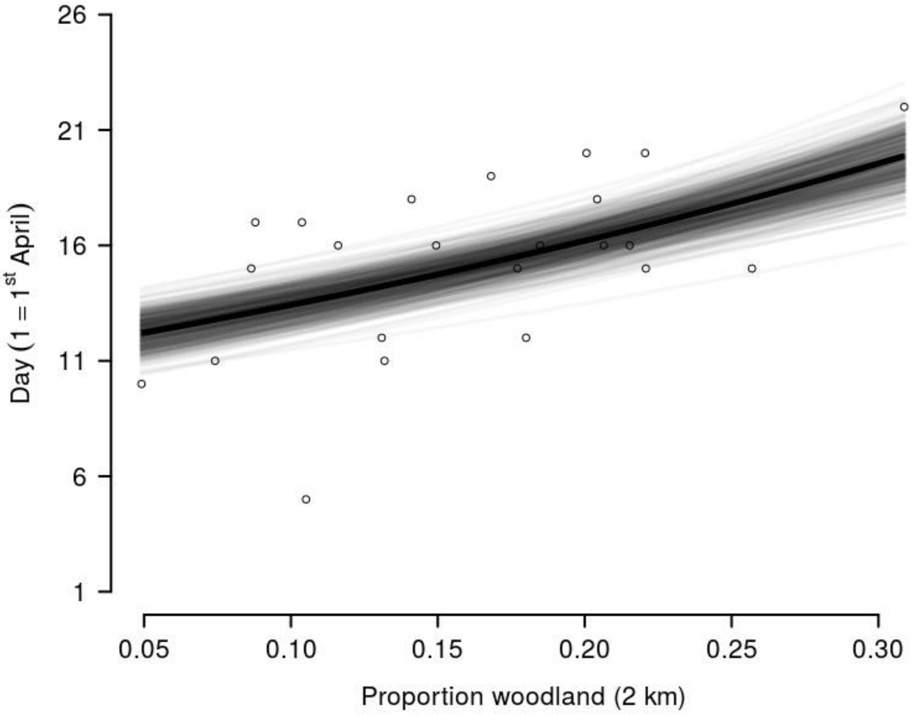


Figure 4.2 Relationship between first *P. trochilus* song date and habitat amount within 2 km of a woodland patch. Circles are observed values and semi-transparent lines are bootstrapped 95% confidence intervals.

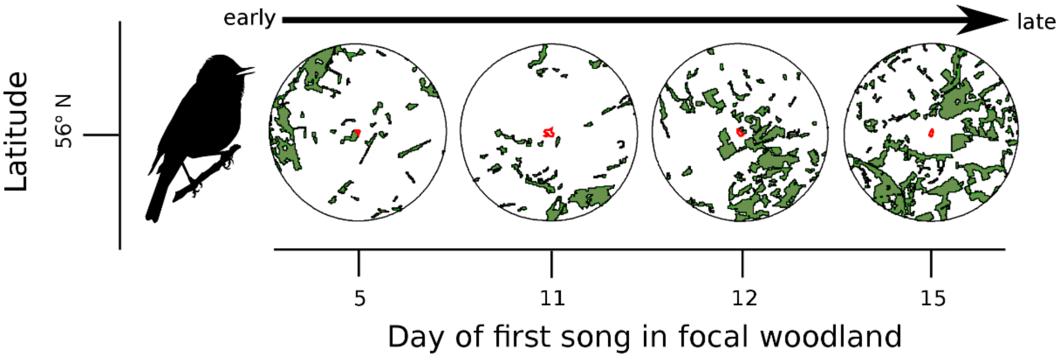


Figure 4.3 Illustration showing the relationship between the amount of woodland in the landscape (green, 2 km buffer) and observed first *P. trochilus* song date (day in April 2016) in four example focal woodlands (red) at similar latitudes (near 56° N).

Table 4.1 Results from the Poisson generalised linear models showing the standardised coefficient estimates for each predictor of interest (β). Northing and easting were included as covariates in each model, but their estimates are not shown. The null model (H_0) included northing and easting only and results are in Appendix 4.2: Table 5.

Model	Focal predictor	β	-95%	+95%	P	ΔAICc from H_0	R^2
1	Proportion any woodland (2 km buffer)	0.12	0.01	0.23	0.04	-1.35	0.36
2	Relative patch size (2 km buffer)	0.01	-0.12	0.13	0.92	2.95	0.23
3	Distance to nearest wood (m)	0.02	-0.09	0.12	0.73	2.84	0.24
4	Canopy cover percent	0.04	-0.09	0.16	0.58	2.65	0.24
5	Tree species richness	0.02	-0.09	0.13	0.68	2.79	0.24
6	Understorey cover percent	0.00	-0.12	0.10	0.93	2.95	0.23
7	Tree DBH mean	-0.01	-0.12	0.10	0.91	2.95	0.23
8	Acoustic complexity index	-0.01	-0.12	0.10	0.91	2.94	0.23
9	ln(area) (ha)	0.04	-0.10	0.17	0.59	2.67	0.24

DISCUSSION

The importance of landscape context for community assembly and dispersal behaviour is well known, but the relationship between landscape context and *colonisation* behaviour is less clear, particularly in terrestrial systems and for organisms that undertake very large-scale, rapid movements. In agreement with experimental work in aquatic environments, results support the “redirection” hypothesis (Stier & Osenberg 2010), and I found little support for the “landscape selection” (Bennet et al. 2004) or “relative patch size” hypotheses. Previous work in the study area also supports the redirection hypothesis and, after controlling for patch size and other factors, the relative abundance of woodland birds was lower in focal patches (*n* = 101) when the amount of broadleaf woodland within 1 km was higher (Figure 2.3b).

Whether this pattern is caused by a random sampling process (i.e. higher probability of “capturing” a colonist when there is less habitat in the landscape), or if individuals are actively selecting patches with low amounts of habitat in the surrounding landscape, cannot be disentangled using these results. Philopatry also plays an important mechanistic role in dictating where birds return to breed each year. Adult males will typically return to their previous territory if they bred successfully, and first year males will return to within 1 km of their natal territory on average. Despite strong philopatry in *P. trochilus*, however, it cannot explain the observed relationship between first song date and the amount of woodland in the landscape based on our *a priori* expectations. Therefore, given the remarkable navigational skills of migrant birds and the cognitive ability of some species to actively select vacant territories based on their relative quality (e.g. prospecting behaviour in Collared Flycatchers *Ficedula albicollis*; Doligez et al. 2004a; Doligez et al. 2004b), I suggest that the relationship between first song date and habitat amount in the landscape is unlikely to be due to a random sampling process, and propose that isolated patches become disproportionally attractive to early colonists in landscapes with less alternative habitat.

The relatively isolated agricultural woodlands studied here probably represent poor quality habitat patches for *P. trochilus*. Yet, when they are situated in landscapes with little alternative habitat they appear to become relatively more attractive because colonists arrive earlier. Paradoxically, this is despite *P. trochilus*' ability to travel more than 100 km per night during migration, which implies that individuals could avoid sparsely wooded landscapes with relative ease. This relationship would have been overlooked by studies of patch occupancy or abundance (e.g. Mortelliti & Lindenmayer 2015; Huber et al. 2017; Chapter 2) because most patches were eventually occupied and thus would appear equally "attractive" if surveys were made at coarse temporal scales or later in the season.

During migration and stopover, body mass gain in *P. trochilus* is higher when landscapes have more forest cover (Ktitorov et al. 2008). It therefore appears perverse that the first songs are detected in the most isolated woodlands since these individuals are likely to experience fitness costs. Perhaps isolated woodland patches are acting as ecological traps (Robertson et al. 2013), leading individuals to trade off current *vs* future fitness potential by avoiding further, potentially risky long distance migratory flights when the landscape appears to have limited habitat availability. Other migratory birds are also attracted to "ecological traps" that arise from novel habitat patterns in the landscape, such as selectively harvested forest (Robertson & Hutto 2007). Considering *P. trochilus* declines across much of their range (Vickery et al. 2014) there is a need to understand if the habitat selection patterns observed here are causing relatively high-quality individuals (as measured by earlier arrival date) to select sub-optimal breeding territories.

Translocation experiments have shown that forest birds (including long-distance migrants such as Ovenbird) return faster to established territories when landscapes are more favourable and have more habitat (Bélisle & Desrochers 2001; Desrochers et al. 2011). This suggests that the same could be true during initial colonisation of breeding territories. However, the drivers that motivate a bird to return to an established territory (perhaps with eggs or nestlings) are quite different to those that motivate initial colonisation or re-colonisation of a territory after spring migration. Results are consistent with colonisation occurring after nocturnal flights that are not constrained by habitat availability in the landscape. In the case of translocation experiments, individuals probably take advantage of available habitat to travel by day and return rapidly to their existing territory, where they have invested significant resources. We should therefore be cautious when extrapolating findings from experimental work on movement ecology to natural systems.

Contradicting expectations, I detected no relationship between acoustic complexity in a patch and first song date, providing no support for heterospecific attraction during initial colonisation. Heterospecific attraction is, however, well supported by evidence from other studies that have tested for its existence experimentally (e.g. Mönkkönen & Forsman 2002; Fletcher 2007). These have shown that migrant bird abundance tracks the abundance of other woodland bird species. I suggest that heterospecific cues might influence migrant bird densities at the local scale once the population has arrived and territorial assortment has begun, but when territories are mostly vacant during initial colonisation early in the season then heterospecific cues are probably less important than large-scale habitat patterns. This hypothesis could be tested more robustly by recording first colonisation events (as here) and then also monitoring post-colonisation dynamics (i.e. migrant density) in a patch, for example by quantifying how heterospecific cues and landscape composition interact to affect migrant bird species accumulation in a patch.

The lack of support for the relative patch size hypothesis was surprising given the apparent importance of patch size for *P. trochilus* and other woodland birds (Bennet et al. 2004; Dolman et al. 2007; Chapter 2). There is ongoing debate surrounding the importance of habitat amount *vs* habitat configuration (i.e. relative patch size in this study) for community assembly in fragmented landscapes (Fahrig et al. 2013; Haddad et al. 2017). This result suggests that habitat amount is more important than habitat configuration for *P. trochilus* during colonisation or re-colonisation of territories after migration.

It is important to acknowledge that these results are from a single year and differences in weather conditions or population densities between years, for example, might also interact with landscape context to influence colonisation and settlement rates. Nonetheless, arrival times were consistent with the historical average in Great Britain and those recorded in 2016, and results supported a well-defined, *a priori* hypothesis. Furthermore, although I detected no effect of patch size or vegetation structure on colonisation rates, this is not necessarily because these factors are unimportant, but because

I was successful in controlling for their effects during site selection. It would be interesting to look at interactions between local and landscape-scale factors when seeking to understand colonisation dynamics under natural conditions, but this would require a substantial numbers of study sites and would be logistically challenging.

I conclude that habitat amount in the landscape can affect *P. trochilus* arrival times in small habitat patches after Spring migration, which is surprising given that movement through the landscape is not constrained by habitat composition or configuration (i.e. nocturnal flights). These results represent an important step forward in understanding how landscape context influences colonisation dynamics by extending results from smaller, experimental systems in aquatic environments to considerably larger scales and to a terrestrial environment under natural conditions. The non-invasive methods used to detect colonisation events also offer considerable promise for studying how landscape composition and configuration influence the colonisation behaviour of other highly mobile, acoustically active taxa that might be too small to track in time and space using existing tracking technology.

ACKNOWLEDGEMENTS

I am grateful to landowners for permitting access to the study sites. The study was funded by the Natural Environment Research Council, the National Forest Company and Forest Research. The WrEN project has been funded by the University of Stirling, Natural England, Forestry Commission, Scottish Natural Heritage, the Department for the Environment, Food and Rural Affairs, the National Forest Company, Forest Research, the Woodland Trust and Tarmac Ltd.

Appendix 4.1 *P. trochilus* relative abundance and habitat amount

Satisfying the assumption that *P. trochilus* densities are proportional to habitat amount

An important assumption is that *P. trochilus* densities are proportional to the amount of habitat in the landscape. This is because when two landscapes have the same proportion of habitat but not the same number of potential territories, the number of potential colonists will also differ between the two landscapes. This could lead to spurious results, especially type II errors (false negatives) where differences in *P. trochilus* densities between landscapes obscure any effect of habitat amount. Ideally, the assumption that densities are proportional to habitat amount should be tested at the landscape scale, for example by quantifying the relationship between *P. trochilus* densities and habitat amount in 10 km grid squares, but this would be logistically challenging. British Trust for Ornithology data could be used to test the assumption but was unavailable at the time of writing. Alternatively, since results from Chapter 2 showed there was a strong positive correlation between patch size and the relative abundance of birds in the study woodlands, it is possible to test if *P. trochilus* relative abundance increases linearly with patch size. Confirming this relationship would support the assumption that the amount of woodland in the landscape is also likely to be proportional to the number of territories.

Methods

To test this assumption I used data collected in Chapter 2 and created a generalised linear model with the relative abundance of *P. trochilus* per patch as the response variable and patch size as a continuous fixed effect (n = 101 patches: see Methods in Chapter 2). The model was fitted using a negative binomial error structure (log-link) to account for over-dispersion. *P. trochilus* were rarer in England than in Scotland, so country was also included as a categorical fixed effect, and a two-way interaction between country and patch size was included because the slope of the relationship was expected to differ between the two regions, since *P. trochilus* have declined significantly in England during recent decades (Balmer et al. 2013). The model was fitted using maximum likelihood estimation (MASS R package; Venables & Ripley 2002) and goodness of fit was assessed by visually inspecting residual plots following Zuur et al. (2010). *P. trochilus* are typically found at densities of approximately 3.3 per ha (see Methods), and the relationship between patch size and relative abundance was expected to be close to this density on average.

Results

As expected, there was a positive relationship between patch size and the relative abundance of *P. trochilus* (Table 1), and the interaction showed that densities in the study sites were lower in England than Scotland, as predicted. In Scotland, mean densities were close to expectations (but with high uncertainty) based on the predicted 3.3 territories per ha (Figure 1a) but this was not the case in England, where densities were significantly lower than expected (Figure 1b).

