

The effects of landscape context and climate on woodland use by bats: implications for habitat creation

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Statement of Original Authorship

I certify this thesis has been composed by myself and the work contained within are the results of my own research, except where specifically stated. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others. The thesis has not previously been accepted for a degree or professional qualification.

Signature:

A handwritten signature in black ink, appearing to read 'Elise', is written over a horizontal line.

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Abstract

There has been growing recognition that simply protecting pristine habitat is insufficient to protect biodiversity in the face of the twin crises of habitat loss and climate change. This, combined with a desire to use functioning ecosystems as carbon sequestration tools, has led to ambitious targets for habitat restoration. Restoration projects are often costly and resource intensive, so strategic planning is required to maximise their benefits. However, evidence is often lacking to inform practitioners of the best strategies. Landscape context can affect the success of restoration projects as edge effects can impact patch quality and the composition and configuration of nearby habitats can promote or impede colonisation. In the UK where habitat loss has been dominated by deforestation, government targets for habitat restoration tend to focus on woodland creation. Bats in the UK use woodland for roosting and foraging and stand to benefit greatly from increased woodland cover resulting from these targets. Here, the impacts of landscape context and climate on bats' use of woodlands are investigated.

Long term population data were used to understand the impacts of heath restoration in conifer forests on bats. In plantations where conifer comprised the majority woodland cover, conversion of conifer to open habitats had negative effects on woodland bats, causing populations to decline or grow at a slower rate.

How bat activity responds to woodland and trees outside woodland cover and spatial configuration was assessed by surveying 60 landscapes in two regions of the UK, with limited impacts found across a number of species. In particular, bat activity in woody habitat patches was consistent along a gradient of woodland cover. However, trees outside woodlands (ToW) were found to be incredibly important aspects of agricultural landscapes. Bat activity at such sites were on par with woodland edge, a key foraging habitat, and landscape ToW cover increased occurrence for *N. noctula*. Activity at ToW sites (and to a lesser extent woodland edge) also increased as the woodland cover was divided into more patches for *P. pipistrellus* and *Myotis spp.* while declining in woodland interior sites, suggesting that ToW increased landscape connectivity and matrix permeability as 'fragmentation per-se' increased.

Multi and cross scale landscape drivers of habitat suitability were investigated at a national scale using nested habitat suitability models. Habitat associations for the 9 most common species of bat in the UK were complex and varied between species and scales considered,

however some general patterns emerged. Broadleaf woodland and ToW cover had a positive impact on all species, however there was no strong indication that any particular range of cover increase was most beneficial across all species and scales. Agricultural habitat had mixed effects but high levels of cover tended to be negative. Urban cover also typically negatively affected suitability, although rural buildings allowed for roosts. Additionally, by using a multi-level approach important cross-scale interactions were identified.

Spatial patterns and potential land use and climate drivers of emerging *Rhinolophus hipposideros* population trends were also investigated. National *R. hipposideros* population recoveries in the UK have slowed in the last decade and this is seemingly driven by declines in the Southwest of England. Yearly growth rates were negatively impacted by winter precipitation anomalies and increasing spring temperatures, while short term (5 year) trends were negatively impacted by increased summer precipitation and urban cover. These impacts did not appear to be concentrated in the Southwest, suggesting that they may not be the main drivers of spatial patterns.

Overall, this thesis has highlighted that landscape context can influence woodland benefits to bats, although the effects of urban, agricultural and woodland cover in the landscape are all species and scale specific, complicating recommendations for spatial targeting. However, it seems that planting woodland in varied landscape contexts will benefit at least part of the UK bat community, although concentrating new planting in a smaller number of patches is likely to have the most benefits for woodland specialists. Trees outside woodland also had an important role to play as habitat for bats in agricultural landscapes, particularly in boosting connectivity between fragmented patches and thus sympathetic management and new planting of these should also be promoted.

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Chapter 1: General Introduction

1.1 Background

1.1.1 Habitat and Biodiversity Loss

Global biodiversity is threatened by a series of anthropogenic pressures, contributing to an estimated wild mammal biomass decline of 83% and plant biomass decline of 50% (Pörtner et al. 2021). Ecosystems and the species they support have intrinsic value and should be protected regardless of their benefits to people. However, biodiversity loss and ecosystem degradation does increase threats to human societies through reduced ecosystem services, such as pollination of food crops, agricultural pest control, carrion removal, flood mitigation and carbon sequestration (Burton et al. 2018, McHugh et al. 2020, Alvarado-Montero et al. 2021). Ecosystem degradation can also lead to increased risk of zoonotic spillovers (Streicker and Allgeier 2016). While historically these declines were largely driven by habitat loss and degradation, increasingly climate change is impacting population trends and causing shifts in species ranges and changes in phenology, all of which interact with modifications to habitats (Eglington and Pearce-Higgins 2012, Howard et al. 2020, Pörtner et al. 2021).

Habitat loss and degradation has been largely driven by conversion of primary vegetation to agricultural and urban land as well as continued degradation by intensification of these processes (Daskalova et al. 2020, Ridding et al. 2020, Pörtner et al. 2021). Native ecosystems are often reduced to divided and isolated habitat patches within a human managed or altered ‘matrix’. While protected areas can play an important role in slowing habitat and biodiversity loss if well managed (Laurance et al. 2012, Gray et al. 2016, Ridding et al. 2020, Kajzer-Bonk and Nowicki 2022), they are not always effective (Laurance et al. 2012, Santana et al. 2014). Additionally, only 15% of land is currently protected, while 77% of land outside Antarctica has already been directly modified by human activities (Pörtner et al. 2021). Habitat loss continues outside (and sometimes within) protected areas with negative impacts both for species outside the protected areas and for those inside through edge effects and increased isolation which are enhanced if nearby habitats are impermeable or hostile (Carroll et al. 2004, Laurance et al. 2012, Di Sacco et al. 2021, Pörtner et al. 2021). Further, as the climate changes, protected areas are likely to become unsuitable for many of the species they are designed for

and if habitat is limited, species may struggle to adjust their geographical range to adapt to new conditions (Hodgson et al. 2011, Hughes et al. 2012, Laurance et al. 2012, Struebig et al. 2015, Smith et al. 2016). Under continued loss, degradation and emerging climate threats, restricting protection to remaining pristine habitat is insufficient (Laurance et al. 2012, Pörtner et al. 2021).

1.1.2 Habitat Restoration

The insufficiency of simply protecting existing habitats has led to ambitious targets for restoring habitat globally, including the UN Decade of Ecosystem Restoration, 2021-2030 (<https://www.decadeonrestoration.org/>). This has been combined with a drive to use native ecosystem restoration to combat climate change. Forest and peat habitats in particular can lead to high rates of carbon-sequestration both directly through photosynthesis and through reductions in soil erosion, partly compensating for continued emissions (Burton et al. 2018, Strassburg et al. 2020, Di Sacco et al. 2021, Pörtner et al. 2021). As much of the world's converted land was originally forested and deforestation continues to be a large part of habitat loss, as well as their particular perceived benefits for carbon sequestration a great deal of focus has been on forest restoration (Strassburg et al. 2020, Di Sacco et al. 2021). Internationally, the Bonn Challenge which started in 2011, aimed to restore 150 million hectares of woodland by 2030 (<https://www.bonnchallenge.org/>).

This is reflected in the UK where there has been a particularly long history of deforestation, with woodland cover dropping to 5% at the beginning of the 20th Century, and still remaining much lower than other European Countries at 13% (Mason 2007, Liu et al. 2023). The previous UK government committed to increasing tree cover in England to 16.5% by 2050, of which 4.5% would comprise trees outside woodlands and with particular promotion of riparian woodlands (DEFRA 2023). It remains to be seen whether the new government will uphold these targets, however their election manifesto included a commitment to create three new national forests while “planting millions of trees” (Labour Party 2024). Devolved governments have committed to similar targets. For example, in Wales targets are to plant 2000ha/year, while encouraging natural regeneration where possible and the government is attempting to tie agricultural subsidies to a minimum of 10% woodland cover on all farms (Welsh Government 2018, Orford 2024). Scottish Government (2020) targets are to plant 18,000ha/year by 2025 and to increase woodland cover to 21% by 2032, while Northern Irish targets are to plant

9000ha by 2030 (DAERA 2020). Actual increases in cover are likely to be lower as planting targets are routinely missed. In 2021-22 only 46% of the yearly planting rate target was met and progress has been similar since 2018 (House of Commons Environmental Audit Committee 2023).

Restored habitats have the potential to be important reservoirs of global biodiversity, for example secondary forests currently account for 64% of all Earth's forests (Arnold et al. 2021). Several habitat restoration studies across a range of taxa and environments have found that new patches are colonised by species relevant to the particular habitat, leading to increased occurrence and abundance (Forup et al. 2008, Laurance et al. 2018, Ashwood et al. 2019, Wolfe et al. 2020, Warner et al. 2021, Wilms et al. 2021, Parkhurst et al. 2022). However, depending on the previous history of the land this can simply result in a turnover of species rather than increases in biodiversity (Burton et al. 2018, Parkhurst et al. 2022). Additionally, at a wider geographical range, increased cover of restored habitats can have mixed impacts on population recoveries (Daskalova et al. 2020, Watts et al. 2020, Bowler et al. 2023). For example, increased broadleaf woodland cover across the UK in the 1980s and 1990s was followed by increases in national population indices for generalist birds (after an 11-year lag, Watts et al. 2020). However even after 30-years woodland specialist birds continued to decline, either due to insufficient or poorly targeted actions or the time required for woodlands to develop the mature habitat characteristics required by these species (Watts et al. 2020). A small increase in woodland associated invertebrates has also been observed in the UK following this increase in broadleaf cover, however this was inconsistent across and within taxa (Bowler et al. 2023).

Habitat restoration can also play a role in mitigating climate change effects for species. Restoration can enhance adaptation by facilitating range shifts through increased connectivity between existing patches (Hodgson et al. 2011, Laurance et al. 2018, Synes et al. 2020). Additionally, improved geneflow in more connected landscape can enhance the propagation of advantageous alleles (Fletcher et al. 2024). This can be achieved through targeted creation of corridors and stepping stones or through simply increasing cover and therefore reducing average inter-patch distances (Andren 1994, Fahrig 2003, Hodgson et al. 2011, Fletcher et al. 2024). Additionally, native vegetation can create microclimatic refuges with a tendency to be cooler than degraded habitats and agricultural land, reducing the direct impacts of increased temperatures (Williamson et al. 2020, Pörtner et al. 2021).

Managed poorly, however, the climate and biodiversity outcomes of restoration projects can be in conflict (Burton et al. 2018, Pörtner et al. 2021). For example, fast growing conifer tree species are perceived to sequester more carbon in the short-term and there are concerns that this could lead to increased creation of large non-native monoculture plantations (Burton et al. 2018, Di Sacco et al. 2021). In the UK, the creation of commercial conifer drove most of the increase in tree cover during the 20th Century and now accounts for 60% of woodlands (Mason 2007). While some woodland species are able to colonise conifer plantations, this is often reliant on sympathetic management, and both abundances and species richness tend to be lower than in native broadleaf woodlands, particularly for specialists (Kirkpatrick et al. 2017a, O’Callaghan et al. 2017, Cook et al. 2023).

A particular concern with both commercial conifer and native afforestation is which habitat they are and have historically replaced (O’Callaghan et al. 2017). The loss of a number of natural habitats such as shrublands, semi-natural grasslands, arid habitats and wetlands can be attributed to afforestation leading to losses of species associated or specialised to those ecosystems (O’Callaghan et al. 2017, Ridding et al. 2020, Strassburg et al. 2020, Di Sacco et al. 2021). In the UK, areas of ancient woodlands, heathland and peatlands were converted to conifer plantations leading to major reductions in their cover with negative knock-on effects for their biodiversity (Mason 2007, Ridding et al. 2020, House of Commons Environmental Audit Committee 2023). These habitats also require restoration, and it is important to understand the impacts this could have on woodland species and whether there are likely to be trade-offs between conservation of species adapted to woodlands and other important habitats.

1.1.3 Passive Restoration

Left undisturbed, many habitats are able to recover naturally, allowing for passive restoration which can be a cost-effective strategy as it requires limited interventions (Holl et al. 2018). In tropical forests, secondary regrowth has been effective in promoting connectivity between mature forest patches and can lead to recovery of populations and communities that suffered declines due to historic deforestation (Farneda et al. 2018, Rocha et al. 2018, Stouffer 2020, Wolfe et al. 2020, Werden et al. 2021). Agricultural abandonment in parts of Europe has also led to forest succession with positive impacts for woodland species (Broughton et al. 2022, Mora et al. 2023). However, the success and speed of natural colonisation can vary, particularly in relation to starting conditions. In tropical regions increased grass cover and time since

original clearance can both negatively affect speed of recovery (Holl et al. 2018). While in temperate regions, browsing pressure, lack of seed sources and soil type have been identified as major challenges (Porton et al. 2024).

In the UK there is huge grazing pressure from livestock and overabundant native herbivores, particularly sheep and deer, which can negatively affect woodland recruitment (Milligan et al. 2016, Burton et al. 2018, Porton et al. 2024). While some studies have found higher rates of sapling growth and recruitment in herbivore exclosures, this is not always the case and grazing does not always preclude successful recruitment (Milligan et al. 2016, Porton et al. 2024). For example, abandoned agricultural fields in Cambridgeshire adjacent to an ancient woodland reached 85% woody cover in 20 years in spite of deer grazing (Broughton et al. 2021a). In many areas, seed sources seem to be the main limiting factor, for example similar agricultural fields to those in Cambridge that were further from existing woodlands did not recruit any trees over 33 years (Broughton et al. 2022). Wind dispersed species in particular can be limited to areas adjacent to parent trees, with studies from across the UK suggesting that natural colonisation is limited to around 100m from existing seed sources (Broughton et al. 2021a, Murphy et al. 2022, Bauld et al. 2023, Porton et al. 2024). The high degree and long-term nature of deforestation in the UK may mean that in many areas natural colonisation is unviable, and woodland restoration will necessitate active restoration through planting.

1.1.4 Spatial Targeting of Conservation

Where natural regeneration is unfeasible or requires initial management to kick-start natural processes, habitat restoration can carry a large cost and high resource intensity. Due to the shortfall between the resources required to restore degraded and lost habitats globally and the realities of those available, many argue that triage is unavoidable, and that strategic planning is required to use resources most effectively (Bottrill et al. 2008). Choosing areas to conserve is complex and reliant on a number of factors, but accounting for the possible biodiversity benefits and probability of success are important to maximise impact and minimise wastage of limited funds and efforts in unsuccessful projects (Scott et al. 2001, Holl et al. 2003, Bottrill et al. 2008, Strassburg et al. 2020). While biodiversity benefits can be conceived of as simply increasing richness or abundance of a particular species or taxa, there is flexibility to place greater importance on distinct and endangered species, or ecosystems of regional importance based on underlying values (Bottrill et al. 2008, Rappaport et al. 2015). Rappaport et al. (2015)

also argue that there is a temporal dynamic, as recently degraded ecosystems may still hold many at risk species due to extinction debts and thus should be prioritised.

Strategic planning can take account of many scales, but for spatial targeting of habitat restoration projects, landscape context is particularly important. Generally, to be successful in promoting biodiversity and species recovery, habitat restoration projects need to be accessible for colonisation and provide good quality habitat (Scott et al. 2001, Whytock et al. 2018b). Landscape context plays an important role in colonisation through its effects on connectivity and species movements (McGarigal and McComb 1995, Scott et al. 2001, Dolman et al. 2007, Whytock et al. 2018b, Watts and Hughes 2024). While patch characteristics play a direct role in habitat quality, landscape context can also affect quality through edge effects, species interactions and by providing supplementary resources (Scott et al. 2001, Tschamntke et al. 2012, Williamson et al. 2020). Successful reforestation projects thus require an understanding of how patch and landscape characteristics, as well as their interactions, affect species colonisation, establishment and persistence in habitats. However, evidence is often lacking to inform the best strategies, largely due to the challenges of conducting experiments on large spatial and temporal scales (Watts et al. 2016, Broughton et al. 2021a). This is exacerbated in studies of woodland restoration due to the length of time it takes for forests to develop (Watts et al. 2016).

1.2 Landscape Context

Early studies of landscape contexts in ecology borrowed from island biogeography and considered remnant natural habitat patches ‘islands’ in an inhospitable ‘matrix’ (Duelli and Obrist 2003, Lesiński et al. 2007, Whytock et al. 2018b, Valente et al. 2023), with island size and isolation having impacts on biodiversity and colonisation. This led to an interest in the impacts of habitat cover and configuration on biodiversity in habitat patches within human modified landscapes (Rogan and Lacher 2018, Valente et al. 2023). However, in recent years a growing interest in the impacts of the matrix itself on ecological processes has emerged (Fletcher et al. 2024).

1.2.1 Landscape Habitat Composition

Many studies have focussed on the impacts of a species' core habitat cover, or semi-natural habitats more generally, commonly finding positive impacts of landscape cover on activity, abundance or occurrence in both remnant (reviewed in, Batáry et al. 2011, Humphrey et al. 2015, Mendes and Srбек-Araujo 2020) and secondary habitats (Naaf and Kolk 2015, Fuentes-Montemayor et al. 2017, Whytock et al. 2018a). However, negative and non- responses are also sometimes found, for example some bat species are more prevalent in landscapes with lower woodland cover, or have the highest abundance in moderate cover, often when they are able to use alternative, usually agricultural, habitats (Mendes and Srбек-Araujo 2020). In particular, hematophagous and frugivorous bat species which can feed on livestock and fruit of early successional plants respectively are often found in higher numbers when forest cover is reduced (Klingbeil and Willig 2009, Mendes and Srбек-Araujo 2020).

Semi-natural habitat amount also sometimes has no, or negative effects on measures of biodiversity or ecosystem services (Batáry et al. 2011). This may be a result of the semi-natural habitat present in the landscape not providing resources for the focal species (Bennett et al. 2006, Haslem and Bennett 2008). For example, semi-natural habitat was not a good predictor of bumblebee colony density, because many of them flowered for limited periods (e.g. woodlands) or had low nectar production per unit area (e.g. pasture, Timberlake et al. 2019, 2021). These studies highlight the fact that different types of semi-natural habitat are not equally beneficial to all species. There are several non-woodland habitats that have suffered losses and are targeted for restoration within the UK (e.g. heath and peatland) and it is important to understand the effects of their expansion on woodland species.

1.2.2 Landscape Habitat Configuration

There is less agreement around the impacts of the spatial configuration of habitat patches on their biodiversity (Haddad et al. 2015, Fahrig 2017, Valente et al. 2023). This debate largely revolves around whether “fragmentation” has positive or negative impacts on species. The fragmentation debate has been described as locked-in, without progress on understanding patterns and drivers behind different responses (Valente et al. 2023). Valente et al. (2023) suggests possible reasons for the equivocal results are differences in study design, particularly the geographic (patch vs landscape) and biological (species vs community) scale at which the impacts are measured as well as how fragmentation is quantified and defined. This latter issue

is an important one in the fragmentation debate as the term has been used to describe two different aspects of habitat configuration.

Some authors use the term to describe the process of habitat sub-division that occurs when continuous habitat is divided into multiple smaller, more isolated patches as a result of habitat loss (Andren 1994, Fischer and Lindenmayer 2007). A review by Haddad et al. (2015) found consistent negative effects of this type of fragmentation on a wide range of biodiversity measures as well as on ecosystem function. There are additionally complex temporal dynamics to the impacts of habitat sub-division. Species abundances can initially increase as species take refuge in remnant patches, but these effects dissipate over time, giving way to progressive and ongoing negative impacts with patch size determining the speed of change (Cosson et al. 1999, Grez et al. 2004, Haddad et al. 2015, Wolfe et al. 2020). In contrast, some studies of small-scale sub-division in landscapes with high habitat cover have found positive impacts on the abundance of some bird species and species richness can be higher in fragmented areas than contiguous habitats (McGarigal and McComb 1995, Estrada and Coates-Estrada 2002, Bernard and Fenton 2007).

Fahrig (2003) argues that this definition conflates the impacts of habitat loss with impacts arising from different spatial configurations of a similar amount of remnant habitat. They use the term ‘fragmentation per-se’ to describe habitat that is split between a larger number of smaller patches (Fig. 1.1). A review by Fahrig (2017) found that such divided configurations of habitat had generally positive impacts, particularly when cover was high, and the effects tended to be smaller (either in effect size or in the number of species affected) than the impacts of habitat cover. However, Fletcher et al. (2018) criticised this study for their selection of papers to include in the review. Additionally, some studies have found negative impacts of ‘fragmented per-se’ habitats on various taxa (Gorresen and Willig 2004, Radford and Bennett 2007, Rodríguez-San Pedro and Simonetti 2015), while some have found positive responses for generalists and negative for specialists (Tscharntke et al. 2002, Alvarado-Montero et al. 2021).

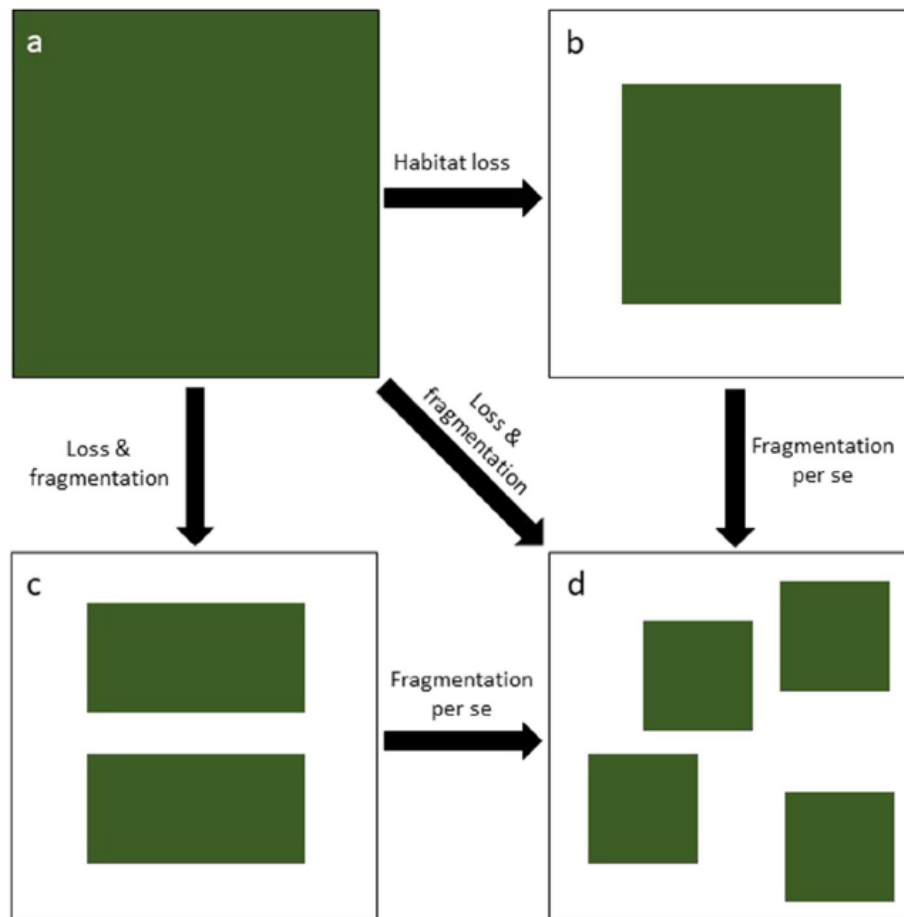


Figure 1.1: An illustration of the relationships between habitat loss, fragmentation and ‘fragmentation per-se’ from (Valente et al., 2023). Landscape (a) is composed of 100% habitat (green), (b) represents habitat loss without fragmentation, however this will impact spatial configuration in the wider landscape. More commonly habitat loss and fragmentation are combined and result in multiple smaller patches (c and d). Increasing the number of patches without changing the total amount of habitat in a landscape is referred to as ‘fragmentation per se’ (b to d and c to d).

The definition of ‘fragmentation per-se’ attempts to separate the impacts of habitat cover from its spatial configuration, however this is complicated by the connection between these measures and the fact that changes tend to occur simultaneously (i.e. it is not possible to lose/gain habitat without affecting the spatial configuration of habitat in a landscape and vice-versa, Fig. 1.1; Andren 1994, Villard et al. 1999, Fletcher et al. 2018). Simulations of landscapes show that when habitat cover is high (>60%) fragmentation is of limited importance, with the habitat largely contained in one contiguous patch and distance between small patches minimal, while loss of habitat has the strongest effects on configuration at low cover (particularly below 20%; Andren 1994).

Additionally, while divided spatial configurations, ‘fragmentation per-se’, are often claimed to have small but positive benefits on biodiversity, many of these studies come from existing landscapes that have been impacted by previous changes. Watts and Hughes (2024) argue that the impacts of spatial configuration on restored habitats are likely to be larger and ‘fragmentation per-se’ will be negative. In remnant habitat patches, communities are likely to be subsets drawn from the species that were present before landscape changes, however the key driver of communities in restored habitat patches is the ease of dispersal and colonisation (Watts and Hughes 2024). Divided habitat patches with limited connectivity will hamper this process, particularly for poor dispersers (Naaf and Kolk 2015, Watts and Hughes 2024). Indeed, studies of secondary woodlands have found that more connected spatial configurations, particularly reduced interpatch distance and presence of woody linear features in the surrounding landscape led to higher activity of bats, as well as greater occurrence and species richness of birds and plants (Fuentes-Montemayor et al. 2017, Whytock et al. 2018a, Brunet et al. 2021, Hughes et al. 2023, de Zwaan et al. 2024)

1.2.3 The Importance of the Matrix

Definitions of the ‘matrix’ vary in landscape ecology, but it generally encompasses areas of land that are not the core habitat of a particular species; in the context of conservation this is usually agricultural or urban areas within which ‘remnant’ habitat patches are found (Fletcher et al. 2024). However, this definition can become somewhat problematic when considering agricultural or urban adapted species (Fletcher et al. 2024). While human modified habitat in landscapes were initially viewed as hostile and unusable, there has been growing recognition that distinctions between different managed land uses are more subtle and that species are able to utilise and disperse through the matrix with varying success (Humphrey et al. 2015). Matrix composition can influence landscape and patch biodiversity in a number of ways. Spillovers between neighbouring habitats can change resource provision, species interactions and community composition in habitat patches (Wethered and Lawes 2005, Tschardt et al. 2012, Humphrey et al. 2015, Mortelliti and Lindenmayer 2015, Stouffer 2020). Additionally, the hostility and permeability of the matrix can impact movements between patches and across the matrix itself (Fletcher et al. 2024).

Edge effects are a form of spillover, caused by the exchange of energy, material and organisms between different habitat types (Fahrig 2003, Tschardt et al. 2012). Within highly modified

landscapes, they are commonly regarded as a negative impact of habitat loss as patch edges are subject to high levels of anthropogenic disturbance, including light and noise pollution in urban landscapes (Lintott et al. 2014a) or chemical inputs in agricultural landscapes (Billeter et al. 2008, Fahrig et al. 2011). This is generally considered to lead to ecological degradation, for example rainforest-palm plantation edges had simpler vegetation structures and communities, lower canopy height and reduced seedling abundance than continuous forest (Williamson et al. 2020). These changes increase wind and light exposure, creating warmer and drier microclimates, with negative effects on invertebrate abundances (Collinge and Palmer 2002, Harper et al. 2005, Tscharntke et al. 2012, Williamson et al. 2020). However, edge effects can also have positive impacts as matrix habitats contribute resources to species within the patch, for example hematophagous bats can feed on livestock in agricultural matrices (Streicker and Allgeier 2016).

Movements of species between neighbouring habitats (especially from the matrix into remnant patches) can directly impact biodiversity and species within habitat patches through increased immigration of matrix-adapted species and resultant interactions, such as predation or parasitism (Ås 1999, Kurki et al. 2000, Fletcher et al. 2024). The most prominent form of this is when the dominant matrix habitat changes through human management. Pine afforestation on previously agricultural or natural grassland habitats in Australia promoted generalist bird species at the expense of rare specialists within adjacent remnant native forest patches, leading to large species turnovers and divergences in community composition (Wethered and Lawes 2005, Mortelliti and Lindenmayer 2015). The effect was most prominent in small woodlands which are able to support fewer forest species while providing more edge habitat for matrix-adapted species to utilise (Ås 1999, Wethered and Lawes 2005). The expansion of pasture around Amazonian rainforest fragments similarly benefited generalist bird species at the detriment of forest bird species, while the regeneration of forest matrix led to the reverse (Stouffer 2020).

The composition of matrix habitats also affects the permeability of landscapes and impacts species movements. Particularly hostile matrices can impede movement altogether, however most evidence suggests movement trajectories are changed rather than halted, although there is large variation in the changes observed (Fletcher et al. 2024). This has knock-on effects for the ability of species to move between patches and thus their sensitivity to habitat cover and configuration, for example in a more permeable landscape isolation of patches may be less

intense as travel between nearby patches will be easier. Rodríguez-San Pedro and Simonetti (2015) found that changes in bat activity in native forest patches were more likely to be associated with native woodland cover and configuration in agricultural landscapes than in pine landscapes. Even when matrices are generally hostile, permeability can differ, for example moth abundance and species richness in woodland fragments within agricultural landscapes increased with the amount of surrounding woodland and semi-natural habitat cover (Fuentes-Montemayor et al. 2012) while in suburban landscapes they did not (Lintott et al. 2014a). Within suburban environments, gardens can act as stepping-stones to facilitate dispersal increasing matrix permeability in comparison to agricultural landscapes (Lintott et al. 2014a). Sensitivity also varies between species (as some will view similar matrices as more or less hostile), and this is thought to be governed by mobility and specialism (Carroll et al. 2004, Tscharntke et al. 2012, Fuentes-Montemayor et al. 2017).

For many woodland species an important factor in the permeability of landscapes, particularly in agricultural areas, are linear woody features including hedges and treelines as well as individual or small clumps of trees (collectively referred to as trees outside woodland – ToW, Frey-Ehrenbold et al. 2013, Humphrey et al. 2015, Scholefield et al. 2016, Broughton et al. 2021b). This is particularly pertinent in the UK where Liu et al. (2023) estimated that 10% of woody biomass and 22% of woody cover is found outside woodlands, the highest in Europe by a wide margin (although some of this difference is likely driven by comparatively low woodland cover). Birds and bats tend to respond positively to local hedge characteristics, particularly increased size (Finch et al. 2020a, Broughton et al. 2021b, Foxley et al. 2023) and connectivity (Frey-Ehrenbold et al. 2013). Many species additionally respond positively to ToW cover in the wider landscape (Sullivan et al. 2017, Wood et al. 2017, Froidevaux et al. 2019, Bellamy et al. 2020), with particular benefits in intensive agricultural areas (Batáry et al. 2011, Sullivan et al. 2017, Alison et al. 2021, Broughton et al. 2021b, de Zwaan et al. 2024). Until recently it has been difficult to map ToW on a large scale limiting their inclusion in landscape ecology studies (Scholefield et al. 2016). However, advances in LiDAR technology have allowed the development of detailed ToW maps over large spatial extents (e.g. Liu et al. 2023, created an EU wide dataset at 30m resolution) allowing for more detailed data on ToW cover and therefore understanding of their impacts on woodland biodiversity.

1.2.4 The Impacts of Landscape Complexity on Restoration Success

While increased habitat cover, configurations that allow for greater connectivity, and more permeable matrices appear to improve species' occurrence in existing patches as well as their colonisation of new habitat patches, the shape of these relationships has important implications for spatial targeting of habitat restoration but are equivocal. Tscharntke et al. (2012) hypothesise that the benefits of landscape complexity on biodiversity follow an S-shaped curve with limited increases in both the simplest and most complex landscapes. As a result, they argue that conservation actions, including habitat restoration will have the biggest impacts in 'simple' (intermediate habitat cover) landscapes as 'cleared' landscapes will suffer from isolated patches and limited colonisation, while in complex landscapes the benefits would be relatively small (Tscharntke et al. 2012, Tambosi et al. 2014). Some studies have found agricultural conservation measures (organic farming or agri-environmental schemes; AES) have most success in landscapes with intermediate remnant semi-natural habitat cover (Geiger et al. 2010, Scheper et al. 2013, Boonchuay and Bumrungsri 2022). However, this likely misses some complexity in the relationship as they bin a continuous gradient of semi-natural cover into 3 groups; simple (<1% cover), intermediate (1-20% cover) and complex (>20% cover) and the thresholds for these categories are seemingly derived from limited data (Tscharntke et al. 2002, 2012).

An alternative possibility is that the benefits of landscape complexity on biodiversity follow a logarithmic curve with increases at low levels but with effects saturating once a sufficient level of habitat is reached (Alison et al. 2021) and thus the benefits are greatest when targeting habitat restorations in low cover landscapes. For example, the benefits of linear features and field margins often increase with agricultural cover and intensity (Batáry et al. 2010, Fuentes-Montemayor et al. 2017, Sullivan et al. 2017, Li et al. 2020, de Zwaan et al. 2024). It may also be that increases are linear and therefore the benefits of adding new habitat are the same regardless of landscape complexity (Villard et al. 1999).

1.2.5 Scales of Effect

As well as sensitivity to habitat composition and configuration varying between species (see: The Importance of the Matrix), the spatial extent over which landscape contexts influence biological processes is also variable (Wiens 1989, Mayor et al. 2009). Identifying this scale of effect and therefore the scale at which to plan and conduct conservation projects, is an

important challenge for landscape ecology (Miguet et al. 2017, Spake et al. 2019, Riva and Nielsen 2020, Yeiser et al. 2021). Species interact with their environments at multiple scales, from individual plants to global ranges and habitat selection can occur across many or all of these scales (Wiens 1989, Mayor et al. 2009, Spake et al. 2019, Bellamy et al. 2020). A species' foraging area for example will be nested within its home range, which includes other resources such as shelter and mating opportunities (Wiens 1989, Mayor et al. 2009, Bellamy et al. 2020). Home ranges are in turn nested within the species range which is limited by regional and biogeographic climate factors (Wiens 1989, Mayor et al. 2009, Bellamy et al. 2020). For example, studies of bat occurrence in the UK found that foraging activity was influenced by habitat cover and configuration at 100-500m while roost locations were influenced at larger scales of up to 6km (Bellamy et al. 2013, Bellamy and Altringham 2015).

Species interactions can complicate these relationships, for example factors that affect the density of wide ranging predators can have knock-on effects for prey species at scales much larger than their home range (Kurki et al. 2000, Leibold et al. 2004, Moll et al. 2019). Additionally, landscape measures at different scales can also interact, such that a species' response to landscape features at one scale is dependent on landscape features at another or multiple other scales (Vergara and Armesto 2009, O'Rourke et al. 2011, Klein et al. 2012, Froidevaux et al. 2021). For example, bat activity increased with proportion of deciduous trees in stands embedded within a conifer dominated landscape, but decreased in stands embedded within a mixed landscape (Froidevaux et al. 2021). Similarly, increased landscape forest cover enhanced the positive benefits of canopy height and patch area for a few bird species in Chile (Vergara and Armesto 2009). These interactions can also affect the success of conservation interventions (Gabriel et al. 2010, Klein et al. 2012). For example, farm biodiversity was higher on organic farms within landscapes with a high proportion of organic farms than those in conventional landscapes (Gabriel et al. 2010).

Life history traits, such as size and mobility are often predicted to affect the scales at which species are likely to respond to landscape characteristics (Wiens 1989, Gehring and Swihart 2003, Mayor et al. 2009, Jackson and Fahrig 2012). Larger and more mobile species are considered to respond to landscape characteristics at larger scales, as they interact with more of the landscape and often require more habitat (Wiens 1989, Gehring and Swihart 2003, Mayor et al. 2009, Jackson and Fahrig 2012). Current evidence supports this hypothesis with vertebrate abundance and occurrence in remnant and secondary woodlands in agricultural

landscapes more likely to respond to landscape as well as patch characteristics than plants and invertebrates (Humphrey et al. 2015, Fuentes-Montemayor et al. 2017, 2020, Fuller et al. 2018a, Whytock et al. 2018a, Waddell et al. 2024). Despite this, Moll et al. (2019) found no relationships between body size or home range on the scale at which urbanisation most affected mammal species ranging from chipmunks to deer. Additionally, while individuals of small, less mobile species may require less habitat and interact less with the matrix, they also tend to be poor dispersers and may be more sensitive to the effects of landscape context at wider scales with regards to immigration supporting healthy metapopulations and colonisation of new patches (Wiens 1989, Watts and Hughes 2024).

As scales of effect are governed by complex mechanisms, it is important to carefully select the scales at which landscape context is measured within studies to ensure results reflect ecological processes rather than being an artefact of study design (Moll et al. 2019, Goicolea et al. 2024). This is reflected in the fragmentation debate where scale of effect is thought to impact whether effects of spatial configuration are positive or negative (Valente et al. 2023). A common method to account for this is to measure landscape characteristics at numerous scales, usually in a series of buffers around a feature of interest, and use model selection tools to determine which scale explains the most variation (Miguet et al. 2017, Yeiser et al. 2021). The scales chosen are often informed by *a priori* knowledge of a species' ecology, however management considerations and logistics can also play a role (Mayor et al. 2009, Spake et al. 2019). Models that select a best scale of effect separately for different variables, have generally been found to outperform models that only measure and include landscape characteristics at one scale (Mayor et al. 2009). Despite this, as scale selection is often done individually for each variable the process ignores the possible effects of covariates and interactions that could influence the chosen 'best' scale (Bellamy et al. 2020, Chandler et al. 2021). However, testing all permutations is often computationally expensive and relies on large amounts of data (Bellamy et al. 2020).

Some authors have criticised the buffer model for not accounting for likely changes in influence with distance and suggest using distance decay functions instead (Miguet et al. 2017, Moll et al. 2019, Yeiser et al. 2021). From these models it is possible to calculate distances at which the influence of a landscape characteristic is strongest and within which e.g. 90% of the impact is had, which can be informative for management (Miguet et al. 2017, Moll et al. 2019). Despite this, there are similar issues to the buffer model in that spatial data must be discretised and the

scale or resolution at which this is done can impact the outcomes, similarly a maximum distance of possible effect and distance decay function shape must be chosen either *a priori* or through model selection (Yeiser et al. 2021). The computational requirements are also much larger, with only limited improvements to model performance (Miguet et al. 2017, Yeiser et al. 2021).

1.2.6 Time Lags

As well as the spatial scale of landscape effect, responses to habitat loss and restoration can also vary over time and thus the temporal scale of a study can impact outcomes. As seen in ‘Landscape Habitat Configuration’, habitat loss can lead to initial increases in species abundance in remnant patches as individuals are concentrated in these areas (Grez et al. 2004, Wolfe et al. 2020). For example, capture rates of birds were elevated in forest fragments for several months post clearance in a fragmentation experiment in Brazil (Wolfe et al. 2020). The negative effects of fragmentation may not be felt in reduced abundance and species loss immediately but accrue over time as extinction debts are paid (Haddad et al. 2015, Watts and Hughes 2024). Analysis of plant communities in remnant woodland suggest debts remain up to 100 years post fragmentation (Vellend et al. 2006) and the process tends to be slower in larger patches and for longer lived species (Haddad et al. 2015, Watts and Hughes 2024).

Similarly, the impacts of restoration or matrix regeneration can take time to emerge (Haddad et al. 2015, Wolfe et al. 2020, Watts and Hughes 2024). Species take time to colonise new habitats, and this is exacerbated in species with poor dispersal and in isolated patches with colonisation credits remaining centuries after establishment of temperate post-agricultural woodlands (Naaf and Kolk 2015, Brunet et al. 2021, Watts and Hughes 2024). Additionally, generalists are often able to make use of new habitats fairly quickly, while specialists may still be absent from well-developed mature habitat (Whytock et al. 2018a). The initial benefit of young restored habitat is likely to be increased connectivity before developing to provide mature habitat (Wolfe et al. 2020).

Due to such time lags, studies measuring the effects of landscape context or change at different times or over different temporal scales may find different outcomes and thus these should be considered carefully. Long term monitoring can give detailed views of changes over time, as in Wolfe et al. (2020) where bird populations were monitored in forest fragments over 30 years tracking different guild responses to initial fragmentation and the development of secondary

forest in the matrix but can be logistically difficult. Even within long term monitoring different temporal scales can give different pictures for example, population monitoring of *Rhinolophus hipposideros* in the UK shows that populations have increased 65% in the past 25 years but have declined 12% in the past 5 years (Bat Conservation Trust 2024). A common alternative to long-term monitoring is to use space-for-time methodologies (Attinello et al. 2023). These compare landscapes or habitat patches along gradients of age, time since interventions or environmental gradients such as habitat cover, connectivity and climate, across space and extrapolate these relationships to changes in time, however the accuracy of such predictions are unclear (Blois et al. 2013, Attinello et al. 2023).

1.3 Bats

During the 20th century bats suffered population declines and range contractions across Europe, including in the UK (Harris et al. 1995, Van der Meij et al. 2015, Browning et al. 2021, Węgiel et al. 2021). Although it is unclear exactly when declines began, they were most significant before the 1980s, and many species have since started to recover (Van der Meij et al. 2015, Węgiel et al. 2021). National monitoring in the UK show that, since 1997, 11 of the 17 breeding bat species have had stable or increasing trends (Barlow et al. 2015, Bat Conservation Trust 2024). Despite this, numbers are estimated to be substantially lower than before the decline and local extinctions still persist (Harris et al. 1995, Schofield et al. 2022). Additionally, these trends are not universal among species or across regions and there is early evidence that recovery for some species is slowing or beginning to reverse (Bat Conservation Trust 2024).

While some drivers of bat population change are clear, evidence for others, their mechanisms, and how drivers interact are more equivocal (Browning et al. 2021). Disturbances of roosts by anthropogenic activity as well as mortality and habitat loss from wind farms and roads are known to have negative impacts on populations (Browning et al. 2021). Persecution and deliberate destructions of roosts are thought to have played a role in recent population declines (Węgiel et al. 2021). Some species roost in buildings which increases their risk of roost loss through development and renovation of barns or lofts as well as mortality through contact with toxic timber treatment chemicals (Afonso et al. 2016, Browning et al. 2021). Legislation has been in place to protect bats and their roosts since 1981, however works can still occur under licence the impacts of which are unclear (Browning et al. 2021).

All bat species in the UK are reliant on woodland as they provide both foraging and roosting habitats (Alder et al. 2020). Changes in woodland cover affect bat populations with loss of woodland having negative impacts (Harris et al. 1995, Borkin et al. 2011, Browning et al. 2021) but conversely responding positively to increased cover (Browning et al. 2021). Habitat loss through historic deforestation as a result of agricultural and urban expansion has left a network of small and isolated woodlands which may not provide sufficient or high-quality habitat for bats (Fuentes-Montemayor et al. 2013, Fletcher et al. 2024). In addition, agricultural intensification is thought to have been an integral driver of 20th century declines. As well as woodland, many UK bat species are adapted to heterogenous landscapes and will use semi-natural open habitats such as heath and unimproved grasslands for foraging, especially if shrubs and tree features are available for shelter (Wood et al. 2017, Put et al. 2019, Ancillotto et al. 2021, Mordue et al. 2023). During the 20th century, many such habitats were converted to improved grasslands/pastures or arable fields leading to landscape simplification (Ridding et al. 2020). Agricultural intensification also increased chemical inputs such as pesticides, which directly reduced insect prey populations (Browning et al. 2021, Rigal et al. 2023). Increasing field sizes also led to the loss of linear woody features and field margins, which can further reduce invertebrate prevalence and remove important foraging and commuting habitats (Frey-Ehrenbold et al. 2013, Wood et al. 2017, Froidevaux et al. 2019, Finch et al. 2020a, Browning et al. 2021, Foxley et al. 2023, Rigal et al. 2023).

