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Spatial Ecology of Species–Habitat Relationships

Applications for Conservation and Rewilding

Pegah Hamedani Raja

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To nature, whose complexity and resilience continue to inspire understanding,
care, and responsibility.

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ABSTRACT

Understanding how species interact with their habitats is central to predicting biodiversity responses to environmental change and to designing effective conservation strategies. This thesis applies spatial ecological methods to examine species–habitat relationships across contrasting ecosystems and to demonstrate how these insights can support evidence-based conservation and rewilding. The research is based on the concept of ecological niche, which links species distribution to environmental conditions, biotic interactions, and spatial structure.

Using passive acoustic monitoring combined with high-resolution spatial data, the first two case studies investigate early-season habitat selection in two boreal forest specialists, the Crested Tit (*Lophophanes cristatus*) and the Willow Tit (*Poecile montanus*).

Crested Tit occurrence increased with pine resources (needle biomass) and decreased with proximity to human settlements.

Willow Tits showed scale-consistent positive associations with the area of pine-dominated peatlands across local (100 m) and broader (400 m) spatial scales. These findings demonstrate that key ecological requirements of specialist birds are governed by fine-grained habitat use, rather than by coarse habitat features captured by conventional management indicators.

The third case study extends the analytical framework to lowland agricultural landscapes in England to evaluate passive rewilding potential under the Biodiversity Net Gain (BNG) policy. By integrating land-cover patterns with deer browsing pressure, the study identifies where natural regeneration is most feasible and quantifies the potential contribution of rewilding to national biodiversity targets.

Collectively, this thesis demonstrates how spatially explicit ecological tools—from acoustic monitoring to landscape-scale modelling—can link ecological theory with conservation action and support resilient species populations and ecosystems in a rapidly changing world.

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TIIVISTELMÄ

Lajien ja niiden elinympäristöjen välisten vuorovaikutusten ymmärtäminen on keskeistä, kun ennustetaan biodiversiteetin vasteita ympäristönmuutoksiin ja suunnitellaan tehokkaita luonnonsuojelustrategioita. Tässä väitöskirjassa sovelletaan spatiaalisen ekologian menetelmiä lajien ja elinympäristöjen välisten suhteiden tarkasteluun erilaisissa ekosysteemeissä sekä havainnollistetaan, miten nämä näkökulmat voivat tukea näyttöön perustuvaa suojelua ja ennallistamista. Tutkimus pohjautuu ekologisen lokeron käsitteeseen, joka liittää lajien levinneisyyden ympäristöolosuhteisiin, bioottisiin vuorovaikutuksiin ja spatiaaliseen rakenteeseen.

Käyttämällä passiivista akustista seurantaa yhdistettynä korkean resoluution spatiaaliseen aineistoon kaksi ensimmäistä tapaustutkimusta tarkastelevat varhaiskevään elinympäristövalintaa kahdella boreaalisen metsän erikoistuneella lintulajilla, töyhtötiaisella (*Lophophanes cristatus*) ja hömötiaisella (*Poecile montanus*).

Töyhtötiaisen esiintymistodennäköisyys kasvoi männyn neulasmassan kasvaessa ja pieneni etäisyyden ihmisasutukseen lyhentyessä havaintopisteen läheisyydessä.

Hömötiainen osoitti mittakaavasta riippumattomia positiivisia yhteyksiä mäntyvaltaisten suometsien pinta-alaan sekä paikallisella (100 m) että laajemmalla (400 m) mittakaavalla. Tulokset osoittavat, että erikoistuneiden lintulajien keskeiset ekologiset vaatimukset liittyvät hienojakoiseen elinympäristön käyttöön pikemminkin kuin tavanomaisten metsänhoidon indikaattorien kuvaamiin karkeisiin elinympäristöpiirteisiin.

Kolmannessa tapaustutkimuksessa analyyttinen viitekehys laajennetaan Englannin alaviin maatalousmaisemiin, joissa arvioidaan passiivisen ennallistamisen potentiaalia Biodiversity Net Gain (BNG) -politiikan puitteissa. Yhdistämällä maankäyttöluokituksia hirvieläinten laidunnuspaineeseen tutkimus tunnistaa alueet, joilla luontainen uudistuminen on todennäköisintä, sekä kvantifioi ennallistamisen mahdollisen panoksen kansallisten biodiversiteettitavoitteiden saavuttamiseen.

Kokonaisuudessaan tämä väitöskirja osoittaa, kuinka spatiaalisti eksplisiittiset ekologiset työkalut — akustisesta seurannasta maisematason mallinnukseen — voivat yhdistää ekologisen teorian käytännön luonnonsuojelutoimiin ja tukea lajipopulaatioiden sekä ekosysteemien kestävyyttä nopeasti muuttuvassa maailmassa.

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Abbreviations

EU	European Union
BNG	Biodiversity Net Gain
PAM	Passive Acoustic Monitoring
GIS	Geographic Information Systems
SYKE	Finnish Environment Institute (Suomen Ympäristökeskus)
ARU	Autonomous Recording Unit
UTC	Coordinated Universal Time
MS-NFI	Multi-Source National Forest Inventory
EMS	Effective Mesh Size
DWP	Dead Wood Potential
VIF	Variance Inflation Factor
GLMMs	Generalized Linear Mixed Models
BTO	British Trust for Ornithology
DEFRA	Department for Environment, Food and Rural Affairs (UK)
IPBES	Intergovernmental Science-Policy Platform on Biodiversity an Ecosystem Services
IPCC	Intergovernmental Panel on Climate Change

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

I Hamedani Raja, P., Baroni, D., Laaksonen, T., & Brommer, J. E. Crested Tits prefer pine forest but not mature forest: insights from an early spring passive acoustic survey. *Ornis Fennica*, 2025; *102*(1): 1–13. https://doi.org/10.51812/of.154972

II Hamedani Raja, P., Baroni, D., Laaksonen, T., & Brommer, J. E. Pine mires as key early-season habitat selection sites for Willow Tits in managed boreal forests. Manuscript.

III Kalliolevo, H., Pérez Chaves, P., Hamedani Raja, P., Vuorisalo, T., Bull, JW. Rewilding for biodiversity offsets: A case study of passive ecological restoration on lowland agricultural land for Biodiversity Net Gain in England. *Global Ecology and Conservation*, 2025; 60, e03603. https://doi.org/10.1016/j.gecco.2025.e03603.

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ROLE	CHAPTER I	CHAPTER II	CHAPTER III
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DATA COLLECTION (FIELD)	DB, TL	DB, TL	NOT RELEVANT
DATA CURATION	PHR, DB	PHR, DB	PHR, HK
SPATIAL DATA PROCESSING & ANALYSIS	PHR	PHR	PHR
STATISTICAL ANALYSIS & VISUALISATION	PHR	PHR	HK, PHR, PPC
WRITING – ORIGINAL DRAFT	PHR	PHR	HK, PHR (METHODS & RESULTS), TV
WRITING – REVIEW & EDITING	PHR, DB, TL, JEB	PHR, DB, TL, JEB	PHR, HK, PPC, TV, JWB

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1 Introduction

1.1 Ecological Theory and Habitat Suitability

The distribution and persistence of species are fundamentally shaped by their interactions with the environment (Hutchinson 1957; Chase & Leibold 2003; Begon *et al*. 2006). In the Hutchinsonian framework, each species occupies a niche defined as an n-dimensional hypervolume — a set of environmental conditions and resources within which populations can sustain themselves (Hutchinson 1957). This niche is shaped by both abiotic factors (e.g., climate, vegetation structure, hydrology) and biotic interactions (e.g., competition, predation, mutualism) (Begon *et al*. 2006). Understanding these relationships remains a central goal of ecology, providing the foundation for predicting species' responses to environmental change and for identifying the conditions necessary to maintain viable populations (Guisan & Zimmermann 2000; Peterson 2001; Pearson & Dawson 2003; Peterson *et al*. 2011).