Table 1. Coefficient estimates, standard errors and *P* values from the generalised linear model (negative binomial error distribution with a log-link function) showing the relationship between *P. trochilus* relative abundance (intercept) and fixed effects of patch size (*n* = 101 patches: see Methods in Chapter 2), country (Scotland or England) and patch-size x country interaction. The shape (dispersion) parameter (θ) for the negative binomial distribution was 0.981 (0.229 SE).

Variable	Estimate	SE	*P*
(Intercept)	-0.12	0.31	0.69
Patch size (ha)	0.06	0.03	0.02
Country (Scotland)	0.80	0.40	0.04
Patch size (ha) * Country (Scotland)	0.49	0.14	0.002

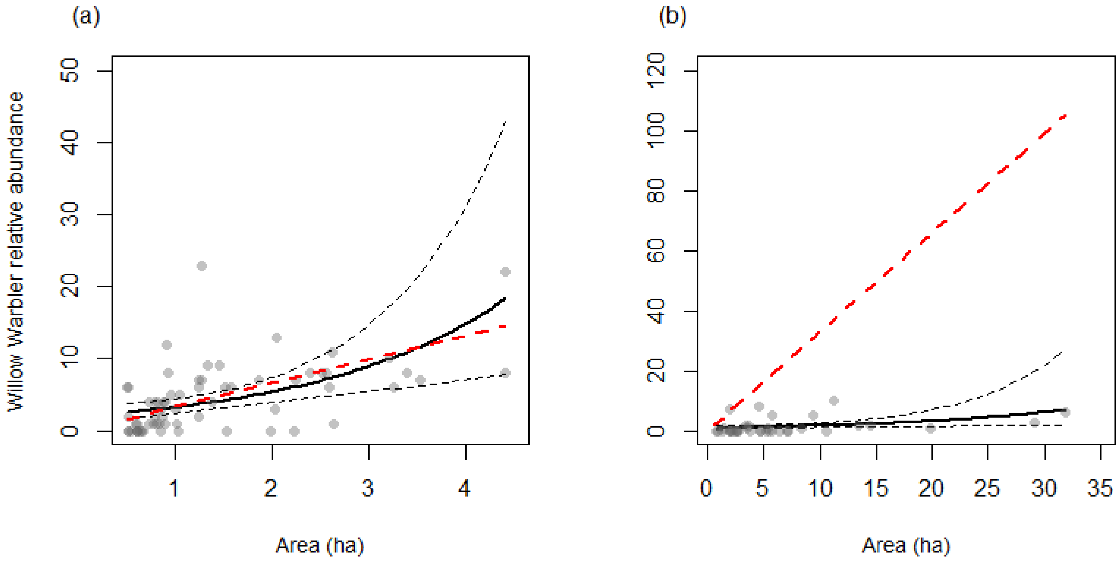


Figure 1. Relationship between patch size (i.e. habitat amount) and the relative abundance of breeding Willow Warblers in 101 woodlands surveyed in 2015 (Chapter 2; Whytock et al. 2017). Plot (a) shows results for Scotland and plot (b) for England. Solid black lines are the back-transformed fitted values from the generalised linear model (Table1) and dashed black lines are 95% confidence intervals. The dashed red line shows the expected relationship based on 3.3 Willow Warbler territories per ha (see Methods). Gray filled circles show the raw data. The x-axis range represents the range of patch sizes in Scotland (a) and England (b), respectively.

Interpretation

These results support the assumption that *P. trochilus* densities increase linearly on average with habitat amount, but only in Scotland (where 20 of the 23 sites used in the analysis were located; Appendix 4.2: Figure 1).

Appendix 4.2 Map of the study sites and microphone detection distances

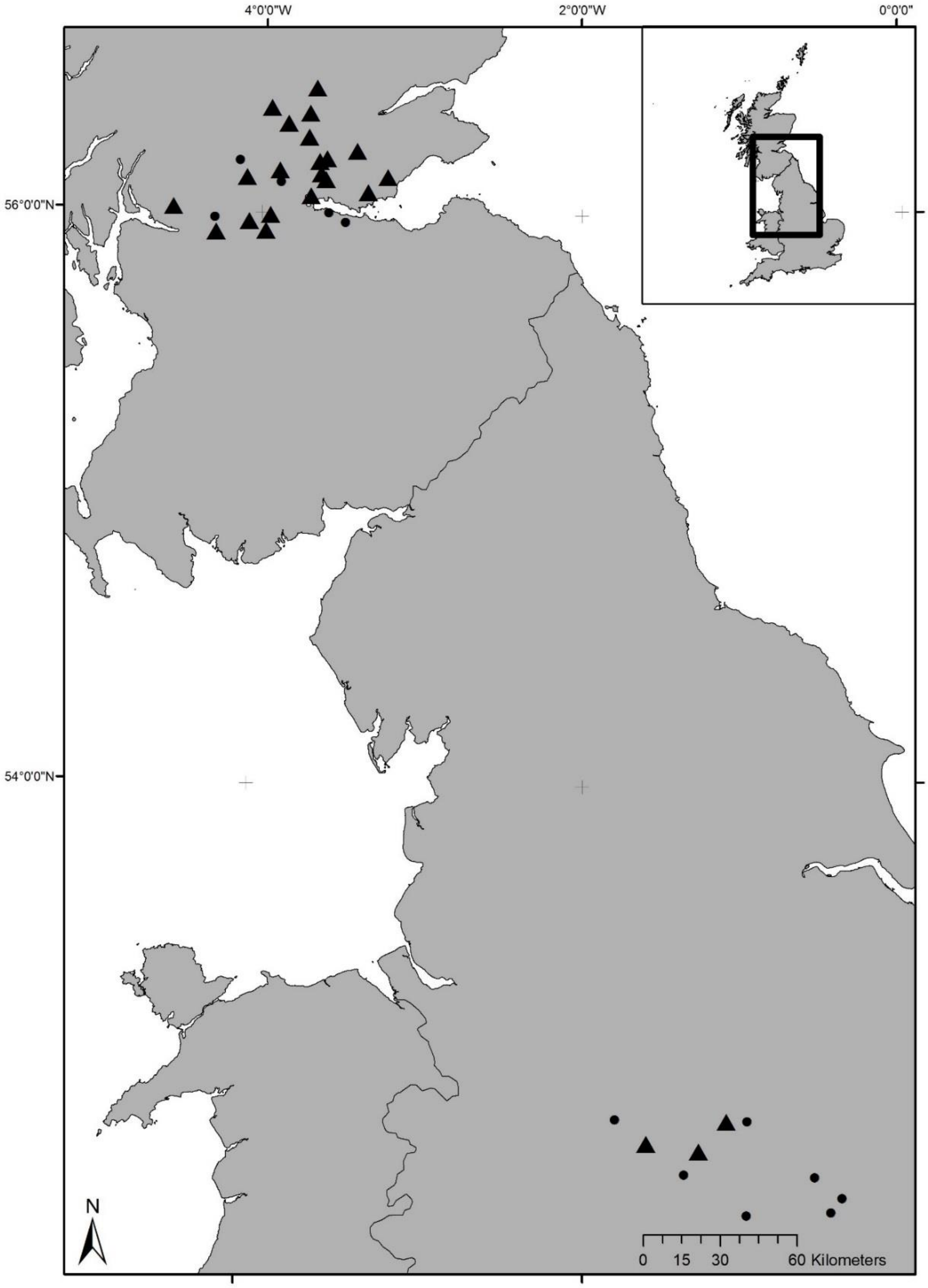


Figure 1. Map of the study sites. Sites colonised by Willow Warblers *Phylloscopus trochilus* and used in analyses (n = 23) are shown as filled triangles. Filled circles indicate sites where acoustic loggers were deployed but no Willow Warblers were detected.

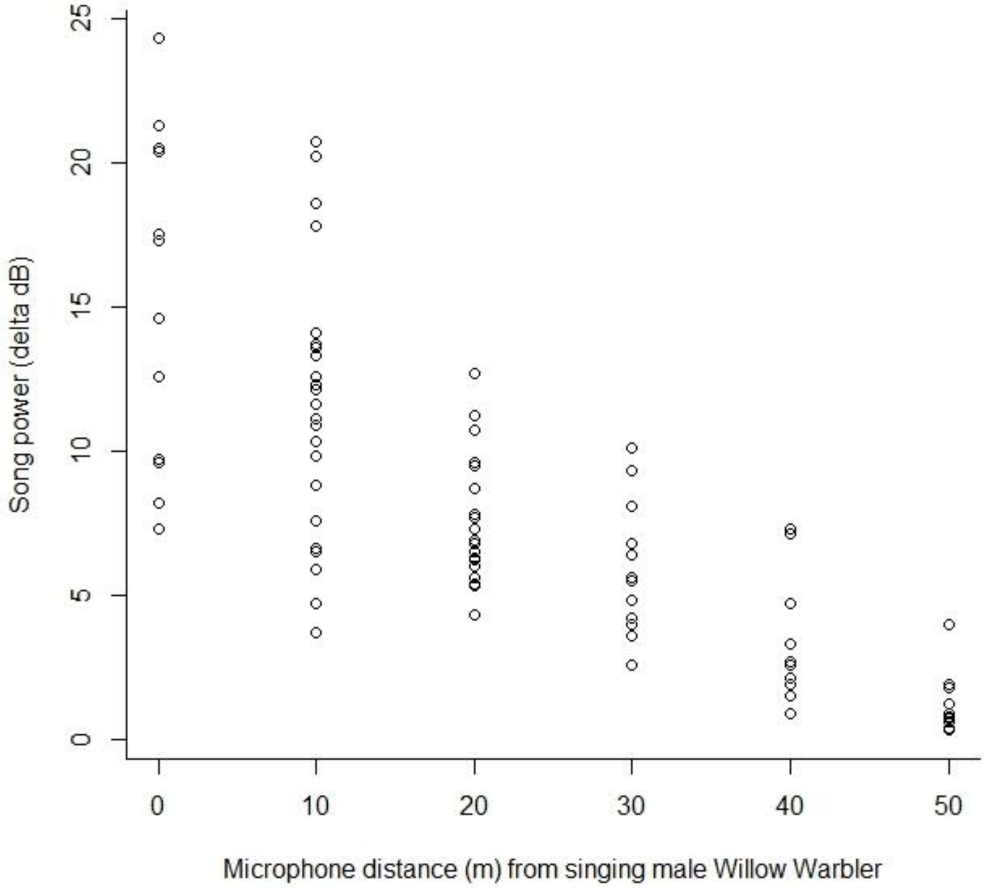


Figure 2. Relationship between microphone (array of *n* = 10) distance from a singing male willow warbler (*n* = 1 territory; *n* = 97 song phrases) and song delta dB (i.e. difference in power between signal and adjacent 1 s of background noise) when the microphone was calibrated to detect song at distances of *c*.50 m. Recordings were made in good weather conditions.

Appendix 4.3 Summary statistics for all local and landscape variables

Table 1. Description and source of local and landscape metrics used in the analysis. Summary statistics for all variables are given in Table 2.

Variable	Description	Source
Landscape context		
Proportion woodland	Percentage cover	GIS NFI dataset [a]
Relative patch size	Ratio between median patch size (mp) in landscape and focal patch size (fp): $mp \div fp$	GIS NFI dataset
Distance to nearest wood (m)	Euclidean distance to nearest patch of any woodland	GIS NFI dataset
Patch 'quality'		
Canopy cover percent	Mean for patch	Field survey 2013/14
Tree species richness	*n* tree species	Field survey 2013/14
Understory cover percent	Mean for patch	Field survey 2013/14
Tree DBH mean (cm)	Mean for patch	Field survey 2013/14
Patch size		
Patch area	Ha, log transformed	GIS NFI dataset [a]
Acoustic complexity		
Acoustic complexity index	Mean for 3x 10-minute audio files (see Methods) on day of first *P. trochilus* song. Calculated in a frequency band between 0.5 and 8 kHz using R package seewave (Sueur et al. 2008; Pieretti et al. 2011).	Audio recordings

[a] Geographic Information System (GIS) data calculated using ArcMap *v*10.2 and National Forest Inventory data (Forestry Commission 2013).

Table 2. Summary statistics for all predictor variables and the response variable (first *P. trochilus* song date).