Continuing agricultural intensification remains a threat to bat populations (Wickramasinghe et al. 2003, Anderson et al. 2020, Finch et al. 2020b). While agri-environmental schemes have been implemented to reduce some impacts of farming on biodiversity, bats appear to have mixed responses to these actions (Fuentes-Montemayor et al. 2011, Froidevaux et al. 2017b, 2019, Angell et al. 2019), although targeted interventions such as sympathetic hedge management, including limited cutting, can increase bat activity (Froidevaux et al. 2019). In agricultural landscapes some species do respond positively to woodland cover (Fuentes-Montemayor et al. 2011, 2017, Monck-Whipp et al. 2018). As a result, it has been proposed that the focus of bat conservation efforts should be on woodland restoration at a landscape scale to increase habitat amount and connectivity and thus bats stand to benefit from increased woodland cover as a result of government targets (Downs and Racey 2006, Fuentes-Montemayor et al. 2011, 2013, Frey-Ehrenbold et al. 2013)

1.4 Thesis Aims and Structure

The aim of this thesis is to determine how landscape context and climate affect woodland use by bats in order to inform spatial targeting of woodland creation and to assess the impacts of restorations of other habitat types. In particular the project aims to:

- 1) Understand the impacts of heath restoration and conifer removal on bat population trends
- 2) Assess the impacts of the cover and configuration of woodland and trees outside woodland in landscapes on bat activity
- 3) Investigate the multi and cross scale landscape drivers of occurrence for bat species across the UK using spatially nested habitat suitability models
- 4) Investigate the spatial patterns and potential land use and climate drivers of emerging population trends of *Rhinolophus hipposideros*

Chapter 2: Effects of Land Cover Change on Bats in Conifer Plantations

2.1 Abstract

Changes in land cover can have profound impacts on a species' population trends. Despite the importance of understanding these changes, research is limited by the paucity of long-term, high-resolution biodiversity and land cover data. This study investigated the impacts of land cover changes resulting from heath restoration in coniferous plantations on the population trends of *Pipistrellus spp.*, *Myotis nattereri* and *Plecotus auritus*. Population trends were calculated using long-term monitoring data from 22 bat box schemes across Purbeck Forest (Dorset, UK). Concurrent land cover change was calculated from the UKCEH Landcover Change Map and the National Forest Inventory. Relationships between population trends and land cover changes were modelled at different temporal resolutions across a 29-year period. *Plecotus auritus* counts decreased across Purbeck Forest and in many individual bat box schemes, while *Myotis nattereri* and *Pipistrellus spp.* counts increased across the forest, with variation across schemes. Since 1991, the study area has undergone declines in coniferous woodland, whilst broadleaved cover remained stable, and heathland increased. *Plecotus auritus* and *Pipistrellus spp.* responded negatively to coniferous woodland loss, with populations declining, or increasing more slowly, in areas where cover decreased. Changes in other land cover types had limited impacts. Despite their perception as providing poor biodiversity, where coniferous plantations comprised the majority of woodland cover, their replacement with other conservation important but structurally different habitats had negative impacts on bats. These results demonstrate the trade-offs that can result from habitat restoration and the lack of a single approach that can deliver conservation gains for all species.

2.2 Introduction

There are a wide array of competing pressures on land cover globally, agricultural intensification and urban expansion have driven significant habitat loss and degradation, acting as major contributors to biodiversity declines (Browning et al. 2021, Rigal et al. 2023). At the same time, there is recognition that stopping or slowing habitat loss through protecting remaining habitats is not sufficient to conserve biodiversity (Pörtner et al. 2021), leading to the adoption of ambitious targets for the restoration and expansion of semi-natural habitats, both nationally and globally.

Many habitat restoration projects have been successful in promoting occurrence or abundances of some individual species across a variety of habitats (Forup et al. 2008, Warner et al. 2021, Wilms et al. 2021). For example, heath restored by clearing conifer stands in Dorset led to the reestablishment of heathland plants and insects, as well as robust pollinator networks comparable to communities on ancient heath sites (Forup et al. 2008). However, evidence for the benefits of habitat restoration on biodiversity as a whole is equivocal. Community turnover, rather than a simple increase in species richness or diversity, is a common result of habitat restoration and thus habitat changes can often result in trade-offs between species (Burton et al. 2018, Warner et al. 2021).

Studying biodiversity responses to land cover changes, such as those caused by habitat loss or restoration can be challenging, especially over long periods (Burton et al. 2018). Long-term landscape scale experiments are useful for studying population trend responses to landscape change but are rare due to their complex nature. Similarly, consistent and frequent long-term monitoring of species can be expensive and logistically complicated; however this has been achieved through the use of citizen science and monitoring projects for some taxa, namely birds (e.g. Breeding Bird Survey in the US <https://www.usgs.gov/centers/eesc/science/north-american-breeding-bird-survey>, and similar projects in many European countries, as well as continent-wide projects) and Lepidoptera (e.g. Rothamsted Insect Survey in the UK <https://www.rothamsted.ac.uk/national-capability/the-insect-survey>). For these taxa, studies relating population trends to land cover changes have been limited by the challenges of quantifying land cover change over time, including lack of data and methodological difficulties such as errors or differences in land cover classification (Fuller et al. 2003).

As a result, a common approach has been to compare the habitat requirements of species with contrasting trends or changes in community composition, to interpret how land cover changes are affecting populations (Kwon et al. 2021, Bowler et al. 2023, Mora et al. 2023). For example, population trends differed between woodland and grassland butterfly species in South Korea, but not between species with different latitudinal distributions, suggesting forest regrowth was driving butterfly trends rather than climate change (Kwon et al. 2021).

Studies directly relating land cover changes to bird population trends have often focused on agricultural landscapes for which data are typically available at high temporal resolutions (often annual) which allows for detailed time series analyses. Data can frequently be obtained from farms or relevant authorities without the requirement for detailed mapping of large areas. Such studies have typically shown that bird population trends are negatively associated with changes related to agricultural intensification, sometimes with lagged responses (Chamberlain et al. 2000, Eglington and Pearce-Higgins 2012, Berg et al. 2015, Jerrentrup et al. 2017, Rigal et al. 2023).

Gathering data on changes to other habitats has previously been more demanding, often involving large mapping efforts. For example, Kajzer-Bonk and Nowicki (2022) mapped the size and prevalence of meadow patches and butterfly abundance across 20 years in an 800ha mosaic landscape near Krakow, demonstrating that the establishment of a Natura2000 site led to reduced habitat loss and butterfly declines compared to control sites. Recent advances in satellite imagery have allowed high resolution mapping of land cover change over time, although these datasets are often variable in their spatial and temporal resolutions, which can limit their usefulness for studying impacts on population trends.

As highly mobile species, bats are predicted to be especially sensitive to the effects of landscape changes (Jackson and Fahrig 2012). Drivers of bat population trends across Europe are poorly understood, however there is moderately strong evidence that habitat changes through woodland management and loss, agricultural (particularly arable) intensification continue to affect populations (Browning et al. 2021). Due to limited long-term monitoring data, space-for-time approaches have dominated studies investigating the effects of land cover change on bat populations (Mendes and Srбек-Araujo 2020, Law and Blakey 2021). These studies have generally reported lower species diversity in human modified habitats (esp. agricultural and urban areas) and mixed, guild-specific responses to landscape forest cover or fragmentation (Ethier and Fahrig 2011, Rodríguez-San Pedro and Simonetti 2015, Mendes and Srбек-Araujo

2020). While space-for-time studies can be very informative of the direction of effect, they may be less reliable in estimating the magnitude of land cover change impacts (Blois et al. 2013, Berg et al. 2015, Attinello et al. 2023). Additionally, the predictive ability of space-for-time approaches can be diminished by shifting baselines and differences between the magnitude and nature of the spatial and temporal gradients (Blois et al. 2013).

There are a small number of studies that have been able to directly investigate bat population responses to land cover change over time, notably Cosson et al. (1999) where flooding from a hydroelectric dam in French Guiana created isolated forest patches in which bat abundance and species richness declined over three years, especially in the smaller islands. Additionally, long-term monitoring at the Biological Dynamics of Forest Fragments Project (BDFFP) in the Amazon showed that the development of secondary forest led to the increased abundance of woodland specialist bats as well as increased functional and taxonomic diversity between 15- and 30-years post clearance (Rocha et al. 2018). More commonly, however, long-term population monitoring studies have been used to compare bat population trends in different landscape contexts (e.g. forests with different disturbance regimes, or industrial and rural areas) but without measuring land cover change directly (Borkin et al. 2011, Froidevaux et al. 2017a, Law et al. 2020).

In this study, the impacts of land cover change, measured at high spatial resolution (25m), on population trends in bat species with contrasting ecologies were investigated. Long-term population monitoring data was used from multiple bat box schemes in Purbeck Forest, a ~3000ha commercially managed conifer plantation in southern England, which is undergoing land use changes from forestry practices and heathland restoration. Specifically, the study seeks to understand whether transitions of forest to heathland in the landscape impacted negatively on bat population trends over a 25-year period, and how this varied between species. Whether co-occurring changes in agricultural patterns and urban cover in the surrounding landscape influenced bat population trends, was also investigated.

2.3 Methods

2.3.1 Study Area

Purbeck Forest in Dorset, Southern England was used as the study system (50.705°N, 2.135°W, Fig. 2.1). The Purbeck Forest is a mosaic of conifer plantations (largely Corsican and Scots Pine), open heathland, and small broadleaf woodland areas which is managed primarily for commercial forestry and recreation by Forestry England. The forest is divided into five areas totalling 2973ha, planted in the 1920s on heathland and scrub. Due to the establishment of this forest and other conifer plantations, as well as agricultural expansion and some successional changes to broadleaf woodland, Dorset's heathland cover suffered a 59% decline during the 20th century (Ridding et al. 2020). Heathland restoration projects across the county have been ongoing since the late 20th century and, as part of this, areas of Purbeck Forest have been restored back into heathland since the early 1990s (Forup et al. 2008, Forestry Commission England 2013). Between 2013 and 2023 the forest management plan included the planned restoration of 195ha of heathland and mire (a 15% increase) as well as 8ha of broadleaf woodland (a 9% increase), although these habitats, especially woodland, will take time to mature. Additional restoration of 96ha of heath (a further 9% increase), 122ha of wooded heath (a 2400% increase), and 4ha of broadleaf woodland (a further 4% increase) is planned for 2023-2033, resulting in a 13% decrease in conifer cover in each period (Forestry Commission England 2013).

2.3.2 Bat surveys

Bat boxes have been installed in Purbeck Forest since 1977 to provide roosting opportunities for bats, as commercial conifer plantations typically have limited roost sites (Borkin et al. 2011, Kirkpatrick et al. 2017a). The bat boxes are grouped into 22 'schemes' across five blocks of the forest. Each scheme consists of 18 boxes across six trees: three boxes per tree (facing North, South East, and South West) and are maintained or replaced as boxes degrade.

Since 1991 a census of the bats occupying the boxes has been conducted by Forestry England twice a year under licence, once pre-parturition (spring – usually May) and once post-parturition (late summer – usually September). In two forest blocks all schemes were surveyed in both censuses every year, in other forest blocks surveys were more variable but each scheme was surveyed at least once a year. During the surveys, bats were identified to species, aged

(immature, juvenile, adult), sexed and female reproductive state assessed (pregnant or not). Bats were also banded with a ring with a unique identifying serial number supplied by the Mammal Society, consistently from 1991 for schemes in two forest blocks, and during the 1990s and from 2014 onwards for the schemes in the other forest blocks.

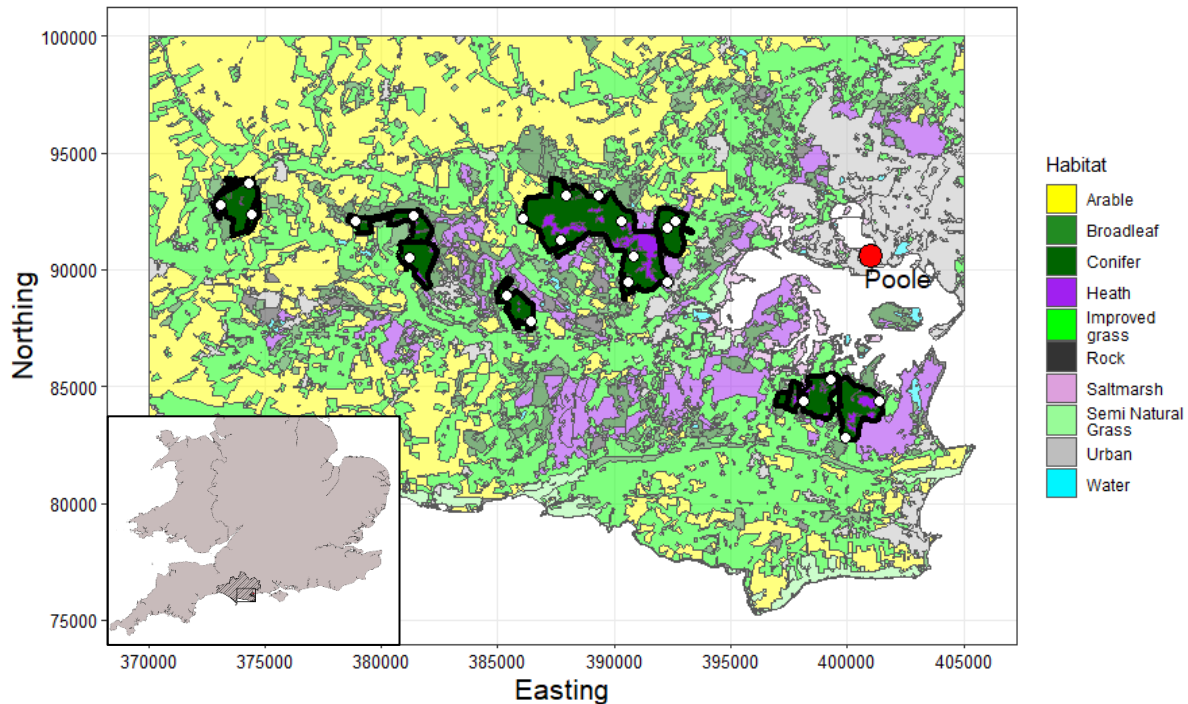


Figure 2.1: Map of the Purbeck Forest Bat Box project, showing simplified land cover from LCCM 2015 with boundaries of forest blocks (geographically distinct sections of forest defined by Forestry England) outlined in black and the location of 22 bat box schemes (white dots). Location of Dorset (hashed), and area covered in map (black box) are highlighted in the inset.

While data were collected on all species that are found in the boxes, this analysis focuses on the three most commonly found species/species groups; *Myotis nattereri*, *Plecotus auritus* and *Pipistrellus spp.* The *Pipistrellus spp.* group includes two species; *P. pipistrellus* and *P. pygmaeus* which only began to be recognised as separate species in 1997 (Barlow and Jones 1997) and so were not recorded separately at Purbeck until the mid-2000s.

2.3.3 Land cover change data

Land cover change data were extracted from the Land Cover Change Map (LCCM) dataset from the UK Centre for Ecology and Hydrology (UKCEH, Rowland et al. 2020). The LCCM dataset displays changes in land cover at a 25m resolution between two years, 1990 and 2015, across six main land cover groups: woodland (including conifer and broadleaf), grassland (including improved pastures and natural grass habitats such as heath), arable, freshwater,

urban and other (e.g. rock and sea). The simplified categories were selected by UKCEH to increase accuracy and increase the likelihood that mapped changes were real (Rowland et al. 2020). Additionally, some artefacts caused by differences in methods and technology between 1990 and 2015, particularly regarding the classification of upland, tidal, and aquatic cover, were corrected (Rowland et al. 2020).

To investigate the effects of woodland cover change at greater temporal resolution than offered by the LCCM dataset, and to distinguish the effects of change in different woodland types, higher resolution temporal data were additionally extracted from National Forest Inventory (NFI) Woodland Maps. NFI datasets are based on 25m resolution satellite imagery and include polygons of woodland over 0.5ha with a minimum of 20% canopy cover and are available at 5-year intervals from 1990 to 2010 (unpublished), and annually thereafter. The older NFI maps (1990-2000) do not differentiate between woodland types, whereas more recent NFI maps (2005 onwards) split woodlands into woodland types (e.g. broadleaf, conifer, mixed). Thus, to focus on the effects of changes in cover of different woodland types and to maintain a (largely) consistent temporal resolution, data from 2005, 2010, 2015 and 2019 were used (2020 NFI data was not used as bat surveys were not conducted during the Coronavirus lockdowns, Forestry Commission 2019).

2.3.4 Land cover change and long-term bat trend models

Overview

To investigate the effects of land cover change on bat population trends, firstly changes in bat abundance between 1990 and 2015 were calculated (hereafter: long-term bat trends) using generalised linear models. Secondly, land cover change between 1990 and 2015 around each bat box scheme was calculated using LCCM data. Finally, the impacts of land cover change on bat populations were modelled using the calculated long-term bat trends as dependent variables and the measured land cover change as independent variables. All modelling was conducted in R (R statistical language, version 4.2.2, R Core Team, 2022).

Calculating long-term bat trends

Long-term bat trends between 1990 and 2015 were calculated as the mean percentage change in bat abundance within each scheme per year using generalised linear models. For each species bat abundance was modelled as a function of year, scheme and their interaction (Bat Count ~ Year + Scheme + Year*Scheme). Counts for each species were the total number of bats found

across all boxes within a scheme in each survey. The interaction between year and scheme allowed the calculation of separate slopes for each of the 22 bat box schemes. Due to skewed data distributions negative binomial models were used to model *Pipistrellus spp.* trends and zero-inflated negative binomial models were used to model *M. nattereri* and *P. auritus* trends. As negative binomial coefficients measure expected change on the log scale, long-term bat trends (change in bat numbers/year) were calculated for each scheme as $(\exp(\text{model coefficient}) - 1) * 100$.

Bat population trends were not calculated for schemes where the species was never or rarely recorded across the whole period; this left 18 schemes for *P. auritus* (minimum N years present = 6), 22 schemes for *Pipistrellus spp.* (minimum N years present = 8) and 11 schemes for *M. nattereri*. (minimum N years present = 10).

Calculating long-term land cover change

Land cover change was calculated within four buffers of different sizes (radius: 500, 1000, 2000 and 3000m) around each bat box scheme (Fig. 2.2). The buffer scales were selected based on *a priori* ecological knowledge of the bat species' home ranges, and are scales at which roosting bats have previously been shown to respond to habitat composition (Boughey et al. 2011, Bellamy and Altringham 2015, Froidevaux et al. 2017a). Overlap of buffers between schemes was common at the larger scales (particularly 2000 and 3000m; mean % of each buffer overlapped with another 500m: 4.3%, 1000m: 22.4%, 2000m: 71.73%, 3000m: 87.63%), however analyses by Zuckerberg et al. (2020) indicate that this does not impact the independence of data. Additionally, all model residuals were tested for spatial autocorrelation using Moran's I through the R package 'DHARMA' (Hartig 2022), with none detected.

The amount of each land cover type present in each buffer was calculated using the zonal histogram tool in QGIS (QGIS Association, 2023). Change was then calculated as the amount of each land cover lost or gained by 2015 as a proportion of that land cover in 1990 (Equation 2.1). Where a land cover category was not present in 1990, a denominator of one was used to avoid division by zero.

$$2.1 \text{ Land Cover Change} = \frac{\text{Land Cover}_{2015} - \text{Land Cover}_{1990}}{\text{Land Cover}_{1990}}$$

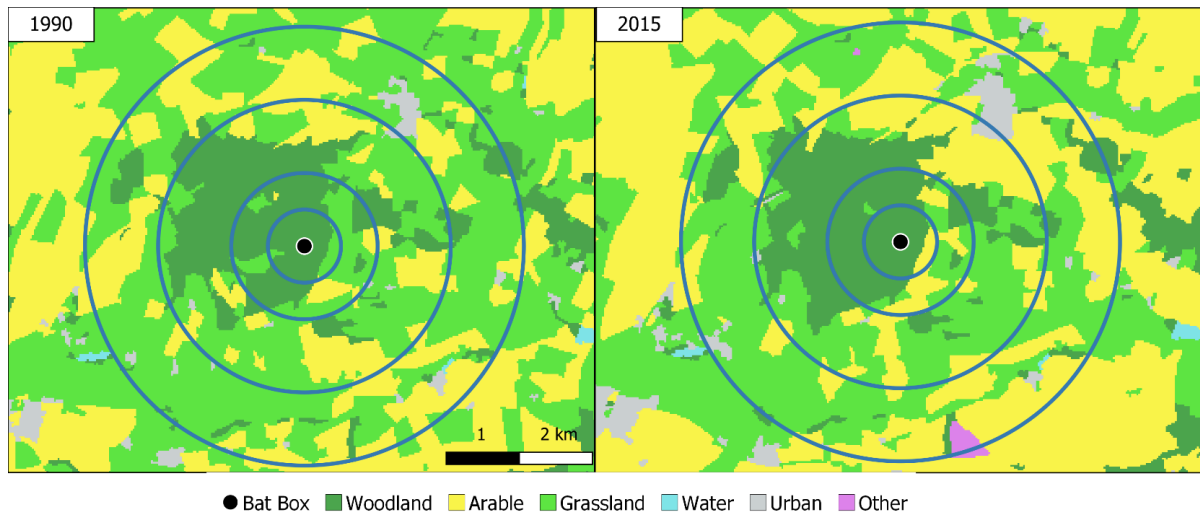


Figure 2.2: Example land cover change map comparing 1990 and 2015 land cover in the vicinity of one of the bat box schemes (black dot) and the 4 buffer sizes (blue circles) within which change was mapped. Changes between the two years include both felling and afforestation within the focal forest block, an increase in arable agricultural areas at the expense of pasture in the surrounding landscape, and the opening of an aggregate quarry to the South (classified as ‘Other’).

Effects of land cover change on long-term bat trends

To evaluate whether changes in land cover were associated with bat population trends, general linear models were fitted using the calculated long-term bat trends as response variables and the calculated land cover change as independent variables, with each bat box scheme as a replicate.

As measures of change at different scales were highly correlated, model comparison was used to select the spatial scale that explained the greatest variation in the bat trends. For each land cover category, separate linear models were run for each of the four scales, logging the variable to account for particularly high leverage datapoints where necessary. The scale which explained the greatest variance in bat trends (assessed using r^2) was then included in the overall model. While scale selection using univariate modelling ignores the possible effects of covariates and possible interactions which can both impact model selection and miss important ecological relationships, testing all permutations and interactions incurs high computational load and was unfeasible without overparametrising models with smaller sample sizes (Bellamy et al. 2020). Due to the limited coverage of the Freshwater and Other categories in this landscape these were not included in the land cover change models. A replicate set of models were also run including baseline land cover in 1990 to control for the effects of initial conditions in each area, but the overall conclusions were the same (Tables S2.3, S2.5 & S2.7).

2.3.5 Woodland cover change and short-term bat trend models

Overview

To investigate the effects of woodland cover change on bat population trends at a greater temporal resolution than available in the land cover change dataset, and to distinguish the effects of different woodland types, the above analysis was repeated over shorter periods with the NFI data. Firstly, changes in bat abundance were calculated across three 5-year intervals between 2005 and 2019 to match the availability of NFI data (hereafter: short-term bat trends). Secondly, total woodland cover change and cover change of various woodland types around each bat box scheme were calculated across these same three intervals (using the historical and current NFI map data). Finally, the impacts of woodland cover change on bat populations were modelled using the calculated short-term bat trends as dependent variables and the woodland cover change measures as independent variables.

Calculating short-term bat trends

Changes in bat abundance over 5 year intervals ‘short-term bat trends’ were calculated as % change in bat abundance in each scheme per year using generalised additive models (GAMs) in R package ‘mgcv’ (Wood 2011, Barlow et al. 2015). For each species bat abundance over time was modelled as a function of year, scheme and their interaction, with a smoothed term for Year (Bat Count ~ smoothed(Year*Scheme) + Scheme). One GAM was run on data for the entire period (2005 - 2019) to reduce the likelihood of calculated 5-year trends being influenced by high leverage counts at the start or end of an interval. The degree of smoothing was specified as the number of intervals-1. Negative binomial models were used to model all species.

As previously, bat population trends were not calculated for schemes where the species was not present at all or only recorded sporadically within this period; reducing the number of schemes for *P. auritus* to 10 (min years present = 4), while other species/groups remained unchanged.

Short-term bat trends (% change in bat numbers/year) were calculated for each scheme as the percentage change in the number of bats predicted by the model from the start to the end of the interval divided by the number of years in the interval (Barlow *et al.*, 2015, Equation 2.2 example using 2005-10 interval).

$$2.2 \text{ Population change} = \frac{\text{Predicted bats}_{2010} - \text{Predicted bats}_{2005}}{\text{Predicted bats}_{2005}} \times 100 \div (2010 - 2005)$$

Calculating short-term woodland cover change

As with the land cover change previously, woodland cover change (total and for each woodland category) was calculated within four buffers around each bat box scheme (radius: 500, 1000, 2000 and 3000m). The amount of each woodland type present in each buffer was calculated using the ‘sf’ R package (Pebesma 2018). Change was then calculated as the amount of each woodland type lost or gained by the end of the interval as a proportion of the cover of that woodland type at the start of the interval. Where a woodland category was not present at the start of an interval, a denominator of one was used to avoid division by zero (Equation 2.3).

$$2.3 \text{ Woodland cover change} = \frac{Cover_{2010} - Cover_{2005}}{Cover_{2005}}$$

Effects of woodland cover change on short-term bat trends

To evaluate the effects of woodland cover change on bat population trends, general linear models were fitted using the calculated ‘short-term bat trends’ as response variables and the calculated woodland type cover change as independent variables, with each scheme in each interval being a replicate. Due to skewed distributions of the short-term bat trends for *P. auritus* and *M. nattereri*, they were log transformed within the model.

As before, model comparison was used to select the spatial scale that explained the greatest variation in the data. For each woodland category in the NFI map, separate linear models were run for each of the four scales and the scale which explained the greatest variance in bat trends (measured using r^2) was then included in the overall model. Only changes in ‘total woodland’, ‘broadleaf’, ‘conifer’ and ‘felled’ categories were included in the models, as other woodland categories comprised only small areas of the forest and changed very little over the period. The felled category is defined in the NFI as “*areas of woodland where the trees have been harvested or felled. Stumps or felled trees may be visible and there may be long heaps of felling debris (windrows)*” and can be interpreted as ‘recently’ felled areas. Conifer loss doesn’t always equate to increases in felled areas over the same period because areas can be restocked or reclassified as another woodland or land cover type within the 5-year interval (correlations between these two variables were $\rho \leq 0.53$ across analysis scales). Additionally, felled areas may provide foraging habitat for some bat species (Kirkpatrick et al. 2017a). For these reasons both land cover types were included in the analysis.

Two replicate sets of models were also run. One including baseline land cover in 1990 to control for the effects of initial conditions in each area, with broadly similar conclusions (Tables S2.4, S2.6 & S2.8). The other included a 5-year time lag to investigate whether bat populations responded more to older than contemporary land use changes, conclusions were broadly similar except for in *Myotis spp.* (Table S2.9).

2.4 Results

2.4.1 Long-term bat population trends overview

Between 1990 and 2015, *P. auritus* counts decreased significantly across Purbeck Forest, and this decrease was largely consistent across the individual bat box schemes – although for some this was non-significant (Figs. 2.3 and S2.3). Conversely *M. nattereri* counts increased significantly across the whole forest, although there was some variation across schemes with some increasing and others showing no significant change (Figs. 2.3 and S2.3). *Pipistrellus spp.* counts similarly increased significantly across the whole forest across the entire period, but numbers fluctuated between 1995 and ~2012 after which they stabilised (Fig. S2.3) and numbers recorded at each bat box scheme tended to increase (Fig. 2.3).

2.4.2 Land cover change overview

Across all bat box schemes and the entire study period, land cover at the smallest scales was dominated by woodland (>70% within 500m) and grassland (>20% within 500m; Table S2.1). The current National Forest Inventory maps (available from 2005 onwards) show that the woodland was primarily coniferous (40-70% depending on scale and interval, Table S2.2). Between 1990 and 2015 woodland cover decreased at all scales, largely replaced by various grass habitats (which in the LCCM dataset included heathland) and to a lesser extent arable habitats at larger scales (Table S2.1). Reflecting the woodland composition, the majority of woodland loss was coniferous, while broadleaf cover remained mostly consistent (although there was a small decrease at the 1000m scale and above between 2015 and 2019, largely in areas outwith the Purbeck Forest; Table S2.2). At larger scales arable cover increased at the expense of grass cover as agricultural patterns changed while urban cover was generally small

and overall increased a small amount at every scale (Table S2.1). Changes in land cover types around each bat box scheme followed these general patterns but varied in magnitude (Figs. S2.1 and S2.2).

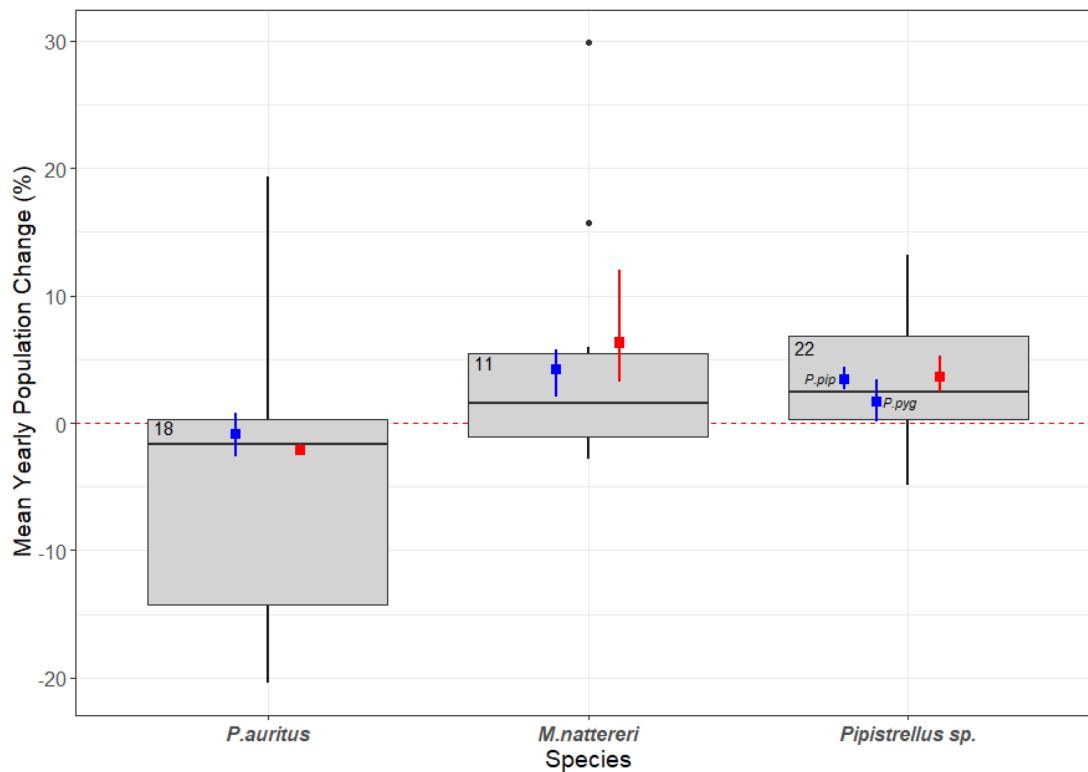


Figure 2.3: Boxplot of population trends for bat species across bat box schemes from 1991-2015, numbers indicate N schemes included. Red squares and error bars display total population growth across all schemes in the forest (predicted from GAMs, Fig. S2.3). Blue squares and error bars display national level trends of each species between 1999 and 2023 (separately for *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*) extracted from the National Bat Monitoring Programme (Bat Conservation Trust 2024). Data were taken from NBMP field surveys for *Pipistrellus* spp. and hibernation surveys for *P. auritus* and *M. nattereri*. (NBMP roost surveys are only considered reliable for *P. auritus*).

2.4.3 Land cover change effects on bat trends

Pipistrellus spp. trends across the bat box schemes were associated with land cover change across a range of scales with significant relationships at smaller scales (500 and 1000m). Slower growing or negative population trends in *Pipistrellus spp.* were observed in bat box schemes where grass cover increased within 500m between 1990 and 2015 (Table 2.1; Fig. 2.4). Similarly, short-term *Pipistrellus spp.* trends were negative or slow growing where conifer cover decreased within 1000m (Fig. 2.5).

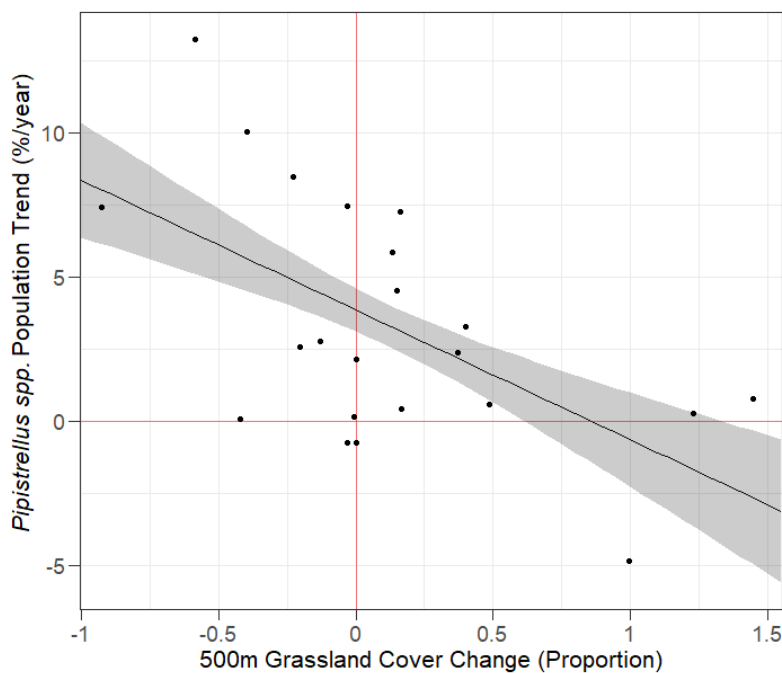


Figure 2.4: Over the long-term, only *Pipistrellus spp.* population trends were associated with land-use change, with populations growing slower or declining where grassland cover increased and growing faster when they decreased. The dark line represents predicted relationship from the linear model with 95% confidence intervals in grey. Datapoints represent each bat box scheme. Red lines indicate 0 population change (horizontal) and 0 land cover change (vertical) dividing into quadrants in which top left = increasing populations with declining land cover, top right = increasing populations with increasing land cover, bottom left = decreasing populations with declining land cover, bottom right = decreasing populations with increasing land cover

Long-term *P. auritus* trends were associated with land cover change at small spatial scales for woodland and arable, but at larger scales for grass and urban. Short-term trends mostly responded to land cover change over larger spatial scales, although this may reflect limited woodland cover changes at smaller scales between 2005 and 2019 (Fig. S2.2). The only significant relationship between long-term *P. auritus* trends and land cover change was a negative response to urban change at the 500m scale, with increasing numbers where urban

cover decreased and vice-versa. However, this relationship was largely driven by the only 6 (of 18) landscapes where urban cover had changed. When 500m urban was replaced by 2000m urban (the next best fitting scale) to ascertain the effect of these high leverage points, the relationship became non-significant (Table 2.1); this also improved model diagnostic plots. Short-term *P. auritus* trends were slower growing or negative in bat box schemes where there was conifer loss at the 3000m scale and increased where felled cover increased at 3000m (Table 2.1, Fig. 2.5). However, the significance of the latter association was driven by one high-leverage data point and became non-significant when it was removed.

Myotis nattereri trends were most associated with land cover change at large scales (2000 and 3000m) over both the long-term (except arable) and short-term (Table 2.1). *Myotis nattereri* numbers increased faster where woodland cover increased, but slower where arable, grassland and urban cover increased, however none of these relationships were significant (Table 2.1). These models were run on limited data points (as *M. nattereri* only occupied a subset of the schemes, N = 11) leading to low model power as well as outlier issues. Shorter-term *M. nattereri* trends also did not respond significantly to any changes, however these models indicated the opposite relationship with woodland change, with population trends decreasing in areas where conifer, broadleaf and total woodland cover increased (and vice versa, Table 2.1).

Table 2.1: Model coefficients for the effects of long-term land cover change and short-term woodland cover change on bat trends. Significant ($p < 0.05$) terms are highlighted in bold, ^a indicates non-robust significant relationship driven by one outlier datapoint

		Land cover	Estimate	Std. Error	P-value
<i>Pipistrellus sp.</i>	Long-term land cover	Wood_3000	14.23	12.38	0.266
		Arable_500 (logged)	-0.41	0.35	0.260
		Grass_500	-4.50	1.65	0.015
		Urban_3000	2.25	2.29	0.338
	Short-term woodland	TotalWood_1000	108.90	212.77	0.611
		Conifer_1000	37.86	16.44	0.025
		Broadleaf_2000	-102.46	56.17	0.073
		Felled_20000	0.05	0.18	0.770
<i>Plecotus autius</i>	Long-term land cover	Wood_500	-2.13	24.75	0.933
		Arable_500 (logged)	1.10	1.35	0.432
		Grass_2000	-3.53	19.68	0.860
		Urban_2000 (logged)	-7.66	6.88	0.286
	Short-term woodland	TotalWood_2000	38.66	34.64	0.275
		Conifer_3000	9.32	2.66	0.002
		Broadleaf_3000	-14.91	11.26	0.198
		Felled_3000 (logged)	0.57	0.20	0.008^a
<i>Myotis nattereri</i>	Long-term land cover	Wood_2000	103.92	97.59	0.328
		Arable_500	-8.56	9.10	0.383
		Grass_3000	-37.83	-1.00	0.366
		Urban_3000	-15.34	-1.31	0.238
	Short-term woodland	TotalWood_3000	-5.38	21.09	0.800
		Conifer_2000	-2.33	2.83	0.419
		Broadleaf_3000	-6.80	9.02	0.457
		Felled_2000 (logged)	0.18	0.16	0.249

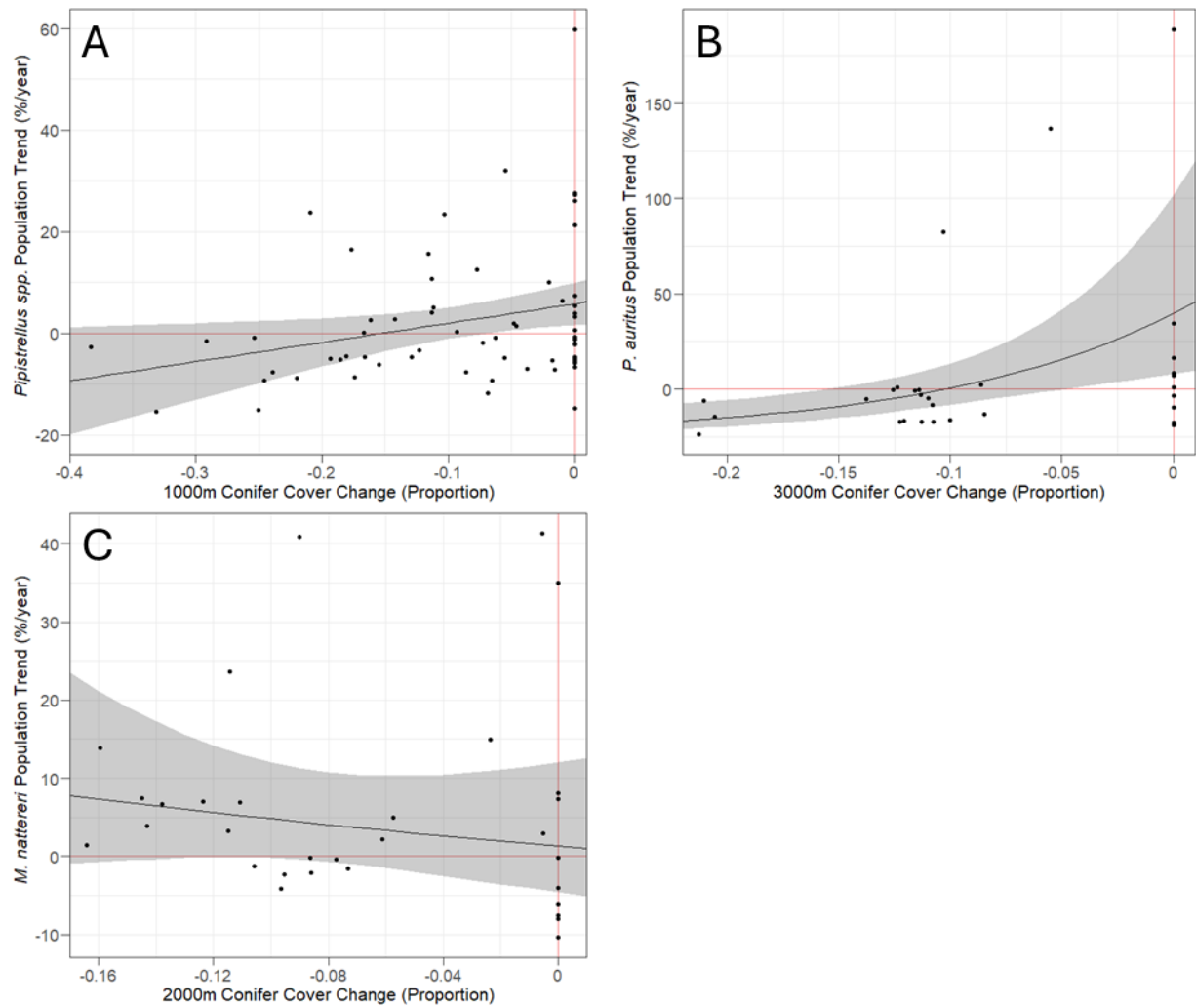


Figure 2.5: Over the short term *Pipistrellus* spp. (A) and *P. auritus* (B) but not *M. nattereri* (C) population trends were negatively associated with conifer loss. Dark lines represent predicted relationships from linear models with 95% confidence intervals in grey. Datapoints represent a bat box scheme/interval replicate. Red lines indicate 0 population change (horizontal) and 0 land cover change (vertical) dividing into quadrants in which top left = increasing populations with declining land cover, top right = increasing populations with increasing land cover, bottom left = decreasing populations with declining land cover, bottom right = decreasing populations with increasing land cover

2.5 Discussion

In this study, long-term monitoring data from bat boxes over ~30 years showed that species responded to land-use change at a range of spatial and temporal scales. There was an overall pattern of negative responses to the loss of woodland, predominantly coniferous plantations, with limited impacts of other land cover changes. This is in line with studies indicating that woodland cover is beneficial to bats for both roosting and foraging activity. However, positive effects of woodland tend to be limited to broadleaf cover with coniferous plantations commonly associated with negative impacts (Boughey et al. 2011, Bellamy et al. 2013, 2020, Bellamy and Altringham 2015). However, Froidevaux et al. (2021) found that bats' preferential use of deciduous or coniferous stands depended on the makeup of landscape level woodland, suggesting a complex interplay of landscape and local woodland type. The results of this study demonstrate that, where it comprises the majority woodland cover, conversion of conifer to open habitats can have a negative effect on woodland bats, in line with other studies of plantation felling impacts (Borkin et al. 2011). In this study, the proportion of broadleaf woodland cover was small, and remained consistent over the study period, so it is not possible to draw inferences about how bat populations respond to changes in broadleaf cover.

Between species, trends varied in the temporal and spatial scale at which they responded to the change in total woodland or coniferous plantation cover. *Pipistrellus spp.* population trends were negatively associated with loss of conifer cover at a relatively small scale (1000m) over the short-term (5 years). Additionally, over the long-term (25 years) they responded negatively to increased grassland cover at the 500m scale; much of the increase in grasslands (including heath) at this scale was caused by the loss of woodland, suggesting an indirect response to reduced tree cover in the vicinity of the bat boxes.