Habitat suitability assessments translate these principles into applied tools for conservation (Guisan & Zimmermann 2000; Franklin 2010). By linking species occurrences with environmental variables, they identify the habitat features most critical for survival and reproduction. This line of thinking follows closely from the Hutchinsonian niche concept, which defines a species' niche as the multidimensional environmental space within which population growth is positive (Hutchinson 1957). However, ecological reality is often shaped not only by abiotic tolerances and resources but also by the Eltonian niche perspective (Elton 1927), which emphasizes the functional role of a species within its community and its interactions with other organisms. In practice, both perspectives are relevant: while species distributions may be constrained by climatic and structural factors, they are also modified by predation, competition, and mutualisms. For example, in boreal forests, the occurrence of small passerines such as the Willow Tit (*Poecile montanus*) may depend on both forest structure and the presence of potential predators like the Pygmy Owl (*Glaucidium passerinum*). Recognizing this duality helps clarify that habitat suitability analyses are not merely correlative descriptions of abiotic requirements but can also integrate biotic interactions to capture the ecological dynamics that shape species persistence. Such an integrated approach is particularly important for species of conservation concern, where mismatches between ecological requirements and available habitat can be driven as much by interactions as by environmental conditions (Boyce & McDonald 1999; Thomas *et al*. 2004). Building on the niche-based understanding of species–habitat relationships, it is equally important to consider the spatial structure and connectivity of habitats across landscapes, particularly in anthropogenically modified environments. Conservation planning increasingly operates in landscapes heavily shaped by human use, such as intensively managed forests and agricultural regions (Foley *et al.* 2005). In these systems, habitat loss, degradation, and fragmentation reduce the spatial extent of environments that match a species' ecological niche, leading to population isolation and disrupting processes such as dispersal and gene flow (Fahrig 2003). Insights from landscape ecology and metapopulation theory (Levins 1969; Hanski 1999) emphasize that maintaining viable populations requires not only sufficient habitat quantity and quality but also the spatial configuration and connectivity of habitats (Taylor *et al*. 1993; Lindenmayer & Fischer 2006).

Beyond protecting remaining habitats, modern conservation depends on ecological restoration and rewilding to recover ecological functions and expand opportunities for species persistence (Hobbs & Harris 2001; Perino *et al.* 2019). Restoration draws on principles of succession and disturbance theory (Clements 1916; Pickett & White 1985) to guide the recovery of degraded ecosystems, while rewilding emphasizes the re-establishment of self-regulating ecological processes, including through species reintroductions (Lorimer *et al*. 2015). Both approaches require a robust understanding of species–habitat relationships: without this knowledge, restoration risks being misdirected or unsustainable (Rey Benayas *et al*. 2009).

Integrating ecological theory with spatial data and quantitative habitat assessments allows conservation to move from reactive protection toward proactive, evidence-based management (Margules & Pressey 2000; Guisan *et al.* 2017). Spatially explicit analyses provide a common framework for quantifying habitat suitability across ecosystems, enabling comparisons between specialist species and broader landscape-scale restoration contexts (Elith & Leathwick 2009; Franklin 2010). Such approaches identify where species can persist under current conditions, where interventions are needed to sustain them, and where landscapes may offer opportunities for restoration or reintroduction (Ferrier & Wintle 2009; Watson *et al.* 2018).

1.2 Habitat in a Changing World

While the previous section outlined the ecological and theoretical basis for understanding species–habitat relationships, this section turns to the real-world pressures that are reshaping habitats and altering the context in which conservation must operate. Across biomes, both natural processes and accelerating anthropogenic change are transforming habitat quality, availability, and spatial structure. Habitats across the globe are being reshaped by a combination of natural processes and unprecedented human-driven change. While ecosystems have always been dynamic, the scale and speed of recent transformations are without historical precedent (Vitousek *et al*. 1997; IPBES 2019). These shifts alter the availability, quality, and spatial configuration of habitats, with direct consequences for the species that depend on them (Foley *et al.* 2005).

In forested ecosystems, intensive management has replaced structurally diverse natural stands with more uniform, production-oriented forests. Practices such as large-scale clear-felling, drainage of peatlands, and the removal of deadwood have simplified habitat structure and reduced the ecological niches available for specialist species (Esseen *et al*. 1997; Kuuluvainen *et al*. 2012). In agricultural and mixed rural landscapes, widespread land-use intensification, including the conversion of semi-natural habitats to farmland, removal of hedgerows and field margins, and expansion of infrastructure—has fragmented the remaining natural areas and eroded habitat connectivity (Donald *et al.* 2001; Tscharntke *et al*. 2005).

Climate change interacts with these pressures by altering temperature and precipitation regimes, shifting growing seasons, and modifying the distribution of both vegetation and wildlife (Walther *et al*. 2002; Parmesan 2006). In northern regions, milder winters and changes in snow cover influence forest composition and structure, with cascading effects on species adapted to cold, stable conditions (IPCC 2014). In temperate zones, changing rainfall patterns and warmer temperatures may compound the effects of land-use change, accelerate habitat degradation, or favour species that thrive in disturbed environments (Williams & Newbold 2020).

These combined drivers of change are particularly significant in landscapes already shaped by centuries of human use, such as boreal forests under intensive commercial forestry regimes and temperate lowland agricultural–forest mosaics. Here, high-quality habitats often persist only as isolated patches within a matrix of less suitable areas, making them especially vulnerable to further degradation (Fahrig 2003; Lindenmayer & Fischer 2006). Understanding how these pressures influence habitat availability is critical for conservation. This thesis focuses on two different landscapes—managed boreal forests and agricultural lowlands—both of which exemplify how habitat change reshapes opportunities for biodiversity persistence and recovery.

1.3 Species–Habitat Relationships for Conservation

The ability of a species to persist in a landscape depends on the match between its ecological requirements and the conditions available within that landscape (Hutchinson 1957; Krebs 2014). When suitable habitats are reduced, degraded, or fragmented, populations may decline even if other threats are absent (Fahrig 2003). For this reason, identifying and understanding the environmental factors that determine species occurrence is a central step in conservation science (Guisan & Zimmermann 2000).

Linking species to their habitats involves more than documenting where individuals are found. It requires assessing the ecological features that support survival, reproduction, and dispersal, and determining how these features vary across space and time (Boyce & McDonald 1999; Morris 2003). In practice, this often entails quantifying habitat characteristics—such as vegetation composition, structural complexity, or proximity to resources—and relating them to patterns of species presence or absence (Elith & Leathwick 2009). By establishing these relationships, it becomes possible to identify core habitat areas, marginal or suboptimal zones, and regions where targeted interventions could enhance habitat quality (Franklin 2010).