Variable	**Mean**	**SD**	**Median**	**Minimum**	**Maximum**
Landscape context					
Proportion woodland (2 km)	0.18	0.07	0.19	0.05	0.33
Relative patch size (2 km)	0.82	0.45	0.72	0.22	1.72
Distance to nearest wood (m)	117.92	127.14	67.85	7.54	530.68
Patch 'quality'					
Canopy cover %	73.38	17.55	78.00	36.00	97.50
Tree species richness	4.83	2.69	4.00	1.00	12.00
Understory cover %	2.12	2.23	1.30	0.00	8.00
Tree DBH (mean)	30.84	13.73	24.93	13.90	61.49
Patch size					
Area (ha)	1.14	0.67	0.78	0.50	2.59
Acoustic complexity					
Acoustic complexity index	134.27	5.86	132.86	122.45	144.79
Response variable					
First willow warbler (1=1st April '16)	15.30	3.81	16.00	5.00	22.00

Appendix 4.4 Acoustic complexity index and species richness

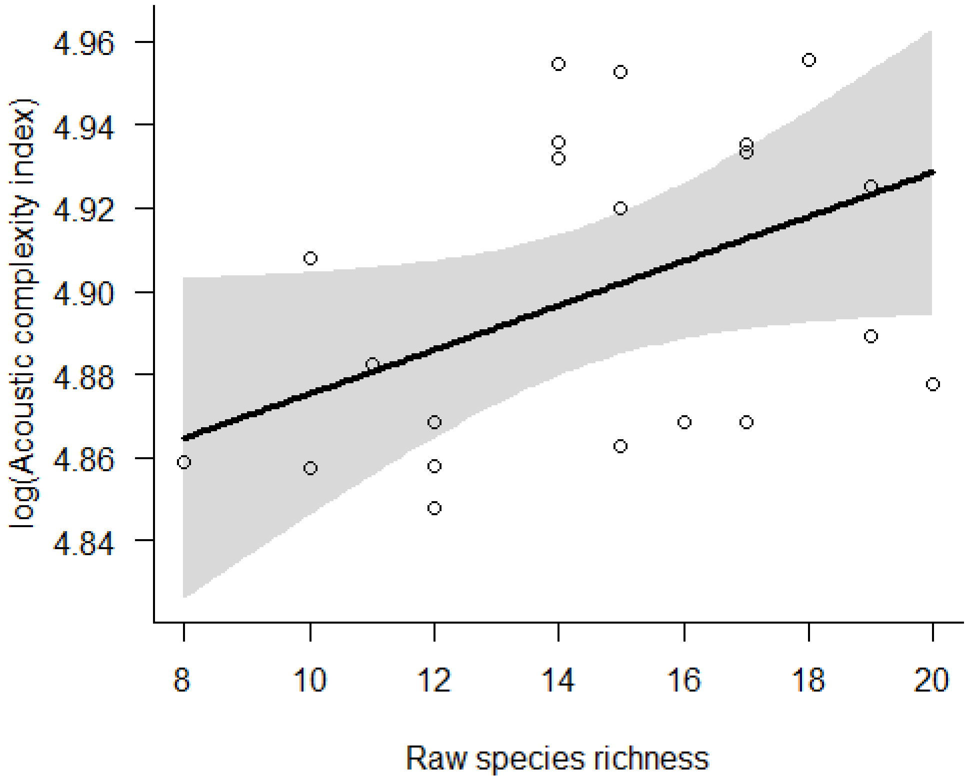


Figure 1. Relationship between acoustic complexity index (log transformed) and raw bird species richness (t_{22} = 1.92, Beta = 0.02, p = 0.066, R^2 = 0.15) in the 23 sites colonised by Willow Warblers *Phylloscopus trochilus*. The black line is the fitted values from a generalised linear model with a Gaussian error structure (identity link) and the grey polygon represents 95% confidence intervals. Circles are observed values.

Appendix 4.5 Correlation matrix and summary statistics for the null GLM

Table 1. Matrix of Pearson's correlation coefficients for all predictor variables

	Easting	**Northing**	**Understory cover %**	**Tree DBH (mean)**	**Canopy cover %**	**Distance to nearest wood (m)**	**Tree species richness**	**Relative patch size (2 km)**	**Proportion woodland (2 km)**	**Acoustic complexity index**
Northing	-0.92									
Understory cover %	0.31	-0.30								
Tree DBH (mean)	-0.19	0.27	0.20							
Canopy cover %	0.31	-0.14	0.28	-0.20						
Distance to nearest wood (m)	0.14	-0.08	0.13	0.08	-0.08					
Tree species richness	0.21	-0.23	0.26	0.14	0.13	-0.03				
Relative patch size (2 km)	-0.38	0.49	-0.03	0.20	0.09	0.13	-0.38			
Proportion woodland (2 km)	-0.19	0.26	-0.23	0.08	-0.01	0.06	-0.15	0.25		
Acoustic complexity index	0.19	-0.20	0.42	0.38	0.22	-0.07	0.50	-0.14	-0.28	
ln(area)	0.61	-0.63	0.13	-0.29	0.19	-0.07	0.26	-0.68	-0.17	0.07

Table 2. Summary statistics for the null model (AIC$_c$ 128.83).

Variable	**β**	**SE**	**Z**	**P**
Intercept	2.72	0.05	50.56	< 0.001
Easting	0.28	0.14	1.96	0.05
Northing	0.34	0.14	2.37	0.02

Appendix 4.6 Patch settlement results

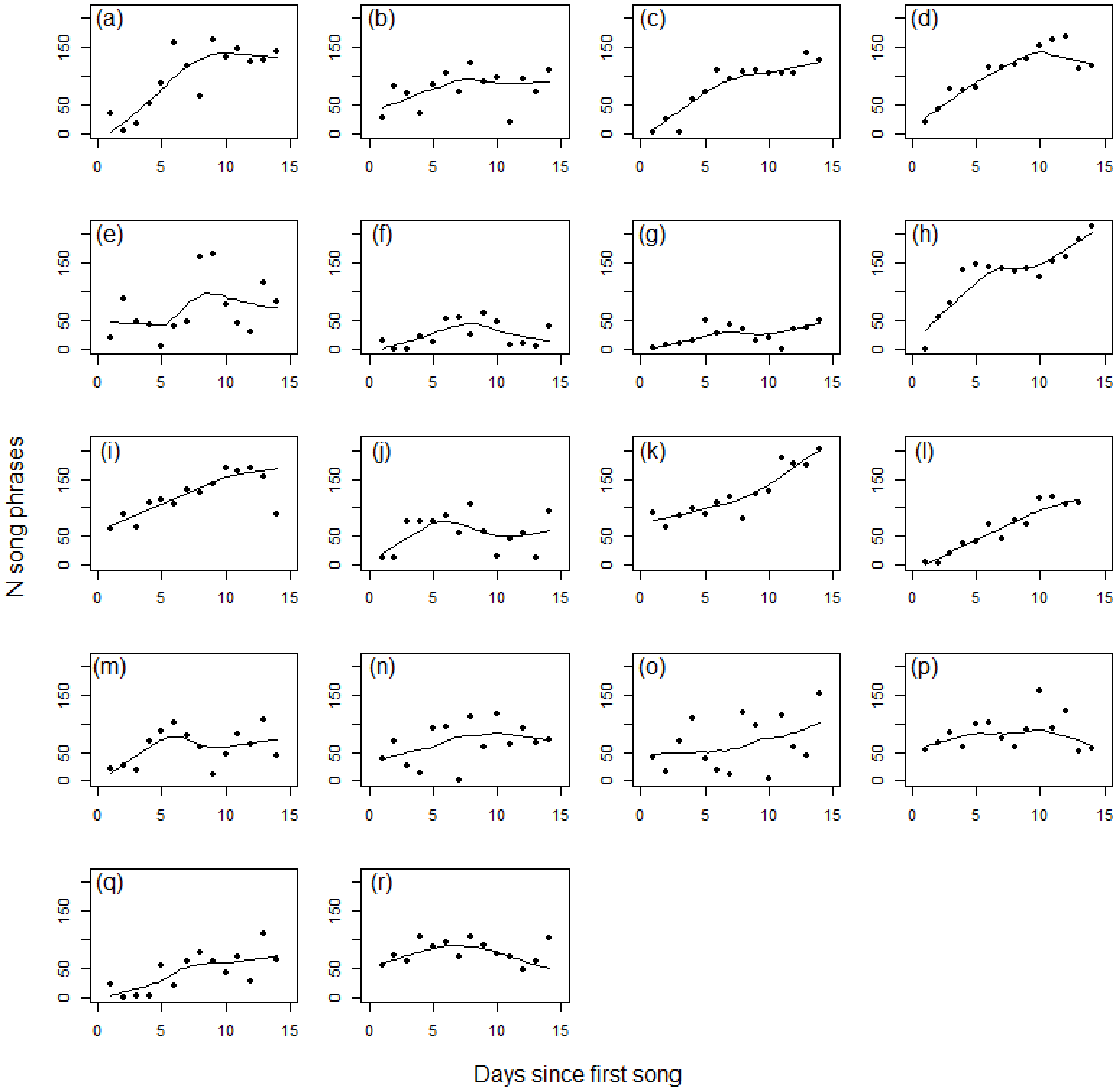


Figure 1. Relationship between *n* days since first song detected and the total number of songs per 20 minutes of sub-sampled audio (points) in 18 patches that were considered colonised after first detection. Lines (LOESS) were fitted using the scatter.smooth() function in R.

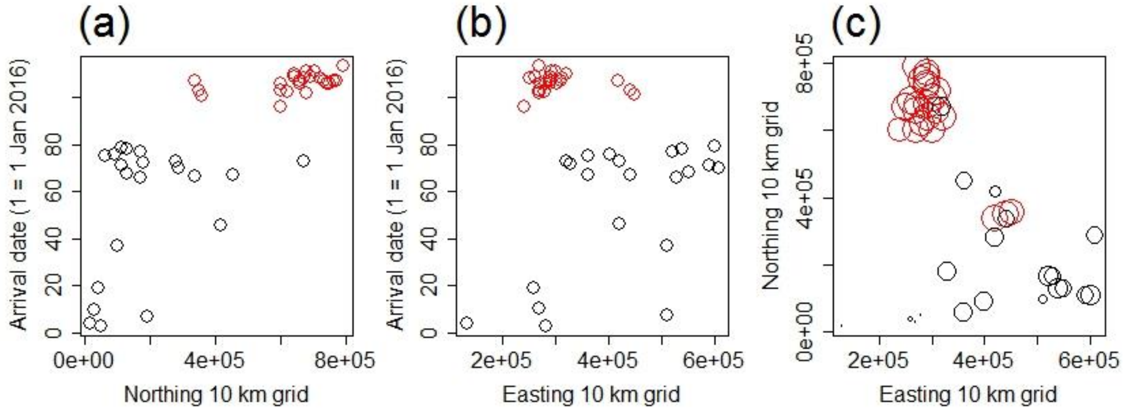


Figure 2 The relationship between geographic position (10 km grid reference) and arrival date (a, b) in the study sites (red circles; *n* = 23). Selected BTO BirdTrack data (available online) from the same year (black circles) are also shown for comparison. Point size in plot (c) is scaled according to arrival date.

CHAPTER 5

PERCEIVED PREDATION RISK IN AGRICULTURAL LANDSCAPES: A CASE STUDY OF THE EURASIAN WREN *Troglodytes troglodytes*

An adapted version of this chapter is being prepared for submission:

Robin C. Whytock, Elisa Fuentes-Montemayor, Kevin Watts, Nicholas A. Macgregor Eilidh Call, Jennifer Mann and Kirsty J. Park. *In prep.* Perceived predation risk in agricultural landscapes: evidence for communication trade-offs in a ubiquitous woodland bird *Troglodytes troglodytes*

Contributions: RCW conceived the study with input from EF-M, KW, NM and KJP. RW collected the data with assistance from EC and JM. RCW analysed the data and wrote the manuscript, and all co-authors commented on an earlier draft.

ABSTRACT

Land-use change and habitat fragmentation are well known drivers of biodiversity declines, but the causal mechanisms are often unclear. In forest birds, increased predation pressure has been proposed as a potentially important driver of community change in fragmented landscapes. Predation can also have non-lethal effects on prey, such as creating ‘landscapes of fear’ that cause individuals to avoid favourable habitat due to higher perceived risk of predation. Such non-lethal effects of predation have received relatively little attention in the context of habitat fragmentation, however. Here, I hypothesised that perceived predation risk is positively correlated with the amount of agricultural land surrounding a woodland fragment in a model woodland bird species, the Eurasian Wren *Troglodytes troglodytes.* I used bioacoustic recorders to quantify Wren alarm call rates and song rates in 32 naturally replicated broadleaf woodlands located in landscapes with varying amounts of agricultural land-cover. As predicted, results showed that perceived predation risk was higher when there was more agricultural land cover in the landscape, but the effects were strongest at the woodland edge (within 20 m). Further work is required to determine if changes in perceived predation risk can affect individual fitness, prey densities, patch attractiveness or demographic rates. Nonetheless, evidence from experimental work on other passerine birds has shown that body condition declines when perceived (but not actual) predation risk increases. If this is also true under natural conditions then the patterns observed here indicate that woodlands with high amounts of agricultural land at their edge could provide relatively sub-optimal habitat for ground-nesting woodland birds such as the Eurasian Wren.

INTRODUCTION

Habitat loss, fragmentation and land-use change disrupt ecological functioning and cause biodiversity loss, but the mechanistic links between pattern and process can be obscure. Behavioural responses to habitat configuration often underlie species responses to landscape change. For example, reduced connectivity between isolated patches can inhibit individual movement through the landscape and impair dispersal and colonisation behaviour. Land-use change can also affect non-movement behaviour, such as predator-prey interactions (Dolman et al. 2007; Thompson 2007). Most work on the relationships between landscape fragmentation, land-use change and predation has focused on lethal effects (e.g. nest predation). However, predators can also have non-lethal effects on prey, for example causing prey to avoid valuable but dangerous foraging habitat (Cresswell 2008), potentially resulting in fitness costs. Although the *lifetime* fitness costs of non-lethal predator-prey interactions can be as great as, or even greater than lethal effects (Cresswell 2008), non-lethal effects have received relatively limited attention in the context of landscape fragmentation and land-use change.

Songbird reproductive fitness is strongly mediated by nest predation (see reviews by Lahti 2001; Thompson et al. 2002; Stephens et al. 2003). Predation pressure operates across a hierarchy of spatial scales ranging from the geographic distribution of predators, predator responses to large-scale habitat patterns, patch-scale effects on predation risk (e.g. patch size, edge effects) and nest site characteristics. In forest passerines, nest predation rates typically increase as forest cover in the landscape declines, probably because predator densities (e.g. corvids) are higher in agricultural or urban environments that replace forest (Thompson 2007). At the local scale, predation rates can increase when nests are closer to patch edges or when patches are smaller, although the evidence is equivocal (Lahti 2001). Very fine scale measures of vegetation structure in the immediate vicinity of the nest site, such as understory cover, can also influence predation rates by affecting nest-detectability. However, predator-prey responses to landscape change are often context-dependent, and most studies are from North America with few comparative studies in Europe, leading to a call for more research (Dolman et al. 2007).

The non-lethal effects of predators on prey include behavioural trade-offs that can incur fitness costs (Cresswell 2008). Examples include opportunity costs when prey avoid foraging in areas with high predation risk (Hilton et al. 1999), or when prey allocate time to predator detection at a cost to other activities such as territorial defence (Krebs 1980). Perceived predation risk can also affect physiology and demography. For example, Great

Tits *Parus major* body mass (fat reserves) declines under increased levels of perceived (but not actual) predation risk (Gosler et al. 1995; Gentle and Gosler 2001). In wild Song Sparrows *Melospiza melodia* the number of offspring declined by 40% per year solely due to the perception of risk (Zanette et al. 2011). Thus, perceived predation risk can incur multiple physiological, demographic and behavioural costs that could have wider consequences for populations.