Pipistrelles tend to avoid foraging in large open areas (especially *P. pygmaeus*) preferring the shelter of hedgerows, woodland edges and interiors (Nicholls and Racey 2006, Kirkpatrick et al. 2017a). Thus, the negative response to conifer loss and related increase in grassland may be driven by the loss of foraging areas or due to changes in woodland structure leading to increased exposure to wind or other adverse weather conditions or reduced shelter from predators near the roost. While both *P. pygmaeus* and *P. pipistrellus* activity have previously been found to be highest in felled areas and to increase after small-scale felling, no effect of felled cover change was found (Kirkpatrick et al. 2017a, 2017b). The positive effects of felled areas tend to

be short lived (<16 months, Kirkpatrick et al. 2017a) and the negative response to woodland loss in this study suggests that when the area remains unstocked and converts to open habitat the benefits disappear and are eventually overtaken by the negative effect of habitat loss.

Plecotus auritus show a strong preference for broadleaf habitats even when conifer habitats are available, both in terms of time spent foraging (Swift and Racey 1983, Roswag et al. 2015, but see Froidevaux et al. 2021) and roost selection (Bellamy et al. 2013, Bellamy and Altringham 2015). The presence of a large *P. auritus* population within the plantations at the start of the study period is thus notable and adds evidence that conifer forests can sometimes provide habitat for this species given roost availability and where a complex habitat structure is allowed to develop (Benzal 1991, Cook et al. 2023). *Plecotus auritus* population trends were not significantly related to land cover change in the long-term analysis. In contrast, the finer temporal resolution analysis indicated that over short-term periods, *P. auritus* trends were negatively associated with conifer loss. This could be driven by loss of foraging areas as the species is rarely recorded feeding outside woodland, especially within 500m of a roost (Swift and Racey 1983, Razgour et al. 2011a, Roswag et al. 2015).

There are a few possible reasons that the relationships between short-term *P. auritus* trends and woodland cover change did not translate to the longer-term models. Firstly, there was a bias towards large changes in population size at the start of the 25 years, with large decreases and complete abandonment of some bat box schemes by *P. auritus* populations between 1990 and 2000 or 2005, rather than a steady decline over the whole period (Fig. S2.3). As a result, the land cover change measured between 1990 and 2015 may not reflect what land cover changes occurred during this crucial time. Additionally, measures of woodland change in this period encompass total woodland loss, making it hard to disentangle separate effects of conifer and broadleaf change.

Myotis nattereri trends were not significantly related to land cover change in the long- or short-term. Over the long-term, populations generally grew at a slower rate where more conifer cover had been lost, but this effect was not significant, and the numbers recorded across the entire site continued to grow despite the overall loss of conifer in the area. Previous studies have found preferential selection of heath as a foraging habitat and thus the addition of heath habitat may be moderating impacts of conifer loss (Mordue et al., 2023), although this is not reflected in these models. The long-term analysis was restricted by small sample sizes which resulted in large standard errors and reduced model power. However, in the short-term analyses woodland

cover change explained very little variation in trends across all scales (Fig. S2.5), and model coefficients were small (particularly in comparison to other species) suggesting a genuine lack of response. *Myotis nattereri* populations grew at a fairly consistent rate over the whole period, similar to, but at a higher rate than, national trends (Figs. 2.3 and S2.3), suggesting that they may be robust to short-term habitat changes and disturbances. Additionally, it is possible that the schemes not used by *M. nattereri* had different land cover change patterns that limit population growth/establishment at these sites but this would not have been picked up in this analysis. That the population is increasing in the conifer plantation adds to evidence that this species will readily use suitable conifer plantations (Mortimer 2006, Kirkpatrick et al. 2017a, Cook et al. 2023) and wider habitats, including heath (Mordue et al. 2023) as well as broadleaf woodland which it has traditionally been considered reliant upon (Smith and Racey 2008, Boughey et al. 2011, Roswag et al. 2015).

Unexpectedly, all species' models had negative coefficients for the effect of broadleaf cover change on population trends (indicating higher population trends where it was lost and lower where it was gained). None of these relationships were significant (although it was marginal for *Pipistrellus spp.*) and the proportion of broadleaf woodland cover was small, and remained fairly consistent over the study period, so drawing inferences from this result should be treated with caution. However, as the direction of this response was largely consistent across scales and species and given the importance of broadleaf woodland for bat species in the UK it bears some discussion.

Firstly, the largest loss of broadleaf cover in this analysis occurred in the most recent interval (2015-2019) and thus the negative impacts of this on populations may not yet be realised due to time lags. Additionally, any effect from recent planting of broadleaf trees in other parts of the forest will take a considerable time to exert any effects, as woodland habitats take a long time to develop, and these areas are at most 5 years old. Studies of bird responses to woodland creation have suggested that there is an 11-year time lag in generalist bird trends responding to increased woodland cover, while woodland specialists can take much longer (Watts et al. 2020). When the models were repeated with a 1 step time lag (e.g. bat trend 2010-2015 ~ broadleaf change 2005-2010) the coefficient became positive for *Pipistrellus spp.* but remained non-significant and did not change for *P. auritus* or *M. nattereri* (Table S2.9). Observations made by Forestry England staff in Purbeck indicate that *P. auritus*, in particular, are now most commonly found in schemes near larger pockets of mature broadleaf woodland (M. Warn, pers.

comm.). Additionally, models controlling for baseline land cover found positive (although non-significant) effects of original broadleaf cover on *P. auritus* and *M. nattereri* trends (Tables S2.6 and S2.8), suggesting that as this woodland matures, positive effects of increased broadleaf woodland for this species would be expected in the future.

Factors other than changes in land cover may also impact bat populations. Changes in habitat configuration connected to land cover changes, e.g. increased edge habitat provided by small-scale felling could also benefit or hinder bat species. Given that *M. nattereri* populations increased over the same period that *P. auritus* populations decreased (Fig. 2.3), the possibility of competition between the species is a consideration. However, a similar divergence in trends is seen at the national level and despite similarities in their diets and foraging ecology there are differences which allow them to coexist at small scales in other areas (Razgour et al. 2011a, Roswag et al. 2015). Competition for roost space is possible, however of the 18 bat boxes at each scheme, bats are only ever found in a small number during each survey, suggesting that limited space is not driving competition. Overall population trends for the whole forest are similar to those seen at a national level (Bat Conservation Trust 2024). This suggests that wider landscape, climate or population recovery dynamics may be driving general trends, but that local land cover changes can moderate these patterns and contribute to the variation in trends between each bat box scheme.

Measuring land cover change has a number of challenges. Errors in classification can lead to both changes being detected where there are none and real change being missed, and error rates in change are greater than in land cover maps of a particular year as misclassifications become compounded (Fuller et al. 2003). The UKCEH land cover change map is designed to minimise these issues but to do so, loses some specificity in habitat types. For example, the grouping of woodland categories may have missed important nuances in bat responses to land cover change, while grouping improved (pasture) grassland with various forms of semi-natural grassland made it difficult to directly investigate the impact of heathland expansion, the largest land-use change in the forest, on bat trends.

Additionally, selecting an appropriate temporal scale at which to investigate relationships between habitat changes and species trends can be challenging. Long-term datasets can miss complexity (e.g. non-linearity or cyclical patterns) in both population and land cover changes, whilst shorter-term datasets may not be as suited to analysing small consistent changes such as the *M. nattereri* models where populations changed at a fairly steady rate over time or where

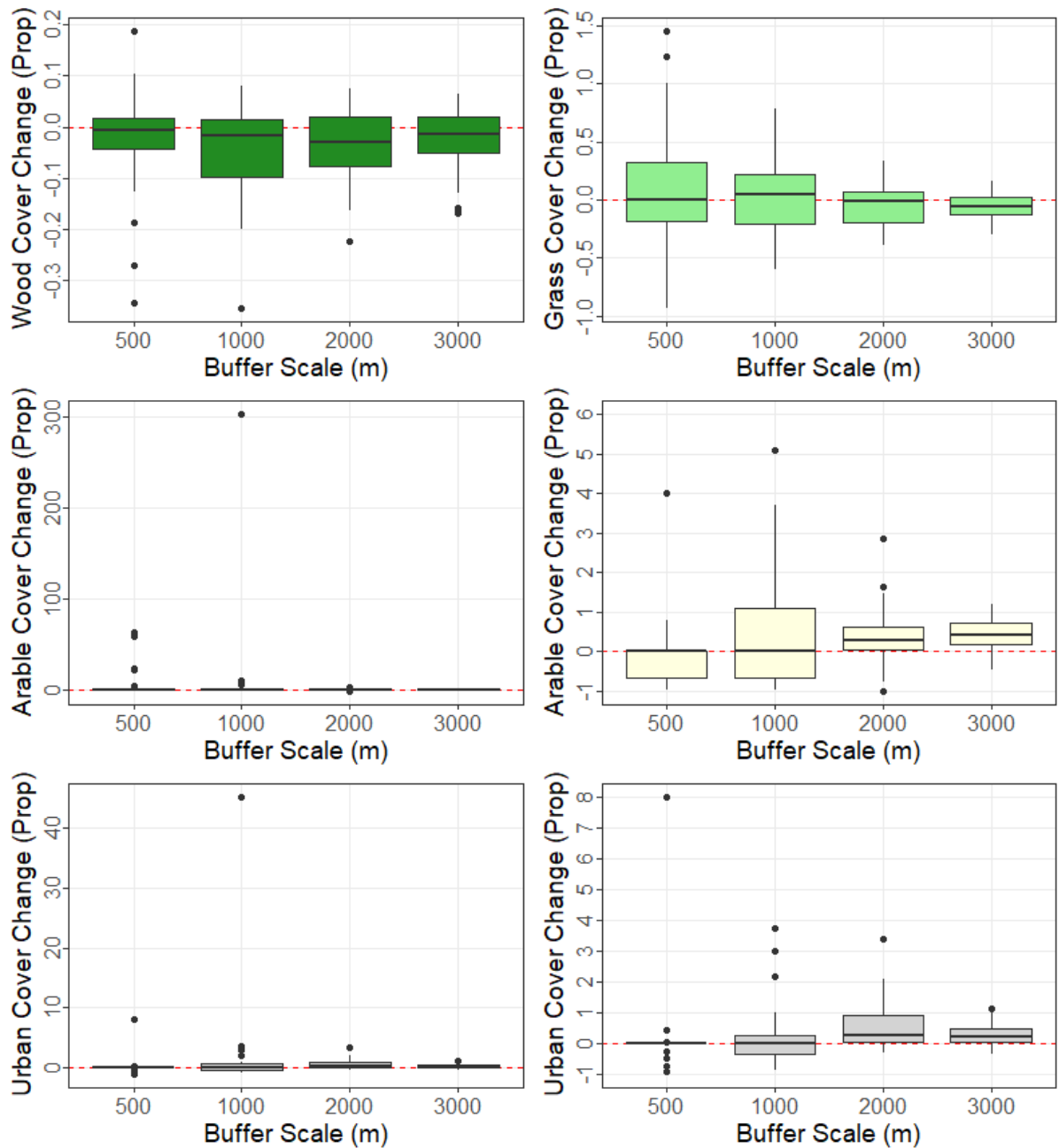
land cover change is gradual and incremental. There is also an inherent assumption that changes are happening on the same timescales in both land cover and species populations, which may not be the case e.g. in the *P. auritus* analyses where population changes were concentrated early in the study period. Similarly, time lags in population responses to land cover changes can also impact the suitability of temporal scales selected for analysis; investigating this was not possible for the long-term analysis as the LCCM only covered change in one interval. For the short-term analysis adding a time lag had limited impacts for *Pipistrellus spp.* and *P. auritus* results but *M. nattereri* displayed significant negative responses to conifer loss but also to total woodland gain (Table S2.9).

In recent years, the availability of land cover data has increased, for example NFI maps have been released yearly since 2011 and UKCEH land cover maps have been released almost yearly since 2015. As data availability increases, methods such as time-series-analyses that have previously been used to study climate change impacts on population trends in bats (Froidevaux et al. 2017a, Law et al. 2020, Ancillotto et al. 2021) as well as climate and land cover change impacts on bird trends (Eglington and Pearce-Higgins 2012, Rigal et al. 2023) could also be used. These methods avoid the need to select a temporal scale and to calculate land cover change, with the associated risk in errors; they are additionally able to incorporate modelling time lags (Froidevaux et al. 2017a, Ancillotto et al. 2021) and causality (Rigal et al. 2023).

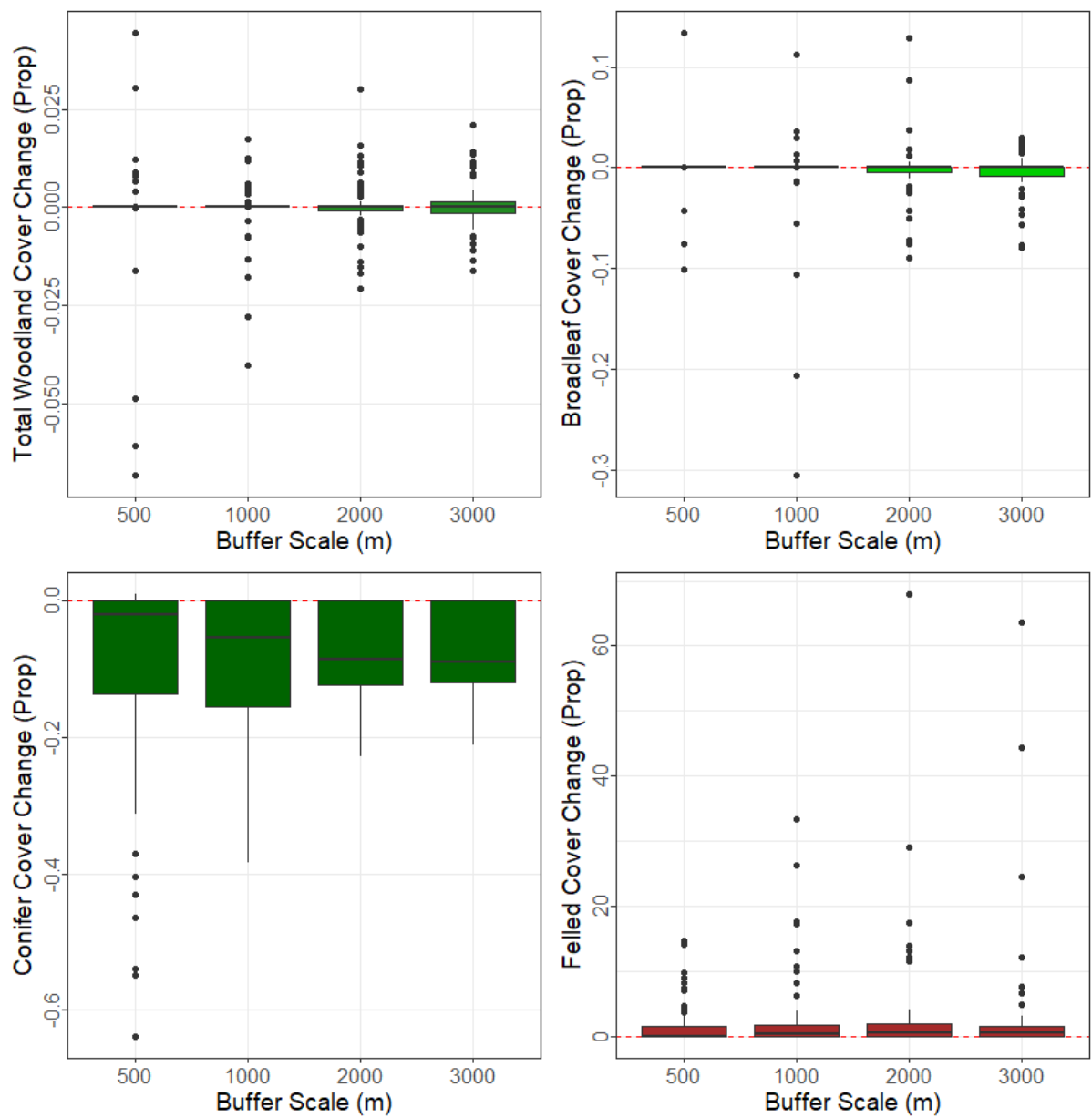
This study focussed on bat trend associations with land cover changes that are related to the management of conifer forests and the restoration of open habitats within them. It was found that conifer replacement with other important but structurally different habitats (in this case heathland) can have negative impacts on bats, especially when broadleaf cover is low. These results demonstrate the trade-offs that can result from habitat restoration and the lack of a single approach that can deliver conservation gains for all species. These dynamics are important to understand as conifer forests account for 60% of woodland in the UK (Mason 2007) and thus make up a large proportion of available bat habitat. Current tree planting initiatives as a climate change mitigation strategy are likely to increase conifer planting as they are fast growing and are perceived to sequester more carbon than broadleaf woodlands in the short-term (Burton et al. 2018). Changes to conifer forests are however only one aspect of the land cover changes facing bats in the United Kingdom and globally in coming years, and similar analyses of bat trends from bat box schemes, or other long running and location specific bat monitoring schemes, would complement the results found here and widen our understanding of how bat

populations will respond as landscapes continue to change, especially as we try to balance conservation aims of multiple species.

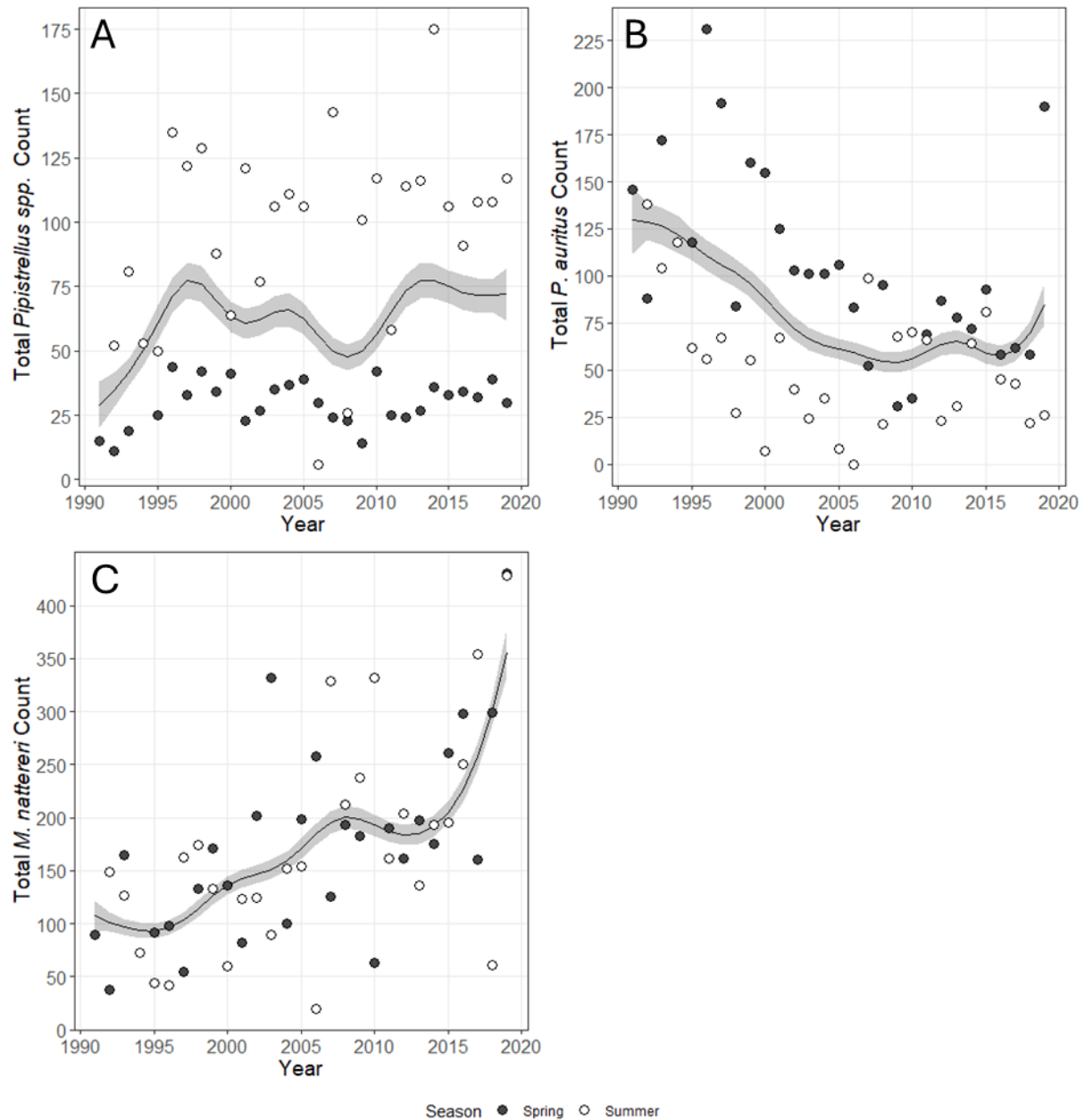
Supplementary Materials 2.1: Additional information on land cover changes and bat trends



Supplemental Figure 2.1: Boxplots of long-term (1990-2015) land cover change at each bat box scheme at different buffer scales both arable and urban change are shown with full and truncated axes to ease visualisation



Supplemental Figure 2.2: Boxplots of short-term (2005-2019) woodland type cover change at each bat box scheme at different buffer scales



Supplemental Figure 2.3: Total counts of A) *Pipistrellus* sp., B) *Plecotus auritus* and C) *Myotis nattereri* across Purbeck Forest recorded in each survey (spring surveys – filled circles, summer surveys -unfilled circles) and population trend calculated by GAMs (black line) with 95% confidence intervals (shaded grey area).

Supplemental Table 2-1: Summary of total land cover measured from LCCM around the bat box schemes at each scale in 1990 and 2015. Values represent percentage of land covered by each habitat

Scale	Percent Land Cover							
	Woodland		Grass		Arable		Urban	
	1990	2015	1990	2015	1990	2015	1990	2015
500	73.5	71.3	21.8	24.4	2.9	3.1	1.2	1.2
1000	54.7	52.2	35.8	37.3	6.0	7.3	1.9	2.0
2000	33.3	32.3	48.5	46.7	11.5	14.2	2.7	2.9
3000	25.3	24.8	51.3	46.7	14.5	19.1	3.3	3.6

Supplemental Table 2-2: Summary of total woodland and woodland type cover from combined buffers around all the bat box schemes, measured from the NFI at 5 year intervals between 1990 and 2019. Values represent percentage of land covered by each habitat. TW = Total Woodland cover, Con = Coniferous cover, BL = broadleaf cover, other categories making up small areas of woodland not included

		Percent Land Cover														
		1990	1995	2000	2005			2010			2015			2019		
		TW	TW	TW	TW	Con	BL	TW	Con	BL	TW	Con	BL	TW	Con	BL
Buffer Scale	500	73.3	73.3	73.3	71.1	48.6	8.5	71.1	48.6	8.5	71.0	43.8	8.5	70.6	36.3	8.5
	1000	55.1	55.1	55.1	53.6	32.7	9.3	53.6	32.7	9.3	53.6	29.2	9.3	53.5	25.0	9.1
	2000	34.5	34.5	34.4	33.9	18.3	9.9	33.9	18.3	9.9	34.0	16.6	9.9	33.9	14.5	9.7
	3000	26.7	26.7	26.6	26.3	13.3	9.3	26.4	13.3	8.9	26.5	12.0	8.9	26.5	10.4	8.8

Supplementary Materials 2.2: Models Controlling for baseline land cover

To determine whether initial land cover conditions impacted bat trends as well as land cover change, models were repeated with the addition of baseline land cover at the beginning of each interval (1990 for long-term models or 2005, 2010, 2015 for short-term models). Where sufficient datapoints allowed, both baseline cover and cover change were included, and the scale for baseline cover matched the scale chosen for cover change during previous scale selection. Where limited data caused issues with collinearity when running full models, the scale and measure (baseline or change) that explained the most variation for each land cover were selected. Baseline land cover was measured as hectares in each buffer using QGIS and the ‘sf’ package in R (Pebesma 2018). Variables were standardised to allow comparison of effect sizes as baseline and change variables were measured on different scales.

Pipistrellus spp.

For woodland and arable, baseline land cover had the biggest effects on long-term *Pipistrellus* spp. trends, for grassland and urban land cover change had the biggest effects. Arable cover change effects on population trends changed direction but remained non-significant. All other land cover change effects matched the directions of those in models without baseline measures but grass cover change became marginally non-significant.

For conifer and broadleaf, land cover change had larger effects on short-term *Pipistrellus* spp. trends than baseline land cover (vice-versa for woodland and felled). All land cover change effects matched the directions those in models without baseline measures but conifer change became marginally non-significant and broadleaf change became significant.

Supplemental Table 2-3: Standardised coefficients for models of baseline land cover and land cover change and long-term Pipistrellus spp. trends, significant ($p < 0.05$) terms are highlighted in bold, marginally non-significant terms are italicised

Land cover	Estimate	Std. Error	P-value
Wood_3000_Change	0.02	1.20	0.985
Wood_3000_Baseline	-0.67	0.93	0.482
Arable_500_Change (logged)	0.40	0.29	0.775
Arable_500_Baseline	1.38	1.14	0.247
<i>Grass_500_Change</i>	<i>-2.07</i>	<i>-1.77</i>	<i>0.100</i>
Grass_500_Baseline	-0.30	-0.33	0.747
Urban_3000_Change	1.30	1.09	0.294
Urban_3000_Baseline	0.66	0.60	0.562

Supplemental Table 2-4: Standardised coefficients for models of baseline land cover and land cover change and short-term *Pipistrellus* spp. trends, significant ($p < 0.05$) terms are highlighted in bold, marginally non-significant terms are italicised

Land cover	Estimate	Std. Error	P-value
Total_Wood_1000_Change	1.26	1.48	0.151
Total_Wood_1000_Baseline	-4.10	2.82	0.401
<i>Conifer_1000_Change</i>	<i>3.82</i>	<i>1.92</i>	<i>0.051</i>
Conifer_1000_Baseline	0.02	2.82	0.996
Broad_2000_Change	-3.93	1.55	0.014
Broad_2000_Baseline	-1.32	1.75	0.454
Felled_1000_Change	1.62	1.96	0.41
Felled_1000_Baseline	-3.00	1.97	0.13

Plecotus auritus

For woodland and grass, baseline land cover had the biggest effects on long-term *P. auritus* trends, and the direction of effect of land cover changed but remained non-significant. For urban and arable, land cover change had the biggest effects and land cover change effects matched the directions those in models without baseline measures but urban change became marginally non-significant.

Supplemental Table 2-5: Standardised coefficients for models of baseline land cover and land cover change and long-term *P. auritus* trends, marginally non-significant terms are italicised

Land cover	Estimate	Std. Error	P-value
Wood_3000_Change	0.73	2.30	0.758
Wood_3000_Baseline	-2.85	3.16	0.391
Arable_500_Change (logged)	3.78	3.53	0.311
Arable_500_Baseline	2.40	2.61	0.381
Grass_500_Change	0.30	2.83	0.917
Grass_500_Baseline	-2.40	2.23	0.310
<i>Urban_500_Change (logged)</i>	<i>-6.31</i>	<i>2.88</i>	<i>0.056</i>
Urban_500_Baseline	-2.42	2.51	0.361

Baseline land cover measures were selected over land cover changes for all woodland types except conifer for short-term *P. auritus* models. Despite this, baseline cover coefficients were small, especially in comparison to conifer change. Similarly to non-baseline models, there was a positive response to conifer change, though this became non-significant. Additionally, there was a marginally significant negative response to baseline felled cover, suggesting an aversion to open areas, or possible time lags in responses to conifer change.

Supplemental Table 2-6: Standardised coefficients for models of baseline land cover and land cover change and short-term P. auritus trends, significant ($p < 0.05$) terms are highlighted in bold. Due to smaller numbers of data points and issues with collinearity when running full models, the scale and measure (baseline or change) that explained the most variation for each land cover were selected

Land cover	Estimate	Std. Error	P-value
Total_Wood_500_Baseline	-0.12	0.17	0.472
Conifer_3000_Change	0.20	0.18	0.265
Broad_2000_Baseline	0.003	0.005	0.444
Felled_3000_Baseline	-0.01	0.004	0.049

Myotis nattereri

For woodland and arable, cover change explained the most variation in *M. nattereri* trends but for urban and grass, baseline cover explained the most variation. However, all relationships remained non-significant.

Supplemental Table 2-7: Standardised coefficients for models of baseline land cover and land cover change and long-term M. nattereri trends, significant ($p < 0.05$) terms are highlighted in bold. Due to reduced numbers of data points and issues with collinearity when running full models, the scale and measure (baseline or change) that explained the most variation for each land cover were selected

Land cover	Estimate	Std. Error	P-value
Wood_2000_Change	0.14	3.16	0.965
Arable_500_Change	-5.59	2.99	0.111
Grass_1000_Baseline	-6.92	3.62	0.104
Urban_3000_Baseline	-1.33	3.44	0.712

Baseline land cover measures were selected over land cover changes for all woodland types except conifer for short-term *M. nattereri* models. Similarly to non-baseline models, there was a negative response to conifer change, though this became significant. The directions of baseline effects differ from those of change effects in non-baseline models but they remain non-significant.

Supplemental Table 2-8: Standardised coefficients for models of baseline land cover and land cover change and short-term M. nattereri trends, significant ($p < 0.05$) terms are highlighted in bold. Due to smaller numbers of data points and issues with collinearity when running full models, the scale and measure (baseline or change) that explained the most variation for each land cover were selected.

Land cover	Estimate	Std. Error	P-value
Total_Wood_500_Baseline	0.09	0.12	0.459
Conifer_2000_Change	-0.36	0.14	0.013
Broad_2000_Baseline	0.28	0.19	0.161
Felled_3000_Baseline (logged)	-0.05	0.20	0.777

Supplementary Materials 2.3: Time Lagged Models

To investigate the possibility of time lags in bat trend responses to land-use change short-term models were also run including a time lag of 1 time step. Population trends were matched to woodland type change in the previous 5-year interval (e.g. 2010-2015 bat trends and 2005-2010 woodland cover change), and models run as previously. While it would be ideal to test varying lengths of time lag the data available only allowed for this approach. Scale selection was re-run to determine whether time lagged effects had greater impacts at different scales.

Pipistrellus spp. trends responded similarly to land cover change in the previous 5-year interval as to the contemporary 5-year interval, conifer loss negatively affected trends but broadleaf change impacts became non-significant. *Plecotus auritus* trends did not respond to any land cover change in the previous 5-year interval. Contrary to many other models in this study *M. nattereri* trends responded significantly to land cover changes, specifically conifer loss negatively impacted trends while woodland gain also negatively impacted trends (and vice-versa, however the relationship seems largely driven by slower growing populations in areas where woodland cover increased). Similar to the discussion on counter-intuitive relationships with broadleaf change, this may be driven by the limited benefits of newer (5-10 year old) woodland.

Supplemental Table 2-9: Coefficients for models of lagged short-term woodland type change and bat population trends, significant ($p < 0.05$) terms are highlighted in bold.

	Land cover	Estimate	Std. Error	P-value
<i>Pipistrellus</i> <i>sp.</i>	TotalWood_500	140.77	108.08	0.200
	Conifer_2000	109.47	39.21	0.008
	Broadleaf_2000	31.54	61.44	0.611
	Felled_3000 (logged)	-0.55	2.36	0.816
<i>P. auritus</i>	TotalWood_2000	49.59	51.37	0.350
	Conifer_3000	8.76	7.20	0.242
	Broadleaf_2000	-9.05	10.59	0.406
	<i>Felled_3000 (logged)</i>	<i>0.68</i>	<i>0.32</i>	<i>0.051</i>
<i>M. nattereri</i>	TotalWood_3000	-45.74	17.36	0.017
	Conifer_1000	5.43	2.11	0.020
	Broadleaf_3000	-8.08	7.13	0.273
	<i>Felled_2000</i>	<i>0.27</i>	<i>0.13</i>	<i>0.055</i>

Chapter 3: Landscape Woody Habitat Cover and Configuration Effects on Bat Activity and Occurrence

3.1 Abstract

Following the negative effects of past deforestation on woodland biodiversity, there is growing interest in using woodland creation to reverse these impacts. The composition and configuration of habitats in surrounding landscapes (landscape context) has been shown to affect habitat restoration outcomes, but information is often limited on how to target projects for the most benefit. Bats use woodland for roosting and foraging and stand to benefit greatly from newly created woodlands. Additionally, as highly mobile species they are predicted to be sensitive to landscape effects. Previous studies of landscape woodland cover on bat activity in temperate regions have found mixed results, but many only surveyed one habitat patch, thus missing information on how bat activity changes in the wider landscape. Increasing cost-effectiveness of acoustic recorders and automatic ID systems allow for surveying wider areas, while LiDAR technologies allow more detailed mapping of trees outside woodlands (ToW). This study takes advantage of these developments to survey bat activity in multiple woodland and ToW habitat patches across landscapes in Scotland and England to investigate how landscape woody features composition and configuration impact bat activity. Landscape composition and configuration measures had limited impacts on overall bat activity except for *Nyctalus noctula*. In particular, activity for all species remained constant along a gradient of woodland cover. Landscape configuration influenced the relative use of different habitat types, as activity increased at ToW features (and to a lesser extent at the woodland edge) but reduced in woodland interiors as woodland cover became more fragmented. Trees outside Woodlands had an important role to play as habitat for bats in agricultural landscapes, especially in boosting connectivity and matrix permeability thus their sensitive management and planting should be further encouraged.

3.2 Introduction

The recognition of the negative effects of habitat loss, including population declines, extirpation and extinction has led to ambitious targets for habitat restoration. In the UK there has been a particularly long history of deforestation, with woodland cover dropping to 5% at the beginning of the 20th Century, although this has since increased to 13% largely through the creation of conifer plantations (Mason 2007). As a result, habitat restoration targets often focus on woodland creation; the previous UK government committed to increasing tree cover in England to 16.5% by 2050, and similar targets are also produced by the devolved governments (Welsh Government 2018, DAERA 2020, Scottish Government 2020, DEFRA 2023) .

Due to the large cost and resource intensity of active habitat restoration projects, strategic planning is required to maximise their conservation benefits from limited funds, but evidence on the best strategies are often lacking (Tambosi et al. 2014, Gilby et al. 2018, Strassburg et al. 2020). This is largely due to the challenges of conducting experiments on large spatial and temporal scales, which is exacerbated for studies of habitats that are slow to mature, such as woodlands (Watts et al. 2016, Attinello et al. 2023). Instead, it is common for studies to employ space-for-time strategies. Originally used particularly for comparison of chronosequences (Arnold et al. 2021, Brunet et al. 2021), this has expanded to include comparing species' responses to environmental gradients - including habitat cover, connectivity and climate - in space and extrapolating these relationships to changes in time (Batáry et al. 2010, Blois et al. 2013, Frey-Ehrenbold et al. 2013, Fuentes-Montemayor et al. 2013, 2017, Alison et al. 2021, Attinello et al. 2023, de Zwaan et al. 2024). For example, de Zwaan et al. (2024) surveyed agricultural habitats in Ontario and found that linear woody features generally had positive impacts on bird abundance, particularly in intensive regions and thus recommended increasing linear woody feature provision especially in arable dominated landscapes to increase populations. There are some caveats for the ability of space-for-time studies to correctly predict the impacts of future changes. For example, the impact of shifting baselines and differences in the magnitude of spatial and temporal gradients used can complicate comparisons (Blois et al. 2013). Despite this, an explicit test by Attinello et al. (2023) found that bird responses to woodland cover change over time and space generally agreed on the direction of effects, although there was some discrepancy in the strengths of the relationships.

Generally, to be successful in promoting biodiversity and species recovery, habitat restoration projects need to provide good quality habitat and be accessible for colonisation, both of which

have the potential to be impacted by landscape context (Gilby et al. 2018, Whytock et al. 2018b). Neighbouring habitats have been shown to impact the quality of remnant habitat patches through edge effects, characterised by the exchange of energy, material and organisms (Harper et al. 2005). Resulting changes in abiotic conditions can affect woodland communities with mixed responses of species abundance to the presence of woodland edges, with specialists tending to respond negatively (Pfeifer et al. 2017, Williamson et al. 2020). Additionally, species from surrounding matrix habitats can influence habitat quality, such as through the presence of livestock or predators and through colonisation of generalist species, impacting community composition (Harper et al. 2005, Lindenmayer et al. 2015, Whytock et al. 2020).

Landscape context can also affect biodiversity in existing habitat patches through the composition and configuration of the surrounding habitats. Many studies have focussed on the impacts of the amount of a species' main habitat or a wider range of semi-natural habitats on biodiversity, commonly finding greater activity, abundance or occurrence with higher cover (although negative and non- responses are also sometimes found, reviewed in Batáry et al. 2011, Humphrey et al. 2015, Mendes and Srбек-Araujo 2020). Spatial configuration of habitat patches is often thought to have smaller impacts on biodiversity (either in effect size or in the number of species affected). 'Fragmentation per-se', the division of a similar amount of habitat between more patches is often argued to have positive effects, through habitat complementation (as dispersed habitats allow easier access to other habitat types) or through increased edge density (particularly for edge species; Fahrig 2003).

Whether the effects landscape context has on biodiversity in remnant habitat patches are similar to landscape context impacts on the development of communities in newly restored habitats is unclear (Watts et al. 2016). The key driver of biodiversity in restored habitat patches is the ability of species to disperse to and colonise them, which may be influenced by different processes than species persistence. Greater habitat cover in a landscape has been found to increase the ease and speed of colonisation of new habitat patches, with higher species richness of plants and birds as well as greater bat activity in secondary woodlands in landscapes with higher woodland cover (Naaf and Kolk 2015, Fuentes-Montemayor et al. 2017, Whytock et al. 2018a).

In contrast to the purported small and positive impacts of 'fragmentation per-se' in remnant habitats, Watts and Hughes (2024) have argued that the impact on restoration is likely to be more pronounced and negative. Habitat configuration will heavily influence how species are

able to move through landscapes and colonise new patches, and fragmented landscapes are more likely to include movement barriers, especially for poor dispersers (Watts and Hughes 2024). Indeed, studies of secondary woodlands have found that those in landscapes with increased connectivity (particularly reduced interpatch distance and presence of woody linear features) had greater structural complexity, higher activity of bats, occurrence and species richness of birds and species richness of plants (Naaf and Kolk 2015, Fuentes-Montemayor et al. 2017, Whytock et al. 2018a, Brunet et al. 2021, Hughes et al. 2023, de Zwaan et al. 2024).

While habitat cover is usually a positive predictor of a species' occurrence or abundance, how the shape of these relationships changes along the habitat cover gradient, and thus where the greatest benefits from adding new habitat are found, is equivocal. Some studies have indicated that increases are linear and therefore the benefits of adding new habitat are the same regardless of existing habitat cover (Frey-Ehrenbold et al. 2013). An alternative possibility is that the effects saturate once a sufficient level of habitat is reached (Alison et al. 2021) and thus the benefits are greatest in targeting habitat restorations in low cover landscapes. For example, the benefits of linear features and field margins often increase with agricultural cover and intensity (Batáry et al. 2010, Sullivan et al. 2017, Li et al. 2020, de Zwaan et al. 2024). Tschardt et al. (2012) hypothesise that local conservation actions will have the largest benefits in 'simple' landscapes that retain some heterogeneity and remnant habitats that support existing populations. Habitat creation in 'cleared' landscapes (<1% non-crop habitat) may be too isolated, limiting colonisation, while in complex landscapes the improvement in biodiversity may be small relative to the existing community (Tschardt et al. 2012, Tambosi et al. 2014, Gilby et al. 2018). Evidence in support of this to date has come from studies which found agricultural conservation measures (organic farming or AES) had best success in landscapes with intermediate remnant semi-natural habitat cover (Klein et al. 2012, Scheper et al. 2013, Boonchuay and Bumrungsri 2022).

All species of bats in the UK are reliant on or use broadleaf woodlands (Alder et al. 2020). As a result, bats stand to benefit greatly from new woodlands created as a result of the governments' tree planting targets. Previous studies of landscape context effects (particularly woodland cover and configuration) on bat activity or occurrence have found mixed results. Some studies have found that bat activity and roost occurrence increases with woody habitat cover and connectivity, sometimes with particular benefits at low cover or connectivity (Boughey et al. 2011, Frey-Ehrenbold et al. 2013). Although some guilds' activity responded linearly to connectivity while others peaked at intermediate values (Frey-Ehrenbold et al.

2013). Other studies have found that activity decreased with landscape woodland cover (although this may be driven by concentration of individuals in isolated habitats, Fuentes-Montemayor et al. 2013, Monck-Whipp et al. 2018). Often, particularly in tropical ecosystems, responses are found to be guild specific, with reduced occurrence or activity in landscapes with more woodland connected to preferences for foraging in open areas (Klingbeil and Willig 2009, Ethier and Fahrig 2011, Rodríguez-San Pedro and Simonetti 2015).

Many previous studies of bat responses to landscape context were conducted by surveying a focal patch and measuring forest cover and configuration in a series of buffers around this patch. However, this can miss information on how bat activity changes in the wider landscape, with implications for interpreting spatial targeting of conservation (Fuentes-Montemayor et al. 2013, Monck-Whipp et al. 2018). The development of low-cost detectors such as audiomoths have made it possible to survey large areas, while automatic classification software makes processing and analysing large amounts of audio data possible and efficient (Barré et al. 2019, Mac Aodha et al. 2022, Foxley et al. 2023). Additionally, LIDAR technology has allowed for detailed mapping of trees outside woodland (Liu et al. 2023). This study takes advantage of these technological advances to survey bat activity at multiple woody habitat patches and types across whole landscapes in both Scotland and England. This data was used to investigate how the composition and configuration of woody features within the landscape influences bat activity at a site level. The impacts of agricultural makeup, urban cover as well as the differences in activity between woody habitat types were also investigated. What the shapes of the relationships between activity and woody cover mean for targeting woodland creation projects is also discussed.

3.3 Methods

3.3.1 Landscape Selection

Study landscapes were centred on woodlands in the WrEN project (Watts et al. 2016). These are secondary woodlands planted on previously agricultural land in landscapes typical of lowland farmland in both central Scotland and central England. A systematic site selection protocol was previously used to identify WrEN woodlands and incorporate combinations of key patch (e.g. size, age) and landscape (e.g. woodland cover in 3km and patch isolation) variables (see Watts et al. 2016 for further details). Extensive mapping of trees outside woodlands (ToW, e.g. hedges and treelines) within a 3km buffer of these sites has also recently occurred.

For this study, landscapes were defined as a 1km buffer around a WrEN woodland, this size was chosen to balance the feasibility of surveying the area and known bat ecology (Fig. 3.1). UK bat species have previously been shown to respond to landscape variables at scales of 1km or less (Boughey et al. 2011, Fuentes-Montemayor et al. 2013, Bellamy and Altringham 2015, Bellamy et al. 2020). A subset of 60 WrEN sites were selected to avoid overlap between landscapes, to minimise non-agricultural or non-woodland habitat (max 20%), and to minimise correlation between predictor variables to allow investigation of the independent effects of woodland cover, configuration and trees outside woodland cover. Landscapes were surveyed in both Scotland (36) and England (24) to include areas with different bat species and agricultural systems.

3.3.2 Survey Sites

Within each landscape, multiple survey sites at least 100m apart were selected. These survey sites were situated in broadleaf and mixed woodlands, as well as ToW features. Only woody features were selected as previous studies have shown that bat activity is very low in open areas (especially over agricultural fields) and that activity steeply diminishes with distance from woodland or ToW features (Lumsden and Bennett 2005, Finch et al. 2020b). To limit the influence of habitats beyond the landscape edge, survey sites were located within the central 800m radius of the landscape. Survey sites within each landscape were initially randomly selected in QGIS but were sometimes replaced with alternative sites due to issues with access, or when ground truthing indicated the area was no longer a woodland or ToW feature.