This approach is especially valuable in landscapes where human activities have altered the natural balance between habitat availability and species needs. In such contexts, conservation planning must be guided by evidence on which habitats are most critical for population viability (Margules & Pressey 2000). For species already in decline, targeted protection of key habitat features can help prevent further losses, while habitat restoration can reverse some of the impacts of degradation (Rey Benayas *et al.* 2009). For species that have been extirpated from parts of their range, understanding habitat requirements is essential for evaluating the feasibility of reintroduction or rewilding (Perino *et al.* 2019).

Integrating species–habitat relationships into conservation decision-making enables practitioners to target resources where they will have the greatest impact, ensuring that actions address the most important limiting factors for populations. It also supports the use of spatial planning tools to map networks of suitable habitat capable of sustaining connected, resilient populations over the long term (Taylor *et al.* 1993; Hanski 1999). This evidence-based approach is increasingly embedded in policy. At the European scale, the EU Nature Restoration Law (European Union, 2024, Regulation (EU) 2024/1991) establishes legally binding targets for ecosystem recovery and emphasises the need to monitor species groups, including forest birds, as indicators of habitat quality. In the UK, the Biodiversity Net Gain (BNG) framework introduced under the Environment Act requires measurable improvements in habitat extent and condition to be incorporated into land-use planning (DEFRA 2024), embedding ecological restoration within development processes. Together, these policy mechanisms highlight the importance of translating ecological evidence into actionable conservation strategies at both continental and national levels.

Focusing on species–habitat relationships is therefore not only a theoretical exercise but also a practical necessity. By quantifying how organisms respond to environmental structure and change, conservationists can identify ecological indicators, prioritize interventions, and anticipate long-term shifts (Soberón & Peterson 2005). This thesis applies such an approach across two contrasting systems—managed boreal forests and temperate agricultural mosaics—to demonstrate how ecological theory can directly inform applied conservation. Modern approaches increasingly rely on spatial ecological methods—remote sensing, passive acoustic monitoring, and spatial modelling—to quantify these relationships and inform decision-making (Guisan *et al.* 2017).

1.3.1 Tools for Species–Habitat Analysis

Modern species–habitat analyses increasingly rely on tools that generate spatially explicit, high-resolution data across broad temporal and geographic scales (Tingley *et al.* 2009). Among the most widely adopted are passive acoustic monitoring (PAM) and geographic information systems (GIS), which together provide powerful means to detect species, assess habitat conditions, and understand ecological processes in changing landscapes.

Passive acoustic monitoring offers a non-invasive and scalable approach to detecting species, especially vocal taxa like birds (Pérez-Granados &

Schuchmann 2021). In forest ecosystems, where visual observation is often limited by dense vegetation, automated sound recorders allow consistent data collection over large areas and extended timeframes. This enables researchers to capture patterns of species presence and activity that might otherwise go undetected. For resident forest specialists, vocal behaviour during key periods such as the early breeding season can reveal habitat use and territory establishment, providing a reliable proxy for habitat suitability. Beyond avian studies, PAM is increasingly recognized as a core method for biodiversity monitoring across taxa and ecosystems, enabling long-term tracking of ecological change (Sugai *et al.* 2020).

Geographic information systems, including remote sensing technologies, provide the spatial framework necessary for relating biological observations to environmental features. By combining field data with landscape-scale information—such as vegetation structure, forest age, or land-use intensity—GIS enables the mapping of habitat characteristics across multiple scales (Bock *et al.* 2003). This is particularly important in landscapes subject to fragmentation or management, where ecological patterns often reflect both fine-scale habitat conditions and broader spatial context. In agricultural systems, for instance, GIS-based approaches are vital for evaluating restoration potential, connectivity, and the ecological suitability of sites for rewilding.

Together, PAM and GIS form complementary foundations for modern ecological analysis. Acoustic monitoring captures species-level signals of habitat use, while GIS situates those signals within a broader spatial and environmental context. Their integration allows for robust, scalable analysis of species–habitat relationships—from understanding forest bird ecology in boreal systems to evaluating the role of large herbivores in regenerating lowland landscapes. Ultimately, these tools bridge theoretical ecology with conservation practice, enabling evidence-based planning in dynamic, human-influenced environments.

1.4 Forest Birds in Boreal Forests

Boreal forests of northern Europe provide essential habitat for many species that are tightly linked to forest structure, composition, and hydrology (Esseen *et al.* 1997; Kuuluvainen *et al.* 2012). In managed boreal forests, logging—particularly clear-felling—has been associated with reduced densities of several cavity-nesting species typical of mature coniferous or mixed stands (Virkkala 2004). Furthermore, many forest specialist species are vulnerable to changes in habitat patch size, connectivity, and the loss of old-forest structures in managed boreal landscapes (Mönkkönen & Mutanen 2003).

To illustrate the responses of boreal specialists to changing forest conditions, this study concentrates on two resident passerines, the Crested Tit (*Lophophanes cristatus*) and the Willow Tit (*Poecile montanus*). Both the Crested Tit and the Willow Tit are included in Finland's official Common Breeding Forest Birds indicator, which is used by the Finnish Environment Institute (SYKE) to monitor the effects of forest management on biodiversity in boreal ecosystems (SYKE 2023). The Crested Tit, a relatively common resident, is associated with pine-dominated stands and often begins breeding early in spring (Cramp & Perrins 1993). The Willow Tit is undergoing rapid decline in parts of Europe, and this has been linked strongly to the loss of suitable nesting sites in decaying wood and reductions in moist, structurally rich habitat (Parry & Broughton 2018; Kumpula *et al.* 2023; Lehikoinen *et al.* 2024). This study focuses on the early spring period, hereafter referred to as the pre-breeding or early breeding season. During this time, both species are largely resident forest birds apart from limited autumnal dispersal of juveniles, and the Crested Tit is preparing to breed, making habitat use particularly informative of conditions relevant to subsequent reproduction.In boreal systems, early-season processes are particularly important, as seasonal constraints and phenological mismatches can strongly influence individual performance and population dynamics (Vatka *et al.* 2014). In Willow Tits, timing has also been shown to be important in a social context, with juvenile survival influenced by the timing of settlement relative to conspecifics rather than food phenology (Pakanen *et al.* 2016). Habitat associations of forest-dwelling Parids have been shown to vary with forest structure, management history, and season, with some studies documenting strong relationships during the winter period (e.g. Siffczyk *et al.* 2003), while fewer studies have focused on habitat use during early spring. Previous studies have linked Crested Tit occurrence to old or mature forests, particularly in protected or near-natural reserves where forest age coincides with high availability of decaying wood (Virkkala *et al.* 1994). However, evidence from managed boreal forests suggests that forest age alone may be an unreliable proxy for habitat suitability, as natural and managed mature stands differ markedly in structural quality (Pakkala *et al.* 2024).

Studying these species provides critical insights into how forest management influences habitat suitability and into the broader conservation challenges facing boreal specialists. By examining Crested Tits and Willow Tits, this thesis not only explores species-specific habitat requirements but also demonstrates how spatial acoustic and remote-sensing methods can be combined to evaluate habitat suitability for boreal specialists.

While boreal systems highlight the vulnerability of specialist birds to intensive management, human-dominated landscapes such as agricultural systems pose distinct restoration challenges, especially in restoring ecological processes. In this context, rewilding has gained prominence as a strategy to recover biodiversity and ecosystem function (Svenning *et al*. 2016; Perino *et al*. 2019).