Vocal communication (singing, alarm calling) is a fundamental behaviour used by passerines for territorial defence, advertising individual quality, attracting a mate, signalling predator presence and signalling hunger. Alarm calls often have several functions and the messages they convey can vary throughout the year. During the breeding season, alarm calls serve multiple functions. For example, nestling begging behaviour, which is noisy and can attract predators, is suppressed by parental alarm calls in the White-browed Scrubwren *Sericornis frontalis* (Platzen & Magrath 2004). Thus, parental alarm calls can serve as an early warning of predation risk to nestlings. Alarm calls can also convey more subtle messages. In Black-capped chickadees (*Poecile atricapilla*) experimental presentation of predators showed that there was a correlation between acoustic features of alarm calls and predator body size, and this information was decoded by conspecifics during mobbing behaviour (Templeton et al. 2005). A recent study showed that when Great Tits perceived an increase in predation risk they traded off territorial communication (i.e. male song) with an increase in alarm-call behaviour (Abbey-Lee et al. 2015). Furthermore, this effect was carried over for days after exposure to the predator cue. Given the almost ubiquitous importance of vocal behaviour such as alarm calling for passerine birds, such patterns are likely to be widespread. The factors that drive behavioural responses to perceived predation risk are also likely to be direct (e.g. increased predator abundance) and indirect, for example through land-use change and its effects on predator behaviour.

Quantifying perceived predation risk under natural conditions is challenging, firstly because it can be difficult to observe predator-prey interactions and secondly because observer presence can interfere with both predator and prey behaviour. To overcome these challenges, studies of birds typically simulate predation risk (e.g. at feeder stations), for example by using dummy predators or by broadcasting predator vocalisations (e.g. Gentle & Gosler 2001; Zanette et al. 2011; Abbey-Lee et al. 2015). However, technological advances such as camera traps have also made it possible to detect attempted or actual predation events under natural conditions, for example at songbird nests (Bellamy et al.

2017), which can complement findings from experimental work. Knowledge of bird communication behaviour has also been greatly advanced by affordable bioacoustic technology (e.g. Chapter 3), and automated detectors can now be deployed to record bird song and other communication behaviour at landscape-scales and for long time periods (Blumstein et al. 2011).

Here, I use a natural experiment approach and a model species (Eurasian Wren *Troglodytes troglodytes*) to assess if agricultural landscapes cause an increase in perceived predation risk. I asked three key questions (i) does perceived predation risk in a habitat patch increase with more agricultural land-use in the landscape?, (ii) what is the scale of effect (local or landscape)?, and (iii) what is the relative importance of landscape *vs* local (e.g. livestock presence) effects on perceived predation risk?

METHODS

Study sites

Thirty-two post-agricultural broadleaf woodlands (Figure 5.1) were selected from a larger sample of 107 woodlands used by the Woodland Creation and Ecological Networks (WrEN) natural experiment (Watts et al. 2016). Patch size is an important predictor of nest predation in woodland birds (Dolman 2012) but the primary aim was to understand how surrounding land-use, and not patch size, affected perceived predation risk. I therefore controlled for area effects as far as possible by selecting woodlands of similar size (0.5 – 2.6 ha), but which were 'naturally replicated' across landscapes that varied in the amount, configuration and types of land management within 3 km. Patches were also *c.*3 km apart, firstly to ensure that they were spatially independent, and secondly because it was considered an ecologically relevant scale, which was sufficiently large to see changes in predator abundance, for example.

Figure 5.1 Map of the 32 study sites in Great Britain.

Study species

The Eurasian Wren *Troglodytes troglodytes* is a ubiquitous woodland bird in Great Britain (Balmer et al. 2013) and during surveys in the study sites in 2015 it was recorded in 96% of 101 woodlands (Chapter 2). Nests are dome shaped and located on or near the ground (usually < 5 m) in thick vegetation or cavities, and constructed from dry leaves, moss, grass and other plant material (Ferguson-Lees et al. 2009). A loud and characteristic ‘chattering’ alarm call is made when the nest site is threatened (Ferguson-Lees et al. 2009) and nest predation is one of the most important factors affecting Wren fecundity (Wesołowski 1983). The predator community in the study areas comprises Sparrowhawk *Accipiter nisus*, Buzzard *Buteo buteo*, Tawny Owl *Strix aluco*, Eurasian Magpie *Pica pica*, Eurasian Jay *Garrullus glandarius*, Carrion Crow *Corvus corone*, Jackdaw *Corvus monedula*, European weasel *Mustela nivalis*, stoat *Mustela ermine*, European badger *Meles meles*, red fox *Vulpes vulpes* and Gray squirrel *Sciurus carolinensis*.

Quantifying perceived predation risk

Solo audio recorders (Chapter 3) were deployed in the centre of each woodland and set to record audio continuously (24 h 7 d) from 1 Mar – 30 Apr 2016, when Wren territories are established and egg laying occurs (Ferguson-Lees et al. 2009). This method allowed alarm calls (an index of perceived predation risk) to be detected at high temporal resolutions in focal patches spread across a large geographic area, but with the trade-off that predator species could not be identified, which would be more feasible at small scales using direct observation or experimental manipulations of predation risk.

Hypotheses

I hypothesised that alarm call rates would be higher when there was more arable and pasture in the landscape. This expectation was based on studies that found songbird nest predation rates were higher in agricultural landscapes (e.g. Andren 1992; reviewed by Thompson 2007). However, since some patches were likely to have higher Wren densities than others, for example because of differences in fine-scale measures of habitat structure, I only expected to see an effect of arable or pasture in the landscape on alarm call rates after controlling for Wren abundance in a patch; using song rates as an index of abundance (Figures 5.2). In addition, song rates are also likely to be directly affected by the proportion of arable and pasture in the surrounding landscape because landscapes with high proportions of arable and pasture also have lower proportions of woodland. Thus, there should be less competition from singing males in neighbouring patches, which is likely to lead to lower singing rates in focal patches when there is a high proportion of arable and pasture in the landscape (Figure 5.2).

Species, communities and individual behaviour are all affected by patterns of land use across multiple spatial scales, which is known as the ‘scale of effect’ (Fahrig 2013). The scale of effect can be linear, non-linear, have a threshold or can operate at a single scale; e.g. Fuentes-Montemayor et al. 2011). No assumptions were made about the scale of effect or its shape here, other than it was expected to be < 3 km (Chapter 2), which is substantially greater than the distance at which Wrens are likely to perceive a threat from a predator.

Woodlands located in agricultural landscapes might also be exposed to higher levels of disturbance from humans, vehicles, livestock and domestic animals such as dogs. Disturbance from livestock (here the presence of horses, cows or sheep), such as trampling of nests, is likely to be perceived as a threat. Livestock could also have indirect effects on perceived predation risk by modifying the understory layer of a woodland through grazing pressure, potentially affecting nest concealment and detection by predators. I therefore predicted (i) alarm call rates would be higher in patches where livestock were present, which would be seen via a direct effect (disturbance; Figure 5.2) and (ii) that livestock would indirectly increase perceived predation risk by reducing the amount of understory cover (Figure 5.2).

Numerous studies have found that predation risk is higher when nests are closer to patch edges or when patches have a high edge to area ratio (Lahti 2001). It was therefore expected that alarm call rates would be higher in patches with a high edge to area ratio. This was captured using the variable ‘patch shape’ (Figure 5.2), which was calculated as the length of the patch perimeter divided by the perimeter of a perfect circle with same area as the patch.

Because Wrens need woodland with sufficient cover for foraging and nest concealment, I expected densities (i.e song rates) to be higher in woodlands with greater structural variation (as measured by tree DBH standard deviation) (Figure 5.2).

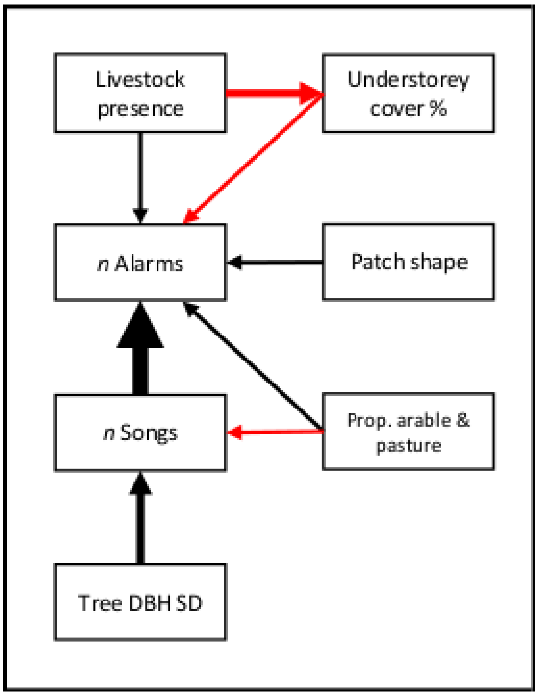


Figure 5.2 Path diagrams illustrating the hypothesised effects of vegetation structure (Tree DBH SD, understory cover %), woodland management (livestock presence), patch shape, song rates (an index of abundance), and the proportion of arable in the landscape on alarm calls in woodland fragments. Black arrows show hypothesised positive effects and red arrows show hypothesised negative effects, and arrow width indicates the expected relative magnitude of the effect.

Data Analysis

I used an unbiased re-sampling approach to quantify alarm (and song) rates in each woodland. Audio sequences were examined on four equally spaced days in April (9th, 16th, 23rd and 30th) to cover the entire month. For each site, I randomly sampled four 10-minute sections of audio (i.e. 40 minutes) from three time periods per day: (i) the 3 hr period after sunrise (morning), (ii) between 1200 and 2 pm (midday), and (iii) the 2 hr period before sunset (evening). Using spectrograms, I then counted the number of songs in the morning (when singing peaks) on each date and counted the number of alarm calls in the morning, midday and in the evening on each date. I then summed the total number of alarm calls and the total number of songs per day in each site.

I used piecewise structural equation modeling (SEM; Lefcheck 2016) to examine local and landscape effects on perceived predation risk and song rates. Figure 5.2 shows the hypothesised direct and indirect relationships tested.

Alarm counts and song counts were log transformed for analyses and linear mixed effects models (Bates et al. 2015) were used to construct the SEMs. Component models were validated following Zuur et al. (2010). All predictors were mean centred and scaled by 1 SD to compare relative effect sizes (β). Because the number of alarm calls and songs were likely to vary as a function of nestling stage (c.f. Southern House Wren *Troglodytes musculus*: Fasanella & Fernandez 2009), and because there was likely to be asynchrony between sites, I accounted for this by including date (n = 4 days) as a random intercept in all constituent models in the SEM. I also initially included date nested in site as a random intercept but models did not always converge, and the site-level effect explained no additional variance so was removed.

To identify the scale of effect of the relationship between alarm call rates and the amount of arable and pasture in the landscape I separately constructed nine SEMs, one for each of the nine scales used (20, 100, 250, 500, 1000, 1500, 2000, 2500, 3000 m GIS buffers). I then compared standardised effect sizes and AIC_c to select the single 'best' scale (n = 9 SEMs).

For all SEMs (i.e. at each scale), I evaluated potentially missing paths and added those that were significant ($P < 0.05$) and ecologically plausible to the model, or they were otherwise specified as having correlated errors. Fitted SEMs were evaluated using Fisher's C. A significance threshold of $P > 0.05$ was used to indicate the model reproduced the data well.

RESULTS

After sub-sampling, a total of 421 Wren alarm calls (median 1, range 0 – 27 per day, n = 35 woodlands) and 7139 songs (median 184, range 0 – 587 per day, n = 35 woodlands) were detected in 280 hours of audio. No Wren alarms or songs were detected in one woodland and it was removed from further analyses. Two other woodlands were also removed due to missing data, leaving 32 woodlands in the analyses.

SEM results (Figure 5.3 and 5.4; Appendix 5.1: Tables 1 & 2) showed that, after controlling for the number of songs (an index of abundance) in a woodland, the number of alarm calls increased significantly when there was proportionally more arable and pasture within 20 m of each patch. This was the only scale found to have a statistically significant effect on alarm call rates, but effect sizes suggested there appeared to be a threshold where the proportion of arable and pasture had no effect beyond 1000 m (Figure 5.3).

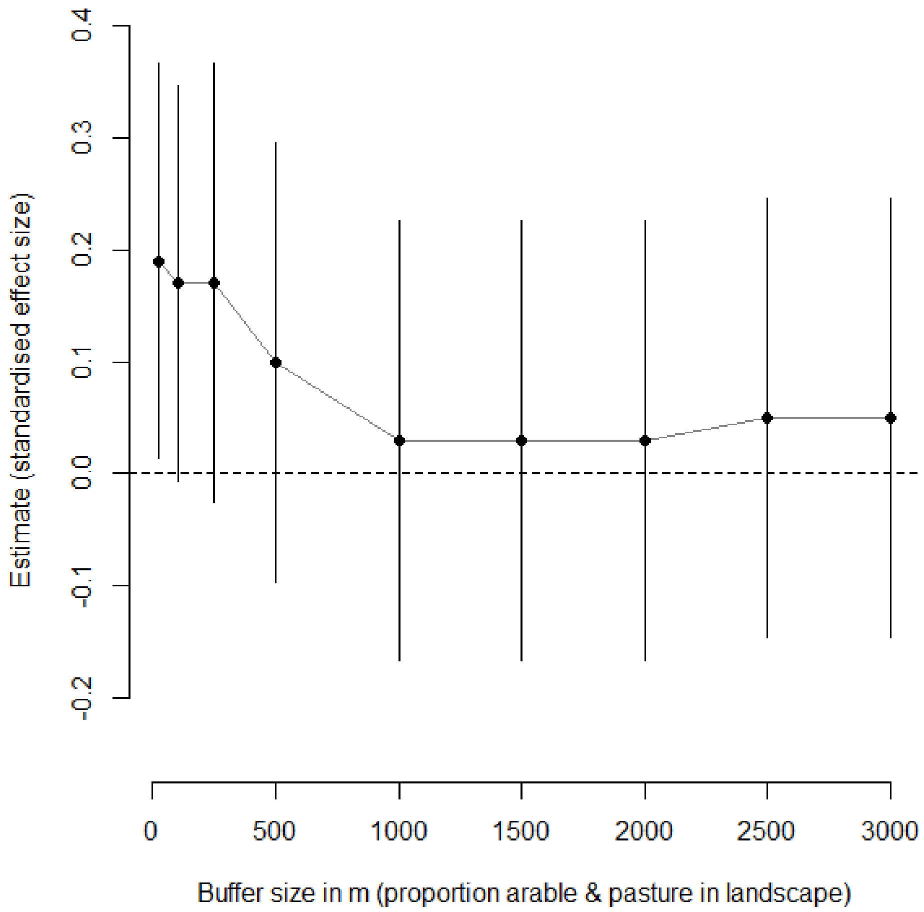


Figure 5.3 Standardised effect sizes (bars show 95 % confidence intervals) for Wren alarm call rates as a function of the proportion of arable and pasture in the landscape at eight nested spatial scales (GIS buffers).