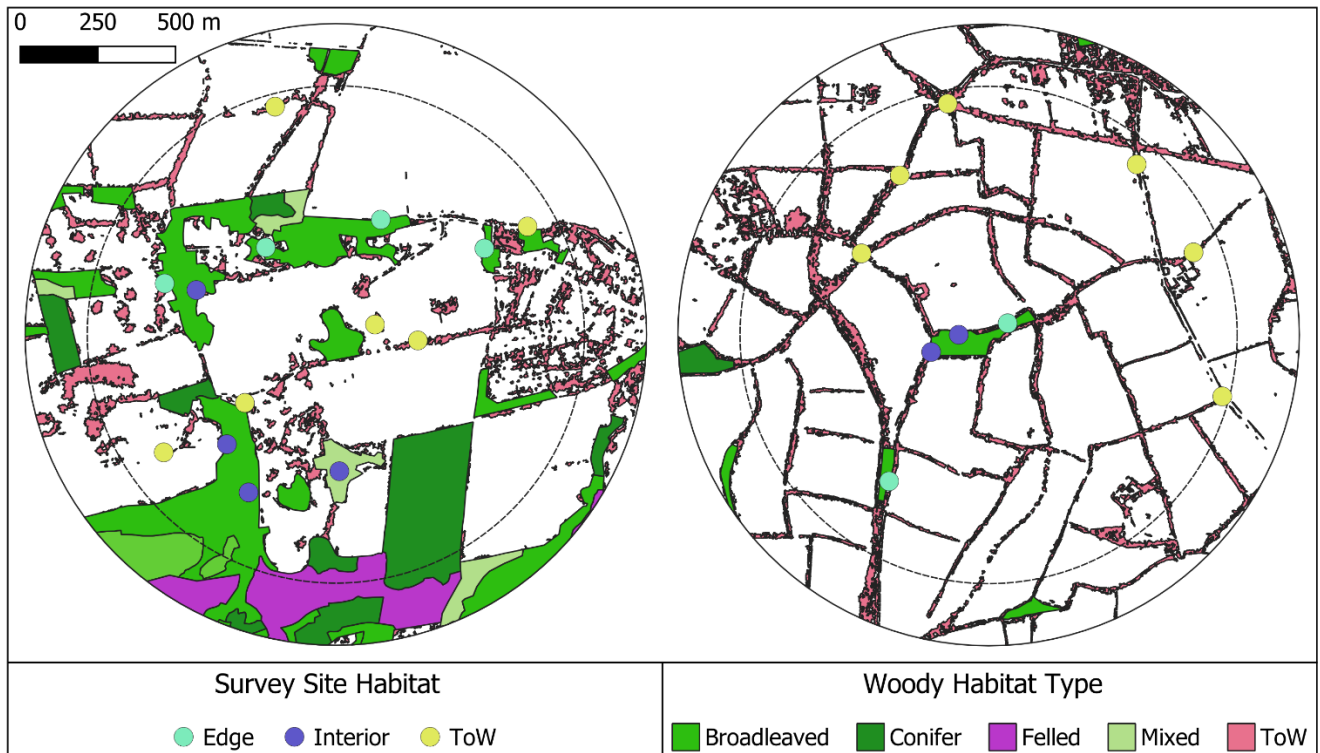


Figure 3.1: Example 1km radius landscapes centered on WrEN woodlands with high (left) and low (right) woodland cover showing woody habitat cover as well as survey points. Dashed line shows the central 800m radius within which all survey points were located.

The total number of survey sites per landscape depended on the area of broadleaf or mixed woodland and ToW available in the central 800m (i.e. the amount of habitat available to survey). Woodland area was divided into 3 quantiles (equal no. landscapes in each category) and assigned 4, 6 or 8 survey sites (for 0.8-7.5, 7.5-19 and 19-52.4ha respectively). Half of the woodland sites were placed in the interior (at least 10m from edge, facing towards the centre of a woodland patch) and half were placed on the woodland edge (on an outermost tree or fencepost facing into the matrix). Trees outside woodland area was similarly divided into 3 quantiles and assigned 2, 4 or 6 survey sites (for 1-7.2, 7.2-13.8 and 13.8-30ha respectively). Each landscape thus had a total number of survey sites ranging from 6-14 (Median = 10, IQR = 2.5).

3.3.3 Surveys

Bat activity was measured at all survey sites within a landscape simultaneously for 7 nights using AudioMoth 1.2.0 detectors. Multiple (up to 4) landscapes were surveyed concurrently. AudioMoths were programmed to start recording 1 hour after sunset (as measured by the middle night of the survey) to avoid peak emergence times and recorded continuously for 4 hours (which is approximately the length of the shortest nights in Central Scotland during the

summer). A high pass frequency filter was used to remove sounds below 6kHz as well as a 1% 2s amplitude threshold to limit recording of quiet periods.

The habitat types adjacent to each survey site (e.g. woodland type, arable, grass, water bodies and urban infrastructure) were recorded, crop type was identified in arable land and the presence of livestock was recorded in grasslands. Temperature was also recorded at 30min intervals at one of the woodland edge sites within each landscape, using an EasyLog EL-USB-LITE Temperature Logger and minimum temperature was calculated for each night. Due to occasional failures of equipment, temperatures for some landscapes were taken from HadUK Grid datasets (Hollis et al. 2019). Data collection in the Scottish landscapes was conducted in summers 2021 (July-September, n=29) and 2022 (June-September, n=7) and in the English landscapes in summer 2022 (June-August, n=24).

3.3.4 Bat Activity

The audio files recorded by the AudioMoths were analysed to automatically detect and identify bat echolocation calls using BatDetect2, a deep-learning trained algorithm provided by the Bat Conservation Trust (BCT, Mac Aodha et al. 2022). BatDetect2 was trained on labelled spectrograms of bat echolocation calls from audio data similar to that in this study, it detects and identifies individual echolocation calls but is able to use context clues (e.g. duration between calls) to aid species identification (Mac Aodha et al. 2022). These algorithms have previously been used to successfully classify UK bat species from passive acoustic recordings (Boughy et al. 2020). The algorithms assign a confidence score to each classification and these were previously calibrated to calculate false positive error rates by BCT (following Barré et al. 2019). A subset of classified pulses across a range of confidence scores were manually verified and an error rate (% false positives) for the algorithm was calculated for each confidence score. General linear models were then used to calculate the confidence score threshold required for different error rates.

Threshold confidence scores equating to a 10% false positive rate were used in this study to filter identifications. Bat calls were identified to species level except for *Myotis spp.*, for which distinguishing between species is difficult due to similarity of calls and so are grouped at the genus level. Site level bat activity was calculated for *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, *Myotis spp.* and *Nyctalus noctula*, the four most commonly detected species/species groups. Activity was initially measured as the number of active minutes per night per site for all species. A species/genus was determined to be active in a particular minute if at least 2

echolocation calls were detected. Due to limited activity, *Myotis spp.* and *N. noctula* activity was collapsed to presence/absence per night per site.

3.3.5 Landscape Measures

For each landscape a number of habitat cover and configuration measures were calculated and tested for collinearity. Total woodland cover in hectares was calculated from the National Forest Inventory 2020 (NFI, Forestry Commission 2022), using package ‘sf’ (Pebesma 2018) in the R statistical software (R Core Team 2024). A variety of landscape level configuration metrics were also calculated from NFI 2020 using the ‘landscapemetrics’ package (Hesselbarth et al. 2019). ‘Number of woodland patches’ showed the least correlation with woodland cover (Correlation coefficient; N patches = 0.36 cf. Mean interpatch distance = - 0.56, Edge density = -0.72, Mean patch area = 0.80) and thus was included as a measure of ‘fragmentation per-se’ (hereafter: “fragmentation”) as it represented similar amounts of cover being divided into a larger number of small patches (Fahrig 2003). Trees outside Woodland cover in hectares was calculated from ToW maps created by Forest Research (ToW - Development version, Forest Research, unpublished data) using the ‘sf’ package (Pebesma 2018). Urban cover in hectares and the proportion of agricultural cover that comprised arable land (cf. improved grassland) were calculated from UKCEH’s Land Cover Map 2020 (Morton et al. 2021). The proportion of agriculture that comprised arable land was used as a proxy of agricultural intensity.

3.3.6 Modelling

For both *Pipistrellus spp.* zero-inflated logistic regression mixed models were used to assess how landscape woody features affected site level bat activity. The dependent variable was number of minutes active linked to number of minutes surveyed, and therefore proportion of survey minutes active. For *N. noctula* and *Myotis spp.* binomial regression mixed models were used to assess how landscape woody features affected site level bat occurrence. The dependent variable was a binomial record of presence or absence for each night at each survey site, an offset term of survey length was used to account for variation in effort caused by AudioMoth/battery failures. All models were run using the ‘GLMMTMB’ package (Brooks et al. 2017).

In both model types, landscape measures, minimum temperature (linear and polynomial if significant), habitat type surveyed (woodland edge, woodland interior or ToW) and country (England or Scotland) were included as independent variables. Polynomial terms were also

tested for woodland cover to investigate the possibility of non-linear effects on bat activity, although none were significant and there not retained in the final models. Random factors were used to account for repeated measures, with survey site nested within landscape (to account for repeated nights at a site and repeated sites within a landscape) and a separate factor for survey date (to account for multiple landscapes surveyed on the same day). The initial model equation for both *Pipistrellus* spp. is therefore summarised as:

$$\begin{aligned} c(N \text{ Mins Active}, N \text{ Mins Surveyed}) \sim & \text{Total Woodland Cover (Ha)} + N \text{ Woodland Patches} + \\ & \text{ToW Cover (Ha)} + \text{Habitat Type} + \text{Minimum Temp} + \\ & \text{Country} + \text{Proportion Agriculture Is Arable} + \\ & \text{Urban Cover (Ha)} + \\ & (1|\text{Landscape/Survey Point}) + (1|\text{Night}), \\ & \text{zeroinflation} = \sim 1 \end{aligned}$$

And the initial model equation for *Myotis spp.* and *N. noctula* is summarised as:

$$\begin{aligned} \text{Presence} \sim & \text{Total Woodland Cover (Ha)} + N \text{ Woodland Patches} + \text{ToW Cover (Ha)} + \\ & \text{Habitat Type} + \text{Minimum Temp} + \text{Country} + \text{Urban Cover (Ha)} + \\ & \text{Proportion Agriculture Is Arable} + \text{offset} = \log(N \text{ mins Surveyed}) + \\ & (1|\text{Landscape/Survey Point}) + (1|\text{Night}) \end{aligned}$$

Two-way interactions were then tested for inclusion. Interactions tested were; 1) country and landscape variables, to test for regional differences in responses to landscape context, 2) habitat type and landscape variables, to test whether there were variations in activity responses to landscape context in different woody habitats, 3) woodland cover and ToW cover as well as number of patches and ToW cover, to test whether ToW cover was particularly important in low cover or fragmented landscapes, and 4) proportion of agricultural habitat that was arable and woodland and ToW cover to test whether agricultural intensity impacted importance of landscape woody features. Interactions were only retained if significant (for *P. pipistrellus* it was necessary to remove proportion agriculture is arable to test interactions, otherwise models did not converge).

3.4 Results

Bat activity was recorded at 590 survey sites across the 60 landscapes for an average of 6.63 nights totalling 15,316 recording hours. The BatDetect2 algorithm detected and identified 20,113,131 echolocation calls to species/genus with a 90% confidence level. The majority of calls detected were from *Pipistrellus spp.* especially *P. pipistrellus*, followed by *Myotis spp.* and *N. noctula* (Table 3.1). Although *Myotis spp.* call numbers were fairly high these translated to very low activity measured as proportion minutes active/night (Mean = 3.02, Median = 1 minutes active per site per night) thus outcomes of occurrence models are presented here (but conclusions were broadly similar from activity models – Supplementary materials 3.1).

Table 3.1: Number of echolocation calls detected at 90% confidence level for all species in each Country. Species which are not found in Scotland only include data for England

Species	N Echolocation Calls Identified		
	Scotland	England	Total
<i>Pipistrellus pipistrellus</i>	3,328,439	8,969,296	12,297,735
<i>Pipistrellus pygmaeus</i>	5,874,746	1,637,314	7,512,060
<i>Myotis spp.</i>	99,194	181,129	280,323
<i>Nyctalus noctula</i>	2668	16,356	19,024
<i>Barbastellus barbastellus</i>	-	3940	3940
<i>Rhinolophus hipposideros</i>	-	38	38
<i>Eptesicus serotinus</i>	-	8	8
<i>Rhinolophus ferrumequinum</i>	-	3	3

The main drivers of bat activity or occurrence at the survey sites were temperature, country and habitat type. Temperature had significant positive impacts (except for *Myotis spp.*) and average activity or occurrence was significantly lower in Scotland for *P. pipistrellus*, *Myotis spp.* and *N. noctula* but non-significantly higher for *P. pygmaeus* (Table 3.2). For *N. noctula* and both *Pipistrellus spp.* activity or occurrence was highest at the woodland edge and ToW sites and significantly lower in the woodland interior (Fig. 3.2). For *Myotis spp.* occurrence was highest at woodland edge and significantly lower at ToW and woodland interior sites.

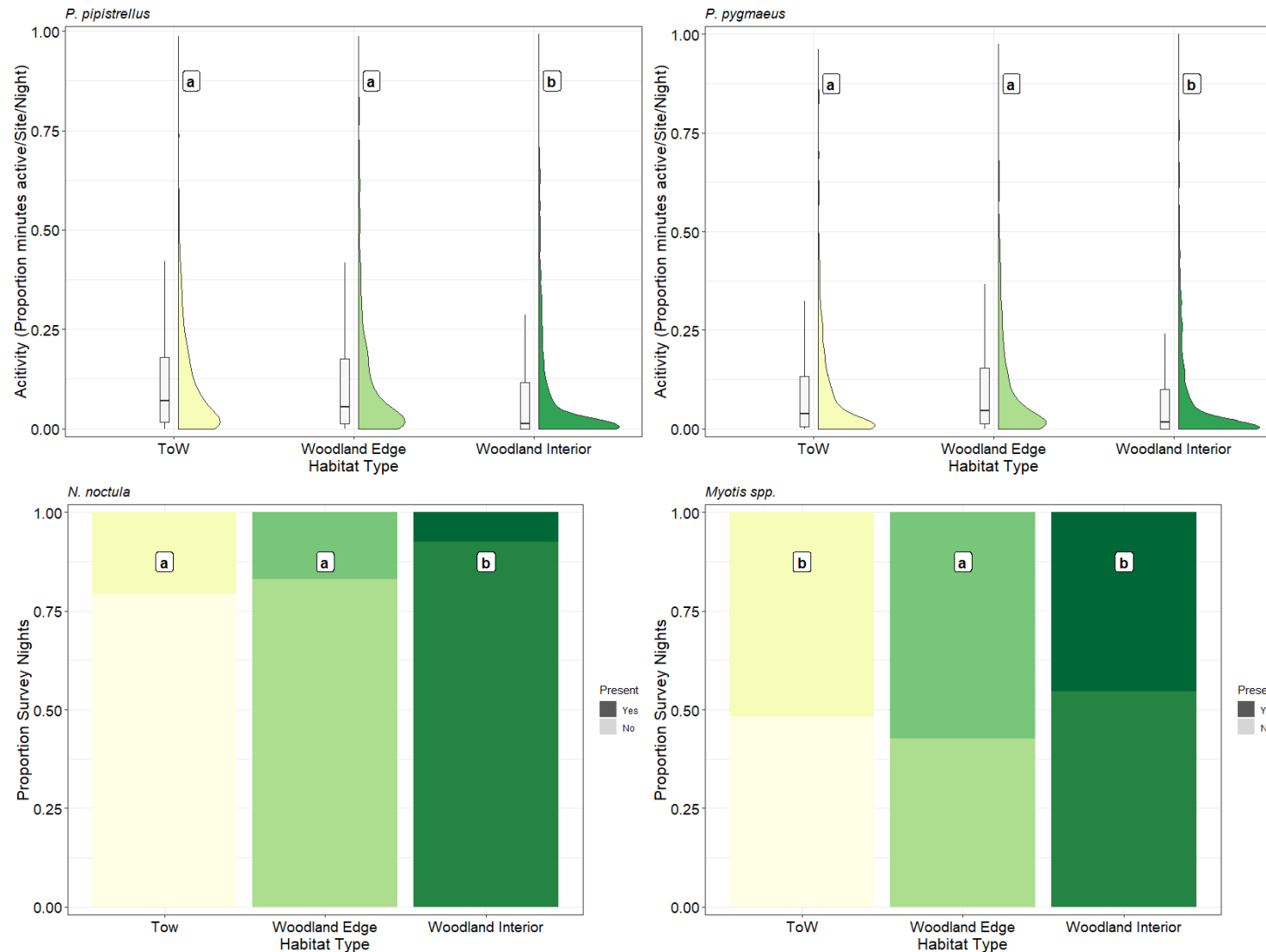


Figure 3.2: Activity (proportion of minutes active per night per site - left) and occurrence (proportion nights species was present: darker colour or absent: lighter colour - right) of bats in different woody habitats. ToW = trees outside woodlands. Letters indicate significance of differences.

Landscape woody habitat cover measures had limited effects on bat activity or occurrence (Table 3.2). Higher trees outside woodland (ToW) cover in the landscape was associated with increased *N. noctula* presence at a site-level (Fig. 3.3) but had no effect on other species. A high leverage landscape where no bats were detected but ToW cover was high was identified, however its removal did not change the results. Activity or occurrence of all species remained similar at a site-level across the range of woodland cover (Fig. 3.4). The proportion of agricultural land that was arable also had no effect on bat activity, however increased urban cover was associated with reduced activity of all species except *N. noctula*.

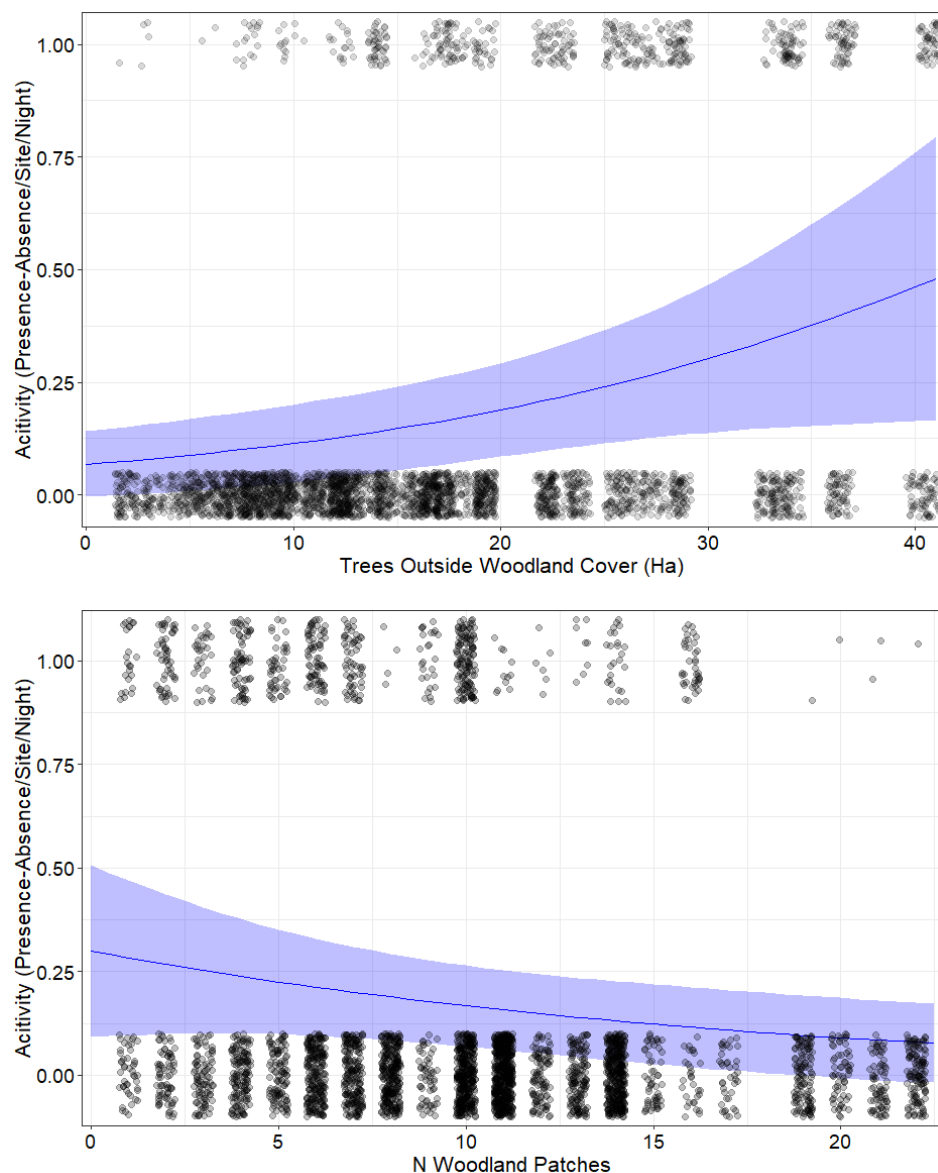


Figure 3.3: Occurrence of *N. noctula* increased significantly with landscape ToW cover (top) and decreased with number of woodland patches (marginal significance $p=0.09$, bottom). Marginal trend (blue line) and 95% CI (shaded area) from model predictions when all other continuous variables held at their means and categorical variables set to reference levels, England and Woodland edge.

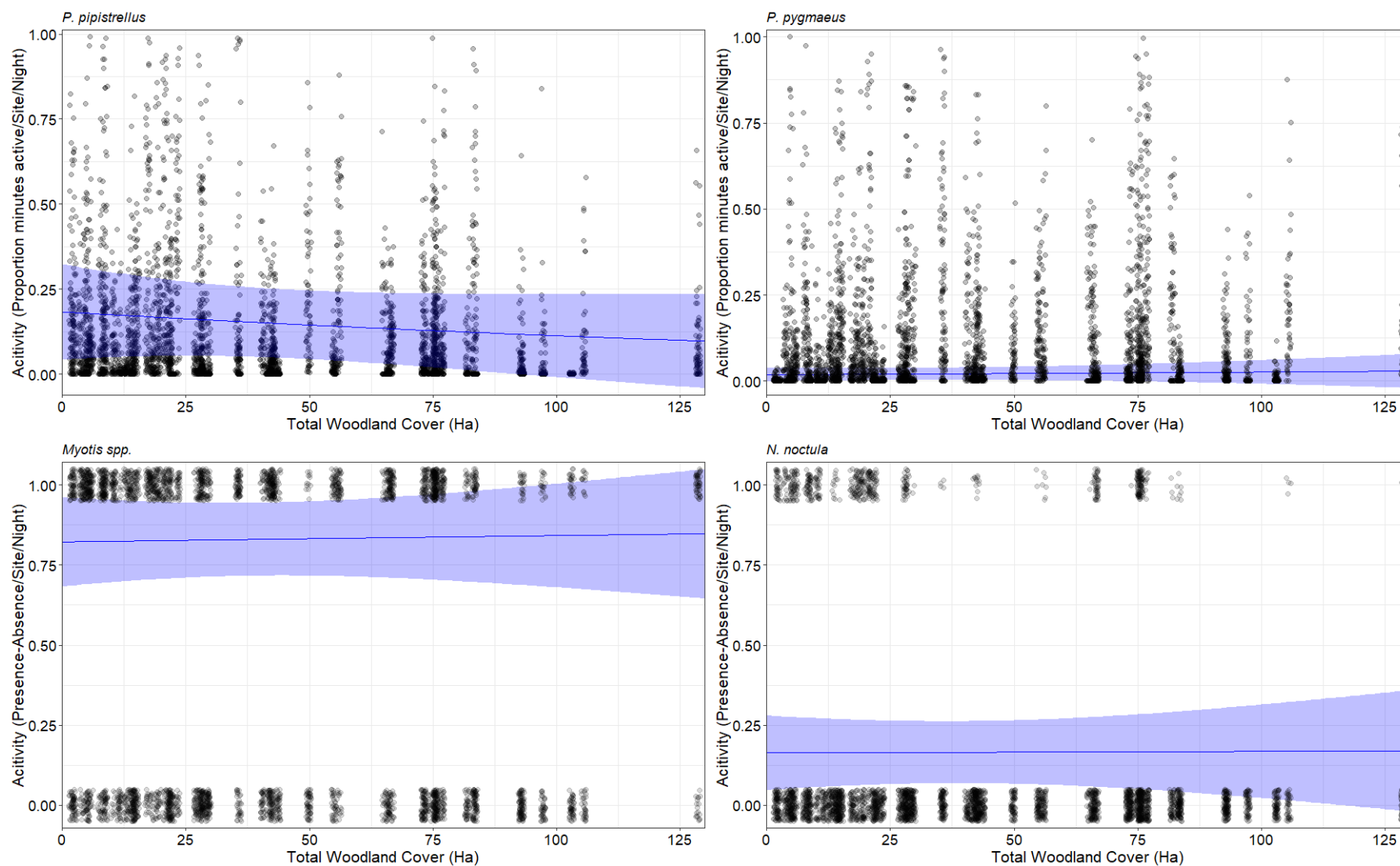


Figure 3.4: Activity or occurrence of all species were not significantly impacted by landscape woodland cover. Marginal trend and 95% CI from model predictions when all other continuous variables held at their means and categorical variables set to reference levels, England and Edge

Landscape habitat configuration had mixed effects on activity and occurrence. Fragmentation per-se, measured as number of woodland patches, was associated with reduced *N. noctula* presence, although this was marginally non-significant (Fig. 3.3, Table 3.2). For *Myotis spp.* and *P. pipistrellus* there was a significant interaction with habitat type surveyed; activity at ToW and woodland edge sites increased with a higher number of patches but declined in woodland interiors (Fig. 3.5, Table 3.2).

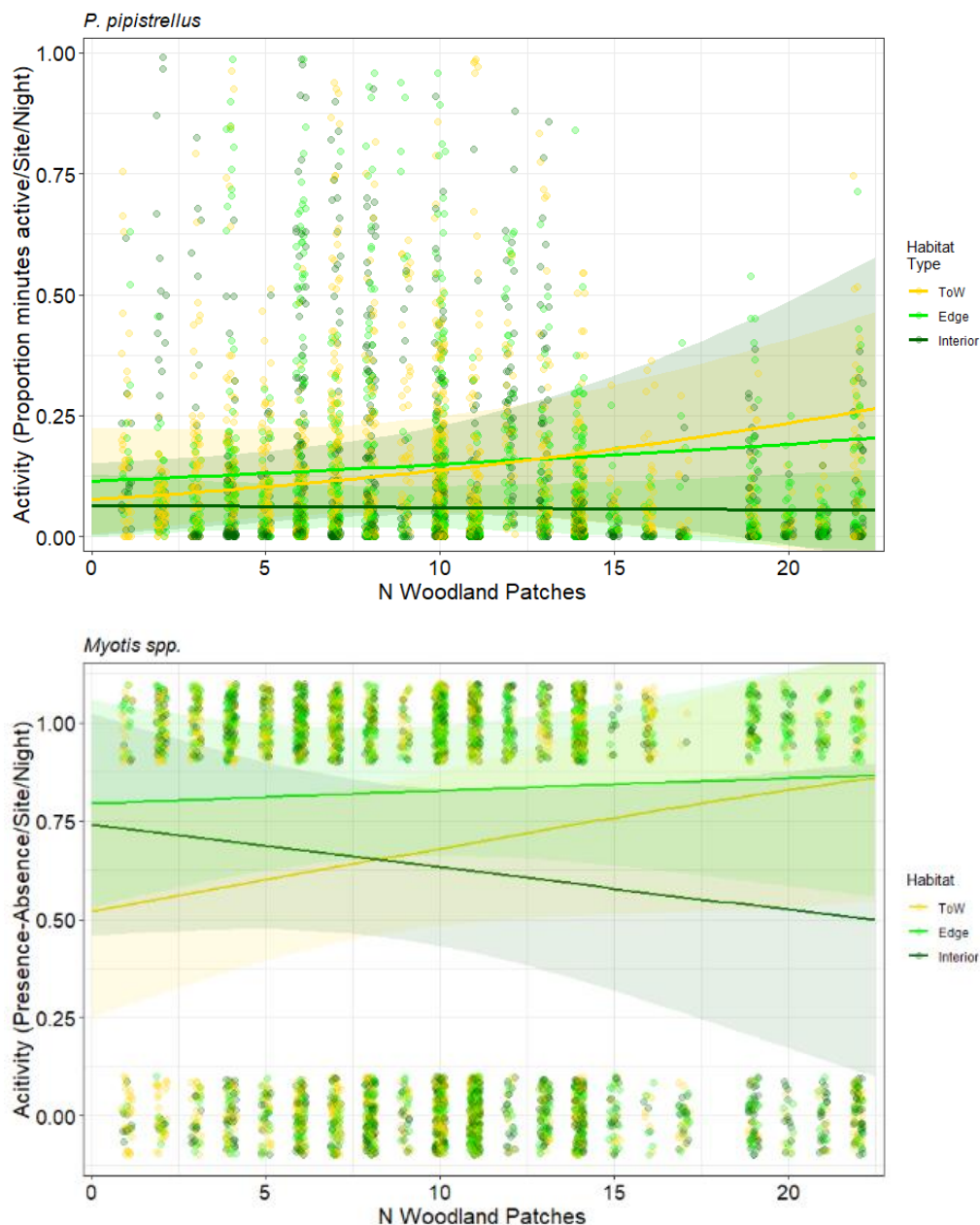


Figure 3.5: Activity of *P. pipistrellus* (top) and occurrence of *Myotis spp.* (bottom) increased in trees outside woodland (ToW) sites and to a lesser extent woodland edge sites but decreased in woodland interior sites as the number of woodland patches increased. Marginal trend (lines) and 95% CI (shaded areas) from model predictions when other continuous variables held at their means and Country set at the reference level of England

Table 3.2: Summary table showing parameter estimates $\pm$ SE and significance (for main effects) of the models. Significant predictors are shown in bold, marginal predictors are shown in italics. Interactions are indicated by the overall anova coefficient for the whole interaction, post hoc comparisons can be found in Table 3.3. Where polynomials or interactions were non-significant and therefore not included in the model, these are left blank. Significance codes: '***' $P \leq 0.001$, '**' $P \leq 0.01$, '*' $P \leq 0.05$, '†' $P \leq 0.1$ and 'ns' $P > 0.1$

Species	Main Effects										Interactions
	Survey Habitat ^a		Country ^b	Wood cover (Ha)	ToW cover (Ha)	N Patches	Urban cover (Ha)	Prop Arable	Min temp	Min temp ²	Type * N Patches
	ToW	Interior									
<i>Pipistrellus pipistrellus</i>	-0.11 $\pm$ 0.14 ^{ns}	-1.00 $\pm$ 0.15***	-2.25 $\pm$ 0.58***	-0.01 $\pm$ 0.01 ^{ns}	-0.04 $\pm$ 0.03 ^{ns}	0.04 $\pm$ 0.05 ^{ns}	-0.03 $\pm$ 0.01*	0.24 $\pm$ 0.72 ^{ns}	0.14 $\pm$ 0.02***	-0.01 $\pm$ 0.0006***	3.36*
<i>Pipistrellus pygmaeus</i>	-0.14 $\pm$ 0.14 ^{ns}	-0.85 $\pm$ 0.15***	0.53 $\pm$ 0.65 ^{ns}	0.003 $\pm$ 0.008 ^{ns}	-0.01 $\pm$ 0.03 ^{ns}	0.07 $\pm$ 0.05 ^{ns}	-0.05 $\pm$ 0.02**	1.22 $\pm$ 0.80 ^{ns}	0.02 $\pm$ 0.005***		
<i>Myotis spp.</i>	-0.67 $\pm$ 0.21***	-0.87 $\pm$ 0.22***	-1.85 $\pm$ 0.58**	0.001 $\pm$ 0.007 ^{ns}	-0.0007 $\pm$ 0.03 ^{ns}	0.02 $\pm$ 0.05 ^{ns}	-0.04 $\pm$ 0.01**	0.51 $\pm$ 0.70 ^{ns}	-0.01 $\pm$ 0.02^{ns}		3.60*
<i>Nyctalus noctula</i>	-0.33 $\pm$ 0.22 ^{ns}	-1.29 $\pm$ 0.26***	-2.41 $\pm$ 0.46***	0.0003 $\pm$ 0.006 ^{ns}	0.05 $\pm$ 0.02**	-0.07 $\pm$ 0.04 [†]	-0.006 $\pm$ 0.01 ^{ns}	-0.54 $\pm$ 0.58 ^{ns}	0.10 $\pm$ 0.03**		

a. Negative values indicate lower activity compared to reference level of Edge

b. Negative values indicate lower activity in Scotland than in England and positive values the opposite

Table 3.3: Post-hoc comparisons of N Patches*Type interaction for *P. pipistrellus* and *Myotis spp.*, showing the difference in NPatches trend coefficient for different habitat types as well as standard error and significance as calculated using R package 'emmtrends' (Lenth 2024). Significant comparisons are shown in bold. Significance codes: '***' $P \leq 0.001$, '**' $P \leq 0.01$, '*' $P \leq 0.05$, '†' $P \leq 0.1$ and 'ns' $P > 0.1$

Species	Reference Level	Comparison Level	Mean Trend Difference $\pm$ SE
<i>P. pipistrellus</i>	Edge	Interior	-0.039 $\pm$ 0.029 ^{ns}
		ToW	0.035 $\pm$ 0.028 ^{ns}
	ToW	Interior	-0.074 $\pm$ 0.029*
<i>Myotis spp.</i>	Edge	Interior	-0.040 $\pm$ 0.028 ^{ns}
		ToW	0.033 $\pm$ 0.027 ^{ns}
	ToW	Interior	-0.074 $\pm$ 0.027*

3.5 Discussion

This study highlights the importance of trees outside woodland in agricultural habitats. Bat activity at such sites was on par with woodland edge, a key foraging habitat, and landscape ToW cover increased occurrence for *N. noctula*. Activity at ToW sites (and to a lesser extent woodland edge) also increased as fragmentation of woodland cover increased for *P. pipistrellus* and *Myotis spp.* while declining in woodland interior sites. This study found limited impacts of landscape composition on bat activity at a site level across a number of species. In particular, bat activity in woody habitat patches was consistent along a gradient of woodland cover.

3.5.1 Activity in Different Habitat Types

Trees outside woodland are known to be important foraging and commuting habitats for bats (Downs and Racey 2006, Wood et al. 2017, Finch et al. 2020b). Shrubs and trees are able to support insect populations and ToW are often coincident with grassy field margins which are important invertebrate habitats, increasing prey availability (Sullivan et al. 2017, Wood et al. 2017). Many bat species avoid large open areas with limited protection and will preferentially use ToW features over fields in agricultural habitats as they provide shelter (Lumsden and Bennett 2005, Finch et al. 2020b). That activity at ToW sites was on par with woodland edge sites which are considered core foraging habitats for many species, especially *Pipistrellus spp.*, is particularly interesting and further highlights their importance as habitat for bats in agricultural systems.

The habitats adjacent to both ToW and woodland edge were similar, in particular features that may have improved activity, such as water, livestock and pastures (in comparison to arable) were equally represented (although ToW features were slightly more likely to border a mixture of arable and grass ~6% vs 1%). The main difference was the increased presence of urban infrastructure (45% vs 25%), especially sealed roads (27% vs 15%) and farm tracks (9% vs 5%) at ToW sites. Roads are generally considered to have negative impacts on bats through noise and light pollution, risk of collision and barrier effects (Berthinussen and Altringham 2012, Finch et al. 2020c) and thus would be expected to comparatively reduce activity at ToW sites. In the study landscapes however, roads tended to be small, quiet and unlit possibly mitigating some of these impacts. Studies of hedge nesting birds have found that abundance was particularly high along farm tracks as they tend to be lined by ToW on both sides, providing additional habitat and enhanced shelter (Walker et al. 2005). It is possible that similar benefits may be experienced by bats, however further analysis on data from only the ToW sites would

be required to test this as in the full models road presence was closely correlated with survey habitat type due to the lack of roads in woodland interiors.

3.5.2 Landscape composition

The consistency of site-level bat activity across a wide range of woodland cover (2-128 Ha) was unexpected. Bats are generally considered woodland species, all UK species are reliant on or heavily use broadleaf woodland for foraging and roosting (Alder et al. 2020, Browning et al. 2021). A large number of previous studies have found bat occurrence and activity increase with proximity to woodland, larger patches as well as greater landscape woodland cover and that woodland is preferentially selected for when foraging (Lesiński et al. 2007, Boughey et al. 2011, Bellamy et al. 2013, 2020, Scherrer et al. 2019, Mendes and Srбек-Araujo 2020, Wright et al. 2021, Foxley et al. 2023). Additionally, loss of woodland cover has been found to have negative impacts on population trends, colony sizes, and abundance (Chapter 2; Borkin et al. 2011, Ancillotto et al. 2021, Carballo-Morales et al. 2021) while recovery of secondary forests improves bat diversity (Farneda et al. 2018).

Some studies have previously found reduced activity or occurrence of bats associated with increased landscape woodland cover (Klingbeil and Willig 2009, Fuentes-Montemayor et al. 2013, Rodríguez-San Pedro and Simonetti 2015, Monck-Whipp et al. 2018, Carballo-Morales et al. 2021, Cook et al. 2023). In the tropics these negative associations are usually found in guilds that prefer foraging in open areas or that are able to make use of resources in agricultural habitat (e.g. frugivores and haemovores; Klingbeil and Willig 2009, Rodríguez-San Pedro and Simonetti 2015, Mendes and Srбек-Araujo 2020, Carballo-Morales et al. 2021). In temperate regions these guilds tend to be limited (including the UK where only insectivorous species are represented) and studies have alternatively hypothesised that reduced activity is due to a dilution effect (Fuentes-Montemayor et al. 2013, Monck-Whipp et al. 2018).

Dilution effects occur when increased habitat cover dilutes or redirects individuals away from a focal habitat patch leading to reduced abundance or activity (Whytock et al. 2018b). It is commonly found in colonisation of marine habitats (Whytock et al. 2018b), as well as pollinator or pest activity in agricultural landscapes (O'Rourke et al. 2011, Desaeher et al. 2021), but has also been applied to studies of landscape composition on bat activity (Fuentes-Montemayor et al. 2013, Law et al. 2018, Monck-Whipp et al. 2018). For example, Fuentes-Montemayor et al. (2013) surveyed central woodland patches in landscapes similar to those in this study and found that bat activity was highest in isolated woodlands. This was hypothesised

to be due to a concentration of activity in the limited available habitat provided by these isolated patches, while in more connected habitats activity was more evenly spread and dispersed throughout the landscape reducing activity in the focal woodland (Fuentes-Montemayor et al. 2013).

Surveying multiple habitat patches across a landscape should reduce the impacts of dilution effects (as areas with limited activity will be surveyed along with concentrated areas). However as acoustic surveys can only measure relative bat activity, similar mechanisms where changes to movement or other behaviours mask changes in abundance could be at play. While comparative studies have found correlations between acoustic activity and trapping rates, especially for *Pipistrellus spp.*, changes in local relative activity do not necessarily translate to changes in landscape scale abundance (Lintott et al. 2014b, Froidevaux et al. 2017a). Radio tracking surveys have found that bats will travel shorter distances in landscapes with more woodland cover and habitat diversity (Mortimer 2006, Laforge et al. 2021). Additionally, as woodland cover has a positive impact on insect populations (Fuentes-Montemayor et al. 2012, Alison et al. 2021) bats may need to spend less time foraging in more wooded landscapes. Both factors could reduce activity levels of individual bats across a night by reducing transit and searching time, reducing relative activity without a change in abundance. Despite this, studies have found that bat activity as measured by acoustic surveys increased with greater woodland cover even in some of the same landscapes surveyed in this study (Fuentes-Montemayor et al. 2011, 2017, Cook et al. 2023).

3.5.3 Landscape configuration

Similar to landscape cover variables, spatial configuration of landscape woodland had limited impacts on overall bat activity other than for *N. noctula*. Despite previous studies finding positive effects of ‘fragmentation per-se’ on bat activity and abundance (Gorresen and Willig 2004, Klingbeil and Willig 2009, Ethier and Fahrig 2011, Rodríguez-San Pedro and Simonetti 2015) in this study fragmentation reduced *N. noctula* occurrence (although this was marginally non-significant). As a specialist species that forages over woodland, this may reflect a need for larger patches (as patch sizes tend to be smaller in more fragmented landscapes) or an aversion to travelling long distances through the surrounding agricultural habitat. The latter is supported by the importance of ToW cover for this species and that an interaction between ToW cover and number of patches, while marginally non-significant and not included in the final model,

did indicate the negative impacts of fragmentation were lessened when ToW cover was higher (interaction coefficient 0.007, $p=0.06$).

Interestingly however, spatial configuration of woodland did affect where bats were most active in the landscape. A significant interaction between habitat type and N patches showed that for both *P. pipistrellus* activity and *Myotis spp.* occurrence increased in ToW (and to a lesser extent woodland edge) habitats in comparison to woodland interior as fragmentation increased (Fig. 3.5). Some of the hypothesised drivers behind the benefits of ‘fragmentation per-se’ are that dispersed habitats allow for landscape complementation as it is easier for species to move between neighbouring habitat types, or that increased edge density provides more foraging opportunities (Ethier and Fahrig 2011, Tschardt et al. 2012). Some bat species do use a mosaic of land covers, particularly semi-natural habitats while others tend to forage at woodland edges (Ancillotto et al. 2017, Put et al. 2019, Mordue et al. 2023).

Increased activity at ToW sites in the matrix and woodland edges could support these theories, however, in the study landscapes, semi-natural habitat cover was low and ToW tended to be found along agricultural fields and roads which bats generally avoid (Lumsden and Bennett 2005, Berthinussen and Altringham 2012, Finch et al. 2020c, 2020b). Additionally, greater activity at the woodland edge simply replaced interior activity rather than having an overall positive impact, possibly indicating diversion from limited woodland interior habitats. Instead, the shift in activity may reflect that bats interact with the matrix more when the available habitat is fragmented, either to find sufficient habitat for roosting and foraging or as a function of reduced interpatch distance increasing ease of movement. Linear ToW features in particular can act as important drivers of connectivity across landscapes for a range of woodland taxa, including bats, and are seemingly used more as habitat fragmentation increases (Frey-Ehrenbold et al. 2013, Humphrey et al. 2015, Scholefield et al. 2016, Broughton et al. 2021a)

While ToW features were more important as woodland fragmentation increased, the effect of ToW on activity did not increase in landscapes with low woodland cover (non-significant interaction with woodland cover, Table 3.2). It could be expected that smaller amounts of woodland would similarly increase the need for bats to move between patches or to forage in agricultural or semi-natural open habitats and thus ToW features would be important in facilitating this. In fact, previous studies have found that ToW cover can have greater benefits for bird communities in more intensive landscapes (Batáry et al. 2010, Sullivan et al. 2017, de Zwaan et al. 2024). The difference in ToW cover modulating the effects of fragmentation and

reduced habitat may be a function of interpatch distance which is often reduced when habitat is more fragmented but increases with reduced cover (mean patch distance correlation: wood cover -0.56, N patches -0.55). As patches become more isolated, the energetic cost and the perceived or real risks of travelling across open areas are increased, reducing movement between patches (Haddad et al. 2015, Pinaud et al. 2018). The presence of ToW may not be sufficient to reduce these impacts and promote movement through the matrix. Alternatively, as inter-patch distances increase, there may be more gaps in ToW coverage which bats avoid (Pinaud et al. 2018).