1.5 Rewilding in Agricultural England

Lowland agricultural landscapes in England have been profoundly shaped by centuries of farming and land-use policies, leading to the simplification of habitats and loss of ecological connectivity (Hodgson *et al*. 2005; Dallimer *et al*. 2009; Williamson 2015). Woodland remnants, hedgerows, and grasslands now persist mainly as small, isolated fragments within intensively cultivated areas, with reduced biodiversity and diminished structural diversity (Firbank *et a*l. 2008).

In response to these challenges, rewilding has emerged as an approach to restore ecological processes in human-dominated landscapes, often through natural regeneration and reduced management intervention (Navarro & Pereira 2012; Svenning *et al*. 2016). Passive rewilding, in particular, highlights the potential for abandoned or de-intensified land to regenerate naturally under suitable conditions (Prach & Hobbs 2008; Perino *et al*. 2019). Large herbivores, such as deer, also shape successional pathways through browsing and grazing, with outcomes ranging from maintaining open habitats to suppressing woodland recovery under high densities (Gill 2000; Vera 2000; Côté *et al.* 2004).

In England, rewilding is increasingly recognized within policy frameworks such as the Biodiversity Net Gain (BNG) requirement, which mandates measurable biodiversity improvements in development projects (DEFRA 2024). Evaluating rewilding potential in these contexts depends strongly on spatial analysis, which can identify where natural regeneration is ecologically viable, where connectivity could be restored, and how restoration potential can be compared across agricultural landscapes (Bergin *et al.* 2024). This spatial perspective also provides a transferable framework, linking fine-scale species–habitat assessments with large-scale mapping of restoration opportunities.

1.6 Aims and Structure of the Thesis

The overarching aim of this thesis is to investigate species–habitat relationships through spatial ecological analyses and to demonstrate how these insights can inform conservation and restoration decision-making (Figure 1). By linking species occurrence data with spatially derived habitat characteristics across contrasting ecological contexts, the research highlights both species-specific requirements and broader landscape-level drivers of habitat suitability. In doing so, it addresses how ecological evidence can support biodiversity protection, habitat restoration, and rewilding in line with current conservation needs and policy frameworks.

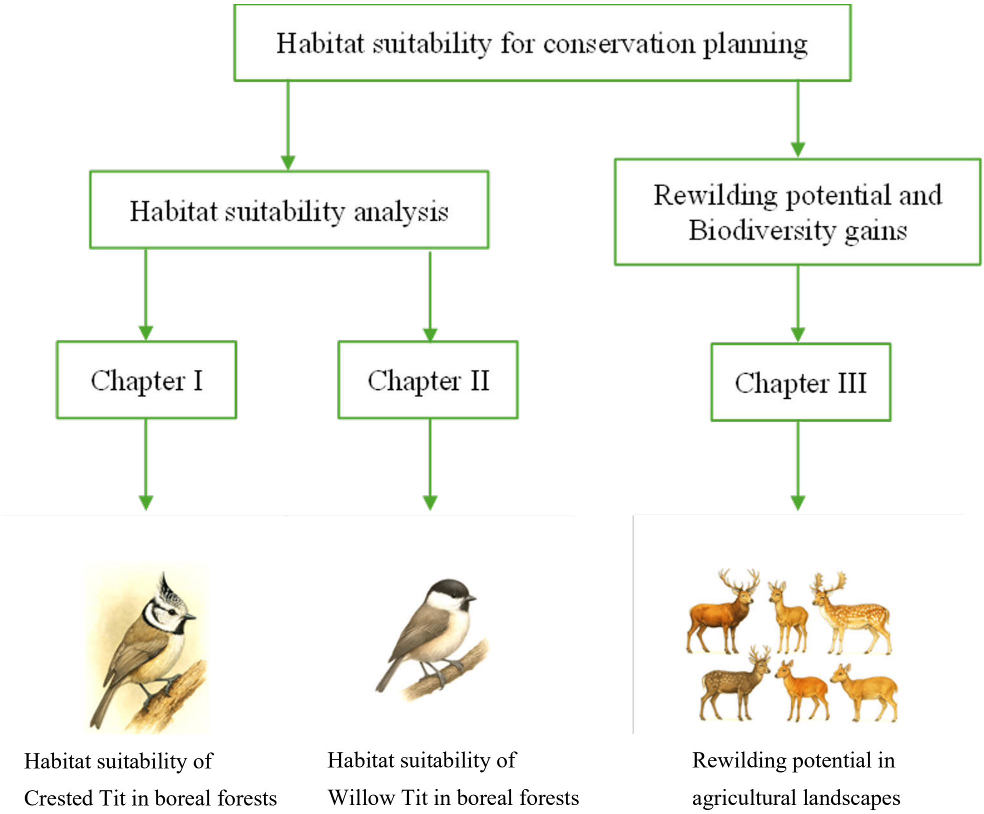


Figure 1. Graphical summary illustrating the main thematic aspects examined in this thesis and the interconnections between the individual chapters.

The thesis is organised into three case studies:

- **Chapters I and II** examine habitat selection in the boreal forests of Finland for two resident bird species, the Crested Tit and the Willow Tit. Using passive acoustic monitoring combined with high-resolution spatial data, these chapters explore how forest structure, composition, and management influence the occurrence of specialist birds during the early breeding season—a critical phase for territory establishment.
- **Chapter III** extends the spatial analysis framework to temperate agricultural landscapes in England, focusing on the potential for passive rewilding. By integrating habitat variables with deer distribution data, this chapter evaluates opportunities for natural regeneration and situates them within the emerging Biodiversity Net Gain (BNG) framework. The purpose of including this case study is to illustrate how the same analytical approach used for boreal forest birds can be scaled up and adapted to human-dominated systems, thereby linking fine-scale ecological analysis with large-scale conservation policy.

Together, the three case studies demonstrate how modern ecological tools—including passive acoustic monitoring, remote sensing, and spatially explicit modelling—can be applied to identify key habitat features, evaluate management impacts, and prioritise restoration opportunities. While each study focuses on a distinct species and landscape, they are unified by a common objective: to bridge ecological theory with applied conservation, and to provide evidence-based approaches that support resilient species populations and ecosystems under ongoing environmental change. In the following chapter, I describe the data sources, spatial analyses, and methodological approaches applied across the three case studies to investigate species–habitat relationships and conservation opportunities.

2 Materials and Methods

Across three case studies, this thesis applies consistent spatial ecological methods to explore species–habitat relationships and assess conservation opportunities. Species occurrence data were obtained through passive acoustic monitoring (**Chapters I and II**) or compiled from ecological and distributional records (**Chapter III**). Habitat characteristics were quantified using spatial datasets, including remote sensing products, land-cover maps, and derived structural variables. These data were then integrated with statistical modelling or index-based approaches to evaluate habitat suitability, management impacts, and restoration potential.