There was a significant negative relationship between the proportion of arable and pasture within 20 m and the number of songs in the woodland (Figure 5.4), but I found no significant direct or indirect relationships between alarm calls or song rates and tree DBH SD, patch shape, livestock presence or understory cover, and standardised effect sizes were relatively small. However, by examining missing paths I found an unexpected positive relationship between livestock presence in the woodland and the number of songs, which was then included in the final models.

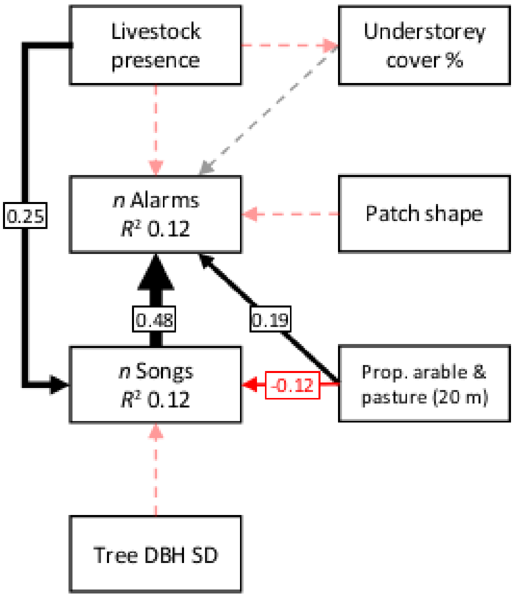


Figure 5.4 Path diagram showing results from the structural equation model with the strongest support, which included a significant, negative effect of the amount of arable and pasture within 20 m of the woodland patch on wren song rates, indicating a communication trade-off (hypothesised in Figure 5.2a).

DISCUSSION

Landscape change due to conversion for agriculture and other purposes threatens species and ecosystems, with forest habitats and species particularly at risk (Haddad et al. 2015). Patterns of species and community responses to habitat fragmentation and loss are well studied but it can be difficult to identify the ecological mechanisms that drive these patterns (Dolman 2012). Evidence from studies of multiple taxa show that when individuals perceive an increased risk of predation, this can have negative, cascading effects on individuals and populations (Cresswell 2008; Ripple & Beschta 2004; Resetarits & Silberbush 2016). Here, I asked if perceived predation risk is greater in agricultural landscapes, and if yes what is the scale of effect? Results suggest that predation risk perceived by Wrens does increase in agricultural landscapes, and the effects are highly local (20 m from woodland edge).

I was not able to identify predator species and can only speculate about the mechanisms that led to higher alarm call rates when there was more agricultural land at woodland edges. One explanation is that predator abundance (e.g. corvids, red fox) increases in agriculturally dominated landscapes, which leads to increased predation rates. However, the very local-scale effect of agriculture on alarm call rates observed here instead suggests that predators could be disproportionally attracted to woodland edges.

This might be because there is higher food availability or because the edge provides cover when traveling, which would be particularly valuable to medium and small mammalian predators such as European weasel, stoat and red fox. However, many of these hypotheses are poorly tested and results are often equivocal (Chalfoun et al. 2002). Quantifying predator functional and numerical responses to habitat configuration and composition therefore remains an important area for future research. Agricultural landscape are also likely to have higher levels of anthropogenic activity (humans, vehicles, dogs), which could cause disturbance and higher alarm call rates. Although this cannot be ruled out as causing the patterns observed here, livestock presence in the woodland was not found to affect alarm call rates, suggesting that the impact of such disturbance is probably minimal. Furthermore, Wrens are also strongly associated with anthropogenic habitats in the UK and elsewhere (Wesołowski T. 1983), suggesting that they are relatively resilient to anthropogenic disturbance.

The highly localised effects of arable and pasture on alarm call rates also probably reflect the distances at which Wren's perceive a threat. There has been substantial research into the distances at which birds will tolerate a threat before fleeing (flight initiation distances; Weston et al. 2012), but surprisingly little research has investigated the same phenomenon for alarm calls, despite the link between the two behaviours (i.e. alarm calls often precede escape behaviour). It has been proposed that flight initiation distances could be used to mitigate against land-management practices that might cause undue disturbance to bird populations (Weston et al. 2012). For example by ensuring that stimuli which cause a disturbance are sighted sufficiently far from potential breeding habitat. It might therefore be possible to use alarm-initiation distances as a similar conservation management tool.

I did not quantify the demographic consequences of increased predation risk, but there is sufficient evidence from studies of other passerines to suggest that an increase in perceived predation risk can impact on demographic rates and thus population persistence in a patch, for example by causing lower fecundity through physiological changes, such as decreased body condition (Gentle & Gosler 2001). Predators can also create 'landscapes of fear', where individuals avoid habitat or foraging opportunities with high predation risk (Ripple & Beschta 2004; Cresswell 2008), which could cause patches with high predation risk to appear relatively unattractive to potential colonisers (Resetarits & Silberbush 2016).

In Great Tits, experimental evidence suggests that even when perceived predation risk is higher, individuals' trade-off territorial defence (i.e. singing rates) (Abbey-Lee et al. 2015). In many birds territory loss can incur substantial lifetime fitness costs, and the risk to life from predation must be very high before individuals risk losing their territory (Abbey-Lee et al. 2015). We did not quantify if such a tradeoff exists in Wrens, but it is plausible that singing rates decline when birds spend more time producing alarm calls, and this should be investigated in future.

Surprisingly, I found that song rates were significantly higher when livestock was present in the woodland. The mechanisms for this are unclear, but in woodland bats detection rates were higher in grazed woodlands, despite these woodlands having lower numbers of invertebrates than woodlands with no grazing (Fuentes-Montemayor et al 2013). Perhaps grazing therefore creates structural features that also favours Wren foraging behaviour and thus Wren densities.

Conclusions

Results show that perceived predation risk is higher in agricultural landscapes, but the effect is highly localised. Many questions remain unanswered however, and it remains unknown if high levels of perceived predation risk affect community assembly in fragmented woodlands. I suggest the following questions are used to guide future research in this area:

- Does an increase in perceived predation risk correlate with actual predation risk?
- Which predators or predator guilds are responsible for causing an increase in perceived predation risk in agricultural landscapes?
- Do agricultural landscapes modify predator behaviour or predator numbers?
- Can these effects be mitigated by ‘buffering’ woodland edges with semi-natural habitat?

I recommend that future studies combine both experimental and observational work to build a more complete picture of why agricultural landscapes cause the patterns observed here. In particular, there is a need to simultaneously quantify both prey and predator numerical and functional responses to large-scale patterns of land-use and land-use change.

ACKNOWLEDGEMENTS

I am grateful to landowners for permitting access to the study sites. The study was funded by the Natural Environment Research Council, the National Forest Company and Forest Research. The WrEN project has been funded by the University of Stirling, Natural England, Forestry Commission, Scottish Natural Heritage, the Department for the Environment, Food and Rural Affairs, the National Forest Company, Forest Research, the Woodland Trust and Tarmac Ltd.

Appendix 5.1 Summary statistics for the structural equation models

Table 1. Estimated coefficients, standard errors (SE) and P-values from each 'scale of effect' structural equation model (20 m to 3 km). Hypothesised relationships (positive or negative), significant missing paths and correlated variables assumed to have no causal relationship (denoted ~~) are also indicated.

Response	**Predictor**	**Hypothesised sign**	**Estimate**	**SE**	**P**
ln(alarm calls)	ln(songs)	+	0.47	0.13	< 0.001
	Prop. arable & pasture (20 m)	+	0.19	0.09	0.026
	Livestock presence	+	-0.09	0.11	0.434
	Understory cover	-	0.04	0.09	0.623
	Patch shape	+	0.00	0.08	0.974
ln(songs)	Livestock presence	Missing path	0.26	0.08	0.001
	Prop. arable & pasture (20 m)	-	-0.12	0.06	0.049
	Tree DBH SD	+	-0.06	0.06	0.384
Understory cover %	Livestock presence	-	-0.04	0.11	0.713
~~ Understory cover %	~~ **Prop. arable & pasture (20 m)**		0.25	-	0.002
ln(alarm calls)	ln(songs)	+	0.47	0.13	< 0.001
	Prop. arable & pasture (100 m)	+	0.17	0.09	0.064
	Livestock presence	+	-0.07	0.11	0.558
	Understory cover	-	0.04	0.09	0.675
	Patch shape	+	0.01	0.08	0.916
ln(songs)	Livestock presence	Missing path	0.23	0.08	0.004

Response	**Predictor**	**Hypothesised sign**	**Estimate**	**SE**	**P**
	Prop. arable & pasture (100 m)	-	-0.14	0.06	0.019
	Tree DBH SD	+	-0.05	0.06	0.441
Understory cover %	Livestock presence	-	-0.04	0.11	0.713
~~ Understory cover %	~~ **Prop. arable & pasture (100 m)**		0.31	-	< 0.001
ln(alarm calls)	ln(songs)	+	0.50	0.14	< 0.001
	Prop. arable & pasture (250 m)	+	0.17	0.10	0.097
	Understory cover	-	0.08	0.09	0.352
	Patch shape	+	0.03	0.09	0.711
	Livestock presence	+	-0.03	0.12	0.780
ln(songs)	**Prop. arable & pasture (250 m)**	-	-0.24	0.06	< 0.001
	Livestock presence	Missing path	0.14	0.08	0.102
	Tree DBH SD	+	-0.03	0.06	0.580
Understory cover %	Livestock presence	-	-0.04	0.11	0.713
~~ Understory cover %	~~ **Prop. arable & pasture (250 m)**		0.05	-	0.306
ln(alarm calls)	ln(songs)	+	0.47	0.14	0.002
	Understory cover	-	0.09	0.09	0.294
	Prop. arable & pasture (500 m)	+	0.10	0.12	0.414
	Livestock presence	+	-0.06	0.13	0.678

	Patch shape	+	0.03	0.09	0.770
ln(songs)	**Prop. arable & pasture (500 m)**	-	-0.38	0.07	< 0.001
	Patch shape	Missing path	-0.20	0.05	< 0.001
	Livestock presence	Missing path	-0.10	0.06	0.074
	Tree DBH SD	+	0.01	0.08	0.896
Understory cover %	Livestock presence	-	-0.04	0.11	0.713

ln(alarm calls)	ln(songs)	+	0.42	0.13	0.002
	Understory cover	-	0.09	0.09	0.299
	Livestock presence	+	-0.10	0.14	0.481
	Prop. arable & pasture (1000 m)	+	0.03	0.12	0.822
	Patch shape	+	0.00	0.09	0.969
ln(songs)	Livestock presence	Missing path	0.22	0.09	0.023
	Patch shape	Missing path	-0.12	0.06	0.045
	Prop. arable & pasture (1000 m)	-	-0.11	0.09	0.202
	Tree DBH SD	+	-0.08	0.07	0.225
Understory cover %	Livestock presence	-	-0.04	0.11	0.713

ln(alarm calls)	ln(songs)	+	0.41	0.13	0.002
	Understory cover	-	0.09	0.09	0.343
	Livestock presence	+	-0.10	0.13	0.439
	Prop. arable & pasture (1500 m)	+	0.03	0.11	0.797
	Patch shape	+	0.00	0.09	0.998

ln(songs)	Livestock presence	Missing path	0.30	0.08	0.001
	Patch shape	Missing path	-0.09	0.06	0.132
	Prop. arable & pasture (1500 m)	-	0.04	0.08	0.574
	Tree DBH SD	+	-0.03	0.07	0.620
Understory cover %	Livestock presence	-	-0.04	0.11	0.713

ln(alarm calls)	ln(songs)	+	0.41	0.13	0.002
	Understory cover	-	0.09	0.09	0.359
	Livestock presence	+	-0.10	0.12	0.400
	Prop. arable & pasture (2000 m)	+	0.03	0.10	0.749
	Patch shape	+	0.00	0.08	0.986
ln(songs)	Livestock presence	Missing path	0.31	0.08	< 0.001
	Patch shape	Missing path	-0.09	0.06	0.121
	Prop. arable & pasture (2000 m)	-	0.08	0.07	0.241
	Tree DBH SD	+	-0.03	0.07	0.693
Understory cover %	Livestock presence	-	-0.04	0.11	0.713

ln(alarm calls)	ln(songs)	+	0.41	0.13	0.002
	Understory cover	-	0.08	0.09	0.376
	Livestock presence	+	-0.10	0.12	0.417
	Prop. arable & pasture (2500 m)	+	0.05	0.10	0.609
	Patch shape	+	0.00	0.08	0.969

ln(songs)	Livestock presence	Missing path	0.31	0.08	< 0.001
	Patch shape	Missing path	-0.09	0.06	0.100
	Prop. arable & pasture (2500 m)	-	0.10	0.07	0.153
	Tree DBH SD	+	-0.03	0.06	0.681
Understory cover %	Livestock presence	-	-0.04	0.11	0.713

ln(alarm calls)	ln(songs)	+	0.41	0.13	0.002
	Understory cover	-	0.09	0.09	0.346
	Livestock presence	+	-0.10	0.12	0.400
	Prop. arable & pasture (3000 m)	+	0.05	0.10	0.630
	Patch shape	+	0.00	0.08	0.954
ln(songs)	Livestock presence	Missing path	0.31	0.08	< 0.001
	Patch shape	Missing path	-0.10	0.06	0.092
	Prop. arable & pasture (3000 m)	-	0.10	0.07	0.130
	Tree DBH SD	+	-0.03	0.06	0.654
Understory cover %	Livestock presence	-	-0.04	0.11	0.713