3.5.4 Insensitivity to Landscape Context

While the lack of response to woodland cover was particularly unexpected, it should be noted that overall, there was a limited response to all landscape composition variables (except urban cover). For example, while high activity at ToW sites indicated they were heavily used, positive impacts of landscape ToW cover were only found for *N. noctula* occurrence in contrast to previous studies where it increased activity for a range of species (Frey-Ehrenbold et al. 2013, Fuentes-Montemayor et al. 2013, Froidevaux et al. 2017a, 2017b, 2019, Bellamy et al. 2020, Finch et al. 2020b). This suggests that particularly at a site level, bat activity in these areas is not strongly driven by landscape context. The random terms used to account for repeated measures contributed more to the model r^2 than the landscape context measures even when accounting for urban cover and agricultural composition (the majority of other habitat in the landscapes) and within landscapes activity between sites varied widely, suggesting a strong effect of local drivers.

Scales of effect in landscape ecology have been found to be predicted by body size and mobility (Wiens 1989, Gehring and Swihart 2003, Mayor et al. 2009, Jackson and Fahrig 2012, Humphrey et al. 2015, Fuentes-Montemayor et al. 2017) but see (Moll et al. 2019), and as wide ranging, mobile species bats are predicted to be sensitive to landscapes at large scales. Despite this, previous studies have found mixed patterns in the relative strength of local and landscape factors on bat activity. Some find local factors, especially woodland structure and biomass of ToW features have the strongest impacts on activity and roost selection (Erickson and West 2003, Perry et al. 2010, Fuentes-Montemayor et al. 2013, Starik et al. 2018, Alder et al. 2020, Cook et al. 2023) while others find the opposite (Hein et al. 2008, Froidevaux et al. 2017a, Fuentes-Montemayor et al. 2017, Boonchuay and Bumrungsri 2022).

Fuentes-Montemayor et al. (2017) further found the importance of local and landscape factors were dependent on species mobility and landscape context, with stronger landscape effects in England compared to Scotland which was hypothesised to be due to the impacts of more intensive agricultural systems. While this study surveyed many of the same landscapes there were no significant interactions between country and landscape measures and the proportion of agriculture that was arable had no impacts on activity nor did it modulate the effects of woodland or ToW cover. Differences in mobility between species also did not appear to impact sensitivity to landscape characteristics as *Myotis spp.*, *P. pipistrellus* and *N. noctula* are all considered high mobility species and only the latter was affected by landscape composition (Fuentes-Montemayor et al. 2017). However, specialists are considered more sensitive to landscape impacts than generalists (Rocha et al. 2018) which may explain the difference in sensitivity between *N. noctula* and other species as they are considered woodland specialists, particularly in comparison to both *Pipistrellus spp.*

3.5.5 Further work

As site-level activity was consistent across a range of landscape woodland cover, and no species displayed non-linear relationships, the differential benefits of adding new woodland to landscapes with varying woodland cover levels are difficult to elucidate. The consistent site-level activity could suggest that at a landscape level, activity increases linearly with new habitat (as new patches will be able to support a similar level of bat activity). Radford and Bennett (2007) similarly suggested that bird species whose incidence within woodland patches remained constant as landscape woodland cover reduced would still suffer population declines in the event of habitat loss. However, Bennett et al. (2006) suggest that emergent properties created by landscape composition and configuration complicate the extrapolation of site-level responses to a landscape level. Thus, directly investigating the effects of landscape woody cover and configuration on landscape-level bat activity would be beneficial. Pooling activity measures from multiple sites across a landscape could allow for this, although care would be required to account for differences in survey effort.

Radio tracking studies could be used to investigate whether habitat use changes with landscape context (Laforge et al. 2021). This could include whether preferential use of particular types of woody habitat e.g. hedges, individual trees, or woodlands vary, whether movement patterns change (for example whether bats travel shorter distances when woodland cover is low or more dispersed), and whether they are active for different lengths of time (e.g. foraging for shorter

periods when there is more habitat). In conjunction, trapping could elucidate whether the number of bats within a patch is increasing even as patch specific activity does not, as well as conducting mark-recapture analyses to calculate landscape population sizes. This would also allow research on species that are difficult to detect through acoustic surveys such as *P. auritus* that was likely fairly common in the surveyed landscapes (Fuentes-Montemayor et al. 2017) but not detected with 90% confidence at any of the sites.

It would also be interesting to investigate these questions using other activity measures particularly ones that give more granularity to the data, as an ‘active minute’ could represent a bat simply passing through an area or more sustained activity. The number of echolocation calls detected per night has the most granularity but was highly overdispersed complicating modelling with generalised linear models and could be more sensitive to misclassifications (as single detections are more likely to be false positives than multiple in close range). Many previous studies have used number of bat passes, usually defined as a set number of echolocation calls within a particular time period (e.g. two or more echolocation calls within 1 second of each other; Fuentes-Montemayor et al. 2017), which could represent a balance between granularity and using multiple calls to increase confidence. Developing a method to calculate bat passes from the BatDetect2 output could thus be beneficial.

Valente et al. (2023) argue that to move our understanding of the effect of fragmentation on biodiversity forward, researchers should focus on the mechanisms behind species responses rather than remaining locked in positive vs negative tallying. Some mechanisms behind the effects of fragmentation in this study have been hypothesised (e.g. reduced patch size limiting *N. noctula* occurrence), however high correlation between habitat spatial configuration metrics and their intrinsic link to cover (Andren 1994, Fletcher et al. 2018) precluded the ability to test these directly. Additionally, it has been suggested that different measures of fragmentation lead to different outcomes between studies and meta-analysis results support this (Valente et al. 2023; Graham, unpublished data).

Statistical techniques that can disentangle the impacts of different aspects of landscape complexity (both cover and configuration) could be investigated to allow comparison of responses to different measures of configuration and their relationships to cover. Previous studies have used ordination techniques such as principal component analysis to create a variable that encompasses a range of aspects of spatial configuration (Pita et al. 2013, Fuentes-Montemayor et al. 2017), however this does not elucidate individual drivers. Structural

Equation Models could be used to investigate the direct effects of woodland cover on bat activity as well as indirect effects through change in configuration. Similarly, the direct and indirect effects (through changes in edge density, patch size or interpatch distance) of fragmentation could be investigated (Fuentes-Montemayor et al. 2020).

3.5.6. Conservation implications

The degree of importance that ToW features played in promoting bat activity, especially in enhancing connectivity in landscapes with greater woodland fragmentation suggests that additional emphasis should be placed on sympathetic management of hedges. Incentives for planting of linear features and small areas of trees, as well as larger woodlands, such as including ToW cover in targets for woodland or biodiversity managed farmland in AES schemes should be enhanced. This study was unable to indicate whether targeting woodland planting at particular landscapes would be most beneficial to bats, however when planting an amount of woodland, concentrating this effort into fewer patches is likely to have more benefits, especially for woodland specialists and in landscapes where ToW cover and connectivity is lower.

Supplemental Materials 3.1: *Myotis spp.* Activity Responses to Landscape Measures

As well as occurrence, models were also run on the impacts of landscape context on *Myotis spp.* activity, measured as number of minutes active per site per night. Conclusions were broadly similar, with activity at woodland edge significantly higher than in both ToW and woodland interior sites (which were not significantly different from each other). Activity was also significantly lower in Scotland than in England. Landscape composition and configuration metrics had no impact on activity except for a negative impact of urban cover. However, there was a significant interaction between number of patches and habitat type with increased number of patches increasing activity in ToW and to a lesser extent woodland edge sites but declining in woodland interior sites.

*Supplemental Table 3-1: Summary table showing parameter estimates $\pm$ SE and significance (for main effects) of the models. Significant predictors are shown in bold. Interactions are indicated by the overall anova coefficient for the whole interaction, post hoc comparisons can be found in Supplemental Table 3.2. Where polynomials or interactions were non-significant and therefore not included in the model, these are not recorded. Significance codes: '***' $P \leq 0.001$, '**' $P \leq 0.01$, '*' $P \leq 0.05$, '†' $P \leq 0.1$ and 'ns' $P > 0.1$*

Species	Main Effects									Interactions
	Survey Habitat ^a		Country ^b	Wood cover (Ha)	ToW cover (Ha)	N Patches	Urban cover (Ha)	Prop Arable	Min temp	Type * N Patches
	ToW	Interior								
<i>Myotis spp.</i>	-0.49 $\pm$ 0.15***	-0.52 $\pm$ 0.16**	-1.38 $\pm$ 0.41***	0.001 $\pm$ 0.01 ^{ns}	0.01 $\pm$ 0.02 ^{ns}	0.02 $\pm$ 0.03 ^{ns}	-0.03 $\pm$ 0.01**	0.34 $\pm$ 0.50 ^{ns}	0.01 $\pm$ 0.01 ^{ns}	6.55**

a. Negative values indicate lower activity compared to reference level of Edge

b. Negative values indicate lower activity in Scotland than in England and positive values the opposite

Supplemental Table 3-2: Post-hoc comparisons of N Patches*Type interaction for *P. pipistrellus* and *Myotis spp.*, showing the difference in NPatches trend coefficient for different habitat types as well as standard error and significance as calculated using R package ‘emmtrends’ (Lenth 2024). Significant comparisons are shown in bold, marginal comparisons are shown in italics. Significance codes: ‘***’ $P \leq 0.001$, ‘**’ $P \leq 0.01$, ‘*’ $P \leq 0.05$, ‘†’ $P \leq 0.1$ and ‘ns’ $P > 0.1$

Species	Reference Level	Comparison Level	Mean Trend Difference $\pm$ SE
<i>Myotis spp.</i>	Edge	Interior	<i>-0.07 $\pm$ 0.03[†]</i>
		ToW	0.04 $\pm$ 0.03 ^{ns}
	ToW	Interior	-0.11 $\pm$ 0.03***

Chapter 4: Multi-Scale Habitat Associations of Nine UK Bat Species

4.1 Abstract

Understanding the habitat associations and preferences of species is important to be able to create targeted and effective conservation programmes. Species interact with their environments at multiple scales, requiring an understanding of landscape context and habitat use across different scales in order to account for context-dependency in conservation. Bats in the UK are recovering from significant declines in the 20th Century, but the drivers of their population changes are unclear. Using national scale data from a range of surveys over 15 years, spatially nested habitat suitability models were constructed to investigate multi-scale habitat associations for nine UK bat species. A multi-species, multi-scale approach allows highlighting of the most effective landscapes for conservation actions and investigation of where they may have wide ranging benefits or where careful consideration is required in the possible trade-offs between species. Habitat associations were species and scale specific. Generally, the amount of broadleaf woodland and trees outside woodland had a positive impact on occurrence likelihood, but the shape of this relationship varied between species and scales such that there was no strong indication of a ‘best target landscape’ for woodland creation to create the most benefit across all bat species in this study. Agricultural cover had mixed effects but in general high levels of cover tended to be negative. Urban cover was also negative, although at a local level proximity to buildings was positive reflecting the use of rural buildings as roosting sites. The cover of other habitats such as urban or agriculture modulated the benefits of woodland and trees outside woodland, but the direction of effect varied between species. To enhance bat populations as a whole, conservation actions should focus on creating or maintaining good quality woodlands and promoting good management of hedges regardless of landscape context.

4.2 Introduction

The twin crises of climate change and habitat loss have caused declines in populations of many species across multiple taxa and increased the need for species conservation, e.g. through habitat protection and restoration (Pörtner et al. 2021). Understanding the habitat associations and preferences of species is important to be able to create targeted and effective conservation programmes. Habitat suitability models (HSM) are a useful and widely employed series of modelling tools used to enhance understanding of species' habitat associations (Guisan and Zimmermann 2000, Valavi et al. 2022). Patchy, biased and occurrence only data are common in species records. Various HSM methods have been developed to account for these characteristics and therefore use these data to calculate relationships between habitat suitability and environmental correlates and to predict species distributions and habitat suitability across large areas. These outputs can fill gaps where surveys have not been conducted, suggest areas to focus future survey effort (Fuller et al. 2018b), and highlight suitable areas outwith a species' known range where management actions are required to protect them (e.g. from invasive species) or to facilitate colonisation for species of conservation concern (Fraser et al. 2015, Ziolkowska et al. 2016, Bellamy et al. 2020).

Species interact with their environments at multiple scales, from global ranges driven by climate niches, home ranges that incorporate foraging, resting and reproductive habitats and local habitat features that impact quality and use of particular habitat patches (Wiens 1989, Mayor et al. 2009, Bellamy et al. 2020). This impacts the scale at which different habitats are most important for species, for example *Pipistrellus pipistrellus* was most sensitive to urban cover at local scales but to woodland cover at landscape scales (Bellamy and Altringham 2015). Additionally, a species can respond differently to the same habitat at a range of scales, and landscape context can impact habitat associations at local scales, leading to differences across regions (Whittingham et al. 2007, Fuentes-Montemayor et al. 2017, Bellamy et al. 2020, Froidevaux et al. 2021, Wright et al. 2021). The modifying effects of landscape context can also influence the effectiveness of conservation actions, for example agri-environment schemes are sometimes found to be most beneficial to biodiversity in 'intermediate' landscapes with moderate cover of remaining natural habitats (Scheper et al. 2013, Boonchuay and Bumrungsri 2022).

Multi-scale habitat suitability models, that account for such scale-dependent effects by selecting the ‘best scale’ for every environmental correlate, have been shown to outperform single-scale models, that use the same scale for every variable (Atzeni et al. 2020, Chandler et al. 2021). Recently developed spatially nested habitat suitability models extend this by allowing models to be sequentially run at different scales, incorporating wider scale outputs at the next, smaller scale, effectively adding a landscape suitability context variable and further improving model performance (Bellamy et al. 2020, Wright et al. 2020, 2021, Adde et al. 2023, Goicolea et al. 2024). This allows incorporation of climate and broad scale habitat variables that control species distribution at global/regional scales with detailed habitat variables that impact occurrence at very local scales in the same model. Integrating these different levels can help balance niche truncation and overly generic covariates, both of which have been highlighted as weaknesses of habitat suitability models (Bald et al. 2024, Goicolea et al. 2024). Niche truncation occurs when models are run on a subset of a species’ geographic or climate niches, leading to underestimations of suitable areas and problems extrapolating to other regions and often results from small geographic scales (Goicolea et al. 2024). On the other-hand, at large geographic scales habitat categories are often broad and can be uninformative, reducing model performance (Bald et al. 2024). Spatially nesting models also allows incorporation of interactions between the higher-level outputs and more local environmental correlates, which can highlight important patterns of context-dependent habitat selection. For example Spake et al. (2020) found that deer damage was described by a complex 3-way interaction between climate, landscape and deer density. Understanding these dependencies can help target conservation actions in the most appropriate/effective areas (Tscharntke et al. 2012).

During the 20th century bats suffered population declines across Europe and while some drivers of population change are clear, evidence for others, their mechanisms, and how drivers interact are more equivocal (Browning et al. 2021). Disturbances of roosts by anthropogenic activity and mortality and habitat loss from wind farms and roads are known to have negative impacts on populations (Browning et al. 2021). Additionally, land use changes are thought to have played a large role in previous declines, in particular through increased chemical inputs and loss of linear features during agricultural intensification reducing insect prey availability as well as foraging and commuting habitats (Harris et al. 1995, Browning et al. 2021). Changes in woodland cover are also known to affect bat populations with loss of woodland having negative impacts through loss of roosting and foraging habitats while populations can

conversely respond positively to increased cover (Chapter 2; Harris et al. 1995, Browning et al. 2021). Urbanisation has more equivocal impacts, with some species seemingly adapting to urban environments, but possibly with less healthy populations or lower densities (Lintott et al. 2016, Browning et al. 2021).

Additionally, climate change is likely to impact bat population trends in the future. In the UK, which is at the latitudinal limit for many bat species, the likely response is a northward expansion but extreme weather events such as heatwaves or storms are likely to have negative impacts (Browning et al. 2021). It is unclear whether this is already playing a role in the UK as recovery from the previous declines may be masking patterns, although it has been suggested that milder winters has helped recoveries of some species (Browning et al. 2021). Climate and land use also have interactive effects which are likely to be enhanced in the future as climate change leads to dispersal away from good quality or protected habitats to newly climatically suitable areas where these may be limited (Hughes et al. 2012, Smith et al. 2016, Law et al. 2018).

Therefore, an understanding of how habitat suitability varies with environmental correlates ranging from climate to landscape habitat cover to local factors such as the occurrence of linear features is important to inform more targeted conservation actions for this at-risk taxon and to consider how they might respond to future changes both positive (e.g. woodland creation) and negative or mixed (e.g. climate change). Due to the complexities of surveying bats arising from their nocturnal behaviour, protected status, and high mobility, habitat suitability models are particularly useful to account for the variety of survey methods used to study them and account for their particular biases, as well as the predominance of bat groups and other citizen-science monitoring that may skew records towards well populated areas. Previous habitat suitability models for bats in the UK have been restricted to small areas and limited scales (Boughey et al. 2011, Bellamy et al. 2013, Bellamy and Altringham 2015) or have used spatially nested models at a regional or national scale but only for a few species (Bellamy et al. 2020, Wright et al. 2021).

Here, spatially nested habitat suitability models across Great Britain were used to investigate associations between bat occurrence and both climate and habitat variables at different scales and examine how those scales interact for nine native bat species. This broad approach allows modelling of both common species that are often overlooked but are still sensitive to environmental change (Lintott et al. 2016), as well as rarer species where occurrence and

ecological data are more likely to be limited (Shcheglovitova and Anderson 2013, Chandler et al. 2021). Additionally, this allows the identification of commonalities or potential conflicts between species, which can highlight conservation actions that may have wide ranging benefits or where careful consideration is required in the possible trade-offs between species and to identify landscapes where these actions may be most effective.

4.3 Methods

Habitat suitability models were conducted for nine species of bat found in the UK using MaxEnt, which is a machine-learning HSM technique that uses the principle of maximum entropy to compare the environment at occurrence-only record locations and a selection of background points or ‘pseudoabsences’ in order to predict habitat suitability across space (Phillips et al. 2006, Elith et al. 2011). MaxEnt has been found to perform well in comparison to other HSM methods and allows models to test for interactions between variables (Valavi et al. 2022). To account for the multiple scales at which bats respond to their environments, a sequential multi-level HSM framework was used as described in Bellamy et al. (2020) and used in Wright et al. (2020, 2021) whereby HSMs are conducted at multiple nested geographical levels, starting with the coarse resolution population range and followed by finer resolution and geographically nested levels. Importantly, the output predictions from a preceding level’s model are incorporated as a predictor at each nested level.

Occurrence records for each species were extracted from Bat Conservation Trust (BCT) roost and hibernation surveys conducted by trained volunteers as part of the National Bat Monitoring Program (NBMP) as well as National Biodiversity Network (NBN) records covering the 15-year period 2007 to 2021. NBMP roost surveys consist of sunset emergence counts of bats conducted at known roost sites located in buildings in the summer (May-July). The hibernation surveys consist of daytime counts of bats conducted at known hibernacula typically located in caves or underground structures in the winter (Jan-Feb, see Barlow *et al.*, 2015 for more details). NBN records were filtered based on rules regarding confidence in the species ID (e.g. those based on only droppings or from visual records without detectors were removed) and on data source (e.g. BCT data were filtered out to avoid duplication with NBMP records, the

former were used as coordinates were provided at a finer resolution). Models were run for the nine most common species in the dataset, beyond this occurrence record numbers were very low (<100) which would have hindered performance, these species (and their UK distributions) were:

- *Pipistrellus pipistrellus* (throughout the UK)
- *Pipistrellus pygmaeus* (throughout the UK, except very north Scotland)
- *Plecotus auritus* (throughout the UK, except very north and west Scotland)
- *Rhinolophus hipposideros* (Confined to southwest England and Wales)
- *Rhinolophus ferrumequinum* (Confined to southwest England and south Wales)
- *Myotis daubentonii* (throughout the UK)
- *Myotis nattereri* (throughout the UK but limited areas of Scotland)
- *Nyctalus noctula* (England Wales and southwest Scotland)
- *Eptesicus serotinus* (south and mid Wales and England)

Many of the occurrence records were collected on an *ad hoc* basis or with varied sampling strategies and designs and were therefore likely subject to sampling biases (Phillips et al. 2009). This can mask true relationships between occurrence and environmental measures, often causing habitat suitability predictions to map sampling effort rather than species presence (Phillips et al. 2009, Barber et al. 2022). One established method to counteract this is to weight the selection of pseudoabsences so that they share the same biases (Phillips et al. 2009). A ‘target group’ approach was used to estimate survey effort across space using all occurrence records found in the datasets used for occurrence data (including species outside the nine that models were run on, Phillips et al. 2009, Mateo et al. 2010). Target group records were filtered for unique coordinates as large numbers of repeated surveys (e.g. known roosts surveyed multiple times a year over many years) overcorrected biases. Large numbers of records in close proximity but with different coordinates were included such that the bias file still represented geographical variation in survey effort. This information was then used to weight selection of 10,000 pseudoabsence points.

We identified three geographically nested levels that are relevant to British bats and for which appropriate records were available. At the ‘regional’ level, the top HSM level, environmental predictors included climate and habitat cover data measured at five or 10km. At the ‘landscape’ level, environmental predictors included cover of the same and additional habitat categories measured at one or three km as well as the predicted suitability from the regional model. At the ‘local’ level, environmental predictions included the same habitat categories at higher

resolution, 100 or 500 m, distance measures to ecological (river, woodland edge and ToW) and anthropogenic (road and building) features, and the predicted suitability from the landscape model. To measure each predictor at the coarser resolution a moving window analysis was used to calculate the mean value of the variable within a radius (10km, 3km or 500m) of each raster pixel at the smaller scale using the focal tool in the raster package (Hijmans 2023). Predicted suitability of the previous level(s) were included by disaggregating the output to the resolution of the next level through bilinear interpolation, which calculates the value of the higher resolution pixel as a mean of the nearest lower resolution pixels weighted by distance.

The range of scales represented by the resolution of the predictors was chosen to encompass the variety of distances within which habitat variables have been shown to previously affect bat occurrence (Boughey et al. 2011, Bellamy et al. 2013, 2020, Bellamy and Altringham 2015, Wright et al. 2021). Habitat suitability modelling on similar bat communities in Britain have found that foraging activity was particularly affected by habitat features within 100-500m of survey locations (Bellamy et al. 2013), while roost selection was generally affected by habitat variables at larger scales, usually one – seven km, although the upper limit is often determined by study design (Boughey et al. 2011, Bellamy and Altringham 2015, Fuller et al. 2018b). The landscape level scales were chosen partly to reflect the lower end of this range and partly as many of the species' home ranges are estimated to be three to four km based on radiotracking data (Boughey et al. 2011). The regional level scales were selected to reflect the higher end of this range and to account for species with slightly larger home ranges as well as dispersal distances (Boughey et al. 2011, Bellamy et al. 2020).

For each model at each level, scale selection was run to determine the optimum scale for each variable to be included by creating univariate models using default settings (for example, at the regional level, did broadleaf cover at five or 10km best explain occurrence?). The scale with the highest training gain was selected. Variables were then tested for collinearity greater than 0.7 using the `layerstats` function in package 'raster' (Hijmans 2023). When collinear pairs were identified, the highest performing univariate model from the scale selection step was used. On occasion, one predictor was collinear with several others and this predictor was removed even if it was higher performing in order to retain as many predictors as possible.

The ENMeval package (Kass et al. 2021) was used to run three-fold cross validation and to identify optimal MaxEnt model settings. Geographically partitioned data folds were created using k means clustering on occurrence data. Pseudoabsence data were assigned to folds based

on the minimum distance to the centre of each data fold. Models were run with combinations of linear (L), quadratic (Q), product (P - interactions) and hinge (H - complex shapes) features; L, H, LQ, LQH, LQP and LQHP (Bellamy et al. 2020). Threshold features were not used to reduce the potential for overfitting. When included in the model, one linear and quadratic feature is created for each variable, product features are created for each pair of variables and the number of hinge features is constrained by sample size. The features allowed by model settings are all explored but only retained if they improve model performance (Merow et al. 2013). A range of regularisation parameter values from 0.5-4 at 0.5 increments were also tested, this controls how localised/closely fit the model is to the data and functions as a penalty for overfitting, with higher values indicating higher penalties (Shcheglovitova and Anderson 2013).

The optimal settings were then used to run a final MaxEnt model in the dismo package (Hijmans et al. 2023). Percentage contribution values (hereafter: ‘variable contribution’) were extracted to evaluate the relative influence of each predictor, this measure is similar to an r^2 but is relative such that values for all variables in a model sum to 100. Species-environment relationships were visualised using marginal response curves produced by r package ‘dismo’ (Hijmans et al. 2023), these plot predicted species occurrence against predictor values while all other predictors are held at their mean. Gridded predictions of logistic habitat suitability across Great Britain were also produced for each species at each level. When optimal model settings included interactions (MaxEnt ‘product’ features), details of those retained in the model, including magnitude and direction of the relationship, were extracted. Significance values of interactions or quadratic curves are not provided using this approach, but they are only retained if they improve model performance.

Model performance was assessed using a range of measures. The area under receiver operator curve (AUC) statistic is a widely used metric in HSMs and measures the ability of the model’s predicted suitability values to correctly rank presence sites as more favourable than pseudo-absences sites (Phillips et al. 2009). It ranges from 0-1 with a value of 0.5 considered no better than random discrimination. AUC has been criticised for a number of biases and sensitivities (Razgour et al. 2016), thus a Maximum Training Sensitivity and Specificity (MTSS) threshold was also used to create binary ‘suitable’ and ‘unsuitable’ areas (Liu et al. 2013). Sensitivity (alternatively; true-presence rate) was then calculated as the proportion of occurrence records found within the ‘suitable’ areas and specificity (alternatively; true-pseudoabsence rate) was

calculated as the proportion of pseudo-absences found within the ‘unsuitable’ areas. The statistical significance of the sensitivity measure was tested using a binomial test.

4.4 Results

4.4.1 Model Performance

Model performance as measured by AUC (area under curve) and sensitivity both varied by species and regional scales, however models had consistently high specificity. As expected, the AUC values were limited by a species’ prevalence, while this is considered a bias of the AUC metric similar patterns were also seen in the sensitivity metrics. For both *Pipistrellus spp.* which are generalist and widely distributed across the UK, AUC was low (<0.7) while *P. pipistrellus* had a non-significant sensitivity of 0 at regional levels and *P. pygmaeus* did not exceed a sensitivity of ~30%. Contrastingly *E. serotinus* and *Rhinolophus spp.*, which have restricted ranges in the UK performed best and had high AUC (>0.77) and sensitivity (~70 - 90%) across all levels. AUC values generally improved at lower model levels, with the exception of *N. noctula*, whose models performed poorly at all levels (AUC = 0.66). This species had low numbers of occurrence records ($n < 600$), particularly at local levels while being fairly widespread (other species had lower sample sizes but were geographically restricted, Table 4.1). Sensitivity similarly tended to increase at lower model levels, especially after the regional level, although there was sometimes a drop between landscape and local levels.

For all but *P. pipistrellus*’ regional output, relationships between habitat suitability at different scales were positive and had high contribution to model performance (Figs. 4.1, 4. 3, 4.5). Interactions between wider landscape suitability and habitat variables were common at both landscape and local levels (Figs. 4.2, 4.4, 4.6). In most cases, previous landscape suitability accentuated the benefits of positive environmental variables and tempered the drawbacks of negative environmental variables (positive interactions when the habitat variable was positively correlated with suitability and negative interactions when the habitat variable had a negative impact).

Table 4.1: Details of models, including number of occurrences, optimal settings (including features allowed and regularisation parameters) selected during tuning and AUC performance metrics. Bold highlights AUC values above 0.7. ME = AUC derived from the final MaxEnt Model; CV = AUC derived from cross-validation. Superscripts indicate level of significance as measured by binomial test: ‘***’ $p < 0.001$, ‘**’ $p < 0.01$, ‘*’ $p < 0.05$ and ‘ns’ $p > 0.05$

Species	Level	N records	MaxEnt Settings	AUC ME	AUC CV	Suitable area (%)	Sensitivity (%)	Specificity (%)
<i>E. serotinus</i>	Regional	366	LQHP_2.5	0.77	0.68	12.2	69.4***	71.8
	Landscape	431	LQ_0.5	0.79	0.75	11.5	68.7***	73.8
	Local	439	LQ_0.5	0.83	0.79	17.0	81.3***	66.7
<i>M. daubentonii</i>	Regional	988	H_2	0.61	0.61	1.1	3.0***	99.1
	Landscape	1239	LQHP_1.5	0.67	0.67	4.4	24.9***	90.9
	Local	1287	LQHP_3.5	0.72	0.74	11.3	52.8***	79.2
<i>M. nattereri</i>	Regional	444	LQHP_2	0.66	0.5	3.2	14.6***	94.1
	Landscape	546	LQ_0.5	0.74	0.66	14.7	58.8***	73.7
	Local	611	LQHP_1.5	0.86	0.83	13.8	34.8***	80.9
<i>N. noctula</i>	Regional	525	LQH_2	0.66	0.63	5.3	24.0***	88.1
	Landscape	590	LQ_0.5	0.67	0.65	8.0	34.7***	82.8
	Local	596	LQ_0.5	0.66	0.62	5.3	28.5***	86.8
<i>P. auritus</i>	Regional	700	LQH_2	0.60	0.47	2.3	8.3***	96.0
	Landscape	840	LQHP_1.5	0.69	0.63	13.3	47.7***	76.7
	Local	904	LQHP_2	0.81	0.78	12.6	64.7***	81.5
<i>R. ferrumequinum</i>	Regional	152	LQ_0.5	0.87	0.84	17.0	82.2***	76.6
	Landscape	206	LQ_0.5	0.91	0.84	11.2	82.3***	83.2
	Local	255	LQ_0.5	0.95	0.93	9.4	85.9***	89.0
<i>R. hipposideros</i>	Regional	394	LQHP_3	0.83	0.74	14.6	77.2***	73.7
	Landscape	625	LQH_1.5	0.90	0.88	10.0	81.0***	82.1
	Local	742	LQHP_2.5	0.95	0.93	8.8	86.7***	87.9
<i>P. pipistrellus</i>	Regional	1313	LQH_4	0.57	0.51	0	0 ^{ns}	100
	Landscape	1596	LQHP_2	0.65	0.64	5.9	24.3***	88.7
	Local	1642	LQHP_2	0.74	0.72	9.9	51.0***	83.6
<i>P. pygmaeus</i>	Regional	1088	LQH_1	0.61	0.55	3.3	5.1**	97.4
	Landscape	1352	LQHP_1.5	0.67	0.64	7.7	30.0***	87.1
	Local	1419	LQHP_4	0.72	0.69	3.7	29.1***	93.2

4.4.2 Regional-level Variables

Climate variables were mostly selected at the larger (10km) scale and had the strongest effect on occurrence for those species with restricted ranges in the UK such as *Rhinolophus spp.* and *E. serotinus* (Fig. 4.1). Habitat suitability for these species was highest in warmer, and for *Rhinolophus spp.*, wetter conditions. These areas are concentrated in their current known ranges in Southern Britain, especially the South-West for *Rhinolophus spp.* The suitability maps also highlighted some areas outside the current range that may be suitable for colonisation if these species’ ranges are able to continue expanding as populations recover (Fig. S4.10).

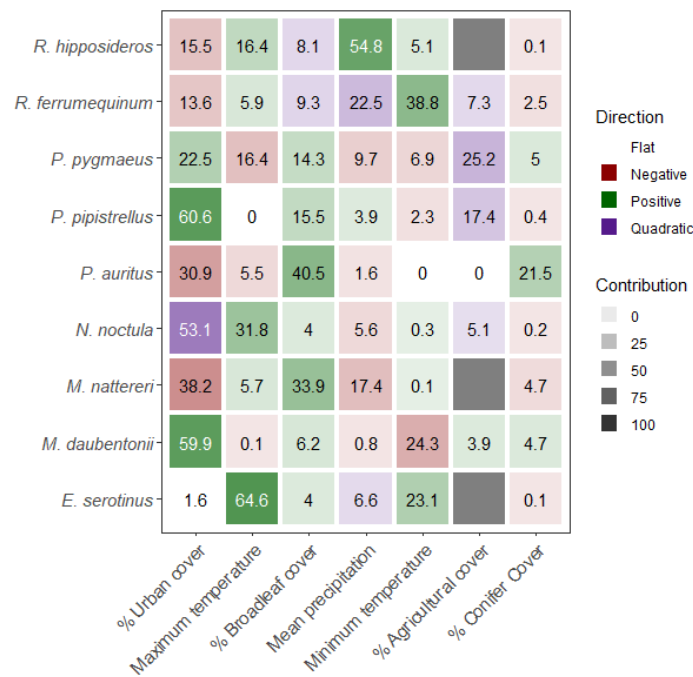


Figure 4.1: Heatmap of variable contribution and direction of relationship for each species in regional models. Relationship directions were estimated from MaxEnt response curves and classified as largely positive (green), largely negative (red), quadratic – when direction of effect varied at different values of the environmental variable (purple) and flat – when there was no relationship (white). Depth of colour and text label indicate variable contribution, this is calculated by MaxEnt as a measure of relative influence in the model (such that all variables sum to 100). Grey tiles indicate a variable that was not included in the model due to collinearity.

Other, widespread species were affected more by land cover and habitat measures, whose selected scales were more varied (Fig. 4.1). Bat species all responded positively to broadleaf cover and to a much lesser extent negatively to conifer cover, except *P. auritus* which had a particularly strong association with broadleaf and a fairly strong positive association with conifer cover. *Rhinolophus spp.* response curves displayed a quadratic response to broadleaf cover with suitability peaking at 10-15% cover (Fig. S4.1), however this is likely an artifact of their range as cover beyond this is not commonly found in this area.

Urban cover had a particularly strong and often negative impact on habitat suitability for many species. Conversely, *Pipistrellus spp.* and *M. daubentonii* were positively associated with urban cover, however this effect plateaued after ~20% for the latter. *N. noctula* had a quadratic relationship between urban cover and habitat suitability which peaked at around 80% cover (Fig. 4.2). Agricultural cover (encompassing both improved grass and arable) had limited effects outside *Pipistrellus spp.* but there tended to be a quadratic association with occurrence,

for some species habitat suitability peaked between 5-30% cover while for others the peak was around 80% cover (Fig S4.1).

Interactions were not very common at the regional level, with models for only three species performing best when they were included. Climatic variables often interacted with each other and there were occasional interactions between maximum temperature and habitat cover. The most consistent was an interaction between urban and broadleaf cover which was positive for *E. serotinus* and *M. nattereri*, indicating that the positive effects of broadleaf cover were accentuated when urban cover was high. Conversely this interaction was negative for *R. hipposideros*.

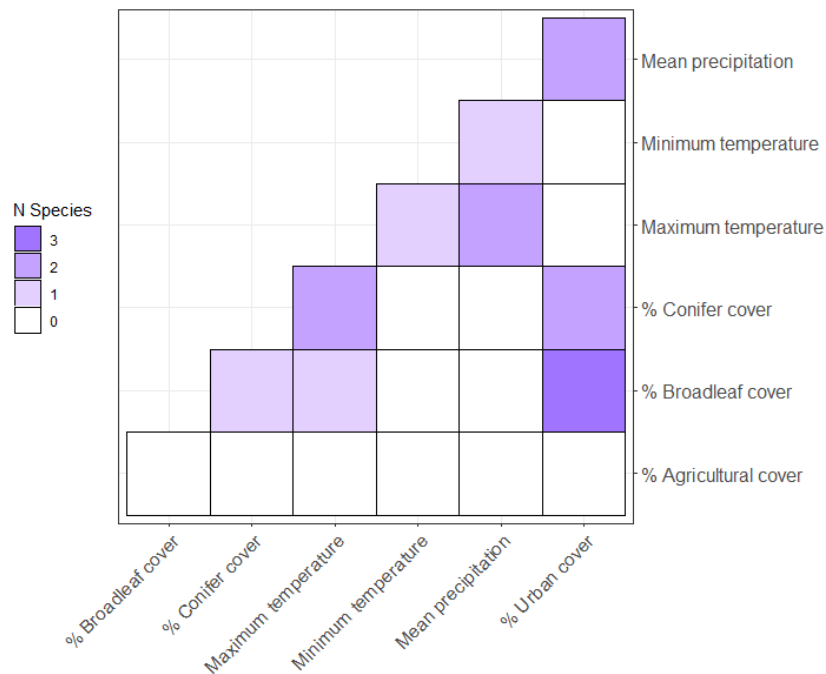


Figure 4.2: Heatmap showing number of species (depth of colour) in which the interaction between each pair of variables was retained in the regional level model. White tiles indicate a variable pair where no species model retained an interaction.

4.4.3 Landscape-level Variables

For species with restricted ranges in the UK such as *Rhinolophus spp.* and *E. serotinus*, climate variables continued to have a strong effect on species occurrence through the dominance of regional suitability in model contributions (70-90%, Fig. 4.3). Regional suitability also had a strong effect on species occurrence for *N. noctula*, despite this species being less geographically restricted in the UK. These species also tended to respond to habitat variables at larger scales. While regional suitability had varied importance in models for other species,

for all except *P. pipistrellus* it was positively associated with occurrence. For *P. pipistrellus* regional suitability had particularly low contribution to model performance (0.9) and the marginal response curve showed a negative relationship (although in a univariate model the relationship was positive, indicating an interaction or covariance with another predictor; Fig. S4.2).

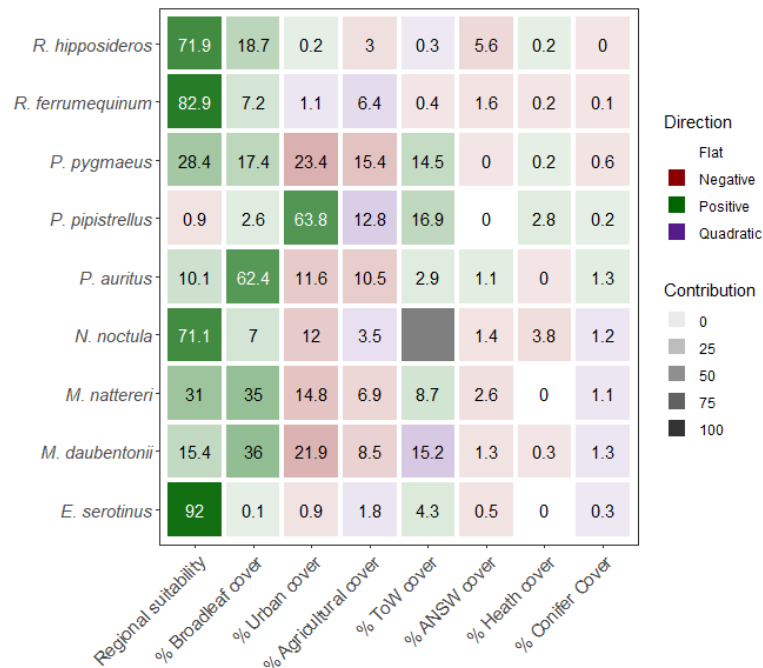


Figure 4.3: Heatmap of variable contribution and direction of relationship for each species in landscape models. Relationship directions were estimated from MaxEnt response curves and classified as largely positive (green), largely negative (red), quadratic – when direction of effect varied at different values of the environmental variable (purple) and flat – when there was no relationship (white). Depth of colour and text label indicate variable contribution, this is calculated by MaxEnt as a measure of relative influence in the model (such that all variables sum to 100). Grey tiles indicate a variable that was not included in the model due to collinearity.

Broadleaf cover continued to have positive associations with habitat suitability and was particularly important for *P. auritus* and *Myotis spp.* at the landscape level. For *M. nattereri*, suitability declined again as broadleaf cover increased beyond 50%, however only <0.01% of background or occurrence points were found in this range of cover, so model accuracy is likely to be low here. Trees outside woodland cover generally had positive (particularly for *M. daubentonii* and *Pipistrellus spp.*) or unimodal effects on habitat suitability, peaking at ~50-60% ToW cover values (Fig. S4.2). Ancient woodland and conifer cover both had limited impacts on habitat suitability, likely due to limited cover and relationships with other woodland cover variables.

Similarly to regional models, urban cover in landscape models continued to have overall negative effects, although for many species there was an initial positive effect below ~5% urban cover. Contrastingly, *P. pipistrellus* responded positively to urban cover (especially below ~40% cover) and this relationship had a strong contribution to the model. Agricultural cover had the strongest effects on *Pipistrellus spp.* and *M. daubentonii* and tended to have a negative association with habitat suitability across the range of cover but especially beyond ~85%. However, for some species the relationship was quadratic with peaks in habitat suitability between 30-55% cover.

Interactions were similarly limited to models for only four species at the landscape level. Agricultural habitat was most often involved in these interactions, particularly with broadleaf, urban and ToW cover. Broadleaf impacts were reduced with increasing agricultural cover whereas ToW and urban impacts increased with agricultural cover (except for *M. daubentonii* where they were reduced).

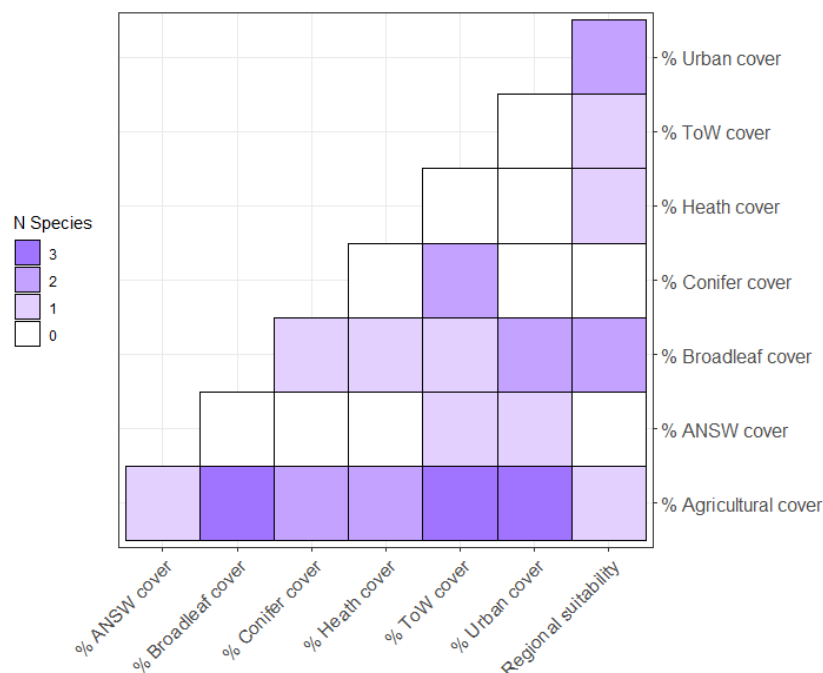


Figure 4.4: Heatmap showing number of species (depth of colour) in which the interaction between each pair of variables was retained in the landscape level model. White tiles indicate a variable pair where no species model retained an interaction

4.4.4 Local-level Variables

In the local level models, habitat variables for most species were largely selected at the 500m scale with the exception of trees outside woodland cover. Conversely, *R. hipposideros* was

more sensitive to 100m effects than other species. For species with restricted ranges in the UK such as *Rhinolophus spp.* and *E. serotinus* climate variables continued to have a strong effect on species occurrence through the dominance of landscape suitability in model contributions (70-80%). Landscape suitability also had a strong effect on species occurrence for *N. noctula*, despite this species being less geographically restricted. (Fig. 4.5).