2.1 Boreal Bird Studies (Chapters I and II)

2.1.1 Study Area and Focal Species

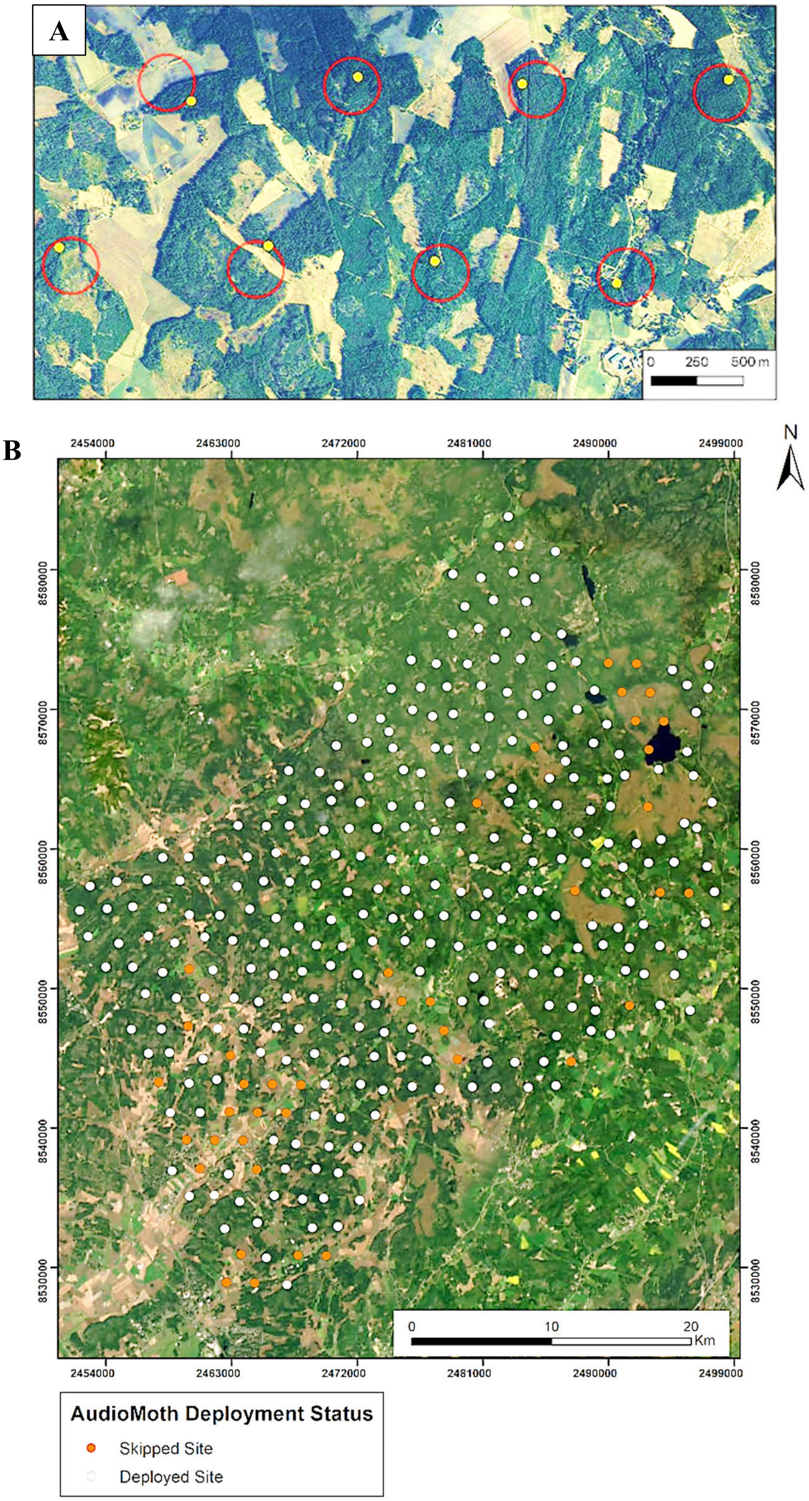
Fieldwork for the boreal case studies was carried out in March–April 2020 in southwestern Finland, north of Turku (60°N, 22°E). The 370 km² study area represents a typical mosaic of managed coniferous and deciduous forests, peatland bogs, and agricultural patches. Dominant tree species include Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birches (*Betula pendula* and *B.* pubescens), and European aspen (Populus tremula). Forest management in the region has reduced structural complexity and deadwood, while drainage of peatlands has altered hydrological conditions, though remnants of more natural habitats still persist.

The focal species, the Crested Tit and the Willow Tit, were chosen because they exemplify different ecological responses of forest specialists to boreal forest management. The Crested Tit is a largely sedentary species that shows a strong association with pine-dominated stands, where it commonly forages among canopy foliage (Cramp & Perrins 1993). The Willow Tit has shown steep population declines in parts of Europe, with recent assessments documenting a dramatic collapse in Northern Europe driven by habitat loss and decreased adult survival (BTO 2024; Lehikoinen *et al.* 2024). Its decline is widely linked to its reliance on moist, structurally diverse forest with decaying wood for cavity excavation, a habitat increasingly degraded by forest management and logging (Kumpula *et al.* 2023). Surveys were conducted in early spring, when both species are typically territorial and highly vocal (Cramp & Perrins 1993), making them well suited to acoustic monitoring. This pre-breeding phase is ecologically important, as individuals occupy established winter territories that transition into breeding territories, and adjust space use and activity in relation to seasonal changes in resource availability and breeding preparation (Cramp & Perrins 1993; Pakanen *et al.* 2016). Vocal activity during this time provides valuable insight into spatial patterns of territory settlement, which in turn reflects habitat preferences and suitability.

2.1.2 Passive Acoustic Monitoring

Species occurrence was measured using passive acoustic monitoring (PAM). A systematic 1 km × 1 km grid was established across the study area, with Autonomous Recording Units (ARUs; AudioMoth v1.1) deployed at the centre of grid cells containing at least 100 m of forest. Non-forested or agricultural cells were excluded, yielding 285 monitored sites. Recording took place from 16 March to 25 April 2020, targeting peak vocal activity during territory establishment. ARUs were programmed to record twice daily (00:00–07:00 and 16:00–20:00 UTC) and rotated weekly to maximise spatial coverage. Recordings were processed using Kaleidoscope v5.4.2 with species-specific classifiers, followed by manual verification. To minimise false positives, species detections were based on full songs and on complex, species-specific calls that could be reliably identified based on their acoustic structure, while alarm calls, very short call fragments, and other ambiguous signals were excluded. Figure 2 illustrates A, the location of AudioMoth devices within 100 m radius buffers, B, their distribution across the study area in southwestern Finland, and C, an example of a device installed on a tree in the field. Passive acoustic monitoring (PAM) provides a non-invasive and scalable alternative to traditional field-based bird surveys, such as point counts or transect walks (Shonfield & Bayne 2017; Darras *et al.* 2018). Unlike in-person surveys, which are constrained by observer availability and limited temporal windows, PAM allows continuous and standardised data collection across large spatial extents, reducing observer bias and enabling detection during periods of peak vocal activity (Shonfield & Bayne 2017; Darras *et al.* 2018; Sugai *et al.* 2020). These advantages make PAM particularly well suited for forest environments, where visibility is limited and access may be restricted (Shonfield & Bayne 2017).

Automated species identification using acoustic classifiers facilitates efficient processing of large datasets, but such tools may be affected by false positives and false negatives, especially for species with overlapping vocalisations or variable song structure (Knight *et al.* 2017; Priyadarshani *et al.* 2018). To address these limitations, all automated detections were manually reviewed and validated by experienced observers, ensuring high confidence in species identification and presence–absence classification (Furnas & Callas 2015).