Table 2. Goodness-of-fit statistics for each ‘scale of effect’ structural equation model

Scale of effect (m)	AICc	K	n	Fisher's C	df	P
20*	56.954	17	128	17.39	12	0.139
20	54.895	18	128	12.62	10	0.246
100	56.575	18	128	14.30	10	0.160
250	58.615	18	128	16.34	10	0.090
500	54.027	19	128	8.99	10	0.533
1000	57.597	19	128	12.56	10	0.249
1500	52.407	19	128	7.37	8	0.497
2000	51.787	19	128	6.75	8	0.564
2500	51.627	19	128	6.59	8	0.582
3000	51.807	19	128	6.77	8	0.562

*Structural equation model with no path between proportion arable and pasture at 20 m and ln(Songs)

CHAPTER 6

GENERAL DISCUSSION

It is widely accepted that forest and woodlands provide significant ecological, economic, environmental and societal benefits, but there is debate over the relative value of primary woodland or forest *vs* secondary habitats. If secondary woodland is to benefit current and future woodland-dependent species, there is a need to carefully strategise woodland creation in the landscape. For the first time, I disentangle the relative importance of temporal, local and landscape scales for bird communities and behaviours (territory selection, communication) in created woodland. I also present an inexpensive, robust and open-source bioacoustic recorder, and use this tool to explore the relationships between landscape configuration and colonisation and communication behaviour in birds. Finally, I examined how ecological time lags – delays between an action (e.g. woodland creation) and species' responses – have implications for conservation evaluation and policy targets. Results from this thesis can be used to inform woodland creation for the benefit of woodland bird diversity in Great Britain. Results are also likely to be relevant to other lowland, temperate agricultural landscapes in the northern hemisphere. Here, I identify several important directions for future empirical and theoretical research.

Optimising woodland creation to benefit biodiversity

Results indicate that post-agricultural woodlands rapidly benefit generalist woodland bird abundance and diversity, but it remains unknown if they will ever benefit species associated with ancient woodland (Chapter 2). Land managers seeking to create woodland on post-agricultural land should maximise patch size (> 5 ha) and limit livestock grazing inside the patch where possible. Although speculative, very isolated woodlands could be acting as ecological traps for migrant birds (Chapter 4) and I therefore suggest that patches are created close to neighbouring woodland whenever possible. Perceived predation risk was greater when woodlands had high proportions of agriculture at their edge (within 20 m; Chapter 5) and there is sufficient evidence from elsewhere to suggest that changes in perceived predation risk can affect individual fitness, demographic rates and perceived patch 'quality'. Because of this, I recommend that a 20 m buffer of semi-natural habitat (any natural land cover that does not include woodland, water, agriculture or urban land) is created between the edge of newly planted woodland and surrounding agricultural fields. If left to go fallow this buffer will eventually become part of the woodland through natural succession, but the time-lag should be sufficient to reduce the potential impact of increased predation or perceived predation risk on new colonisers (i.e. founding individuals).

Biodiversity pattern in fragmented landscapes

Studies that identify patterns of species and community responses to local and landscape-scale habitat patterns dominate landscape ecology. This has been especially true for birds. Many studies have found that large scale measures of landscape composition and configuration play a role in shaping bird communities (Chapter 2; Dolman 2007; Dolman 2012), but I found that their relative importance was low compared to local-scale factors, such as patch size or livestock presence.

The importance of patch size (i.e. area) for woodland birds is long-established, but surprisingly its *relative* importance has rarely been quantified. Here, I found that the standardised effect of patch area was almost double that of other variables. In Southeast England, patch size was also the most important predictor of bird species richness in small agricultural woodlands of unknown age (Bellamy, Hinsley & Newton 1996). However, in many regions, a significant barrier to effective landscape-scale woodland creation is the limited space available. In Great Britain, private land ownership and agricultural management restrict the number and size of woodland patches that can be created or extended. Where it is impossible to create a large patch or increase the size of an existing patch, there should be a focus on improving habitat quality. For example, increased tree species richness in a patch had positive effects on total species richness (Chapter 2). Care should also be taken to balance the relative economic cost and logistical feasibility of potential actions with their statistical effect sizes. For example, whilst it may not be feasible to plant a single large woodland patch, it might be possible to plant two individual, smaller patches. In this situation, the land manager could offset the small size of the patches by erecting stock fences to exclude livestock.

There remains significant debate surrounding the processes that make patch size important for woodland birds. The area-quality hypothesis predicts that habitat heterogeneity increases incidentally as a function of area (Dolman 2012), resulting in greater niche diversity. However, the woodlands used in this study were generally homogenous plantations created by woodland grant or conservation schemes, as shelter belts or for rearing game. Furthermore, measures of habitat heterogeneity such as tree species richness, tree size, understorey cover and the amount of coarse woody debris were not correlated with area. Instead, species richness and abundance probably increased with area because territory sizes are limited by a minimum threshold at which individuals will tolerate inter- or intraspecific competitors. Thus, only a limited number of bird territories can ever be present per unit-area of woodland.

Although Chapter 2 focused on obligate and facultative woodland species, other groups such as farmland seed-eaters were also common in the study sites. These species are not typically the primary conservation focus of woodland creation, but I did find some interesting results. For example, the amount of arable or improved grassland in the landscape (2500 m) had a strongly negative effect on farmland seed eater abundance and therefore richness in woodlands (Appendix 2.5: Table 4). This supports existing evidence that links intensive agricultural practices to farmland bird declines (Donald et al. 2001). Thus, although woodlands are not necessarily the favoured habitat of this species group (with the exception of Chaffinch), the negative influence of intensive agriculture in the surrounding landscape is clear.

Tree and building nesters, which prefer to nest in cavities, were also rare in our woodlands (Chapter 2: Figure 2.2). It was predicted that the abundance and richness of this group would be correlated with woodland age, because older trees typically have more cavities for nesting purposes. However, results did not support this hypothesis, and instead the most important, positive predictor of abundance and richness of this group was livestock presence in the patch. This is probably because the species in this group (e.g. Starling *Sturnus vulgaris*, Pied Wagtail *Motacilla alba*) prefer to feed on grassland with an open understory and low sward, which is common in grazed woodlands. This result highlights the trade-offs that can occur when undertaking conservation actions. Removing livestock from a woodland is likely to benefit most woodland birds, but the subsequent closure of the understory will disadvantage other species that feed on grassland. Quantifying these trade-offs should be prioritised in future work that examines biodiversity responses to habitat creation.

Processes underlying biodiversity patterns in fragmented landscapes

An important aim of this thesis was to move away from focusing exclusively on pattern and instead focus on identifying and quantifying underlying processes. There are several reasons why studying process is more challenging than studying pattern in landscape ecology. For vertebrates and invertebrates, changes in landscape configuration and composition largely affect movement behaviour, which includes foraging, dispersal, colonisation and prey avoidance. These are difficult behaviours to quantify under natural conditions at the best of times because it can be difficult to achieve sufficient replication. In landscape ecology, the problem is greatly magnified when there is a need to conduct behavioural studies at km scales whilst also ensuring that replicates are spatially independent.

Remotely operated technology such as bioacoustic sensors or GPS tracking devices can overcome some of the challenges of scale in behavioural ecology. However, for small passerine birds, high end satellite tracking technology is currently too large, preventing its use. Smaller ‘geolocators’ have been used to study passerine movements during migration by estimating longitude and latitude from sunrise and sunset times, but data are very coarse (typically > 100 m accuracy) and birds must be re-trapped to retrieve the data.

Audio sensors can be used to detect acoustically active taxa at large spatial scales. However, many of the commercial systems are expensive and thus most bioacoustic studies are often limited in spatial extent because of economic reasons. Since many birds communicate vocally, it is possible to make inferences about their movement behaviour by recording their presence using audio recorders. To overcome budget limitations and extend bioacoustic studies to large spatial scales, I co-developed the open-source ‘Solo’ bioacoustic system (Chapter 3; Whytock & Christie 2017).

Using the Solo system, I was able to determine which local and landscape-scale cues are used by migratory birds during territory selection (i.e. colonisation) in spring. This experimental design has never before been used to understand avian colonisation behaviour, and it offers substantial opportunities for future research. Superficially, the method is similar to that used in the study of movement behaviour in microchiropteran bats. The primary difference is that it is possible to explicitly relate local and landscape factors to colonisation events in migratory birds, and not just to foraging or commuting behaviour, which is typical in studies of bats.

Results in Chapter 4 indicated that the amount of woodland in the landscape acted as an important cue during territory selection and settlement. The direction of the effect contradicted expectations, however, and patch colonisation was earlier when the amount of habitat in the landscape was low. I discussed the possibility that such isolated woodland patches could be acting as ecological traps, and recommended that future work investigates the fitness consequences of breeding in highly isolated patches. I predict that, after controlling for male age (which is also correlated with fitness in Willow Warblers), highly isolated patches will attract ‘fitter’ males (i.e. better body condition) earlier in the season, but their annual reproductive output will be lower relative to males in landscapes with high amounts of woodland. If this prediction is confirmed, it would be indicative of an ecological trap, where high quality males are selecting sub-optimal breeding territories.

In North America, several studies have found links between landscape composition and configuration and nest predation pressure. Outside of North America, however, this topic has received relatively little attention. As a consequence, it has been unclear if links between predation pressure and landscape structure are generalisable, or if they are highly context dependent. In Chapter 5, I found that perceived predation risk increased when there was more agricultural land at the woodland edge, which confirms results from experimental studies in other species (Abbey-Lee et al. 2015). An increase in perceived predation risk can create a ‘landscape of fear’. Thus, even though I did not investigate the demographic consequences of predation risk, patches with higher perceived predation risk might appear relatively unattractive to prospective colonisers. This process could affect community assembly in a patch but results presented in Chapter 2 contradict this expectation, and no strong relationship between the amount of agriculture at the woodland edge and bird diversity or abundance was detected. This suggests that the effects of increased perceived predation risk in agricultural landscapes are probably relatively small at the community level.

Policy implications

Woodland creation has become a popular conservation action that has strong public support. In January 2018, the British Government announced plans to spend £5 million creating the ‘Northern Forest’, which will involve planting 50 million trees over the next 25 years, and with careful planning this could provide significant benefits to the environment and society. However, conservation as a discipline suffers from an ‘implementation gap’; where the latest scientific evidence is not always applied in practice. The results and data contained in this thesis will contribute to the wider WrEN project, which aims to inform future habitat creation efforts by looking to the past. The WrEN project is built on a foundation of knowledge exchange, where stakeholders working in applied conservation collaborate with WrEN project scientists to identify key research themes. Several of the WrEN stakeholders, such as the National Forest Company and the Woodland Trust, are central to the creation of the Northern Forest. These organisations are therefore well-placed to take the results from this thesis and the wider WrEN project into practice, demonstrating the value of the knowledge-exchange model and early involvement of important stakeholders when developing scientific research.

There is little doubt that we need to create more woodland to address historic losses, not only to benefit biodiversity but also to benefit the environment, the economy and society. However, it must be acknowledged that there will be ecological, economic and cultural trade-offs. Economically, woodland creation might result in the loss of productive agricultural land, but this could be offset in part by exploiting timber and other resources through careful woodland management. Ecologically, woodland often replaces grass fields, which provide habitat for non-woodland species such as declining lapwing *Vanellus vanellus* and other waders. From a cultural perspective, it has been argued that Britain is unique in Europe because its landscape is a product of long-term cultural management, and its open spaces attract tourists and country sports enthusiasts from across the world. We must therefore ask if the benefits of large scale woodland creation are sufficient to offset these potential losses.

When creating new habitat, the goal is often to replicate the ecological communities found in ancient or natural habitats. I propose that we should not be overly concerned about perfectly replicating ‘natural’ habitats such as ancient woodland - because we risk disappointment, at least over measurable timescales. After all, the ecological and environmental processes that precede the establishment of natural, climax woodland operate over millennia and there is no quick fix. The scale of forest loss in Britain and other countries is enormous, and in Britain very little ancient woodland remains. I believe we should focus on protecting and restoring those ancient woodlands that do remain, but we should also seek to plant new woodlands at large-scales that are as species-diverse and as large as possible. Finally, if we actively manage created woodlands in diverse and creative ways, we will not only increase their broader cultural and biodiversity benefits, we will greatly increase their ecological and economic value to society in the long term.

Limitations

One of the main limitations with the study design used here was that I did not account for historic temporal and spatial changes in the landscapes surrounding each patch. Thus, it is possible that a patch might appear relatively isolated using present-day spatial data, but the surrounding landscape might have had historically high proportions of woodland habitat that has now disappeared. The consequence of this scenario is that we might wrongly conclude the present-day bird community assembled in an unfavourable landscape (i.e. low woodland availability), and landscape composition or configuration are not therefore important. However, most large-scale losses of forest or woodland habitat in Britain occurred long before the 1900s. Because most of the study sites were < 50 years old, there is unlikely to have been significant changes in landscape structure during this time-period, although many hedgerows have been lost in recent decades, but I did not explicitly examine the influence of hedgerows here due to a lack of available data.