Habitat suitability generally reduced with increasing distance from buildings, reducing steeply within a few 100m of buildings and continuing to reduce until 2km for many species. However, for *R. ferrumequinum* the relationship was unimodal, and suitability increased again beyond this distance (Figs. S4.3). Despite this positive association with buildings, which are often used as roosts, most species (exc. *P. pipistrellus*) continued to display a negative relationship to urban cover and to a lesser extent a positive relationship to distance from roads (Fig. 4.5).

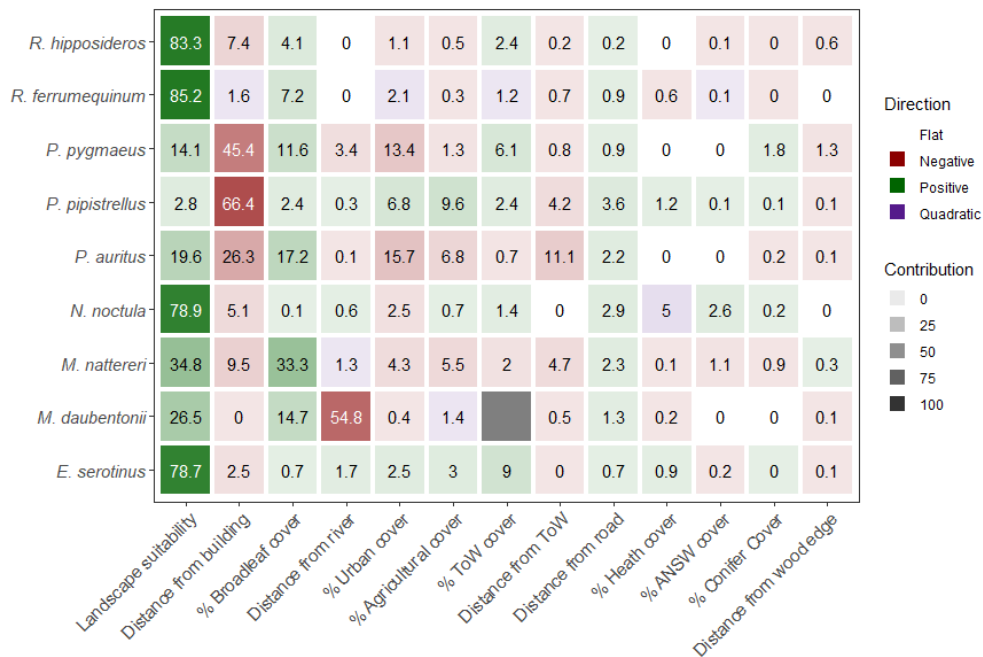


Figure 4.5: Heatmap of variable contribution and direction of relationship for each species in local level models. Relationship directions were estimated from MaxEnt response curves and classified as largely positive (green), largely negative (red), quadratic – when direction of effect varied at different values of the environmental variable (purple) and flat – when there was no relationship (white). Depth of colour and text label indicate variable contribution, this is calculated by MaxEnt as a measure of relative influence in the model (such that all variables sum to 100). Grey tiles indicate a variable that was not included in the model due to collinearity.

Broadleaf cover also continued to have positive associations with habitat suitability at this level and had a particularly high variable contribution for *M. nattereri* (Fig. 4.5). While overall contribution was low, broadleaf was also the most important variable to *R. ferrumequinum* after

landscape suitability. Trees outside woodland cover and distance from nearest ToW feature had small impacts but habitat suitability was highest with increased cover and reduced distance from ToW (particularly within a few 100m). Ancient woodland, conifer and distance from woodland edge again had limited impact on habitat suitability, likely due to limited cover and relationships to other woodland cover variables.

Distance from rivers had limited effects on species other than *M. daubentonii* for which suitability dropped steeply as distance from rivers increased from 0 to ~100m. Agriculture and heath also had limited effects on species. Agriculture showed a strong negative relationship with *P. auritus* and *M. nattereri* occurrence.

Interactions were much more common at local levels, with six species' models performing best when included and a greater number of interactions. As with landscape level models, agricultural cover was most often involved in these interactions, particularly with broadleaf, urban and ToW cover. The effect of broadleaf and urban cover increased with agricultural cover, and ToW similarly positively interacted with agriculture except for *P. auritus* and *M. nattereri* indicating that agricultural habitats were more attractive when some woody or urban habitat were also present. There was also a positive interaction between broadleaf cover and ToW cover for 3 species (*P. auritus*, *R. hipposideros* and *M. nattereri*)

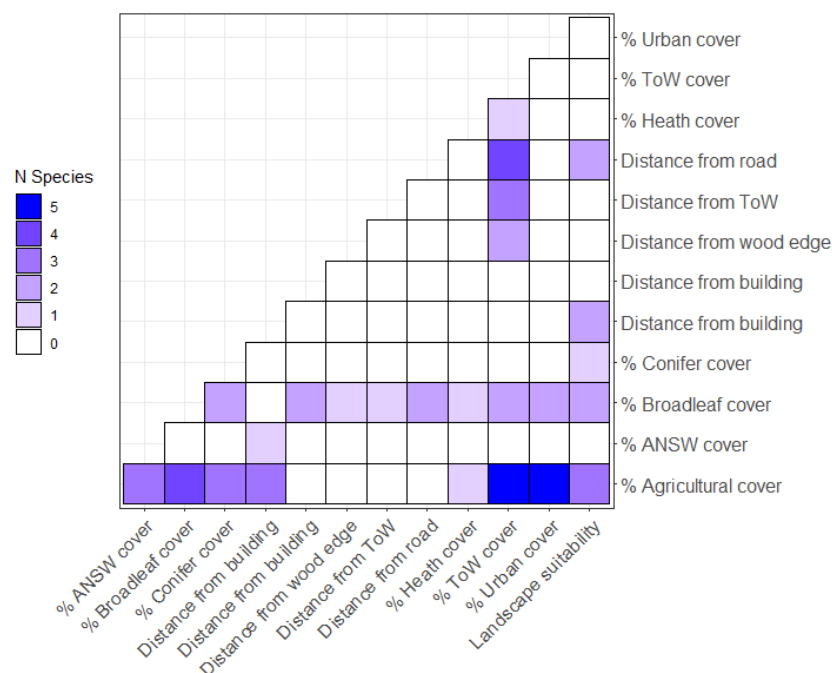


Figure 4.6: Heatmap showing number of species (depth of colour) in which the interaction between each pair of variables was retained in the local level model. White tiles indicate a variable pair where no species model retained an interaction.

4.5 Discussion

4.5.1 Model Performance

Overall, the habitat suitability models performed well, with all but one achieving significance and with most species exceeding an AUC score of 0.7 in the final model at the local level. Specificity (ability to correctly predict pseudo-absences) was high across species and levels, but sensitivity (ability to correctly predict presences) and AUC varied according to how widespread the species is. Species that have limited ranges in the UK performed very well at all levels of the model, while widespread generalist species' models tended not to perform as well at regional and landscape levels. At the local level, species that are considered woodland specialists performed better than those considered generalist species which reflects previous poorer performance of generalist species, particularly *P. pipistrellus* due to limited difference in occurrence and absence locations (Boughey et al. 2011, Bellamy et al. 2013, Razgour et al. 2016, Wright et al. 2021).

Model performance increased at lower (greater spatial grain) levels, which incorporated predictions from higher levels. For all but *P. pipistrellus*' regional model, relationships between habitat suitability at different levels were positive and higher-level suitability generally had high contribution to model performance. In general, regional or landscape suitability had the highest, or second highest, model contribution (after urban or broadleaf at landscape level and after distance from buildings at the local level). One notable exception was the consistent lack of connections between suitability at different scales for *P. pipistrellus*, a finding that is most likely driven by the poor performance leading to fairly uniform suitability predictions across the UK, particularly at the regional level (Fig. S4.11). This poor regional level performance may be driven by niche truncation, as models conducted across a wider portion of *P. pipistrellus*' global range is likely to have highlighted stronger associations with climate variables. Additionally, this suggests that *P. pipistrellus* is mostly impacted by local conditions within its British range, rather than the wider landscape or regional context. This reflects previous results on activity where this species had no or limited response to landscape measures in comparison to local features (Lintott et al. 2015b, Fuentes-Montemayor et al. 2017, Kirkpatrick et al. 2017a, Foxley et al. 2023), although other studies have found the opposite in some areas (Fuentes-Montemayor et al. 2017, Froidevaux et al. 2021).

Interactions between wider landscape suitability and habitat variables were common at both landscape and local levels and reflect interplays between environmental drivers of species occurrence across different scales (Spake et al. 2019, Bellamy et al. 2020). With only a few exceptions, high landscape suitability accentuated the benefits of positive environmental variables and tempered the drawbacks of negative environmental variables (positive interactions when the habitat variable was positively correlated with suitability and negative interactions when the habitat variable had a negative impact). This suggests that conservation measures to improve local habitat features for bats are likely to be most beneficial in more suitable landscapes, in agreement with previous studies (Vergara and Armesto 2009, O'Rourke et al. 2011, Ponisio et al. 2019). In contrast, some studies have found that the largest benefits of local habitat improvements were in more hostile landscapes (Batáry et al. 2010, Sullivan et al. 2017, de Zwaan et al. 2024). Vergara and Armesto (2009) found that local variables were more commonly dependent on landscape context for habitat specialists, but this was not the case in this study where the majority of species including the more generalist and more specialist species all displayed interactions.

4.5.2 Climate

Climate variables had the highest contributions to models where the known range of the species within the UK is restricted. This agrees with previous studies that have found that spatial truncation of species occurrences (as when models are run on one country) can limit performance of habitat suitability models as variables may only cover a subset of those experienced by a species in its global range, although this is less of an issue when models cover the edges of a habitat or climate niche (Di Febbraro et al. 2015, Razgour et al. 2016, Bellamy et al. 2020, Goicolea et al. 2024). Species in the UK that are not at their latitudinal limit are unlikely to be strongly impacted by the relatively limited climate differences across the country (in comparison to what is experienced across their global range). Contrastingly, both *Rhinolophus spp.* and *E. serotinus* are at their latitudinal limits and thus climate plays a large role; *N. noctula*, which is less restricted in the UK but is still absent from central and northern Scotland, had moderate importance of climate variables.

Interestingly, although *Rhinolophus spp.* have more restricted ranges than *E. serotinus* the overall contribution of climate variables was higher for the latter (94.3 cf. 76.3 for *R. hipposideros* and 67.2 for *R. ferrumequinum*). This could be driven by a greater sensitivity to

land use variables in *Rhinolophus spp.* as percent contribution values calculated by MaxEnt are relative (such that all variables sum to 100) and in connection reflect a larger difference between fundamental and realised niches for *Rhinolophus spp.* Gridded predictions of suitability for *E. serotinus* did not highlight areas outside of their current known range as suitable, suggesting that climate is the main limit on their regional distribution in the UK. For *Rhinolophus spp.* predictions highlighted suitable areas outside of their current range and they were previously more widespread in Britain, including the Southeast and, for *R. hipposideros*, some areas in the north of England, suggesting that they are not occupying all areas of the UK within their climatic niche (Harris et al. 1995). Habitat changes thus likely drove range contractions in the 20th Century and are possibly limiting their recovery to these areas. Some recovery of the former range has already occurred during the early 21st century, while this is often attributed to milder winters allowing population growth (Browning et al. 2021) targeting habitat improvements in these areas could support further range expansion.

4.5.3 Habitat Associations

In agreement with known ecological preferences and previous HSM studies, all species responded positively to broadleaf cover (Boughey et al. 2011, Bellamy et al. 2013, Tournant et al. 2013, Browning et al. 2021). A few species had unimodal responses, particularly *Rhinolophus spp.* at regional levels, where declines in habitat suitability occurred beyond 10-15% cover however this is most likely driven by cover above 15% being rare within their current range. Previous HSMs found the biggest impact on roost probability occurred when broadleaf cover increased between 0-20% for some species (Boughey et al. 2011). Here, visual inspection of marginal response curves did not indicate that any particular range of cover increase was most beneficial across species and scales (Figs. S4.1, S4.2, S4.3). While for some species curves were steepest at the low end of broadleaf cover, especially at regional and landscape scales, for some the steepest increases were at higher values of cover and, especially at local scales, some species responses were fairly uniform across the range of cover. This suggests that while the benefits to particular species may vary, on the whole promoting woodland expansion will have positive impacts on bat communities regardless of existing woodland cover.

Broadleaf cover benefits were modulated by the landscape context, particularly through interactions with agricultural and urban cover. Urban cover tended to enhance the benefits of

broadleaf cover. It is possible that the co-occurrence of both habitats allows for provision of roosts near foraging areas and that small-scale fragmentation can increase the density of woodland edge which is an important foraging habitat for some species. Alternatively, woodland patches could function as particularly important remnant habitat areas in highly urban areas, in line with previous studies that found increased tree cover improved the suitability of urban areas for some species (Dixon 2012, Lintott et al. 2016). Conversely, for *R. hipposideros* and *P. auritus*, urban cover reduced the benefits of broadleaf woodlands suggesting that these species are particularly sensitive to urbanisation and that woodlands in urban areas provide fewer benefits than those in rural areas.

At landscape scales, agricultural cover had a dampening effect on the benefits of broadleaf cover, suggesting that woodland within highly agricultural areas is of poorer quality. This could possibly be due to poor foraging opportunities in the surrounding agricultural land due to pesticide use and lack of invertebrate habitat, or loss of connectivity to other woodland habitats (Browning et al. 2021). At local scales the interaction had the opposite effect with agricultural cover enhancing the benefits of broadleaf cover. As with interactions with urban cover, this may indicate the benefits of increased edge density and habitat complementation when woodland patches are dispersed through a matrix (Fahrig 2003). Alternatively, the more hostile landscape created by greater agricultural cover may make bats more sensitive to woodland cover, as there are limited foraging opportunities outside these habitat patches. Previous studies have found that increased matrix permeability (reduced contrast with a species' main habitat) reduces the effects of habitat cover on a species' presence (Carroll et al. 2004, Humphrey et al. 2015, Rodríguez-San Pedro and Simonetti 2015, Otálora-Ardila and López-Arévalo 2021). Fuentes-Montemayor et al. (2017) similarly found that for a number of bat species, relationships between activity and landscape variables, including woodland and semi-natural habitat cover and proximity, were higher in England than in Scotland which was argued to be due to higher intensity agricultural patterns.

There were limited impacts of conifer cover on habitat suitability, with low model contributions across species and especially at lower scales. One notable exception is that *P. auritus*, considered a broadleaf specialist, responded positively to conifer cover at regional scales with good model contributions, contrary to previous studies where no response was found (Bellamy et al. 2013, Bellamy and Altringham 2015). Previous studies have found that *P. auritus* will utilise conifer cover when it is the most prevalent woodland habitat and provided that roost

structures are available nearby (Chapter 2; Benzal 1991, Kirkpatrick et al. 2017a, Cook et al. 2023). Additionally, at a coarse scale, conifer forests are likely to co-occur with areas of mixed woodlands, which was not included as a predictor, but has previously been found to positively impact habitat suitability (Bellamy et al. 2013). Ancient semi-natural woodland had limited impacts on habitat suitability, likely due to generally small coverage and limited variation in cover across the UK and limitations of the existing spatial dataset, which only maps areas >2ha. This is currently being improved (C. Bellamy, pers. comm.) and future research should incorporate these updated datasets to further investigate the impacts of ancient woodland for bats.

Trees outside woodlands are estimated to make up 22% of woody cover in the UK (Liu et al. 2023), and they had a mostly positive impact, with suitability for most species highest with greater cover and closer to ToW features. Woody features have previously been difficult to map (Scholefield et al. 2016) and thus limited in their inclusion in habitat suitability models. However some studies using previous, less detailed linear features datasets similarly found higher suitability closest to these features for some species (Bellamy et al. 2020, Wright et al. 2021). These results are also in agreement with previous field studies showing higher activity and a preference for feeding and commuting around such elements (Chapter 3, Downs and Racey 2006, Frey-Ehrenbold et al. 2013, Froidevaux et al. 2019, Finch et al. 2020b, Browning et al. 2021).

Studies of other taxa have often found that the effects of ToW are landscape dependent, with benefits highest in intensive agricultural areas for birds (Batáry et al. 2010, Sullivan et al. 2017, de Zwaan et al. 2024) and increasing with semi-natural cover habitat for bees (Ponisio et al. 2019). Similarly, interactions between ToW and agricultural cover were common in the models and the majority of these were positive suggesting ToW provide the highest benefits to bats in areas with higher agricultural cover. Some interactions however were negative (*M. daubentonii* at landscape scale; *M. nattereri* and *P. auritus* at local scales) suggesting that for these species the negative impacts of agricultural cover are not alleviated by ToW cover. Greater agricultural cover usually comes at a cost of reduced woodland area, so it may be that ToW are of limited benefit when the core woodland habitat patches are missing. This is supported by the fact that *Myotis spp.* and *Plecotus spp.* activity at ToW is reduced when connectivity to other woody habitats is low (Frey-Ehrenbold et al. 2013) and that all these species also had positive interaction between ToW and broadleaf cover in the HSM models.

The impact of ToW on habitat suitability was generally limited compared to broadleaf cover, except for *P. pipistrellus* and *E. serotinus* for which ToW contributions exceeded those of woodland cover. Contrastingly, previous studies have found smaller effects of ToW on activity for medium and long-range echolocation guilds, to which these species respectively belong (Frey-Ehrenbold et al. 2013) and negative responses of *Eptesicus spp.* activity to ToW cover (Froidevaux et al. 2019). Both of these species had quadratic and positive responses to agricultural cover (at landscape and local scales respectively) suggesting they are regularly using areas with high agricultural cover; while these species may not intensively use linear elements, their occurrence may act as a measure of agricultural intensity and prey availability (Foxley et al. 2023). They are also generalist species that are considered less reliant on broadleaf so it may be that quality of agricultural areas (e.g. occurrence of ToW features) is more important than woodland cover.

Anthropogenic habitats and sources of disturbance generally had negative impacts, with habitat suitability for the majority of species decreasing with increased urban cover in agreement with previous habitat suitability modelling across a range of species and countries (Tournant et al. 2013, Fuller et al. 2018b, Bellamy et al. 2020, Cable et al. 2021, Wright et al. 2021). The drivers of negative bat responses to urbanisation are commonly attributed to habitat loss, hunting by domestic cats, and light, noise and chemical pollution which are particularly present on roads which also bring the risk of mortality from vehicle collisions (Browning et al. 2021, Foxley et al. 2023). While buildings can provide roosting opportunities, the loss of woodland and other native vegetation removes foraging habitats and reduces invertebrate prey availability (Browning et al. 2021).

Species were also more likely to occur near buildings as in Bellamy et al. (2020). This may seem counter to the negative impact of urban cover, however this effect was greatest at the local scale and was limited beyond a few 100 meters and likely reflects the large proportion of building roosts found in the occurrence datasets. Taken together these relationships suggest that suitable roost habitat is found in buildings in rural areas away from conurbations. Similarly, most species had a small increase in suitability at very low levels of urban cover despite an overall negative response, possibly reflecting a similar relationship where very low densities of buildings allow for roosting without the negative impacts of more urbanised areas outlined above.

Pipistrellus pipistrellus was an outlier with positive responses to urban cover at all scales, a similar response was found in Bellamy and Altringham (2015). National monitoring additionally suggests this species' populations are currently doing best in greater London (K. Boughey, pers. comm.), which suggests some adaptation to urbanisation. However, it is worth noting that previous analyses of *P. pipistrellus* occurrences in field surveys conducted as part of the NBMP found negative impacts of urban cover (Lintott et al. 2016). Additionally, urban cover in greater London varies greatly from fairly suburban areas with gardens that provide habitat for bats and their prey to high density areas in the centre where vegetation is limited and urban pressures will be very high (at the 1km scale, urban cover values across all London Boroughs has a median of 81% IQR 46%). It has previously been theorised that bat populations' equivocal responses to urban cover may result from stable abundances and high densities but with lower condition and reproduction rates (Lintott et al. 2015a, Browning et al. 2021).

Roads also had a negative impact on all species, with habitat suitability increasing with distance from these features. Negative impacts from roads can be direct, through roadkill, and indirect through avoidance and noise pollution causing reduced activity and barriers (Berthinussen and Altringham 2012, Finch et al. 2020c). Avoidance caused by noise and light pollution are thought to be very localised with impacts limited to a few hundred meters (Berthinussen and Altringham 2012, Finch et al. 2020c). This study found increases in habitat suitability continued multiple kilometres from roads, in agreement with Berthinussen and Altringham (2012)'s findings that bat activity and diversity increased up to 1.6km from roads. Impacts at this scale are more likely to be driven by increased mortality and barrier effects reducing foraging areas and disrupting commutes which both reduce reproductive output and cause relocation of nearby roosts (Berthinussen and Altringham 2012).

Previous habitat suitability models on bats in the UK and Europe found more mixed responses to road cover, with both positive (Scherrer et al. 2019) and quadratic responses, where suitability peaked at 10-20% cover (Bellamy et al. 2013). These differences may be driven by the localised nature of these studies. Bellamy et al. (2013) note that most roads in the area are minor with likely low traffic volumes and are lined with features such as hedges that bats use for commuting and foraging (Scherrer et al. 2019). This study included only major and main roads which are likely to be more impactful than minor roads, acting as larger barriers and

causing more disturbances. Additionally, trees outside woodland were included separately reducing the conflation of linear elements and roads.

Responses to agricultural cover were more equivocal but generally high agricultural cover had a negative effect in line with previous studies (Bellamy et al. 2020, Cable et al. 2021). At regional levels the relationship was generally quadratic, increasing with low cover but decreasing with high cover but had limited contribution outside the *Pipistrellus spp.* (although it should be noted that for some species, 10km scale agricultural cover was removed from the model as it was correlated with maximum temperature, $\rho = 0.77$, which generally explained higher variation in univariate models). At landscape scales, responses were a mixture of negative and unimodal (with habitat suitability peaking around 40-50% cover) and at local scales negative responses remained in those species but the unimodal ones tended to become positive. Agriculture also exerted influences on the effects of other habitats being by far the variable most often found in interactions with other variables at landscape and local levels.

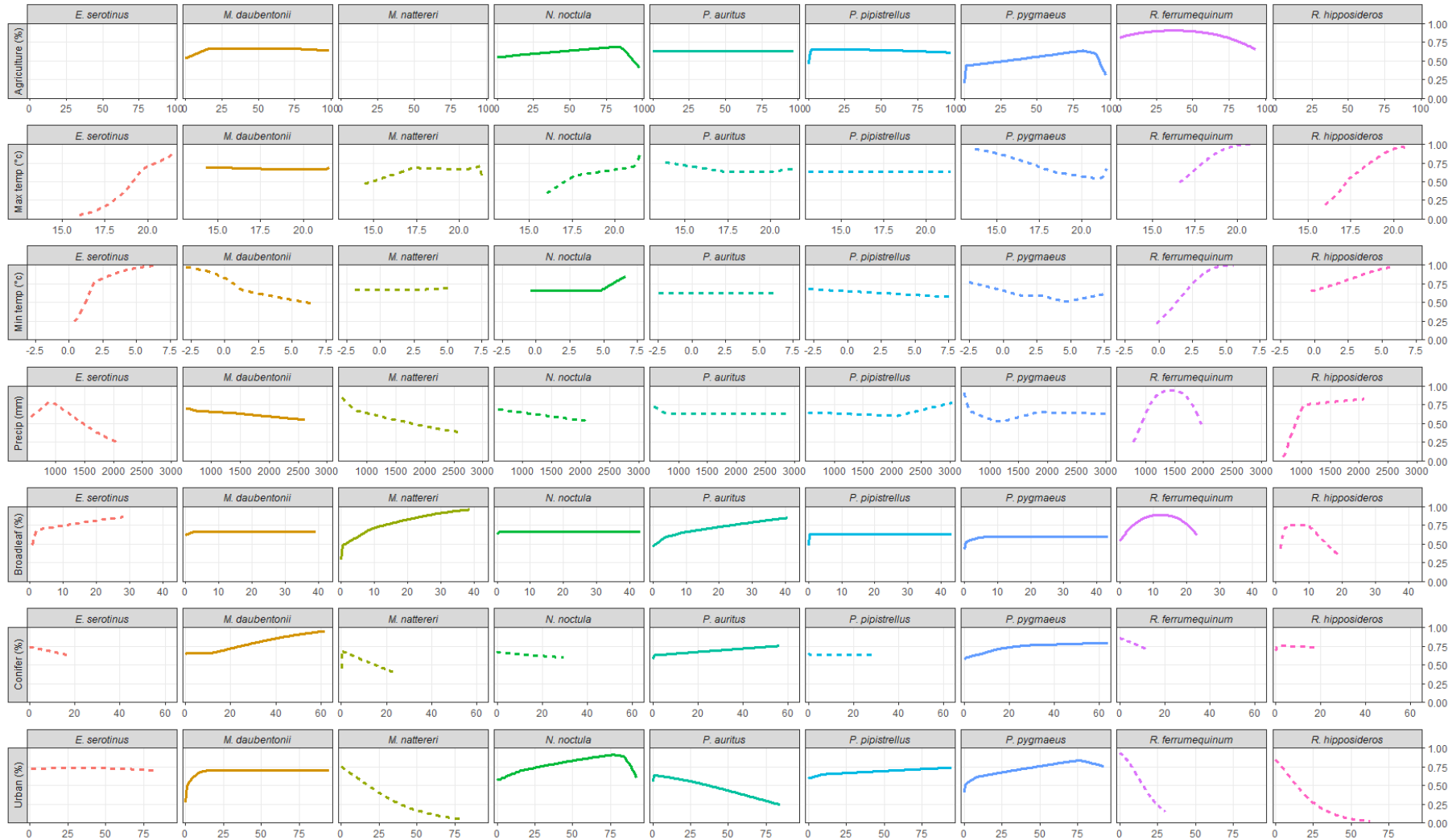
At low levels of cover, agricultural areas provide foraging habitats as the occurrence of livestock can attract insect prey and margin vegetation like hedges or grass strips can also provide habitats for invertebrates (Ancillotto et al. 2017, Wood et al. 2017, Anderson et al. 2020, Foxley et al. 2023). Some species have also been recorded as highly active over improved grasslands (Browning et al. 2021, Foxley et al. 2023) and this is reflected in Boughey et al. (2011) where improved grass had positive impacts on habitat suitability for a range of species at landscape scales. At higher levels of cover, agricultural practice is likely to be more intensive, with pesticides and a lack of margins reducing insect availability and likely loss of other important habitats such as woodlands and trees outside woodlands (Browning et al. 2021).

4.5.4 Conclusions

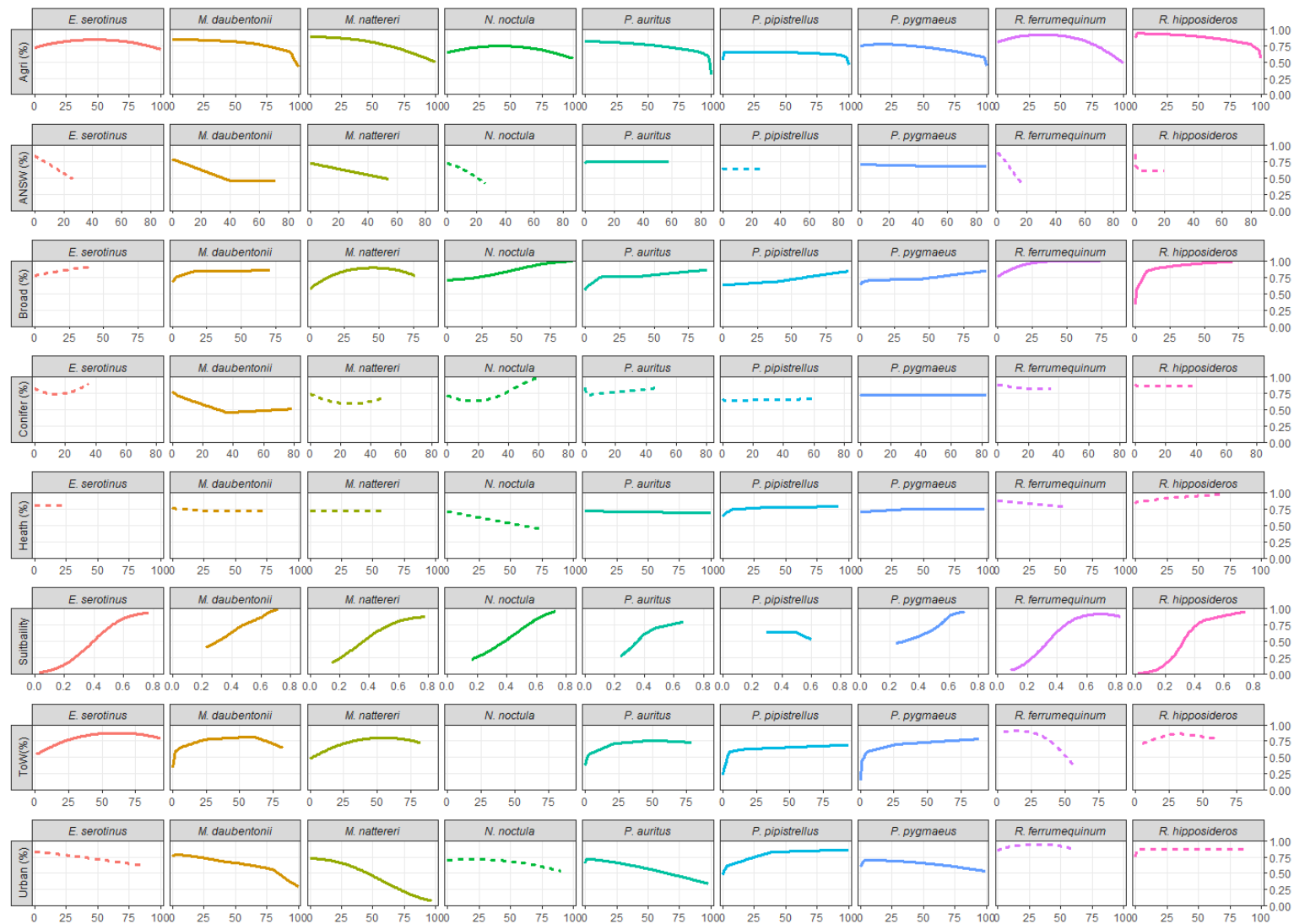
This study has highlighted habitat associations for many of the most common species of bats in the UK and by using a multi-level approach has identified important cross-scale interactions. The picture is complex and varies between species and scales considered, however some general patterns emerged. Broadleaf woodland and trees outside woodland had a positive impact on all species, adding to evidence that promoting woody cover expansion will be of conservation benefit to bats (Browning et al. 2021). While some previous studies have found the greatest benefits of new woodland below certain levels of existing cover (Boughey et al.

2011), in this study there was no strong indication that any particular range of cover increase was most beneficial across all species and scales. Some species had the steepest association between habitat suitability and broadleaf cover at low cover, but others had the opposite. Similarly, some species saw increased benefits of woodland and ToW cover in high agricultural cover or urban areas while others saw reduced benefits. While the benefits to species may vary, on the whole, promoting woodland expansion will have positive impacts on bat communities in all landscapes. Agricultural cover had mixed effects, but on the whole high levels of cover tended to be negative. Urban cover also typically negatively affected suitability, although rural buildings allowed for roosts. Conservation actions should generally focus on creating good quality woodlands and promoting sympathetic management of hedges regardless of landscape context as there is a lot of evidence that increasing woodland structural complexity and diversity (Fuentes-Montemayor et al. 2013, 2017, Kirkpatrick et al. 2017b, Alder et al. 2020, Cook et al. 2023) and conserving or creating larger, sensitively managed ToW increase bat activity (Froidevaux et al. 2019, Finch et al. 2020b, Foxley et al. 2023). In addition, gridded suitability outputs can be used to identify and target habitat improvement in areas where poor quality areas present barriers to range recovery (as in *Rhinolophus spp.*) or future climate range-shifts.

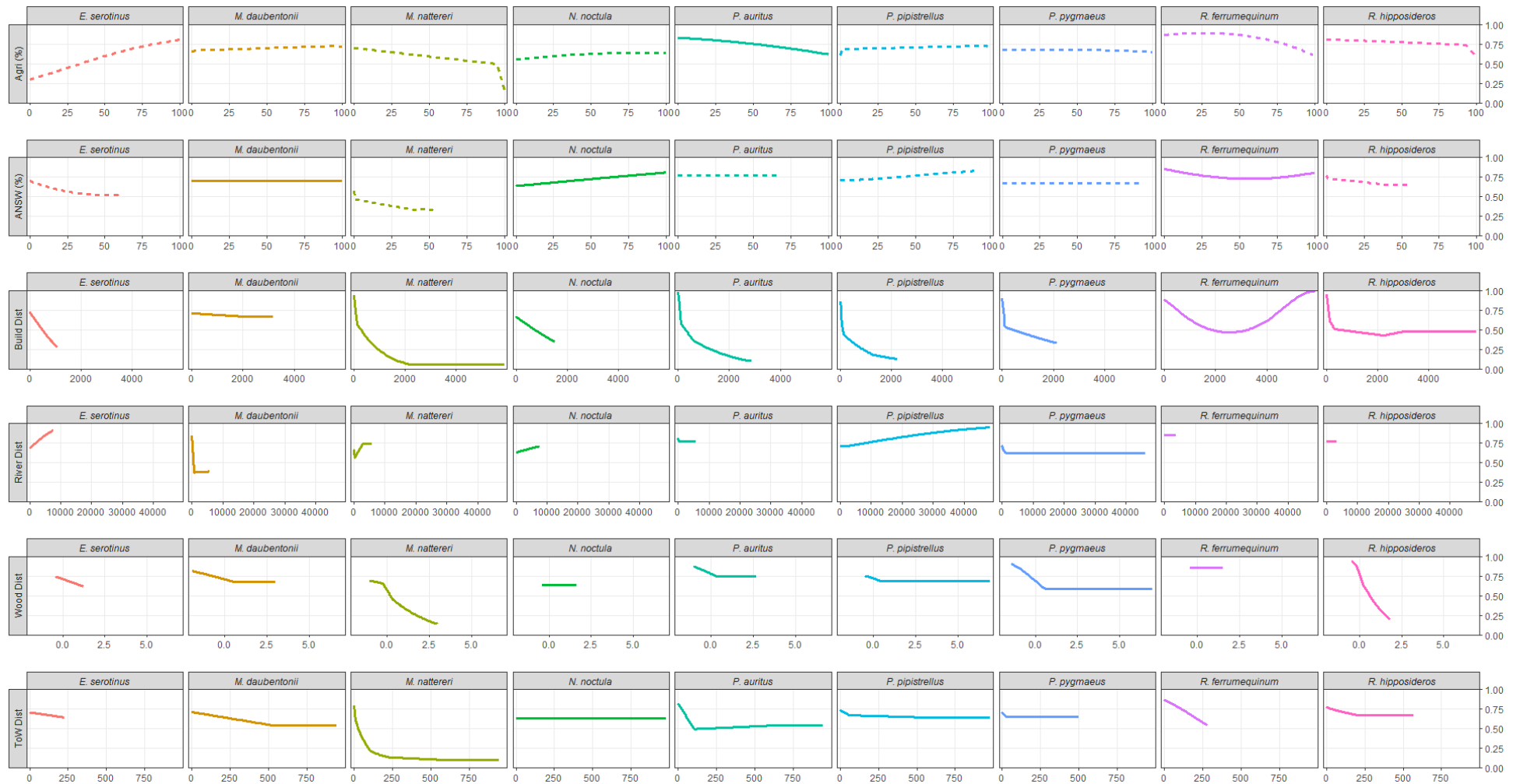
4.6 Supplementary Materials 4.1 – Marginal Response Curves

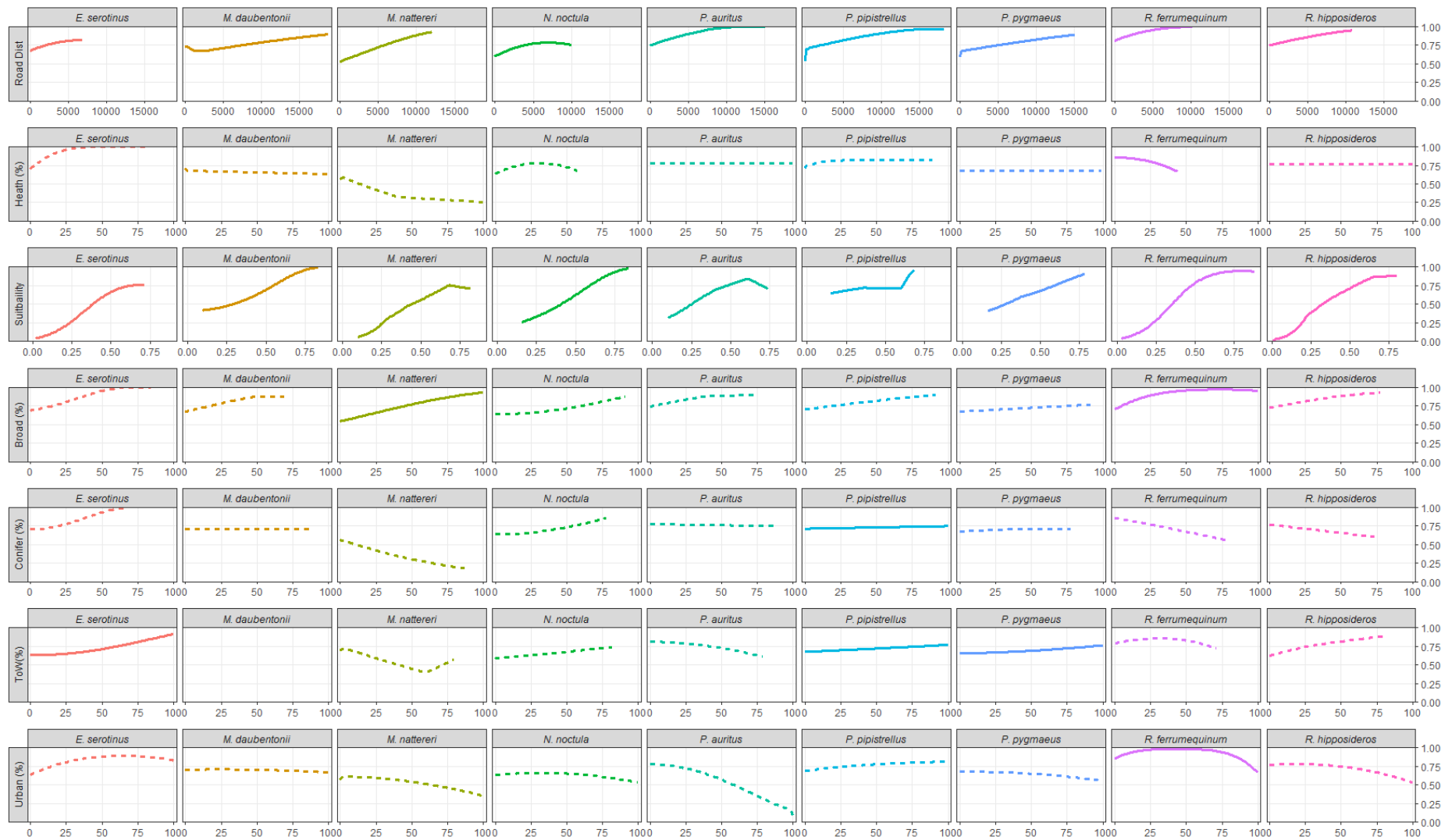


Supplemental Figure 4.1: Response curves displaying relationships between habitat suitability and environmental variables at the regional level. Full lines indicate 5km scale and dashed lines indicate 10km scale. Blank graphs indicate where variables were removed due to collinearity.



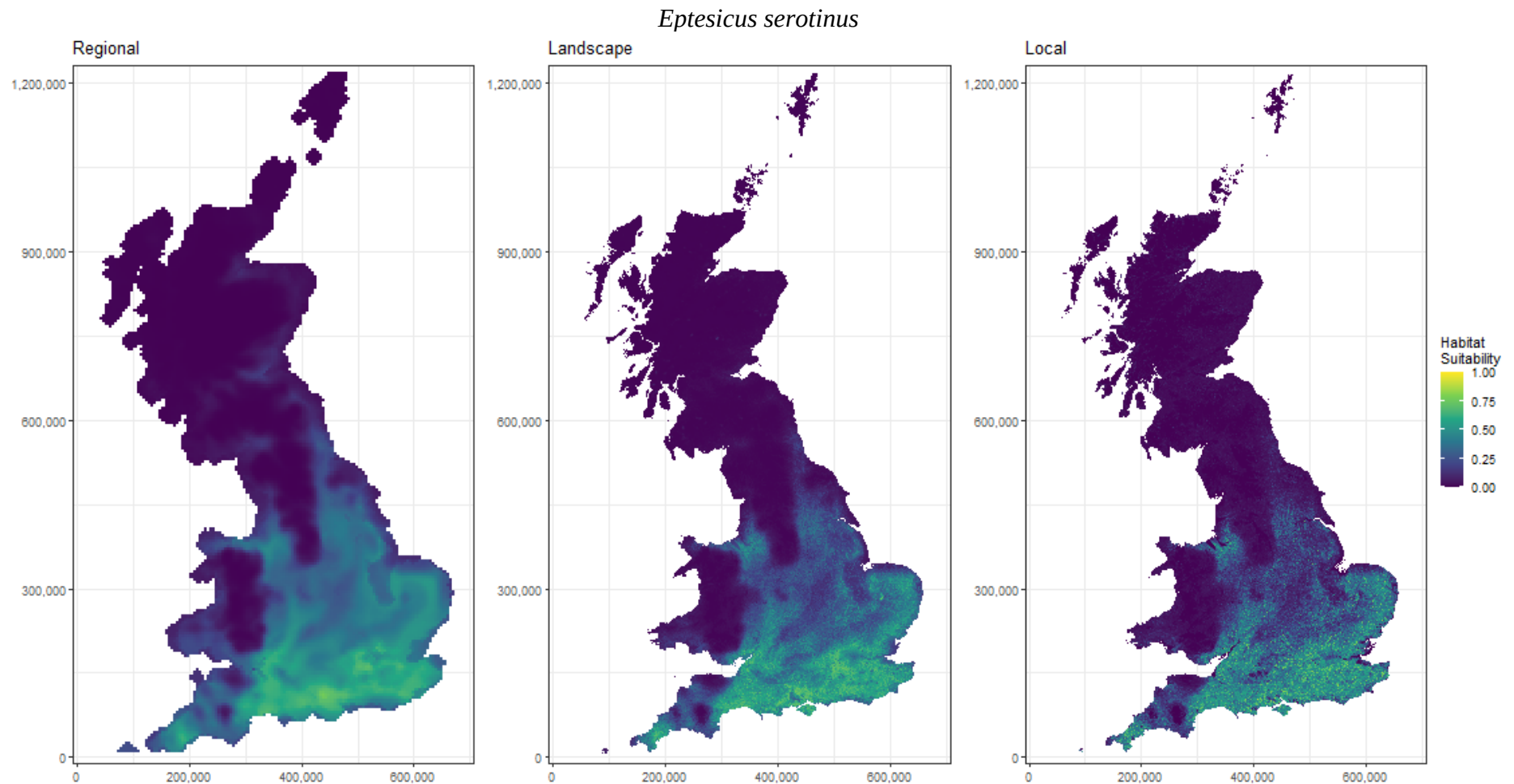
Supplemental Figure 4.2: Response curves displaying relationships between habitat suitability and environmental variables at the landscape level. Full lines indicate 1km scale and dashed lines 3km scale. Blank graphs indicate where variables were removed due to collinearity.