A
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2463000
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2481000
2490000
2499000
8580000
8570000
8560000
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8530000
N
0 10 20 Km
AudioMoth Deployment Status
● Skipped Site
○ Deployed Site

Figure 2. **A**: Locations of AudioMoth devices (yellow dots) within 100 m radius buffers centered on grid cells (red). **B**: Placement of AudioMoth devices across the study area in southwestern Finland, with grey dots showing deployed devices and red dots showing excluded sites with insufficient forest cover. **C**: Example of an AudioMoth device installed on a tree in the field (original photograph by Daniele Baroni). Panel A is adapted from Hamedani Raja *et al.* (2025), **Chapter I** of this thesis; panels B and C are adapted from Hamedani Raja *et al.* (Manuscript), **Chapter II** of this thesis.

Because exact detection distances cannot be determined from autonomous recordings, analyses were conducted using fixed spatial buffers, which represent analytical scales rather than strict limits of sound detectability.

2.1.3 Environmental Variables

Habitat variables were quantified at two spatial scales: 100 m radius buffers, approximating the core territory size of the species, and 400 m buffers, capturing broader landscape influences. Forest composition was quantified using foliage biomass (kg/ha) for pine, spruce, and deciduous trees, derived from the Finnish Multi-Source National Forest Inventory (MS-NFI; Mäkisara *et al.* 2016). From the same dataset we calculated the mean, standard deviation, and summed values of foliage biomass, as well as mean and standard deviation of canopy cover. Peatland habitats (pine mires, spruce mires, and treeless peatlands) were also delineated from MS-NFI layers. Forest age was classified into young (<15 years), mid-aged (15–80 years), and mature (>80 years) stands, based on historical aerial photographs (dating back to 1949) and recent satellite imagery; these classifications were used to derive the area of clearcuts, forest cover (>15 years), and mature forest within each buffer, as well as to quantify forest fragmentation using the Effective Mesh Size (EMS) index (Jaeger 2000; Baroni *et al.* 2023). Forest age classes were used as coarse proxies for stand maturity and structural conditions relevant to cavity-nesting forest birds. Evidence from Willow Tit ecology indicates that very young or recently regenerated stands generally lack suitable cavity substrates, while habitat suitability increases in mid-aged forests as dead wood begins to accumulate, even in the absence of old-growth conditions (Kumpula *et al.* 2023). Forest age does not capture important management-related factors such as thinning history and stands of similar age may therefore differ substantially in structural quality; this limitation is acknowledged in the interpretation of the results. Modeled deadwood availability was obtained from the Dead Wood Potential (DWP) model (Mikkonen *et al*. 2020), from which we extracted mean expected deadwood values. Agricultural areas were identified from MS-NFI, and total raster area within buffers was included to standardize habitat cover estimates. Human disturbance was represented by the Euclidean distance to the nearest residential building and to the nearest main road. Biotic interactions were represented by the presence of Pygmy Owl (*Glaucidium passerinum*), a known predator of small passerines (Baroni *et al.* 2023), and by the co-occurrence of Crested and Willow Tits as potential competitors. Julian date was included as a covariate to account for seasonal changes in vocal activity. A full list of habitat variables, their definitions, data sources, and summary ranges (100 m scale) is provided in Table 1.

Table 1. Habitat variables included in the analysis in **chapters I and II**, with explanations, data sources, and summary ranges (100 m radius).

Variable title	Explanation	Resource	Amount of variable within 100m radius in applied sites
Julian date	Start date of recording, used to account for seasonal variation in vocal activity	Recording metadata	March 16–April 25
Pygmy owl	Presence/absence of Pygmy Owl	Passive acoustic monitoring (Baroni *et al.* 2023)	Present in 63 sites (22%)
Distance to house	Minimum distance to the nearest inhabited houses	Cartographic maps	43–3249 m (mean = 715.4)
Sum pine foliage	Sum of pine foliage biomass (kg/ha)	Multi-source National Forest Inventory	30–2.79×10^4 kg/ha (mean = 1.55×10^4)
Sum deciduous foliage	Sum of deciduous foliage biomass (kg/ha)	Multi-source National Forest Inventory	84–1.65×10^4 kg/ha (mean = 4.05×10^3)
Mean expected dead wood	Modeled deadwood availability	Dead wood potential (DWP) modelling (Mikkonen *et al.* 2020).	0.08–1 (mean=0.62)
Area of mature forest	Forest area > 80years old	Aerial photographs and satellite imagery	0–3.17 ha (mean= 0.27)
Area of clearcut	Forest <15 years old	Aerial photographs and satellite imagery	0–3.05 ha (mean = 0.33)
Area of Pine mire	Forested peatland dominated by pine	Multi-source National Forest Inventory	0–2.48 ha (mean= 0.2)
Area of spruce mire	Forested peatland dominated by spruce	Multi-source National Forest Inventory	0–1.02 ha (mean= 0.18)
Area of treeless peatland	Open bogs and fens	Multi-source National Forest Inventory	0–0.74 ha (mean= 0.01)
Initial variables were excluded to avoid redundancy	Mean and standard deviation of Pine foliage biomass, Mean and standard deviation of spruce foliage biomass, Mean and standard deviation of deciduous foliage biomass, mean and standard deviation of canopy cover, minimum distance from main road, ems (Fragmentation index), Forest cover, i.e. forest >15 years old, Area of agricultural areas, Area of peatbogs, Total area of the raster layers included in the buffers		

2.1.4 Data Analysis

Presence/absence of Crested Tit and Willow Tit in the passive acoustic monitoring data was determined from call detections (0 = not detected, 1 = detected) using Kaleidoscope version 5.4.2. To minimize false positives, we applied advanced classifiers and initially trained the software with publicly available reference calls of both species. The classifier then used statistical pattern recognition to sort similar vocalizations. All automated identifications were subsequently verified by at least two bird specialists (PHR, DB) to further reduce potential misclassifications. Prior to modelling, collinearity among explanatory habitat variables was assessed using a Pearson correlation matrix in the usdm package (Naimi *et al.* 2014). When two variables were strongly correlated ($|r| > 0.70$), one was excluded to reduce redundancy and avoid interpretational ambiguity, following the recommendations of Zuur *et al.* (2010) and Dormann *et al.* (2013). The final set of variables retained for analysis is listed in Table 1. Residual multicollinearity was further evaluated using Variance Inflation Factor (VIF) values, all of which were well below the commonly applied threshold of 5 (Naimi *et al.* 2014), indicating acceptable independence among predictors.

The relationships between species presence/absence (Crested Tit and Willow Tit) and environmental variables were analysed with binomial generalized linear mixed models (GLMMs). To account for spatial dependence among observations, we included an exponentially decaying spatial autocorrelation term. For the Willow Tit, Julian date was included as a fixed effect to account for changes in vocal activity and detectability as the breeding season progressed. Models were implemented in glmmTMB (Brooks *et al*. 2017) in R version 1.3.959 (R Core Team 2020).

2.2 Rewilding Study (Chapter III)

This case study extended the analytical framework to temperate lowland England (<250 m a.s.l.), where centuries of agricultural land use have left woodland remnants embedded in an intensively farmed matrix. The spatial analysis focused on evaluating rewilding potential defined as an index reflecting the relative suitability of sites for passive restoration.