Secondly, there is evidence to suggest the regional populations of a species can differ in their responses to landscape composition and configuration. For example, the Eurasian Wren is closely associated with ancient, contiguous forest in mainland Europe. In Britain, however, the Wren is a ubiquitous species found in urban areas, moorland, coastal habitat and grassland. Thus, the Wren population in Britain will respond differently to land-use change compared to the mainland population in Europe. The same could be true for other species in Britain, which has experienced comparatively long periods of large-scale habitat fragmentation and loss, which is likely to have exerted selective pressures on local populations that may now be well-adapted to living in fragmented landscapes.

CONCLUSIONS

In this thesis I aimed to quantify the relative importance of local and landscape scales for woodland birds in secondary, post-agricultural woodlands. The rationale behind this aim was to better inform conservation and land-management decisions. For example, when seeking to increase woodland bird diversity in a newly created woodland, should there be a focus on improving habitat extent in the landscape or improving habitat 'quality' in the patch itself. Although large scale habitat patterns at the landscape-scale contribute to bird abundance and diversity in post-agricultural woodlands, their relative effects on bird diversity and abundance appears to be small compared to factors at the patch-level, such as patch size and the presence of livestock (Chapter 2). Nonetheless, results presented in Chapters 4 & 5 suggest factors at the landscape-scale can be important predictors of bird behaviour, including first song dates in the migratory Willow Warbler, and alarm calling behaviour in the ubiquitous Eurasian Wren. However, these effects were only detected after experimentally controlling for patch size, which would likely have obscured results because of its very high relative importance.

It has long been known that patch size is an important predictor of bird diversity and abundance in habitat fragments, but surprisingly few studies have quantified its relative importance compared to other local- and landscape-scale factors. In particular, there is a need to consider its relative importance compared to alternative land-management actions that could be implemented during woodland creation. Results from this thesis suggest that the greatest relative returns from woodland creation will be gained by making patches as large as possible. In light of this, I conclude that local-scale factors are relatively more important than landscape factors for woodland bird diversity and abundance in Great Britain. When faced with making complex decisions during woodland creation, I recommend that land-managers focus on maximising patch sizes if the aim is to benefit woodland birds.

LITERATURE CITED

Abbey-Lee RN, Kaiser A, Mouchet A, Dingemanse NJ. 2015. Immediate and carry-over effects of perceived predation risk on communication behavior in wild birds. *Behavioral Ecology* **27**:708-716.

Aide TM, Corrada-Bravo C, Campos-Cerqueira M, Milan C, Vega G, Alvarez R. 2013. Real-time bioacoustics monitoring and automated species identification. *PeerJ* DOI: 10.7717/peerj.103.

Andren H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* **73**:794-804.

Arvidsson BL, Neergaard R. 1991. Mate choice in the willow warbler - a field experiment. *Behavioral Ecology and Sociobiology* **29**:225-229.

Baker AJ, Gonzalez PM, Piersma T, Niles LJ, do Nascimento ID, Atkinson PW, Clark NA, Minto CDT, Peck MK, Aarts G. 2004. Rapid population decline in Red Knots: Fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society B-Biological Sciences* **271**:875-882.

Balmer D, Gillings S, Caffrey B, Swann B, Downie I, Fuller R. 2013. Bird Atlas 2007 – 2011: The breeding and wintering birds of Britain and Ireland. British Trust for Ornithology, Thetford.

Bardeli R, Wolff D, Kurth F, Koch M, Tauchert K-H, Frommolt K-H. 2010. Detecting bird sounds in a complex acoustic environment and application to bioacoustic monitoring. *Pattern Recognition Letters* **31**:1524-1534.

Bates D, Maechler M, Bolker B, Walker S. 2015. lme4: Fitting linear mixed-effects models using lme4. *Journal of Statistical* Software **67**:1-48.

Bayard TS, Elphick CS. 2010. How area sensitivity in birds is studied. *Conservation Biology* **24**:938-947.

Bélisle M. 2005. Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* **86**:1988-1995.

Bélisle M, Desrochers A, Fortin MJ. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* **82**:1893-1904.

Bélisle M, Desrochers A. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology* **17**:219-231.

Bellamy PE, Hinsley SA, Newton I. 1996. Factors influencing bird species numbers in small woods in south-east England. *Journal of Applied Ecology* **33**:249-262.

Bellamy PE, Hill RA, Rothery P, Hinsley SA, Fuller RJ, Broughton RK. 2009. Willow Warbler *Phylloscopus trochilus* habitat in woods with different structure and management in southern England. *Bird Study* **56**:338-348.

Bellamy PE, Burgess MD, Mallord JW, Cristinacce A, Orsman CJ, Davis T, Grice PV, Charman EC. 2017. Nest predation and the influence of habitat structure on nest predation of Wood Warbler *Phylloscopus sibilatrix*, a ground-nesting forest passerine. *Journal of Ornithology* DOI:10.1007/s10336-017-1527-7

Bennett AF, Hinsley SA, Bellamy PE, Swetnam RD, Mac Nally R. 2004. Do regional gradients in land-use influence richness, composition and turnover of bird assemblages in small woods? *Biological Conservation* **119**:191-206.

BirdTrack: BTO/RSPB/BirdWatch Ireland/SOC/WOS. 2017. Available from www.birdtrack.net [accessed June 2017].

Blumstein DT, Mennill DJ, Clemins P, Girod L, Yao K, Patricelli G, Deppe JL, Krakauer AH, Clark C, Cortopassi KA, Hanser SF, McCowan B, Ali AM, Kirschel ANG. 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. *Journal of Applied Ecology* **48**:758-767.

Bohenek JR, Pintar MR, Breech TM, Resetarits WJ. 2017. Patch size influences perceived patch quality for colonising Culex mosquitoes. *Freshwater Biology* **62**:1614-1622.

Boitani L, Falcucci A, Maiorano L, Rondinini C. 2007. Ecological networks as conceptual frameworks or operational tools in conservation. *Conservation Biology* **21**:1414-1422.

Bregman TP, Sekercioglu CH, Tobias JA. 2014. Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. *Biological Conservation* **169**:372-383.

Briedis M, Hahn S, Adamík P. 2017. Cold spell *en route* delays spring arrival and decreases apparent survival in a long-distance migratory songbird. *BMC Ecology* **17**:11.

British Ornithologists' Union. 2013. The British list: a checklist of birds of Britain (8th edition). *Ibis* **155**:635-676.

British Trust for Ornithology. 2016. BTO/JNCC/RSPB breeding bird survey trends 2015 - UK. BTO, Thetford. Available from https://www.bto.org/volunteer-surveys/bbs/latest-results/population-trends [accessed March 2017]

Cerquiera MC, Aide TM. 2016. Improving distribution data of threatened species by combining acoustic monitoring and occupancy modeling. *Methods in Ecology and Evolution* DOI: 10.1111/2041-210X.12599.

Convention on Biological Diversity. 2017. Recommendation adopted by the subsidiary on scientific, technical and technological advice: Scenarios for the 2050 Vision for Biodiversity. CBD/SBSTTA/REC/XXI/1 Montréal, Canada.

Cowlishaw G. 1999. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. *Conservation Biology* **13**:1183-1193.

Cresswell W. 2008. Non-lethal effects of predation in birds. *Ibis* **150**:3-17.

Cristofoli S, Mahy G. 2010. Colonisation credit in recent wet heathland butterfly communities. *Insect Conservation and Diversity* **3**:83-91.

Davies, ZG, Tyler C, Stewart GB, Pullin, AS. 2008. Are current management recommendations for saproxylic invertebrates effective? A systematic review. Biodiversity and Conservation, **17:**209-234.

del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds). 2017. Handbook of the Birds of the World Alive. Lynx Editions, Barcelona. Available from http://www.hbw.com/, [accessed June 2017].

Desrochers A, Bélisle M, Morand-Ferron J, Bourque J. 2011. Integrating GIS and homing experiments to study avian movement costs. *Landscape Ecology* **26**:47-58.

Diamond JM. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* **7**:129-146.

Doligez B, Pärt T, Danchin E. 2004a. Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? Animal Behaviour **67**:457-466.

Doligez B, Pärt T, Danchin E, Clobert J, Gustafsson L. 2004b. Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. *Journal of Animal Ecology* **73**:75-87.

Dolman PM, Hinsley SA, Bellamy PE, Watts K. 2007. Woodland birds in patchy landscapes: the evidence base for strategic networks. *Ibis* **149**:146-160.

Dolman PM. 2012. Mechanisms and Processes Underlying Landscape Structure Effects on Bird Populations. Pages 93 - 23 in Fuller RJ. ed., Birds and Habitat: Relationships in Changing Landscapes. Cambridge University Press, UK.

Donald PF, Green RE, Heath MF. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society B: *Biological Sciences* **268**:25-29.

Donald PF, Sanderson FJ, Burfield IJ, Van Bommel FP. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems & Environment **116:**189-196.

Efford M, Dawson D, Borchers D. 2009. Population density estimated from locations of individuals on a passive detector array. *Ecology* **90**:2676-2682.

ESRI 2011. ArcGIS Desktop: Release 10.2. Redlands, CA: Environmental Systems Research Institute.

Ewers RM, Didham RK, Fahrig L, Ferraz G, Hector A, Holt RD, Kapos V, Reynolds G, Sinun W, Snaddon JL, Turner EC. 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. Philosophical Transactions of the Royal Society B: Biological Sciences **366**:3292-3302.

Fahrig L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* **40**:1649-1663.

Fasanella M, Fernández GJ. 2009. Alarm calls of the Southern House Wren *Troglodytes musculus*: variation with nesting stage and predator model. *Journal of Ornithology* **150**:853-863.

Ferguson-Lees IJ, Castell R, Leech DI. 2009. A field guide to monitoring nests. British Trust for Ornithology, Thetford.

Fletcher RJ. 2007. Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology* **76**:598-606.

Foppen R, Reijnen R. 1994. The effects of car traffic on breeding bird populations in woodland. II. Breeding dispersal of male willow warblers (Phylloscopus trochilus) in relation to the proximity of a highway. *Journal of Applied Ecology* **31**:95-101.

Forestry Commission 2013. National Forest Inventory. Available from http://www.forestry.gov.uk/inventory/ [accessed April 2015].

French DD, Picozzi N. 2002. Functional groups of bird species, biodiversity and landscapes in Scotland. *Journal of Biogeography* **29**:231-59.

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

Fuentes-Montemayor E, Goulson D, Cavin L, Wallace JM, Park KJ. 2013 Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. *Agriculture, Ecosystems & Environment* **172**:6-15.

Fuller RJ, Noble DG, Smith KW, Vanhinsbergh D. 2005. Recent declines in populations of woodland birds in Britain. *British Birds* **98**:116-143.

Galitsky C, Lawler JJ. 2015. Relative influence of local and landscape factors on bird communities vary by species and functional group. *Landscape Ecology* **30**:287-299.

García-Ruiz JM, Beguería S, Arnáez J, Sanjuán Y, Lana-Renault N, Gómez-Villar A, Álvarez-Martínez J, Coba-Pérez P. 2017. Deforestation induces shallow landsliding in the montane and subalpine belts of the Urbión Mountains, Iberian Range, Northern Spain. *Geomorphology* **296**:31-44.

Gentle LK, Gosler AG. 2001. Fat reserves and perceived predation risk in the great tit, *Parus major*. *Proceedings of the Royal Society B: Biological Sciences* **268**:487-491.

Gibson L, Lynam AJ, Bradshaw CJ, He F, Bickford DP, Woodruff DS, Bumrungsri S, Laurance WF. 2013. Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science* **341**:1508-1510.

Gil D, Graves JA, Slater PJ. 1999. Seasonal patterns of singing in the Willow Warbler: evidence against the fertility announcement hypothesis. *Animal Behaviour* **58**:995-1000.

Gill R, Fuller RJ. 2007. The effects of deer browsing on woodland structure and songbirds in lowland Britain. Ibis **149:**119-127.

Gosler AG, Greenwood, JJ and Perrins C. 1995. Predation risk and the cost of being fat. Nature 377:621-623.

Gregory RD, Vorisek P, Van Strien A, Gmelig Meyling, AW, Jiguet F, Fornasari L, Reif J, Chylarecki P, Burfield IJ. 2007. Population trends of widespread woodland birds in Europe. *Ibis* **149**:78-97.

Haddad NM. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications* 9:612-622.

Haddad NM. 2012. Connecting ecology and conservation through experiment. *Nature Methods* **9**:794-795.

Haddad NM, Gonzalez A, Brudvig LA, Burt MA, Levey DJ, Damschen EI. 2017. Experimental evidence does not support the Habitat Amount Hypothesis. *Ecography* **40**:48-55.

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances* **1**:e1500052.

Hanski I. 1994. A practical model of metapopulational dynamics. *Journal of Animal Ecology* **63**:151-162.

Hanski I. 2015. Habitat fragmentation and species richness. *Journal of Biogeography* **42**:989-993.

Hanski I, Ovaskainen O. 2002. Extinction debt at extinction threshold. *Conservation Biology* **16**:666-673.

Harmer R, Watts K, Ray, D. 2015. A hundred years of woodland restoration in Great Britain: changes in the drivers that influenced the increase in woodland cover. Pp. 299-320 in John A. Stanturf, ed. Restoration of boreal and temperate forests. 2nd edition. CRC Press, Boca Raton, Florida.

Hedenström A, Petterson J. 1987. Migration routes and wintering areas of Willow Warblers *Phylloscopus trochilus* (L.) ringed in Fennoscandia. *Ornis Fennica* **64**:137-143.

Hedlund JSU. 2015. Climate change effects on migratory birds and on the ecology and behaviour of the willow warbler (*Phylloscopus trochilus*). PhD thesis. Department of Zoology, Stockholm University, Sweden.

Hilton GM, Ruxton GD and Cresswell W. 1999. Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. *Oikos* **87**:295-302.

Hoctor TS, Carr MH, Zwick PD. 2000. Identifying a linked reserve system using a regional landscape approach: the Florida ecological network. *Conservation Biology* **14**:984-1000.

Hodgson JA, Moilanen A, Wintle BA, Thomas CD. 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology* **48**:148-152.