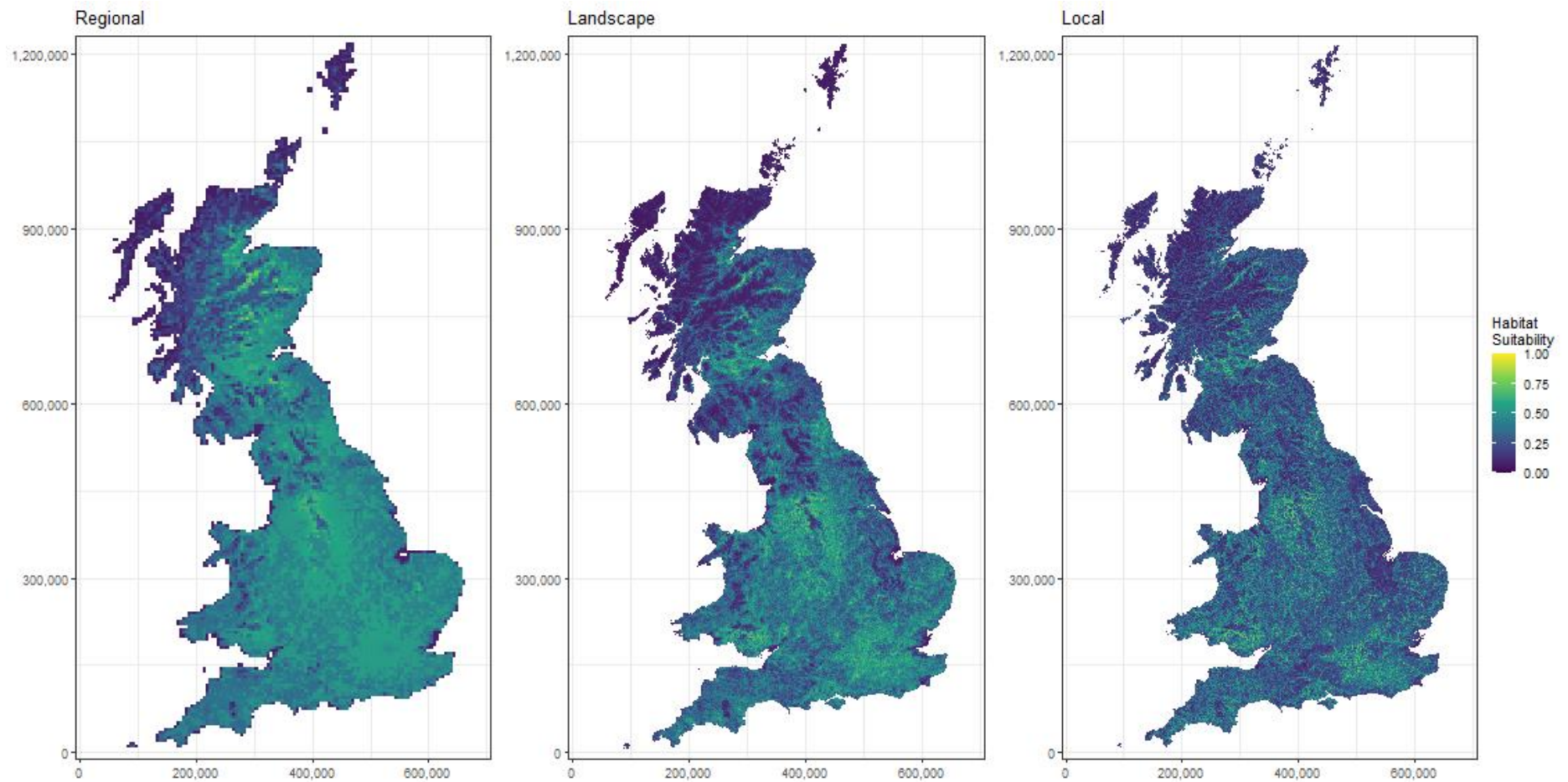
Supplemental Figure 4.3: Response curves displaying relationships between habitat suitability and environmental variables at the landscape level. Full lines indicate 1km scale and dashed lines 3km scale. Blank graphs indicate where variables were removed due to collinearity. Distance variables were measured in meters.

4.7 Supplementary Materials 4.2 – Gridded Habitat Suitability Maps



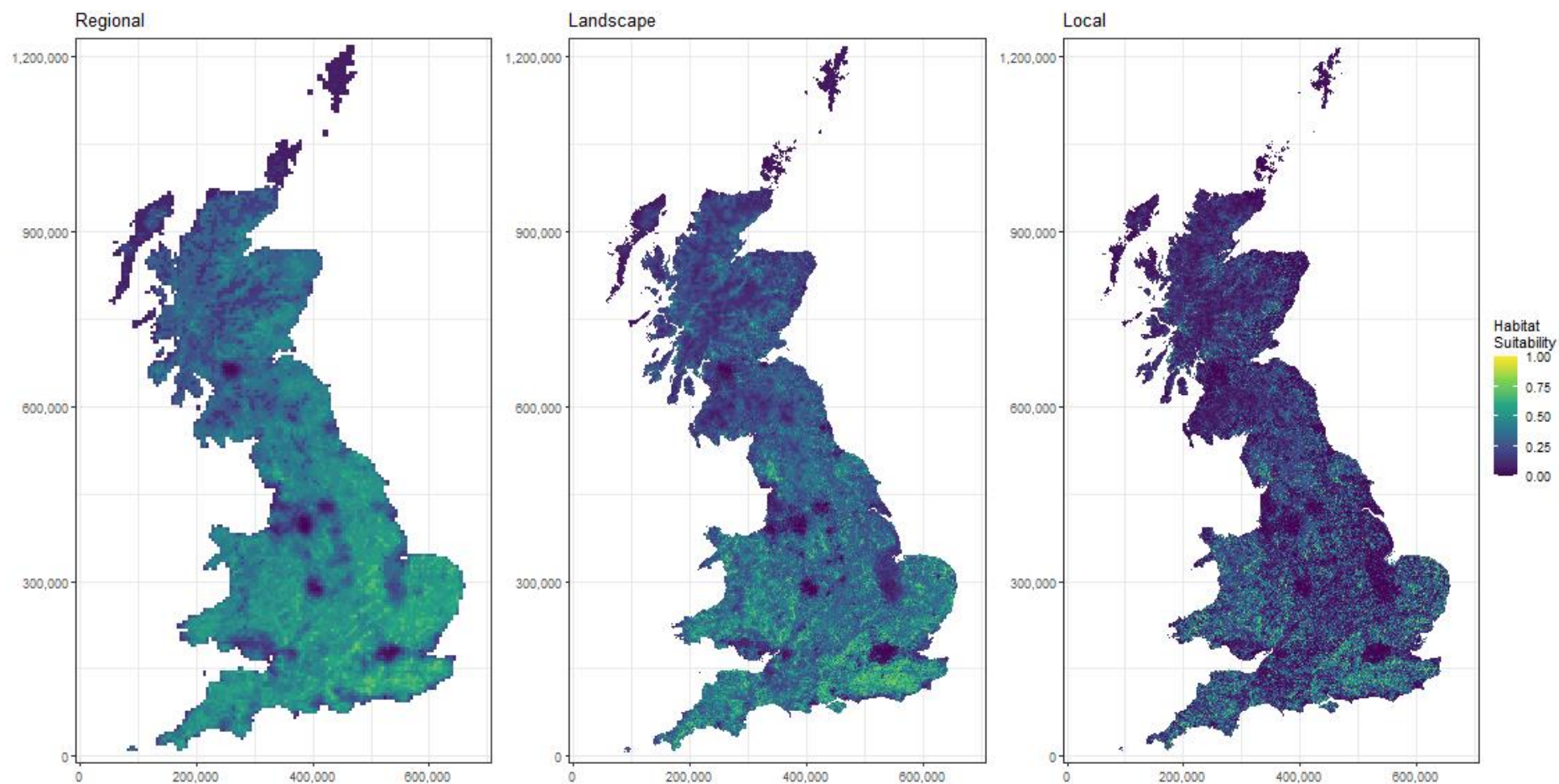
Supplemental Figure 4.4: Gridded maps of logistic predicted habitat suitability across Great Britain for *E. serotinus* at each level of the spatially nested model. Regional; 5km resolution based on climate and coarse habitat cover, Landscape; 1km based on wider habitat cover and regional output, Local; 100m resolution based on habitat cover, local features and landscape output

Myotis daubentonii



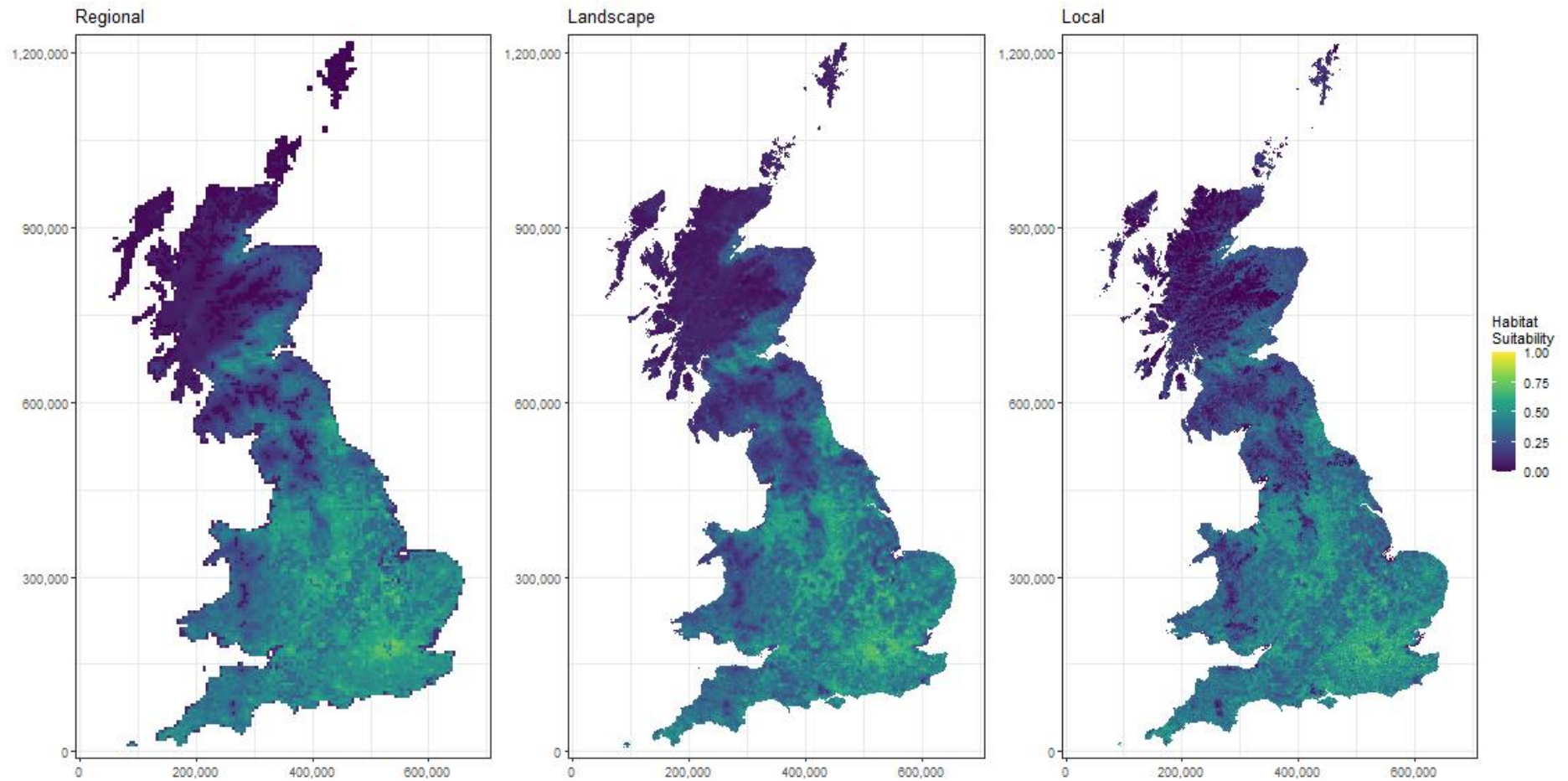
Supplemental Figure 4.5: Gridded maps of logistic predicted habitat suitability across Great Britain for *M. daubentonii* at each level of the spatially nested model. Regional; 5km resolution based on climate and coarse habitat cover, Landscape; 1km based on wider habitat cover and regional output, Local; 100m resolution based on habitat cover, local features and landscape output

Myotis nattereri



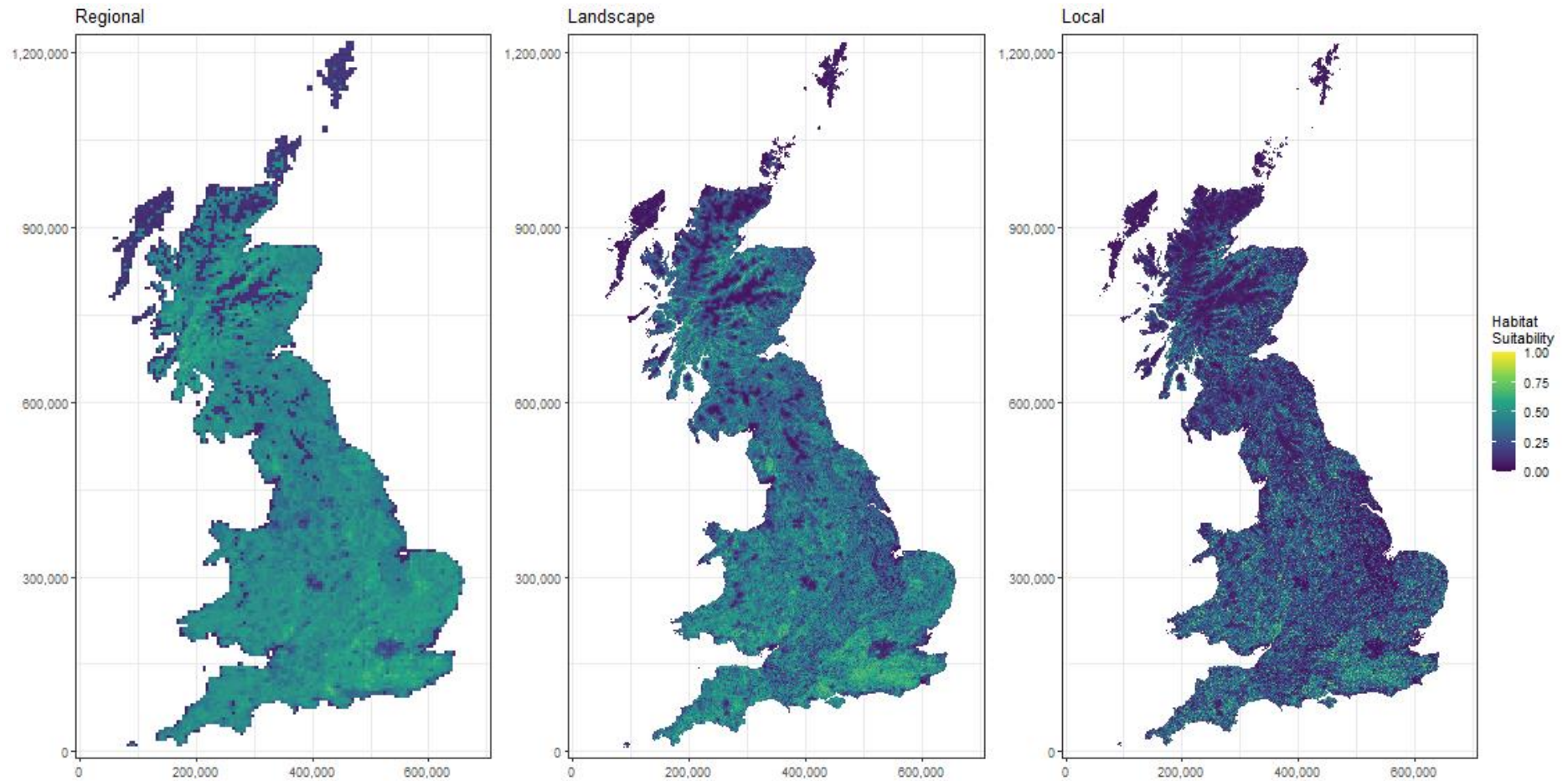
Supplemental Figure 4.6: Gridded maps of logistic predicted habitat suitability across Great Britain for *M. nattereri* at each level of the spatially nested model. Regional; 5km resolution based on climate and coarse habitat cover, Landscape; 1km based on wider habitat cover and regional output, Local; 100m resolution based on habitat cover, local features and landscape output

Nyctalus noctula



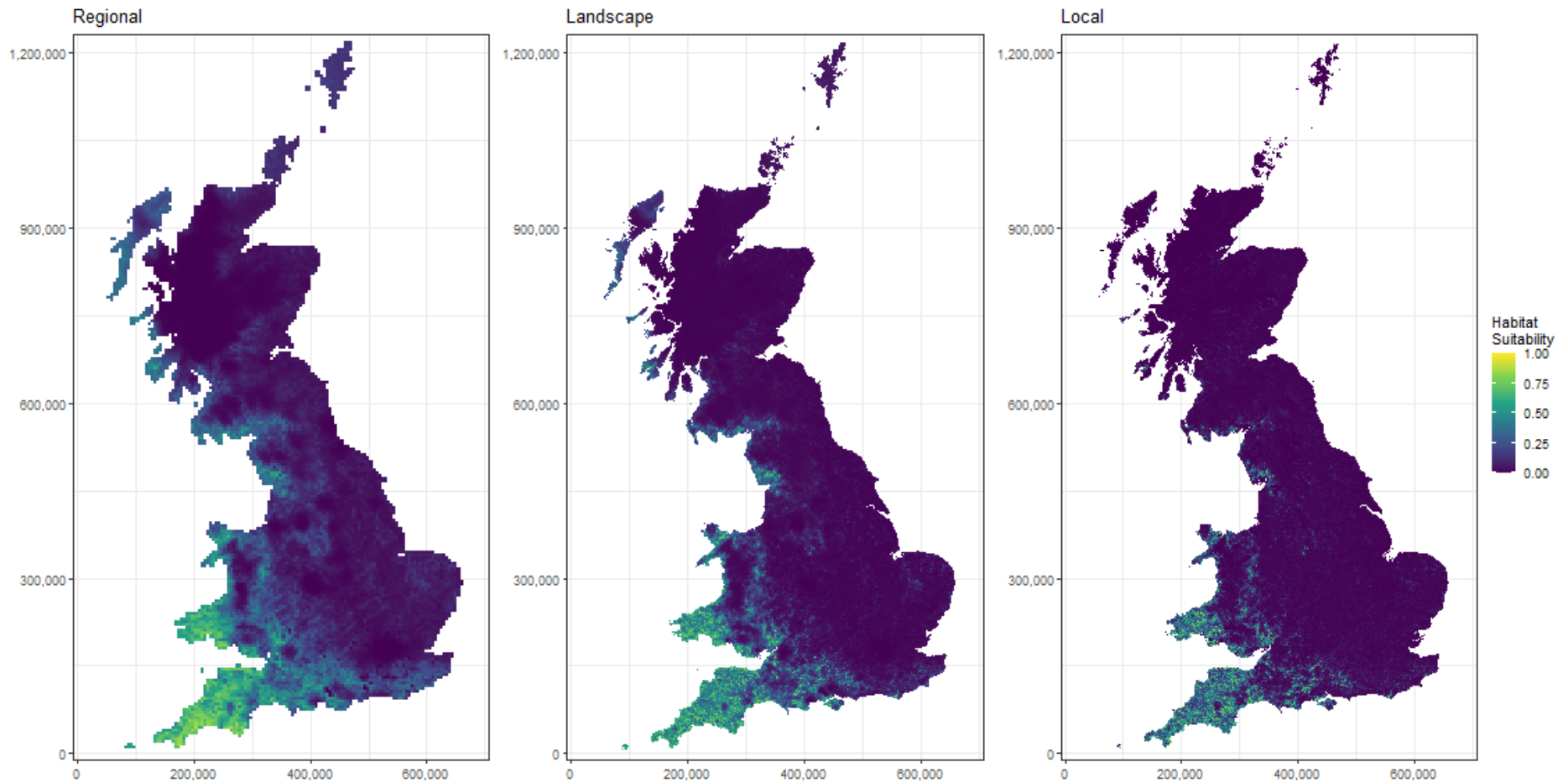
Supplemental Figure 4.7: Gridded maps of logistic predicted habitat suitability across Great Britain for *N. noctula* at each level of the spatially nested model. Regional; 5km resolution based on climate and coarse habitat cover, Landscape; 1km based on wider habitat cover and regional output, Local; 100m resolution based on habitat cover, local features and landscape output

Plecotus auritus



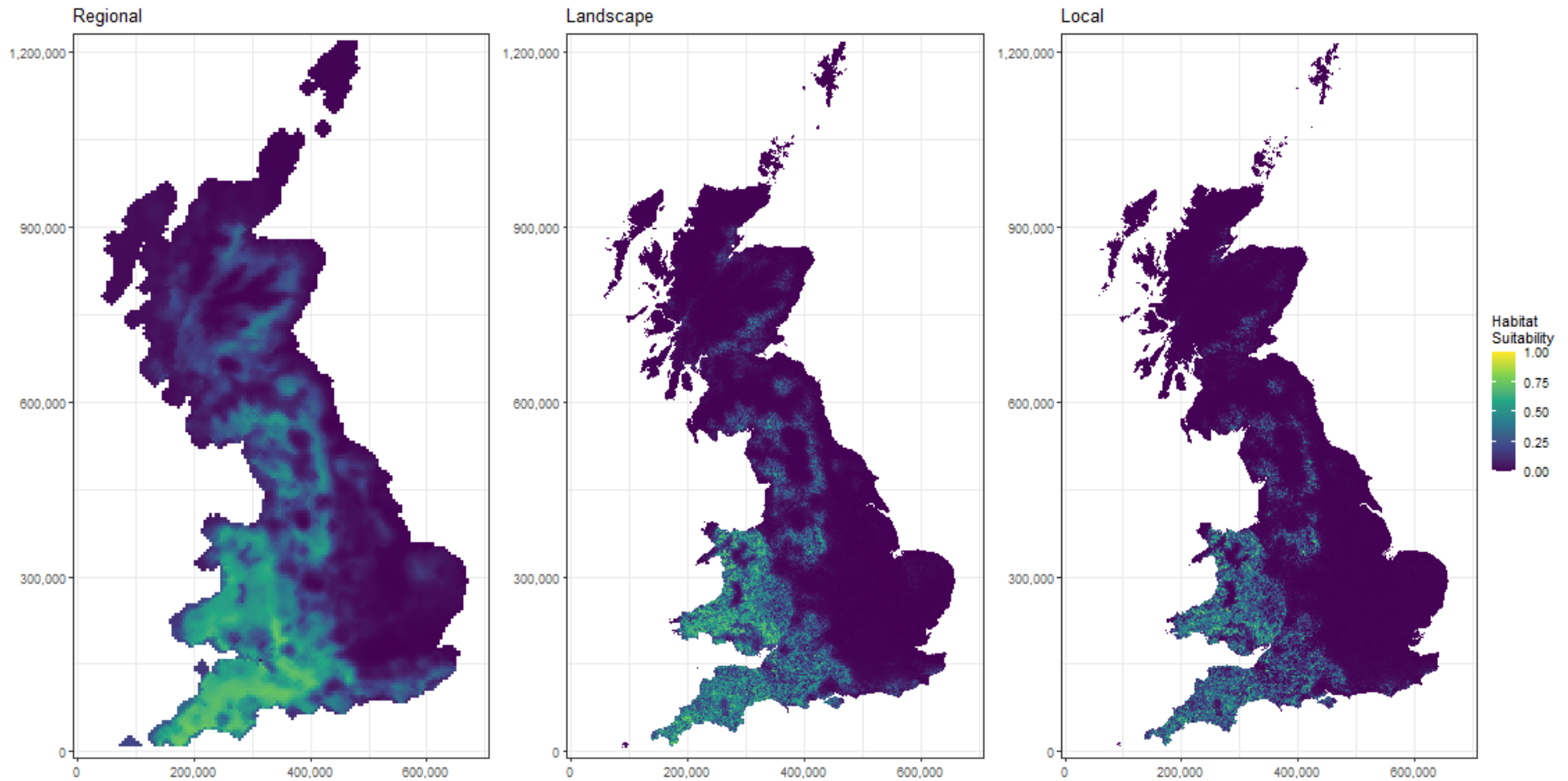
Supplemental Figure 4.8: Gridded maps of logistic predicted habitat suitability across Great Britain for *P. auritus* at each level of the spatially nested model. Regional; 5km resolution based on climate and coarse habitat cover, Landscape; 1km based on wider habitat cover and regional output, Local; 100m resolution based on habitat cover, local features and landscape output

Rhinolophus ferrumequinum



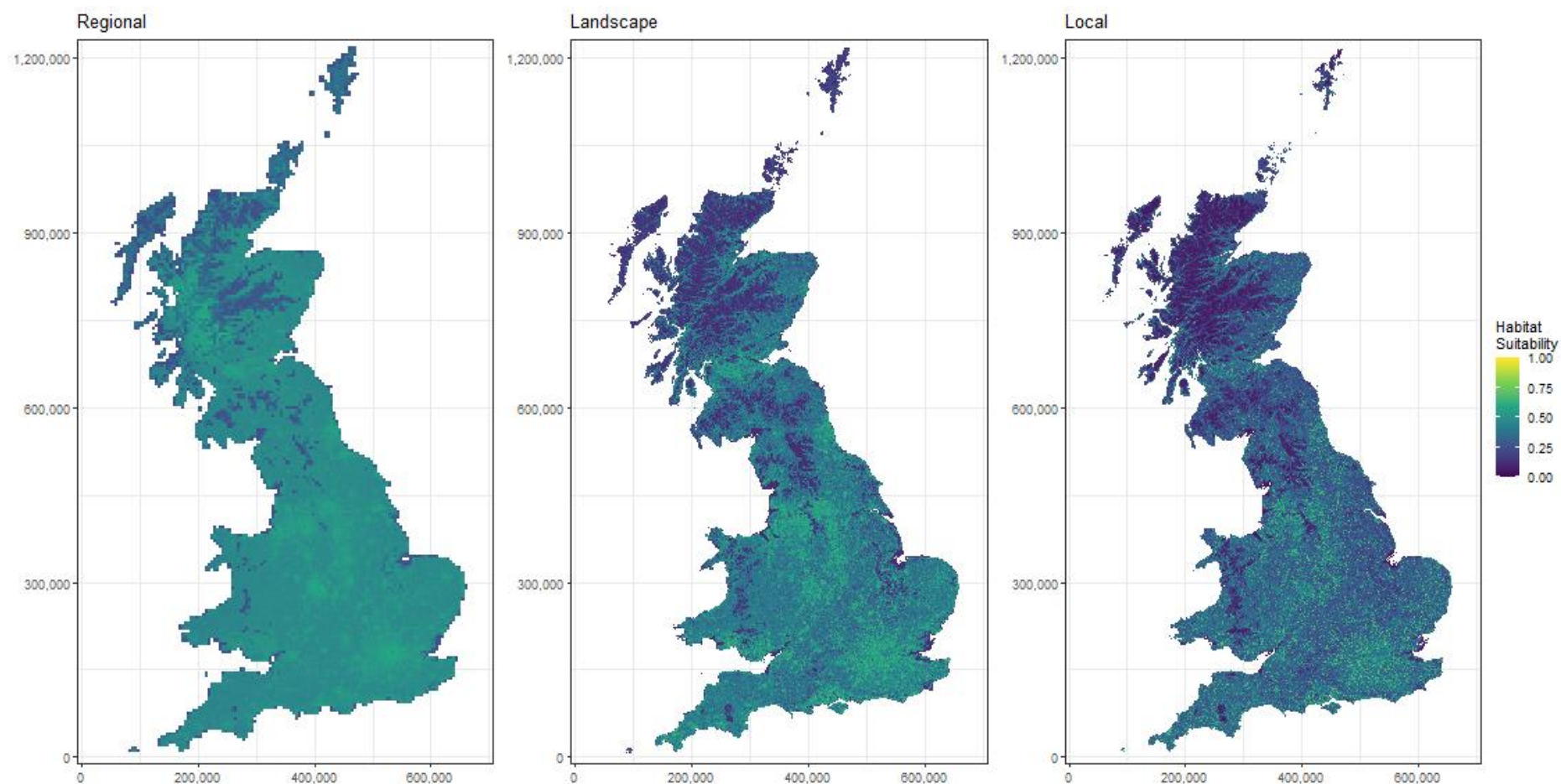
Supplemental Figure 4.9: Gridded maps of logistic predicted habitat suitability across Great Britain for *R. ferrumequinum* at each level of the spatially nested model. Regional; 5km resolution based on climate and coarse habitat cover, Landscape; 1km based on wider habitat cover and regional output, Local; 100m resolution based on habitat cover, local features and landscape output

Rhinolophus hipposideros



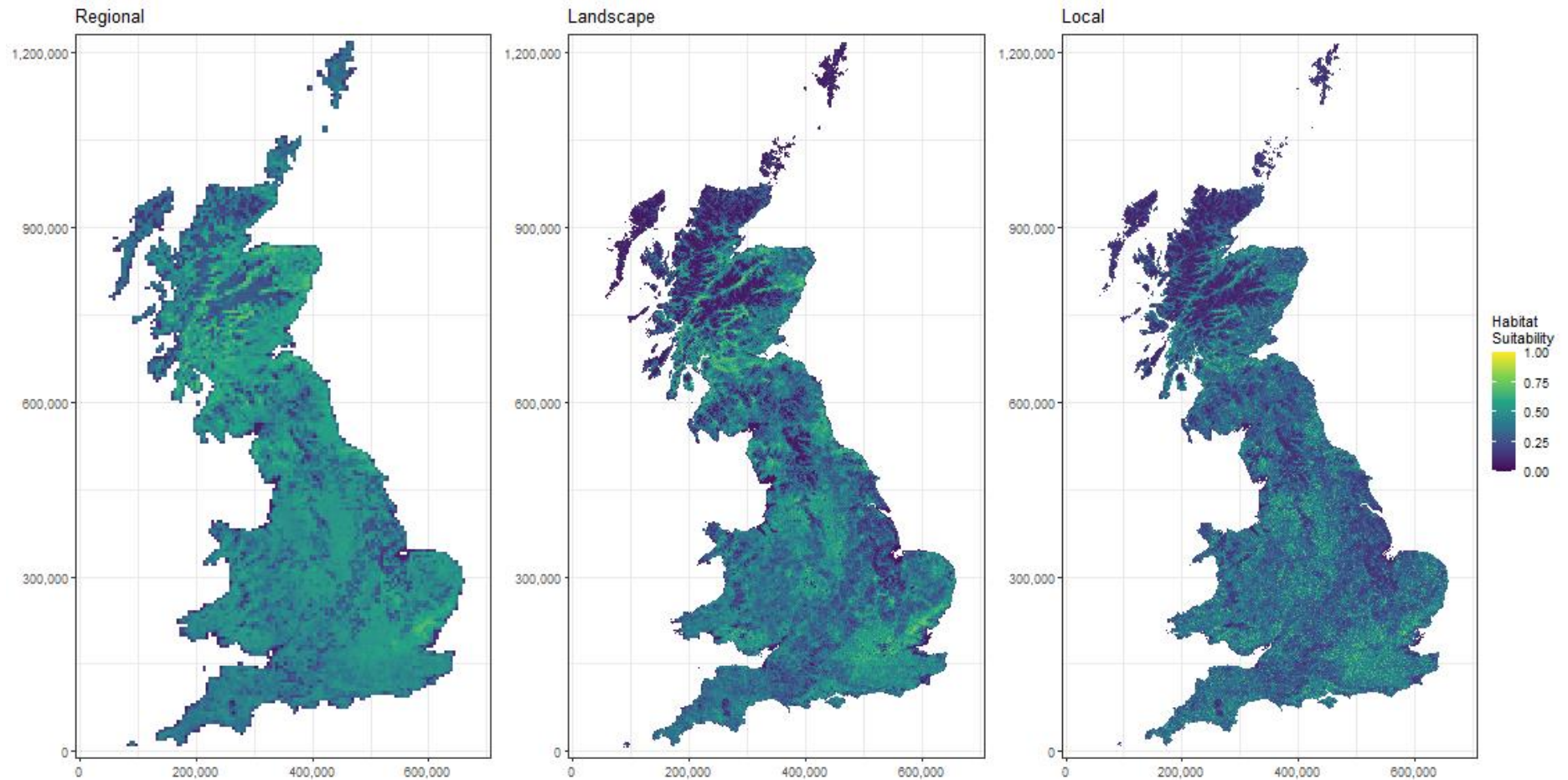
Supplemental Figure 4.10: Gridded maps of logistic predicted habitat suitability across Great Britain for *R. hipposideros* at each level of the hierarchical model. Regional; 5km resolution based on climate and coarse habitat cover, Landscape; 1km based on wider habitat cover and regional output, Local; 100m resolution based on habitat cover, local features and landscape output

Pipistrellus pipistrellus



Supplemental Figure 4.11: Gridded maps of logistic predicted habitat suitability across Great Britain for *P. pipistrellus* at each level of the spatially nested model. Regional; 5km resolution based on climate and coarse habitat cover, Landscape; 1km based on wider habitat cover and regional output, Local; 100m resolution based on habitat cover, local features and landscape output

Pipistrellus pygmaeus



Supplemental Figure 4.12: Gridded maps of logistic predicted habitat suitability across Great Britain for *P. pygmaeus* at each level of the spatially nested model. Regional; 5km resolution based on climate and coarse habitat cover, Landscape; 1km based on wider habitat cover and regional output, Local; 100m resolution based on habitat cover, local features and landscape output

Chapter 5: Investigating Emerging Spatial Patterns in *Rhinolophus hipposideros* Population Trends

5.1 Abstract

Understanding the drivers of population trends is important to be able to plan effective conservation action. Despite initial recoveries from historic declines in the 20th Century, *R. hipposideros* trends in Great Britain have begun to stabilise, with evidence of declines in some regions. Using summer roost count data from the National Bat Monitoring Program this study investigated spatial patterns in trends over 26 years and investigated possible land use and climate drivers. The slowing in population recovery appeared to be largely driven by an increase in roosts where populations are declining, especially in the Southwest of England, a spatial pattern that only appeared in the past decade. Yearly growth rates were negatively affected by anomalously high winter precipitation and warmer spring temperatures while 5-year trends were negatively affected by urban cover and increasing summer precipitation. While this revealed important drivers of *R. hipposideros* trends, none appeared to be localised to the Southwest indicating further analysis is required to understand the drivers of these spatial patterns.

5.2 Introduction

While historic biodiversity declines were largely driven by land-use change, the influence of climate change on population trends has increased in recent decades and is likely to further increase in coming decades. (Lemoine et al. 2007, Eglington and Pearce-Higgins 2012, Pörtner et al. 2021). Climate change is already having negative impacts on bat populations in some areas, for example Ancillotto et al. (2021) found survival of *Plecotus sardus* decreased with increased heatwave prevalence and with extremes of summer precipitation. In addition to direct impacts such as extreme weather events and climates becoming unsuitable, climate change is also likely to interact with the impacts of land use changes (Hughes et al. 2012, Smith et al. 2016, Pörtner et al. 2021).

In regions facing high land use pressures, protected areas are important refuges for species but these may become unsuitable under future climate scenarios while newly favourable areas may have already been converted to unsuitable habitats (Hughes et al. 2012, Smith et al. 2016, Mora et al. 2023). Habitat loss may also cause barriers to climate driven range shifts, although it may conversely be possible to facilitate movements with targeted habitat restoration (Hodgson et al. 2011, Hughes et al. 2012, Struebig et al. 2015, Smith et al. 2016, Synes et al. 2020). The relative importance of land use and climate and therefore the degree of threat from related changes varies between species but also across a species' range (Harrison et al. 2014, Howard et al. 2020, Rigal et al. 2023). For example, Howard et al. (2020) found that population trends of migrant birds in Europe were driven more by land use in non-breeding grounds and climate in breeding grounds, suggesting different conservation actions would be required in each. Disentangling the relative importance of climate and land use changes on populations and biodiversity are thus important for understanding the relevant conservation actions required.

Like many bat species in Great Britain (GB), *Rhinolophus hipposideros* suffered major population declines in the 20th century, and additionally underwent a large range contraction (Harris et al. 1995). While the species is thought to have previously inhabited the South East and parts of Northern England, they are now restricted to Wales and the South West (Harris et al. 1995, Matthews et al. 2018). Estimates of when this decline began vary, but it was most significant before the 1980s with similar patterns seen across Europe but especially at its Northern limit (Harris et al. 1995, Van der Meij et al. 2015, Browning et al. 2021, Węgiel et al. 2021, Schofield et al. 2022). The drivers of this decline are unclear, with hypotheses including

agricultural intensification, roost destruction and disturbance and habitat loss (Harris et al. 1995, Barlow et al. 2015, Matthews et al. 2018, Browning et al. 2021, Węgiel et al. 2021).

Roost destruction and disturbance can cause increased mortality, reduced abundance and possibly reduced reproductive success (Browning et al. 2021). *Rhinolophus hipposideros* tend to roost in buildings and show high site fidelity, and thus renovations are a common source of disturbances and historically used timber treatment chemicals caused high mortality (Afonso et al. 2016, Browning et al. 2021). Conversely, degradation of old buildings can also reduce suitability of roosts (Wright et al. 2022). Changing agricultural practices during the 20th century included increasing chemical inputs such as pesticides which can reduce insect populations both directly and indirectly through reduced availability of host plants (Browning et al. 2021, Rigal et al. 2023). Intensification also led to direct loss of open and woodland habitat, for example in Dorset between 1930 and 2015 agricultural intensification resulted in huge losses of semi-natural grasslands and heath, important invertebrate habitats, as well as some deforestation (Ridding et al. 2020). Increasing field sizes also led to the removal of linear woody features, which can further reduce invertebrate prevalence and is also an important commuting and foraging habitat for bats (Wood et al. 2017, Browning et al. 2021, Rigal et al. 2023).

Since the late 20th century, populations have been recovering with increases seen across Europe (Van der Meij et al. 2015). From a baseline in 1999, *R. hipposideros* populations across GB are estimated to have increased 73.5% or 202.4% depending on survey method (Bat Conservation Trust 2024). Protection legislation is likely to have reduced intentional persecution, however many roosts are still subject to works under licence (K. Boughey, pers. comm.). Similarly, many chemical pollutants used in the 20th century have been outlawed, but some are still persistent in the environment and continue to be found in guano (Afonso et al. 2016). The provision of agri-environmental schemes may have reduced some impacts of intensive farming, however evidence of their effectiveness for *R. hipposideros* and bats as a whole are equivocal (Fuentes-Montemayor et al. 2011, Froidevaux et al. 2017b, 2019, Angell et al. 2019). Increased cover and sympathetic management of hedges can increase activity, likely through increased insect prey populations (Chapter 4; Froidevaux et al. 2019, Bellamy et al. 2020, Foxley et al. 2023). However, arable cover still tends to have a negative impact on activity and occurrence (Bellamy et al. 2020, Foxley et al. 2023). It has also been suggested that warmer winters are assisting species recovery by increasing overwinter survival (Browning et al. 2021). Węgiel et al. (2021) found increases in *R. hipposideros* populations in the late 20th and early 21st centuries correlated

with increasing temperature and Jan et al. (2017) found increased temperatures in various months increased colony size and fecundity. Similarly, Froidevaux et al. (2017a) found warmer spring temperatures increased population growth rates of the closely related *R. ferrumequinum* in the UK.

Despite this recovery, numbers are still estimated to be lower than before the decline and local extinctions, such as in the Netherlands and the North and East of the UK, persist (Harris et al. 1995, Schofield et al. 2022). While protection and conservation action have had positive impacts, bats are still exposed to many threats (as outlined above), while continued climate change is likely to bring new pressures (Browning et al. 2021, Schofield et al. 2022). This is exemplified by the fact that in recent years, evidence has begun to emerge that population recoveries in some areas of Great Britain have stopped or has even started to decline. The most recent National Bat Monitoring Programme (NBMP) report showed that short-term (5-year) trends of *R. hipposideros* calculated using Roost Count data were overall stable with a 0.9% increase (95% CI; -6.8 - 9.6%) but this was not equal across GB, with declines of -12.3% in England (95% CI; -23.1 – 1.0%) and increases of 6.5% in Wales (95% CI; -3.7% to 17%; Bat Conservation Trust, 2024). These patterns are not as apparent in other areas of Europe; Węgiel et al. (2021) found consistent increases to 2020 in Poland and short-term trends in Ireland continue to be positive (Aughney et al. 2022). This study uses 26 years of data from NBMP Roost Count surveys to investigate these emerging spatial patterns in *R. hipposideros* population trends. The study especially seeks to answer how population trends have varied spatially across Great Britain since the 1990s, whether the differences between England and Wales are isolated to outlier roosts or areas and how climate, climate change and land use may be driving these patterns.

5.3 Methods

5.3.1 Bat Surveys

Rhinolophus hipposideros roost count data were taken from the National Bat Monitoring Programme Roost Count survey, in which known summer roosts are surveyed via an emergence count at sunset on at least two evenings during the breeding season following an established protocol (Barlow et al. 2015, Dambly et al. 2021). Surveys have been conducted annually as part of the NBMP since 1997, although data exists from similar roost surveys previous to this.

5.3.2 Population Trends

Following Barlow et al. (2015) and Fewster et al. (2000), generalised additive models (GAMs) were used to fit smoothed trends to *R. hipposideros* roost counts across the time series at different spatial scales. Where more than one survey was conducted in a year, the maximum annual count was included in the model. GAMs were fit with a Poisson error distribution and a site term to account for differences in abundance between roosts, using package ‘mgcv’ in R statistical software (Wood 2017, R Core Team 2024). The degree of smoothing was controlled by specifying a maximum degrees of freedom of 0.3 times the number of years roost data was available (Fewster et al. 2000, Barlow et al. 2015). Where data from before 1997 existed, this was included in the GAMs to improve estimation of early trends.

Models were run at national scales (GB, Wales and England), regional scales (ranging from 10-300km), and for individual roosts. To model national population trends, all roosts within each country with data from surveys in at least 2 years were included and roost ID was included in the model as a factor (Bat Conservation Trust 2024). To model regional trends, roosts were first assigned to regional clusters using hierarchical clustering. Regional clusters were defined as groups of roosts where no roost was more than a given distance from another roost. Cluster distances tested were 10, 50, 100, 200 and 300km. Similar studies investigating regional trends in e.g. birds have used 100km OS grid squares to delineate regions (Harrison et al. 2014, Oedekoven et al. 2017), however for the *R. hipposideros* data this was not a useful subdivision as it created highly uneven sample sizes between regions. Regional models were run using all roosts within the relevant cluster with data from surveys in at least 2 years and roost ID included as a factor. Models were also run separately for each individual roost which had at least 4 years of data (a higher threshold was used to allow GAMs to run and to avoid large trends predicted from limited data).

To calculate trends at a more granular temporal scale, the time period covered by the data was subdivided into 5-year intervals (1998-2003, 2003-2008, 2008-2013, 2013-2018, 2018-2023; 2024 data was not published at time of analysis). This was chosen to reflect the short-term trend interval in use by the National Bat Monitoring Programme. Predicted mean roost counts were standardised at 100 in 1997 to create a population index and the population index for the relevant region/roost was extracted at the start and end of each interval. Mean percentage population change per year was then calculated in each interval as;

$$\frac{N_{tEnd} - N_{tStart}}{N_{tStart}} \times \frac{1}{5}$$

For individual roost trends this was only conducted if data were available in at least 2 years within the interval. To determine if individual roost trends were different in each region in different intervals, linear models were conducted with an interaction term between region and interval. Due to skewed trend data, this was log transformed within the model.