2.2.1 Focal Species and Ecological Role

The rewilding study focused on six free-ranging deer species: Red Deer (*Cervus elaphus*), Roe Deer (*Capreolus capreolus*), Fallow Deer (*Dama dama*), Sika Deer (*Cervus nippon*), Reeves's Muntjac (*Muntiacus reevesi*), and Chinese Water Deer (*Hydropotes inermis*). These herbivores are key drivers of woodland dynamics through browsing, which can maintain habitat heterogeneity but also suppress natural regeneration when densities are high (Gill 1992; Côté *et al.* 2004). Their distribution and density were therefore central to assessing rewilding potential (Cooke & Farrell 2001).

2.2.2 Environmental Variables and Index Construction

Spatial data included the Land Cover Map (Centre for Ecology and Hydrology 2017), used to categorize agricultural and forest land, and Terrestrial Ecoregions of the World (Olson *et al.* 2001), used to classify original English habitat types. Deer distribution maps were obtained from the British Deer Society (2016). Deer presence was digitised to a 10 × 10 km grid and combined with literature-based estimates of species-specific browsing pressure in broadleaved woodlands.

Separate raster layers were created for arable land and forest cover, categorized into three classes (1–3) based on percentage cover within each grid cell. Thresholds were defined by dividing the maximum observed cover values (38% for forest, 95% for arable) into three equal categories. Browsing pressure was also classified into three categories. The three variables—arable cover, forest cover, and deer browsing pressure—were summed to produce scores of 3–9, which were then classified as poor (3–4), moderate (5–7), or good (8–9) rewilding potential. These categories were aligned with the DEFRA Biodiversity Metric 3.1, which scores habitat condition from 1 (poor) to 3 (good) (Table 2).

Table 2. Scoring of the sites used in **Chapter III**, based on deer browsing pressure and the amount of forest and arable land cover in a 10 km × 10 km pixel. The variables are given scores from 1 to 3 based on the rewilding potential.

Deer browsing pressure		**Forest cover**		**Arable land cover**	
Threshold population density per 100 ha	Score	Cover (%)	Score	Cover (%)	Score
>25	1	<13	1	<32	1
5–25	2	13–25	2	32–63	2
0-5	3	>25	3	>63	3

2.2.3 Biodiversity Net Gain (BNG) Scenarios and Sensitivity Analysis

To evaluate uncertainty, a sensitivity analysis was performed on the thresholds used for habitat suitability scoring. Forest thresholds were varied by ±5%, and arable thresholds by ±10%, reflecting their different maximum coverages (38% forest, 95% arable). Cross-testing of these changes produced eight alternative versions of the rewilding index.

3 Results

3.1 Crested Tit – Habitat Suitability in Boreal Forests (Chapter I)

Crested Tits were detected at 195 of 285 sites (68%) during the one-week recording period (Figure 4).

At the 100 m scale, occurrence showed a positive association with pine foliage biomass (Figure 4A; **Chapter I**, Table 2A) and with distance from the nearest house (Figure 4B; **Chapter I**, Table 2A). While these relationships did not reach conventional levels of statistical significance, they may still indicate ecologically meaningful patterns, with local pine resources and avoidance of human settlements influencing Crested Tit presence.

At the 400 m scale, no strong associations were detected between Crested Tit presence and any of the measured habitat variables. Weak, non-significant trends were observed for both pine foliage and distance from houses, but the area of mature forest had no effect on occurrence (**Chapter I**, Table 2B).

The presence of Pygmy Owls was not associated with Crested Tit occurrence at either scale (**Chapter I**, Table 2).

Predicted probabilities further illustrate these patterns (Figure 4). At the 100 m scale, Crested Tit presence increased with higher pine foliage biomass and greater distance from houses, suggesting sensitivity to local foraging resources and anthropogenic disturbance. These results indicate stronger associations with local-scale habitat characteristics, although this pattern may partly reflect the effective detection range of acoustic monitoring relative to broader (400 m) landscape variables.

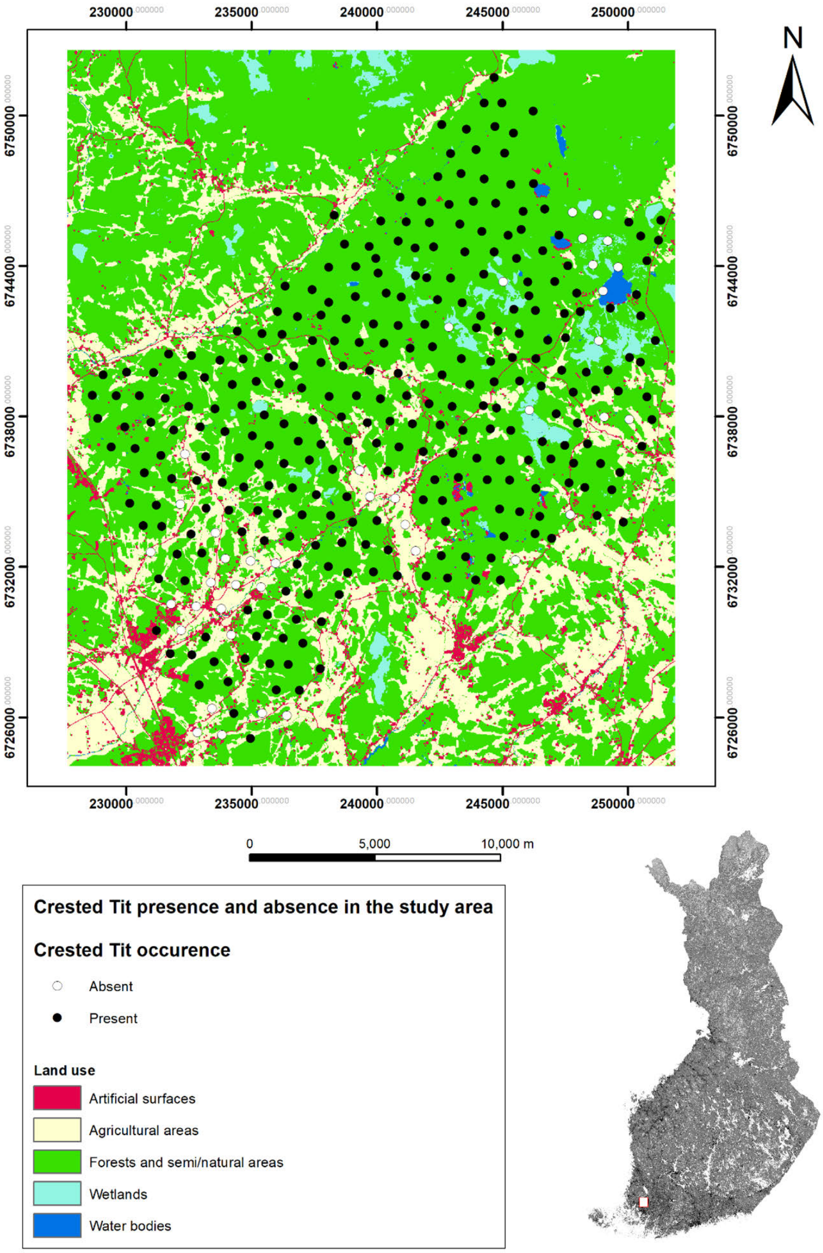


Figure 3. Map of the study area in southwest Finland, showing the study grid and the presence–absence records of Crested Tits obtained from passive acoustic surveys across different land-use types. Figure issued from Hamedani Raja *et al*. (2025), **Chapter I**.