Hollander FA, Titeux N, Van Dyck H. 2012. Territorial resource valuation deviates from habitat quality in an ecologically trapped, long-distance migratory bird. *Behavioral Ecology and Sociobiology* **66**:777-783.

Huber N, Kéry M, Pasinelli G. 2017. Occupancy dynamics of the Wood Warbler *Phylloscopus sibilatrix* assessed with habitat and remote sensing data. *Ibis* **159**:623-627.

Humphrey JW, Watts K, Fuentes-Montemayor E, Macgregor NA, Peace AJ, Park KJ. 2015. What can studies of woodland fragmentation and creation tell us about ecological networks? A literature review and synthesis. *Landscape Ecology* **30**:21-50.

Jackson ST, Sax DF. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology and Evolution* **25**:153-160.

Jenerette GD, Shen W. 2012. Experimental landscape ecology. *Landscape Ecology* **27**:1237-1248.

Jones GP. 1997. Relationships between recruitment and postrecruitment processes in lagoonal populations of two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **213**:231-246.

Jongman RH, Bouwma IM, Griffioen A, Jones-Walters L, Van Doorn AM. 2011. The pan European ecological network: PEEN. *Landscape Ecology* **26**:311-326.

Kavanagh RP, Stanton MA, Herring MW. 2007. Eucalypt plantings on farms benefit woodland birds in south-eastern Australia. *Austral Ecology* **32**:635-650.

Kobori, H, Dickinson, JL, Washitani I, et al. 2016. Citizen science: a new approach to advance ecology, education, and conservation. *Ecological Research* **31**:1-19.

Krebs JR. 1980. Optimal foraging, predation risk and territory defence. *Ardea* **68**:83-90.

Ktitorov P., Bairlein F., and Dubinin M. 2008. The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover. *Landscape Ecology* **23**:169-179.

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Rodà F, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution* **24**:564-571.

Lahti DC. 2001. The "edge effect on nest predation" hypothesis after twenty years. *Biological Conservation* **99**:365-374.

Lambin EF, Turner BL, Geist HJ, Agbola SB, Angelsen A, Bruce JW, Coomes OT, Dirzo, R, Fischer G, Folke C, George P. 2001. The causes of land-use and land-cover change: moving beyond the myths. *Global Environmental Change* **11**:261-269.

Laurance WF, Camargo JL, Luizão RC, Laurance SG, Pimm SL, Bruna EM, Stouffer PC, Williamson GB, Benítez-Malvido J, Vasconcelos HL, Van Houtan KS. 2011. The fate of Amazonian forest fragments: a 32-year investigation. *Biological Conservation* **144**:56-67.

Law B, Chidel M, Brassil T, Turner G, Kathuria A. 2014. Trends in bird diversity over 12 years in response to large-scale eucalypt plantation establishment: implications for extensive carbon plantings. *Forest Ecology and Management* **322**:58-68.

Lawn MR. 1994. Site fidelity and annual survival of territorial male Willow Warblers *Phylloscopus trochilus* at four adjacent sites in Surrey. *Ringing and Migration* **15**:1-7.

Lawton JH, et al. 2010. Making space for nature: a review of England's wildlife sites and ecological network. DEFRA, London.

Lefcheck JS. 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution* **7**:573-579.

Legrand et al. 2012. The metatron: an experimental system to study dispersal and metaecosystems for terrestrial organisms. *Nature Methods* **9**:828-833.

Lindenmayer DB. 2009. Large-scale landscape experiments: lessons from Tumut. Cambridge University Press, Cambridge, UK.

Loyn RH, McNabb EG, Macak P, Noble P. 2007. Eucalypt plantations as habitat for birds on previously cleared farmland in south-eastern Australia. *Biological Conservation* **137**:533-548.

MacArthur RH, EO Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Magrath RD, Haff TM, Horn AG, Leonard ML. 2010. Calling in the face of danger: predation risk and acoustic communication by parent birds and their offspring. *Advances in the Study of Behavior* **41**:187-253.

Marchant JH, Hudson R, Carter SP, Whittington PA. 1990. Population Trends in British Breeding Birds. British Trust for Ornithology, Tring.

Marques TA, Thomas L, Martin SW, Mellinger DK, Ward JA, Moretti DJ, Harris D, Tyack PL. 2013. Estimating animal population density using passive acoustics. *Biological reviews of the Cambridge Philosophical Society* **88**:287-309.

Martin TG, McIntyre S. 2007. Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats. *Conservation Biology* **21**:504-514.

Maxwell SL, Fuller RA, Brooks TM, Watson JE. Biodiversity: The ravages of guns, nets and bulldozers. *Nature* **536**:143-145.

McGarigal K, Cushman SA. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* **12**:335-345.

Mennill DJ, Battiston M, Wilson DR, Foote JR, Doucet SM. 2012. Field test of an affordable, portable, wireless microphone array for spatial monitoring of animal ecology and behaviour. *Methods in Ecology and Evolution* **3**:704-712.

Metzger JP, Martensen AC, Dixo M., Bernacci LC, Ribeiro MC, Teixeira AMG, Pardini R. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. *Biological Conservation* **142**:1166-1177.

Moilanen A, Hanski I. 2001. On the use of connectivity measures in spatial ecology. *Oikos* **95**:147-151.

Moilanen A, Nieminen, M. 2002. Simple connectivity measures in spatial ecology. *Ecology* **83**:1131-1145.

Mönkkönen M, Forsman JT. 2002. Heterospecific attraction among forest birds: a review. *Ornithological Science* **1**:41-51.

Mortelliti A, Lindenmayer DB. 2015. Effects of landscape transformation on bird colonization and extinction patterns in a large-scale, long-term natural experiment. *Conservation Biology* **29**:1314-1326.

Morton D, Rowland C, Wood C, Meek L, Marston C, Smith G, Wadsworth R, Simpson IC. 2011. Final report for LCM 2007 – the new UK land cover map. Countryside survey technical report 11/07. Centre for Ecology & Hydrology, Edinburgh.

Munro NT, Lindenmayer DB, Fischer J. 2007. Faunal response to revegetation in agricultural areas of Australia: a review. *Ecological Management & Restoration* **8**:199-207.

Musgrove A, Aebischer N, Eaton M, Hearn R, Newson S, Noble D, Parsons M, Risely K, Stroud D. 2013. Population estimates of birds in Great Britain and the United Kingdom. *British Birds* **106**:64-100.

Naaf T, Kolk J. 2015. Colonization credit of post-agricultural forest patches in NE Germany remains 130-230 years after reforestation. *Biological Conservation* **182**:155-163.

Newson SE, Evans HE, Gillings S. 2015. A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biological Conservation* **191**:38-49.

Oliver TH, Marshall HH, Morecroft MD, Brereton T, Prudhomme C, Huntingford C. 2015. Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change* **5**:941.

Opdam P, Steingröver E, Rooij S van. 2006. Ecological networks: A spatial concept for multi-actor planning of sustainable landscapes. *Landscape and Urban Planning* **75**:322-332.

Palmer MA, Ambrose RF, Poff NL. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* **5**:291-300

Pärt T. 1994. Male philopatry confers a mating advantage in the migratory collared flycatcher, Ficedula albicollis. Animal Behaviour. **48**:401-409.

Paradis E, Baillie SR, Sutherland WJ, Gregory RD. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* **67**:518-536.

Pollock ML, Milner JM, Waterhouse A, Holland JP, Legg CJ. 2005. Impacts of livestock in regenerating upland birch woodlands in Scotland. *Biological Conservation* **123**:443-452.

Powell LL, Stouffer PC. 2015. Experimental translocations: pitfalls and alternatives for quantifying animal movement in fragmented landscapes. *Brazilian Journal of Ornithology* **22**:311-316.

Pieretti N, Farina A, Morri D. 2011. A new methodology to infer the singing activity of an avian community: the Acoustic Complexity Index (ACI). *Ecological Indicators* **11**:868-873.

Platzen D, Magrath RD. Parental alarm calls suppress nestling vocalization. 2004. *Proceedings of the Royal Society B: Biological Sciences* **271**:1271-1276.

R Core Team 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Radesäter T, Jakobsson S, Andbjer N, Bylin A, Nyström K. 1987. Song rate and pair formation in the willow warbler, *Phylloscopus trochilus*. *Animal Behaviour* **35**:1645-1651.

Robertson BA, Hutto RL. 2007. Is selectively harvested forest an ecological trap for Olive-sided Flycatchers? *Condor* **109**:109-121.

Robertson OJ, Radford JQ. 2009. Gap-crossing decisions of forest birds in a fragmented landscape. *Austral Ecology* **34**:435-446.

Robertson BA, Rehage JS, Sih A. 2013. Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology and Evolution* **28**:552-560.

Resetarits WJ. 2005. Habitat selection behaviour links local and regional scales in aquatic systems. *Ecology Letters* **8**:480-486.

Resetarits WJ, Binckley CA. 2009. Spatial contagion of predation risk affects colonization dynamics in experimental aquatic landscapes. *Ecology* **90**:869-876.

Resetarits WJ, Silberbush A. 2016. Local contagion and regional compression: habitat selection drives spatially explicit, multiscale dynamics of colonisation in experimental metacommunities. *Ecology Letters* **19**:191-200.

Ripple WJ, Beschta RL. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience* **54**:755-766.

Savory C. 2016. Colonisation by woodland birds at Carrifran Wildwood: the story so far. *Scottish Birds* **36**:135-49.

Şekercioğlu ÇH, Daily GC, Ehrlich PR. 2004. Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences* **101**:18042-18047.

Secretariat of the Convention on Biological Diversity. 2014. *Global Biodiversity Outlook 4* Montréal, Canada.

Soulé ME, Bolger DT, Alberts AC, Wrights J, Sorice M, Hill S. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* **2**:75-92.

Sueur J, Aubin T, Simonis C. 2008. Seewave: a free modular tool for sound analysis and synthesis. *Bioacoustics* **18**:213-226.

Simberloff, DS, Abele LG. 1976. Island biogeography theory and conservation practice. *Science* **191**:285-286.

Southern HN. 1938. The spring migration of the Willow Warbler over Europe. *British Birds* **32**:202-206.

Stephens SE, Koons DN, Rotella JJ, Willey DW. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Biological Conservation* **115**:101-110.

Stevens VM et al. 2014. A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecology Letters* **17**:1039-1052.

Stier AC, Osenberg CW. 2010. Propagule redirection: Habitat availability reduces colonization and increases recruitment in reef fishes. *Ecology* 91:2826-2832.

Stokstad E. 2012. The Metatron: Experimental Ecology Gets Connected. Science **337**:279.

Taylor PD, Fahrig L, Henein K, Merriam G. 1993. Connectivity is a vital element of landscape structure. *Oikos* **68**:571-573.

Templeton CN, Greene E, Davis K. Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science* **308**:1934-1937.

Tewksbury JJ, Hejl SJ, Martin TE. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* **79**:2890-2903.

Tilman D, May RM, Lehman CL, Nowak MA. 1994. Habitat destruction and the extinction debt. *Nature* **371**:65-66.

Tittensor DP, Walpole M, Hill SL, Boyce DG, Britten GL, Burgess ND, Butchart SH, Leadley PW, Regan EC, Alkemade R, Baumung R. 2014. A mid-term analysis of progress toward international biodiversity targets. *Science* **346**:241-244.

Thompson FR III. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* **149**:98-109.

Thompson FR III, Donovan TM, DeGraaf RM, Faaborg J and Robinson SK. 2002. A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. *Studies in Avian Biology* **24**:8-19.

Tiainen J. 1983. Dynamics of a local population of the Willow Warbler *Phylloscopus trochilus* in southern Finland. *Ornis Scandinavica* **14**:1-15.

Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

Vergara PM, Armesto JJ. 2009. Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. *Landscape Ecology* **24**:25-38.

Vesk PA, Nolan R, Thomson JR, Dorrough JW, Mac Nally R. 2008. Time lags in provision of habitat resources through revegetation. Biological Conservation, **141:**174-186.

Vickery JA, Ewing SR, Smith KW, Pain DJ, Bairlein, F, Škorpilová J, Gregory RD. 2014. The decline of Afro-Palearctic migrants and an assessment of potential causes. *Ibis* **156**:1-22.

Villard MA, Merriam G, Maurer BA. 1995. Dynamics in subdivided populations of neotropical migratory birds in a fragmented temperate forest. *Ecology* **76**:27-40.

Villard MA, Trzcinski MK, Merriam G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* **13**:774-783.

Ward JH. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* **58**:236-244.

Watts K, Handley P. 2010. Developing a functional connectivity indicator to detect change in fragmented landscapes. *Ecological Indicators* **10**:552-557.

Watts K, Fuentes-Montemayor E, Macgregor NA, Peredo-Alvarez V, Ferryman M, Bellamy C, Brown N, Park KJ. 2016. Using historical woodland creation to construct a long-term, large-scale natural experiment: the WrEN project. *Ecology and Evolution* **6**:3012-3025.

Wesołowski T. 1983. The breeding ecology and behavior of Wrens *Troglodytes troglodytes* under primaeval and secondary conditions. *Ibis* **125**:499-515.

Weston MA, McLeod EM, Blumstein DT, Guay PJ. 2012. A review of flight-initiation distances and their application to managing disturbance to Australian birds. Emu-Austral Ornithology. *Emu - Austral Ornithology* 112:269-286.

Whittingham MJ, Evans KL. 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* **146**:210-220.

Whytock RC, Fuentes-Montemayor E, Watts K, Barbosa de Andrade P, Whytock RT, French P, Macgregor NA, Park AJ. 2017. Bird community responses to habitat creation in a long-term, large-scale natural experiment. *Conservation Biology* DOI: 10.1111/cobi.12983

Whytock RC, Christie J. 2017. Solo: an open source, customizable and inexpensive audio recorder for bioacoustic research. *Methods in Ecology and Evolution* **8**:308-312.

Zanette LY, White AF, Allen MC, Clinchy M. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* **334**:1398-1401.

Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**:3-14.