5.3.3 Climate

Climate data were extracted from HadUK Grid, seasonally and at a 1km resolution (Hollis et al. 2019). Variables used were minimum temperature (average of daily minimum air temperature over the season), maximum temperature (average of daily maximum air temperature over the season) and precipitation (total amount over the season). HadUK Grid define the seasons as Winter (December-February), Spring (March-May), Summer (June-August) and Autumn (September-November). Following Oedekoven et al. (2017) climate data was broken into 3 components in order to disentangle differences in climate across space and time. These components were 1) spatial; the average value across all years in each grid cell, 2) temporal; the average value across all grid cells for each year, and 3) anomalies; the additional variation in each grid cell each year.

The impacts of climate on yearly growth rates of individual roosts were modelled using generalised linear mixed models, allowing for lags up to 3 years. Following Lemoine et al. (2007) a balanced yearly growth rate was calculated for each year in each roost as;

$$\frac{Count_t - Count_{t-1}}{(Count_t + Count_{t-1}) * 0.5}$$

providing surveys were conducted in both years. Balanced yearly growth rates were used as traditional growth rates can get very large (for example a count of 242 was recorded after a

count of 1 in the previous year, equivalent to a growth rate of 241000%) which can complicate modelling. The measure ranges from -2 (extirpation) to +2 (colonisation).

The season and lag duration that best explained growth rates were tested using univariate models, the season and lag duration that performed best as measured by r^2 were included in the final model. The final model consisted of a GAMM with a 2D- thin-plate regression spline to account for the effect of x and y coordinates which was allowed to vary with year. Climate variables were included as linear terms and roost ID was included as a random effect to account for repeated measures.

To further investigate the impacts of climate change over time on roost trends, GAMs similar to those run on roost counts were run on climate records for the 1km grid cells where roosts were located, and the 5-year trends estimated. Five-year population trends were then modelled against climate trends using GLMs, again roost trends were log transformed within the model to account for skewed data.

5.3.4 Land cover

The UK Centre for Ecology and Hydrology (UKCEH)'s land cover maps were used to extract land cover data. Land cover data were limited before 2015 and as spatial patterns in bat trends were most prominent in the last 10 years, the land cover analysis was limited to the 2 most recent intervals. The land cover maps for 2020 and 2015 were used as midpoints in these intervals (Rowland et al. 2017, Morton et al. 2021). The percentage cover of a range of land covers were extracted around each roost at 0.5km intervals from 0.5-3km based on *R. hipposideros*' home range and propensity to forage within 2-3km of a roost (Bouhey et al. 2011). Land covers measured were arable, improved grass, broadleaf, semi-natural grass, suburban and urban, additionally arable and improved grass were combined to measure agricultural cover and suburban and urban cover were combined to measure 'built' cover. The scale that best explained trends were tested using univariate models, and the best performing scales as measured using r^2 were included in the final models. The final models consisted of a GAM with a 2D- thin-plate regression spline to account for the effect of x and y coordinates which was allowed to vary with interval. Land use variables and interval were included as linear terms. Models were run with agricultural and built cover combined or separated into arable and improved grass or suburban and urban to see which performed best. Roost trends were log transformed within the model to account for skewed distributions.

5.4 Results

Generalised additive models showed that the number of *Rhinolophus hipposideros* recorded in roosts across their GB range has increased since 1997, agreeing with trends estimated by the National Bat Monitoring Programme. This increase was steepest in the 1990s-2000s and plateaued somewhat from around 2015. Patterns of trends in individual roosts show that this reduction in growth rate is reflected in an increase in the percentage of roosts with declining counts, and an increase in those declining at the fastest rates in the last 10 years, rather than just roost populations stabilising (Fig. 5.1). From 1993-2013 the percentage of roosts with declining trends in each 5-year interval was around 30% whereas since 2013 this increased to ~50% for each 5-year interval.

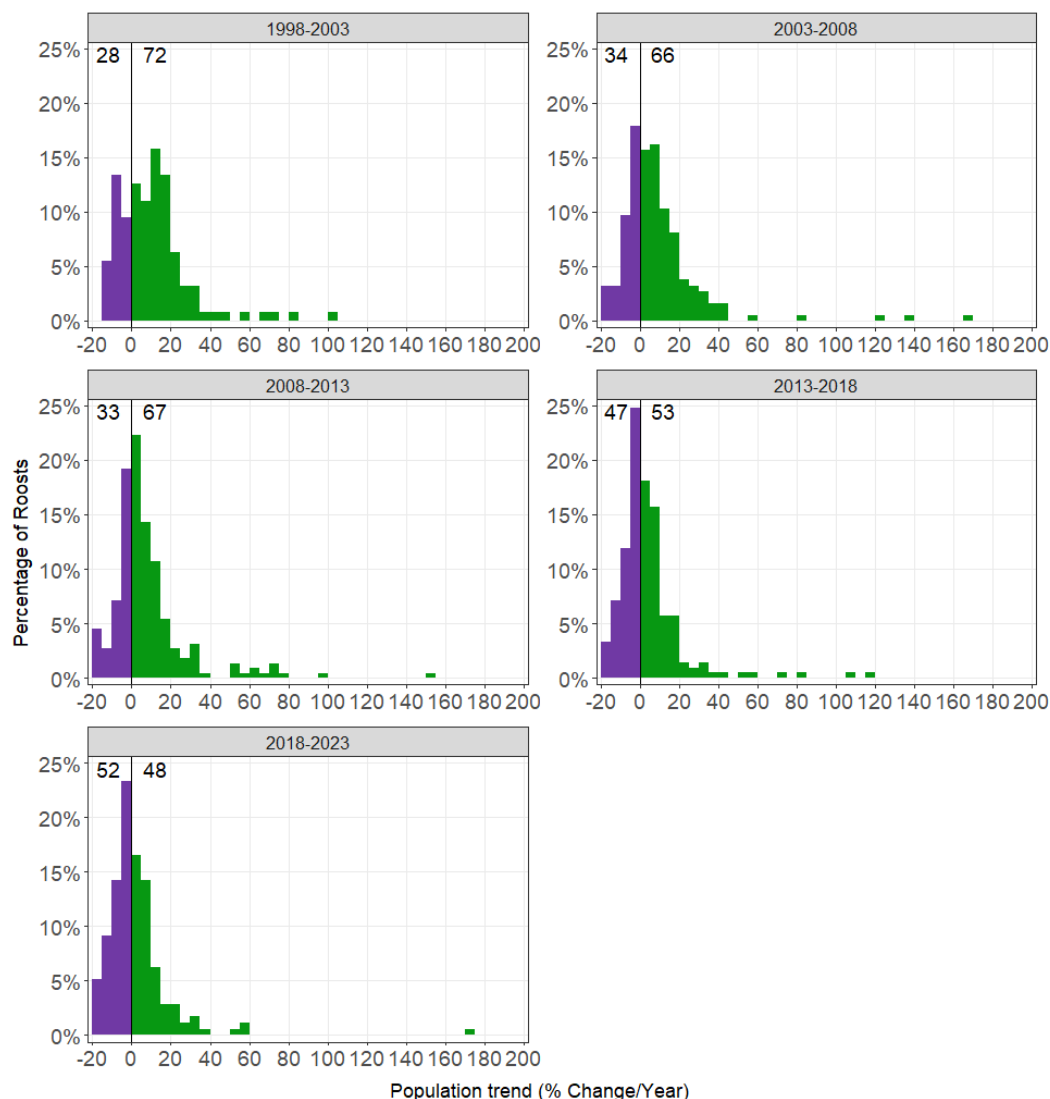


Figure 5.1: The distribution of trends in individual roosts within each 5-year interval, bars represent the percentage of roosts falling within each 5% quantile of trend values. Horizontal line delineates negative (purple) from positive (green) trends. Black numbers at top of panels indicate the percentage of roosts with positive (right) or negative (left) trends

At a national scale the smoothed population index has increased in comparison to the baseline year in both England and Wales (Fig. 5.2), however the two trends have diverged in recent years, with the trend in England declining while the trend in Wales continues to increase.

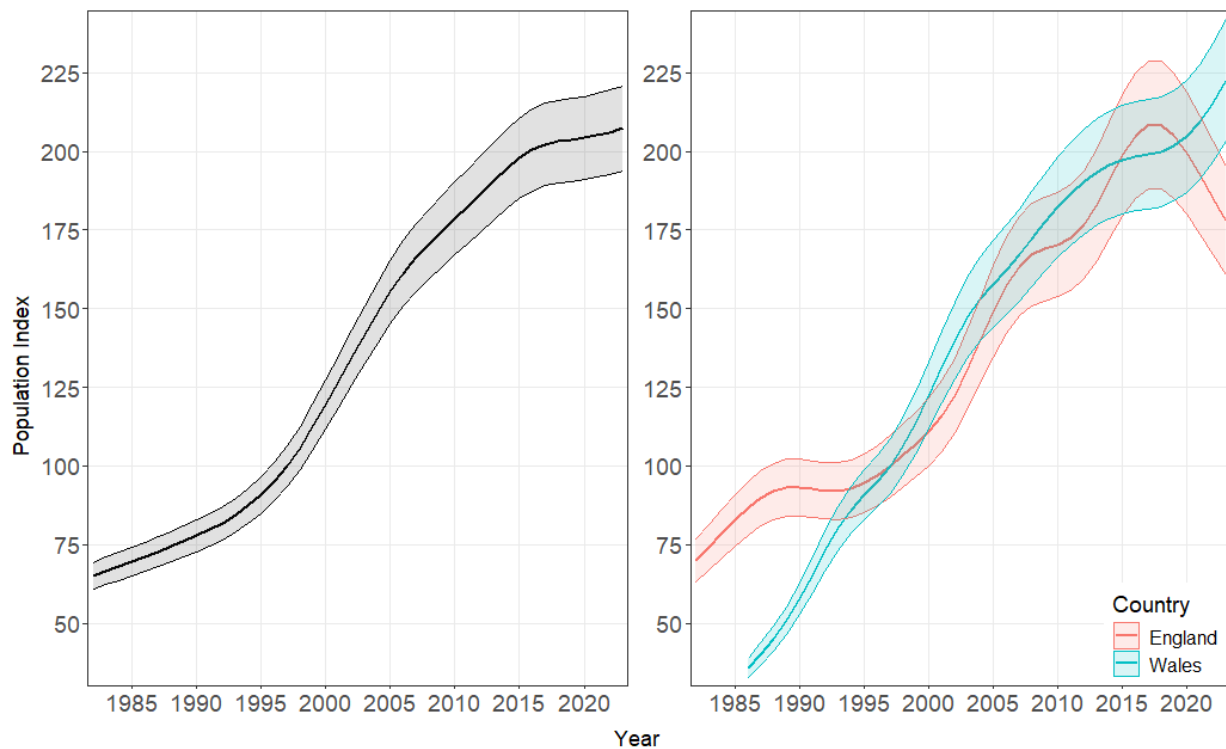


Figure 5.2: Predicted *R. hipposideros* population indices calculated from roosts across the UK (left) and for England (red) and Wales (blue, right). NBMP surveys began in 1997 but proceeding data from similar surveys are included for context (earliest in England: 1982 and Wales: 1986)

These national differences were also reflected in the regional cluster trends, where a north-south trend pattern was apparent across different scales (Fig. 5.3). Roost clusters created using a 10km threshold were too granular with a limited number of roosts in each (<7) while using a 300km threshold only created 2 large clusters, thus these were not included in further analysis. For the cluster scales retained (200, 100 and 50km) similar spatial patterns were seen across all scales, with increases across the whole range, excepting some local fluctuations, from 1998-2013 followed by regional declines appearing in the South during 2013-2018 and expanding in 2018-2023. In the Southwest of England trends are particularly consistent at all scales with only a few clusters not declining, suggesting regional drivers. However, the picture is more mixed in areas across the Southern end of the England/Wales border, at 200km this shows a small decrease in 2018-2023, but this appears to largely be driven by a local decline in the South and East of this region.



Figure 5.3: Map of regional trends at different scales in different intervals. Region polygons were created by dissolving Voronoi polygons around each roost within a cluster. Labels indicate the number of overall roosts in each cluster, the number of roosts surveyed in each cluster each interval may vary slightly.

Within regions, there was variation in trends between individual roosts (Fig. 5.4). At all regional scales, five-year trends at individual roosts did vary over time, in particular trends in 2013-2018 and 2018-2023 were significantly lower than in other intervals (Table 5.1). At larger scales, significant differences between regions were only present in 2018-2023, in particular, individual roost trends were significantly lower in England than Wales and 200km clusters in Cornwall and Devon/Somerset had lower trends than in North Wales (Fig. 5.4A, clusters 1, 2 and 5 respectively). At 100km there were variations between regions, generally with lower trends in Pembrokeshire (Fig. 5.4B, cluster 6) but this did not vary between intervals.

Table 5.1: Linear model outputs comparing individual roost trends grouped by country and regions across temporal intervals, bold values represent significant effects

Region	Variable	Df1	Df2	F ratio	P value
Country	Region	1	913	0.034	0.8532
	Interval	4	913	11.079	<0.0001
	Interval: Region	4	913	4.164	0.0024
200km Clusters	Region	4	898	4.591	0.0011
	Interval	4	898	9.570	<0.0001
	Interval: Region	16	898	1.869	0.0199
100km Clusters	Region	10	868	3.882	<0.0001
	Interval	4	868	9.198	<0.0001
	Interval: Region	40	868	1.297	0.1053
50km Clusters	Interval	4	918	8.317	<0.0001

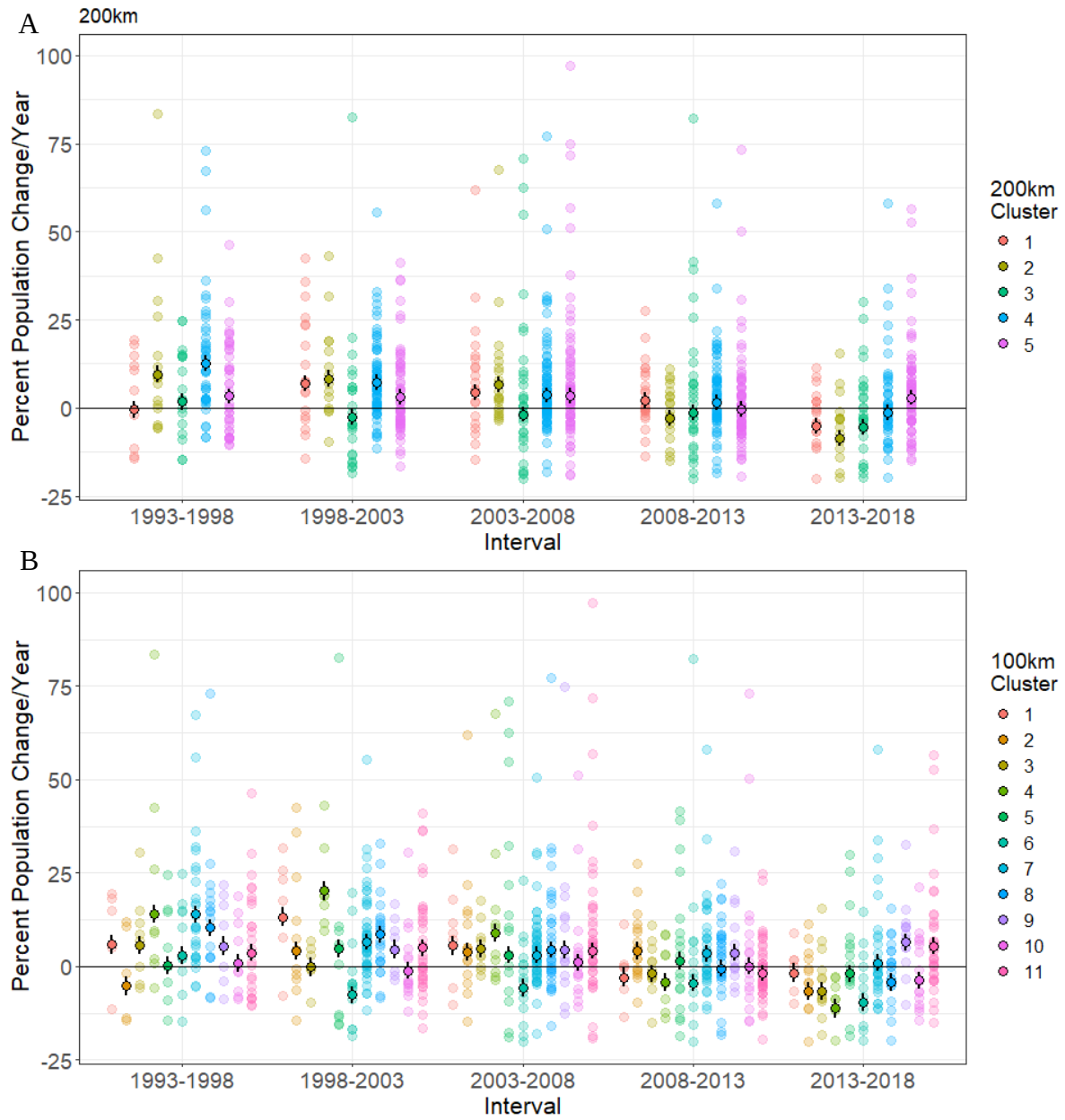


Figure 5.4: Five-year trends for individual roosts, grouped by 200km (top) and 100km (bottom) cluster regions for each period, mean and 95% confidence intervals displayed by large points and lines. Clusters have been arranged (and numbered) by ascending mean Y coordinate (South – North). Trends were log transformed within the model but have been backtransformed for the graph. The y axis has been truncated for ease of visualisation, 9 outliers above 100% change/year are missing (representing <1% data).

Local climate impacts on balanced growth rates in individual roosts each year were impacted most by winter precipitation with a lag of 3 years and spring temperature (both minimum and maximum) with a lag of 1 year (Table 5.2). Growth rates were negatively affected by precipitation anomalies. Where winters were wetter than expected yearly growth rates were reduced. Years with higher temperatures also had lower growth rates.

Table 5.2: Model outputs for climate impacts on balanced growth rates, bold values represent significant effects

	Estimate	Std Error	P-value
Winter precipitation spatial	-6.17e-06	8.94e-05	0.94
Winter precipitation anomalies – lag 3	-3.31e-04	1.29e-04	0.01*
Winter precipitation temporal – lag 3	-4.47e-06	9.76e-05	0.96
Spring max temp spatial	-6.00e-03	1.72e-02	0.73
Spring max temp anomalies – lag 1	-2.80e-02	5.19e-02	0.59
Spring max temp temporal – lag 1	-4.07e-02	1.13e-02	3.35e-04***

Climate change also had impacts on 5-year trends in each roost, in particular increased summer precipitation had negative impacts (-0.01 ± 0.006 , $p=0.035^*$). Temperature change had the biggest impacts in the spring, although in opposite directions with increased maximum temperatures associated with bigger short-term trends and increased minimum temperatures associated with smaller short-term trends, but neither were significant. Five-year trends in each roost in 2013-2018 and 2018-2023 were mostly related to land use at 3km, however most no significant effect, including woodland. Only urban cover had significant effects with trends lower in areas with higher urban cover (-0.08 ± 0.03 , $p= 0.012^*$).

5.5 Discussion

National (GB-scale) *Rhinolophus hipposideros* population growth, as estimated from summer roost counts, has slowed in the last decade. This is seemingly driven by regional population declines in the Southwest of England. This spatial divergence in population trends is most apparent in 2018-2023 and to a lesser extent 2013-2018, although there were previous localised fluctuations in trends. Regional patterns were largely reflected by trends at individual roosts, suggesting regional trends are being driven by regional-scale factors, rather than outlier roosts. Yearly growth rates were negatively impacted by winter precipitation anomalies and higher spring temperatures, while short term (5 year) trends were negatively impacted by increased summer precipitation and urban cover.

This analysis highlights the importance of considering trends at different scales. At a GB-scale *R. hipposideros* trends estimated from Roost Count data do not show any significant change in the last 5-years (Bat Conservation Trust 2024), which could be interpreted as a period of slow growth or as populations stabilising after a recovery from previous declines (Van der Meij et al. 2015). However, regional and individual trends show a divergence along a North-South gradient and highlights areas of concern where urgent conservation action may be needed. Van der Meij et al. (2015) similarly found that a European wide index of all bat species trends showed large recoveries, but that this masked regional patterns where increases were prominent in Atlantic regions but stable in Continental regions, highlighting conservation issues at a regional scale.

The negative impacts of increased precipitation, in both winter (on yearly growth rates) and summer (on short term trends) are in line with previous studies of *Rhinolophus spp.* colony growth and fecundity (Froidevaux et al. 2017a, Jan et al. 2017). Both studies found negative precipitation effects although the season where this had the most effect varied, indicating that *Rhinolophus spp.* are sensitive to inclement weather year-round (Froidevaux et al. 2017a, Jan et al. 2017). That impacts on growth rates were most evident after 3 years was unexpected as Froidevaux et al. (2017a) found lags of 1 year most important, despite testing up to 3 years. Increased mortality of adults during hibernation might be expected to have impacts in the same year while the impacts of reduced juvenile survival might be expected to be delayed by a year or two as *R. hipposideros* usually reach maturity at 1, birthing their first pups at 2 years of age (Schofield et al. 2022). Short term trends were additionally negatively related to increased summer precipitation. Inclement summers are likely to reduce female and pup survival through

reduced foraging opportunities and prey availability during lactation, the most energy intensive time of year. As the trend has been towards drier summers in the past decade, these are unlikely to be driving the recent differences in trends and are more likely to explain local variations across the entire time period.

In contrast to Jan et al. (2017) and Froidevaux et al. (2017a), this study found that years with particularly warm springs had negative impacts on growth rates. This difference may be due to the later period of this study, both used data to 2014, while this study added more recent data where the impacts of climate change were likely higher and more chronic. Despite this, warmer weather has been linked to positive population trends up to 2020 in Poland (Węgiel et al. 2021). Additionally, in the UK *R. hipposideros* are at their latitudinal limit, and thus populations can tolerate higher temperatures in other areas of their global range (Schofield et al. 2022). The drivers behind this are unclear, it is possible that warmer temperatures lead to earlier emergence which may not be matched by a similar shift in insect prey emergence. Alternatively, Jan et al. (2017) highlighted that meteorological variables covary in complex ways and that counter-intuitive results such as these may be influenced by these relationships. So far, increasing temperatures at roosts have not yet impacted short-term trends, although interactions with interval were not tested so it is possible that this is due to differences in effect in earlier and later periods or only having effects in more recent times.

In agreement with previous patterns of negative urban impacts on *R. hipposideros* occurrence, short-term trends were negatively related to urban cover at 3km (Chapter 4; Tournant et al. 2013, Bellamy et al. 2020). Although changes in urban cover were not directly measured, increases were apparent in the last 10 years, but these did not seem particularly localised to the Southwest. Additionally, increases were also seen from 1990 to 2015, and populations were able to grow in that period. This suggests that urban cover either reduces the robustness of populations to other drivers or changes within urban areas separate to increased cover are having negative impacts. Light pollution, associated with roads and buildings has been highlighted as a risk to *R. hipposideros* as a particularly light phobic species (Schofield et al. 2022). Streetlights have been shown to negatively impact landscape connectivity for *R. hipposideros* (Finch et al. 2020a) and colony growth rates for *R. ferrumequinum* (Froidevaux et al. 2017a). Citizen science projects have indicated a 6.5% increase in light pollution since 2011 across Europe and monuments and infrastructure are increasingly lit at night (Schofield et al. 2022, Kyba et al. 2023). However, it is again unclear that these drivers would be particularly strong in the Southwest.

While some drivers of *R. hipposideros* population trends have been elucidated, none appear to be particularly localised to the Southwest or more prevalent in the last decade. This suggests that further analysis is required, either to investigate the spatial patterns of these stressors or to identify possible alternative drivers. One possibility is roost disturbance and management. It is estimated that just under 20% of *R. hipposideros* roosts in England have been subject to works under licence (K. Boughey, pers. comm.). Licenses are required for works that will disturb bats, or that will damage or remove roosts (even if unoccupied). Given the negative impact of roost disturbances, particularly structural changes, it is likely that this could lead to reduced numbers in these roosts (Browning et al. 2021). Data on the spatial pattern of these works were unavailable for this study. The effects of such works would be expected to be localised to the affected roost, however at such high volumes, this may be sufficient to drive regional trends. This could also explain differences between countries if the prevalence of licenced works is not as high in Wales, where licencing is managed by a different organisation.

Conversely, some roosts are also subject to enhanced protection, either through management by organisations such as the Vincent Wildlife Trust (VWT) or through Special Areas of Conservation (SAC). Analysis by VWT suggested roosts managed by their organisation had stronger long-term trends, although this may be confounded by roost size, and it would be interesting to see if this also held for short-term trends and for SACs, especially in the Southwest (Wright et al. 2022). If trends are more positive in these roosts it could further indicate roost disturbance or condition is an ongoing problem, however if protection is not sufficient this would suggest landscape or climate drivers.

It would also be interesting to complete a parallel analysis on hibernacula trends as roost counts can be subject to biases, particularly when roost switching commonly occurs and when inter-annual variability in abundance is high (Dambly et al. 2021). *Rhinolophus hipposideros* tend to be faithful to roosts, and do not switch as commonly as other species, however abandonment of disturbed roosts could play a role in reduced counts if new roosts are not identified for surveying (Dambly et al. 2021). Despite this, a similar but less extreme divergence between England and Wales is seen in trends estimated using hibernation survey data, suggesting a genuine regional population decline (Bat Conservation Trust 2024). Hibernacula counts in the short term have increased 22.1% (95% CI: 11-35.5) for GB as a whole, although this is largely driven by an increase of 31.2% in Wales (95% CI; 18.5%-49.8%), while in England numbers have declined -2.1% (95% CI; -25.6-21.9%). Comparing the regional patterns and drivers of

trends in hibernacula could further elucidate drivers of population change and conservation actions required to protect the future of *R. hipposideros*.

Chapter 6: General Discussion

Long-term population monitoring indicates that most surveyed bat species in the UK are recovering from previous declines in the 20th Century and, as woodland species, they stand to gain from increased woodland cover. Understanding landscape context effects on bat populations is crucial for understanding how different habitat restoration strategies, particularly spatial targeting will impact upon bats. The importance of ongoing conservation has been highlighted by emerging evidence of slowing recoveries and regional declines for some species (Chapter 5, Bat Conservation Trust 2024). In this thesis, trees outside woodlands (ToW), including hedges treelines and individual trees were found to be incredibly important aspects of agricultural landscapes for bats. Habitat suitability increased with both ToW cover in the landscape as well as proximity to woody features (Chapter 4) and activity of *N. noctula* increased with landscape ToW cover (Chapter 3). Across many species, activity at ToW sites was on par with activity at woodland edges which are generally considered important foraging habitats, especially for *Pipistrellus spp.* (Chapter 3; Kirkpatrick et al. 2017a, Cook et al. 2023). In addition, ToW played an important role in landscape connectivity and matrix permeability within agricultural landscapes, supporting previous studies (Frey-Ehrenbold et al. 2013, Froidevaux et al. 2017b, Finch et al. 2020a). As expected, woodland cover was positive for bat population trends and occurrence (although this was not the case for relative activity measured by acoustic surveys), but there was no strong indication that targeting woodland creation to particular landscapes had the most benefits across all species. Bat activity was affected more by spatial configuration of woodland, as fragmented woodlands had negative effects for *N. noctula* and influenced the relative use of different habitat types by *P. pipistrellus* and *Myotis spp.*

6.1 The Importance of Trees Outside Woodlands

Trees outside woodlands are used for shelter and navigation, with bats often avoiding large open areas and preferentially flying over ToW compared to agricultural fields (Lumsden and Bennett 2005, Finch et al. 2020b) and in this thesis these features were found to be especially important in more fragmented landscapes (as in Fahrig 2003 where existing habitat is distributed between more and dispersed patches). For *P. pipistrellus* and *Myotis spp.* activity at ToW sites

increased when woodland cover in the surrounding landscape was more fragmented (Chapter 3) while for *N. noctula*, landscapes with more fragmented woodlands reduced occurrence, however this impact was less pronounced when landscapes also included high ToW cover (although the interaction was non-significant). In fragmented landscapes ToW features likely facilitate movement between dispersed woodland patches, allowing bats to access sufficient roosting and foraging resources (Mortimer 2006, Laforge et al. 2021).

While connectivity provided by ToW was particularly important in landscapes with more fragmented woodland, the effect of ToW on activity did not increase in landscapes with low woodland cover (Chapter 3, Chapter 4). In fact, habitat suitability models often included a positive interaction between woodland and ToW cover, indicating ToW benefits increased in landscape with more woodland (Chapter 4). Similarly, Frey-Ehrenbold et al. (2013) found increased connectivity (proximity and cover of other ToW features and woodlands) increased bat activity at ToW. This may be due to increased interpatch distances in low cover landscapes creating barriers to movement that ToW cannot moderate. Despite this, some species did show higher benefits of ToW in highly agricultural areas in habitat suitability models (Chapter 4), in line with previous studies on ToW benefits to birds (Batáry et al. 2010, Sullivan et al. 2017, de Zwaan et al. 2024).

As new technologies allow more detailed mapping of ToW its inclusion in models of landscape context should be encouraged, both on its own and in interaction with other landscape variables to further our understanding of their role in matrix permeability (Scholefield et al. 2016, Liu et al. 2023). Additionally, in this thesis only ToW cover was measured but the development of configuration metrics for ToW would also be useful (for example gap-ness or aggregation indices).

6.2 Targeting Increased Woodland Cover

Woodland cover was generally found to have positive impacts on bats, in line with known ecology and previous studies, (Boughey et al. 2011, Fuentes-Montemayor et al. 2011, Alder et al. 2020, Browning et al. 2021, Foxley et al. 2023). For example, habitat suitability increased with woodland cover at a range of scales across all species tested and reduced conifer cover had negative impacts on population trends (Chapter 2, Chapter 4). Conversely, bat activity at a site level did not seem to be affected by landscape woodland cover (Chapter 3). In contrast to

these results, a number of studies have found that bat activity increased with greater woodland cover in agricultural landscapes (Fuentes-Montemayor et al. 2011, 2017, Frey-Ehrenbold et al. 2013). When taken in line with the overwhelming evidence that bats use and respond positively to woodland cover the result in Chapter 3 is possibly related to the lack of a direct link between local relative activity and wider abundance rather than bats' ambivalence to woodland cover (Fuentes-Montemayor et al. 2013, 2017, Lintott et al. 2014b, Monck-Whipp et al. 2018).

It has been proposed that conservation actions, including restoration of habitats would create the most benefit in landscapes with low (Batáry et al. 2011) or intermediate (Tschardt et al. 2012, Tambosi et al. 2014) amounts of remnant habitat. Previous studies of roost selection by bats suggested that increasing woodland amount was most beneficial in landscape with <20% cover (Boughy et al. 2011), however this thesis found that the most beneficial landscapes for targeting woodland varied between species. Response curves from habitat suitability models (Chapter 4) showed that for some species the relationship between woodland cover and habitat suitability was steepest (i.e. the largest increases in activity per unit increase in cover) in landscapes with low cover while for others it was steepest at intermediate levels of cover while others still had linear relationships indicating that benefits were equal across the whole range of woodland cover.

The benefits of woodland cover for several species did, however, depend on the cover of other habitats but this also varied between species and scales. Some species, particularly woodland specialists (*R. hipposideros* and *P. auritus*) saw lower benefits of woodland cover in urbanised landscapes, indicating a high sensitivity to stressors such as light and noise pollution, roads and habitat loss (Lintott et al. 2016, Browning et al. 2021). For other species (both *Pipistrellus spp.* and *E. serotinus*), woodland appeared to moderate the negative impacts of urban cover suggesting woodlands in this area act as important refuges, or that woodlands near urban areas allow for complementation of roosting and foraging habitat. For agricultural cover, the interaction effects depended on scale. Generally, at a landscape (1-5km) scale woodland had fewer benefits in highly agricultural areas, conversely at the local scale (100-500m) woodland moderated negative impacts of agricultural cover. In contrast, in Chapter 3 the (lack of) impact of woodland cover on bat activity was not modulated by intensity of agriculture (measured as arable vs pasture cover) nor by country (where England tends to have more intensive agricultural landscapes). This highlights some of the complexities of determining a 'best landscape' for woodland creation to benefit bats.

While encouraging woodland restoration wherever possible is likely to benefit at least some bat species, spatial targeting should also consider other species, particularly those negatively impacted by increasing woodland cover. Many taxa, including ground nesting birds require large areas of fallow ground or upland grasslands and have been found to reduce in abundance following woodland succession in former agricultural lands (O’Callaghan et al. 2017, Sanz-Pérez et al. 2021, Mora et al. 2023). Woodland restoration projects must be careful not to have significant negative effects on other aspects of biodiversity. Societal considerations, such as equitable access or protecting communities from flooding can also be incorporated into woodland targeting choices (Burton et al. 2018, DEFRA 2023).

6.3 Targeting Restoration of Other Habitats

This thesis found that spatial targeting of non-woodland habitats, especially in relation to the habitat being replaced, is likely to have impacts on bats. Some species use a mosaic of open habitats for foraging (Razgour et al. 2011b, Roswag et al. 2015, Mordue et al. 2023) and an increase in open semi-natural habitat cover could have positive impacts, especially if targeted at poor quality areas of bat habitat such as urban or intensive agricultural landscapes (Boughey et al. 2011, Fuentes-Montemayor et al. 2017). Many priority habitats such as peat and heath in the UK were planted with conifer historically, and these areas are now being targeted for semi-natural habitat restoration through thinning or removal of trees. While the benefits of woodlands for bats are often considered to be limited to broadleaf habitats, commercial conifer forests in the UK and Europe have been found to support a range of bat species, particularly when roosting opportunities are provided by built structures or bat boxes (Benzal 1991, Kirkpatrick et al. 2017a). Similarly, increased structural diversity, reduced density and broadleaf cover can increase benefits of conifer stands (Kirkpatrick et al. 2017a, Cook et al. 2023).

Using long-term census and land cover data in Chapter 2, it was found that reduced conifer cover had negative impacts on population trends, in agreement with previous studies (Borkin et al. 2011). While small scale felling has previously been found to increase particularly *Pipistrellus spp.* activity in the short term by providing thinned stands and forest edges for foraging (Kirkpatrick et al. 2017b), a felled area remaining unstocked and converting to open habitat can have negative impacts on population trends (Chapter 2; Borkin et al. 2011). Thus,

in landscapes where conifer cover is high and provides most available habitat, their replacement with open semi-natural habitats may have negative impacts for bats.

This is an example of a situation in which habitat restorations can lead to community turnover rather than necessarily an increase in biodiversity, with the possibility of trade-offs between different endangered or conservation important species (Dornelas et al. 2014, Mortelliti and Lindenmayer 2015, O’Callaghan et al. 2017, Burton et al. 2018).

6.4 Spatial Configuration of Woodland

While habitat suitability models and population trend analysis indicated an important role of high woodland cover on bat occurrence and abundance, bat activity largely responded to spatial configuration (Chapter 3). ‘Fragmentation per se’ is argued to have largely positive (albeit small) impacts on biodiversity, including on bats (Klingbeil and Willig 2009, Ethier and Fahrig 2011, Rodríguez-San Pedro and Simonetti 2015) but see (Bernard and Fenton 2007). In contrast, this thesis found that for woodland specialist *N. noctula* occurrence was reduced with fragmentation. Previous studies have suggested that fragmentation tends to have negative impacts on specialists while generalists benefit (Alvarado-Montero et al. 2021), however an overall increase in activity or occurrence for generalist bat species was not found. For these species, the spatial configuration of the landscape had more impacts on the relative use of different habitat types. In particular, fragmentation increased use of woodland edges and ToW features in comparison to woodland interiors.

Valente et al. (2023) advocate for a move towards mechanistic understandings of fragmentation effects in order to advance habitat fragmentation research. For this thesis it was difficult to elucidate the drivers behind the effects of fragmentation due to high correlation between spatial configuration metrics and their intrinsic link to cover (Andren 1994, Fletcher et al. 2018). For example, it was hypothesised that fragmentation had negative impacts on *N. noctula* due to reduced patch sizes, and that reduced cover leads to greater inter-patch distances limiting the ability of ToW features to enhance connectivity. However, it was not possible to include those measures in the models due to collinearity. Fragmentation experiments at this scale are costly and logistically complex, thus statistical techniques, such as Structural Equation Models that can disentangle the direct and indirect effects of landscape habitat cover and configuration

measures (and account for correlated errors) could be investigated (Fuentes-Montemayor et al. 2020).

6.5 Bat Survey Techniques

Throughout this project, data from a variety of bat survey techniques have been used, including long-term population monitoring from both bat box captures and roosts emergence counts, acoustic surveys and occurrence records (including records from trapping as well as hibernacula, roost and acoustic surveys collapsed to presence locations). All bat survey techniques have different biases for the species captured, for example *P. auritus* has very quiet echolocation calls and is regularly under detected in acoustic surveys (including in this thesis where none were found at 90% confidence), while *Myotis spp.* are difficult to distinguish without capturing. Some species are also trap shy while roosting behaviours of others preclude population monitoring through these methods (Lintott et al. 2014b, Barlow et al. 2015, Bat Conservation Trust 2024). However, using complementary methods allowed this project to investigate a wide range of demographic responses to landscape context and habitat restoration as well as a range of different species (Lintott et al. 2014b).

Interestingly, studies using long-term monitoring and occurrence records tended to have similar results, in particular that positive outcomes (increasing trends or habitat suitability) were reliant on sufficient woodland cover. In contrast, results from acoustic surveys were more ambivalent about the responses of bats to woodland cover. Acoustic surveys facilitated data collection over large spatial areas. This has been enhanced recently with the development of cheaper recorders (e.g. Audiomoths ~£70 cf. SongMeter SM4 ~£750) which allowed for simultaneous deployment at multiple survey sites across 60 landscapes. However, acoustic surveys can only measure relative activity as it is not possible to directly link echolocation calls to bat abundance (Froidevaux et al. 2017a). An increase in ‘activity’ may relate to an increase in number of bats or a similar number of bats using an area more intensively (e.g. foraging vs commuting). A comparison by Lintott et al. (2014b) did suggest a close relationship between trapping captures and activity measures, especially for *Pipistrellus spp.* at a local scale, however the relationship to landscape scale population sizes is less understood (Froidevaux et al. 2017a). In addition, differences in activity types can be difficult to elucidate, some studies have separately analysed feeding buzzes and general bat passes but these tend to be closely correlated (Ancillotto et al. 2017, Froidevaux et al. 2017b) and display similar responses to habitat type or landscape context (Fuentes-Montemayor et al. 2011, Wood et al. 2017, Finch et al. 2020c). Additionally,

while the BatDetect2 algorithm developed by the Bat Conservation Trust is able to identify feeding buzzes to species, it does not specifically distinguish them from other echolocation calls and accuracy is likely to be lower as they are more similar between species.

Long-term population monitoring can provide a direct measure of changes in bat abundance, provided species do not frequently roost switch (Bat Conservation Trust 2024) and can be used to investigate local or regional drivers of trends. However, this requires a significant level of effort especially at a national level. For example in 2023, 15,833 volunteer hours were contributed to the NBMP (Bat Conservation Trust 2024). Similarly, occurrence data from a range of survey methods but collapsed to avoid issues with estimating abundances can be directly comparable across space and time, although misidentifications are possible. While data from citizen science projects can be subject to biases and draw data from a range of methodologies, habitat suitability models have been developed to deal with these issues allowing the use of a wide range of data sources (Phillips et al. 2009).

Emergence roost counts, occurrence data (especially gathered from a range of sources) and acoustic surveys are often missing demographic data that could highlight landscape context effects on particular ecological processes. For example, Fuentes-Montemayor et al. (2020) found differences in adult and juvenile responses of *Myodes glareolus* to landscape ToW cover, highlighting their particular importance in facilitating dispersal of young. Being able to test for differences in the effect of landscapes on use of habitats between sexes or between adults and juveniles or on fecundity could add useful context to the studies presented here. While trapping could have allowed for the collection of this information alongside the acoustic surveys, trapping requires greater effort and the logistical complexities of surveying multiple sites across a 1km radius landscape precluded this. Captures from bat boxes can also provide this information, and in combination with banding can allow for mark-recapture studies. These methods can facilitate investigating whether population declines result from reduced fecundity or increased emigration or death. While this would have been interesting to study for Purbeck Forest to elucidate the drivers behind negative responses to conifer loss in Chapter 2, a lack of funding meant that for half the bat boxes in the middle of the monitoring period only numbers of bats were counted rather than banding and demographic data collection occurring (M. Warn, pers. comm.) which precluded this analysis.

Radio tracking can provide information on how individuals move through landscapes with varying habitat compositions and configurations and, as capturing bats is required, can be

combined with demographic information. There is evidence, for example, that bats have smaller home ranges in more diverse and more forested landscapes (Mortimer 2006, Laforge et al. 2021). They can also allow analysis of habitat selection and preferential use for foraging or commuting (Mortimer 2006) as well as mapping landscape connectivity (Finch et al. 2020a). However, radio tracking is particularly resource intensive and typically results in small sample sizes. Individuals of some bat species show highly divergent habitat use and selection (Mordue et al. 2023) and thus to get a representative sample across 60 landscapes (or even a subset of landscapes) would not have been feasible for this thesis. Emerging technologies that could allow for remote data downloads or drone receivers to track multiple bats could make this possible in future.

6.6 Management Recommendations

Where conifer forests are being earmarked for restoration of non-woodland habitats, consideration should be afforded to the possible negative impacts of conifer loss on woodland species in the area. Actions such as supplying roost boxes or promoting broadleaf and/or ToW expansion in the wider landscape could be considered to mitigate some of these impacts. However in weighing the trade-offs between conifer and non-woodland priority habitats value judgements are likely to determine the favourable outcome (e.g. higher importance of creating habitat for highly endemic heath species in comparison to reductions in abundance of woodland species that are more widespread, Fischer and Lindenmayer 2007, Bottrill et al. 2008)

Considering the importance of trees outside woodland, retaining existing ToW and managing them sympathetically should be promoted. Larger, more diverse hedges, with few gaps are known to benefit bats (Pinaud et al. 2018, Froidevaux et al. 2019, Foxley et al. 2023), although even highly managed, poor-quality ToW can increase landscape connectivity (Finch et al. 2020a). Planting of new ToW between existing woody habitats should also be encouraged to enhance connectivity, particularly in landscapes where woodlands are present but fragmented and poorly connected (Chapter 3; Frey-Ehrenbold et al. 2013).

The benefits of targeting new woodlands in particular landscapes are complex and species dependent, thus it is difficult to recommend approaches to spatial targeting to benefit bat communities as a whole. However, encouraging woodland restoration where possible is likely to benefit at least some bat species. While the mechanisms behind the impacts of fragmentation

per-se are unknown, this thesis shows that for woodland specialists, restoration should focus on aggregating new cover in a small number of patches (Chapter 3). This is especially important in poorly connected landscapes with limited ToW cover.

Overall, this thesis has shown that increased woodland cover has benefits for bats as has been seen with several other woodland species. While habitat restoration is partly driven by biodiversity concerns, especially among conservation organisations, in many sectors the emphasis is largely on climate mitigation through increased carbon sequestration. Government targets, for example, often talk about net-zero emission targets with smaller emphasis on biodiversity and societal benefits (DEFRA 2023). The growing carbon finance industry is also highly focussed on carbon sequestration. These competing motivations could have possible negative impacts for biodiversity, for example the perceived higher sequestration of conifer trees could promote afforestation of dense monoculture conifer plantations rather than diverse native broadleaf woodlands (Burton et al. 2018). Thus, care should be taken to ensure new woodlands are created with consideration for biodiversity as well as carbon benefits, especially as questions are being raised about the efficacy of tree planting as a strategy to reduce climate change, while its benefits for conserving woodland biodiversity are clear.

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