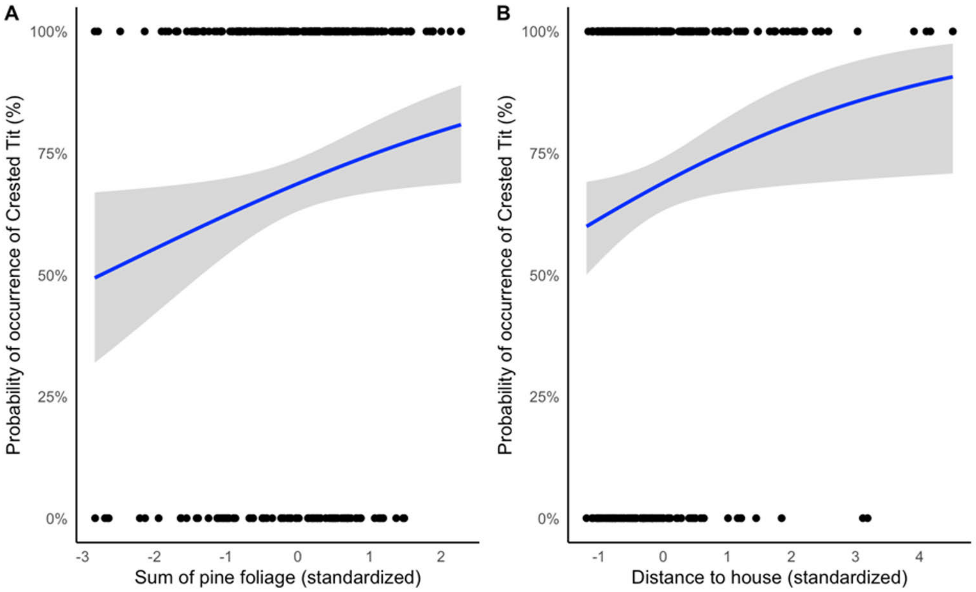


Figure 4. Figure 4. Probability (expressed as a percentage) of Crested Tit presence in relation to **A**: Sum of pine foliage and **B**: distance to the nearest house, within a 100m radius buffer around the detector. In both graphs, the variables were standardized to a mean of zero and a unit standard deviation to allow comparison. The fitted relationships are represented by solid blue lines, with 95% confidence intervals around each line to indicate uncertainty. Data points are plotted as dots, showing Crested Tit presence (1) or absence (0) at each detector location. Figure issued from Hamedani Raja *et al.* (2025), **Chapter I**.

3.2 Willow Tit – Early Season Habitat Selection in Boreal Forests (Chapter II)

Willow Tits were detected at 103 of 285 sites (36%) during one-week recording sessions (Figure 5). Habitat models showed that pine mire area was a consistent positive predictor of Willow Tit occurrence at both the 100 m and 400 m scales (Figure 6A, C; **Chapter II**, Table 2). Pine foliage biomass showed a marginally positive effect at the 400 m scale (**Chapter II**, Table 2B), though no association at the finer scale.

Pygmy Owl presence was also positively associated with Willow Tits at the 100 m scale (Figure 6B; Chapter II, Table 2A), suggesting that both species may co-occur in areas not fully captured by the available habitat variables. In contrast, modelled deadwood potential was negatively associated with Willow Tit presence at the 400 m scale (Figure 6E; **Chapter II**, Table 2B).

Detection probability declined with advancing Julian date, significantly at the 400 m scale (Figure 6D; **Chapter II**, Table 2B) and marginally at 100 m (**Chapter II**, Table 2A), likely reflecting reduced vocal activity later in the early breeding season. Mature forest area did not emerge as a significant predictor at either spatial scale.

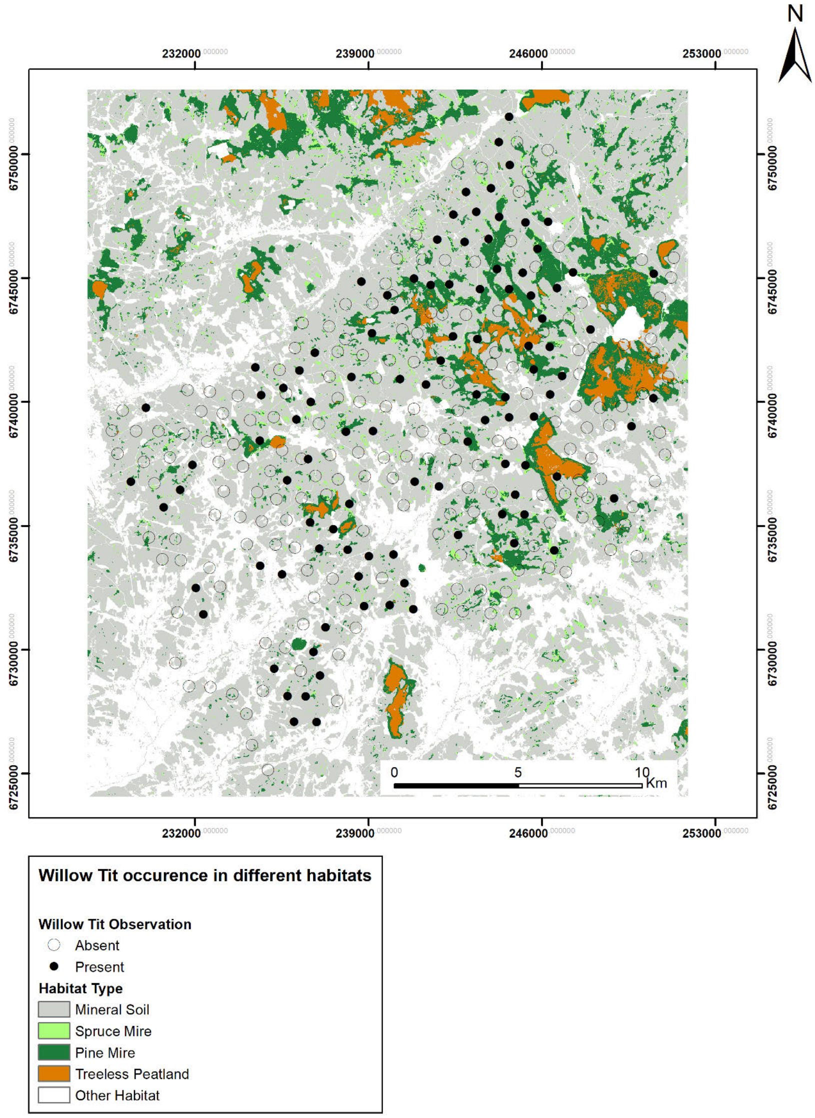


Figure 5. Willow Tit presence (black dots) and absence (open circles) across the study area, displayed over dominant habitat types. Habitat types include pine mires (dark green), spruce mires (light green), treeless peatlands (orange/brown), and other habitats (white). Areas classified as mineral soil forests (light grey) are shown for spatial context but were not included as separate variables in the habitat analysis. Figure issued from Hamedani Raja *et al*. (Manuscript), **Chapter II**.

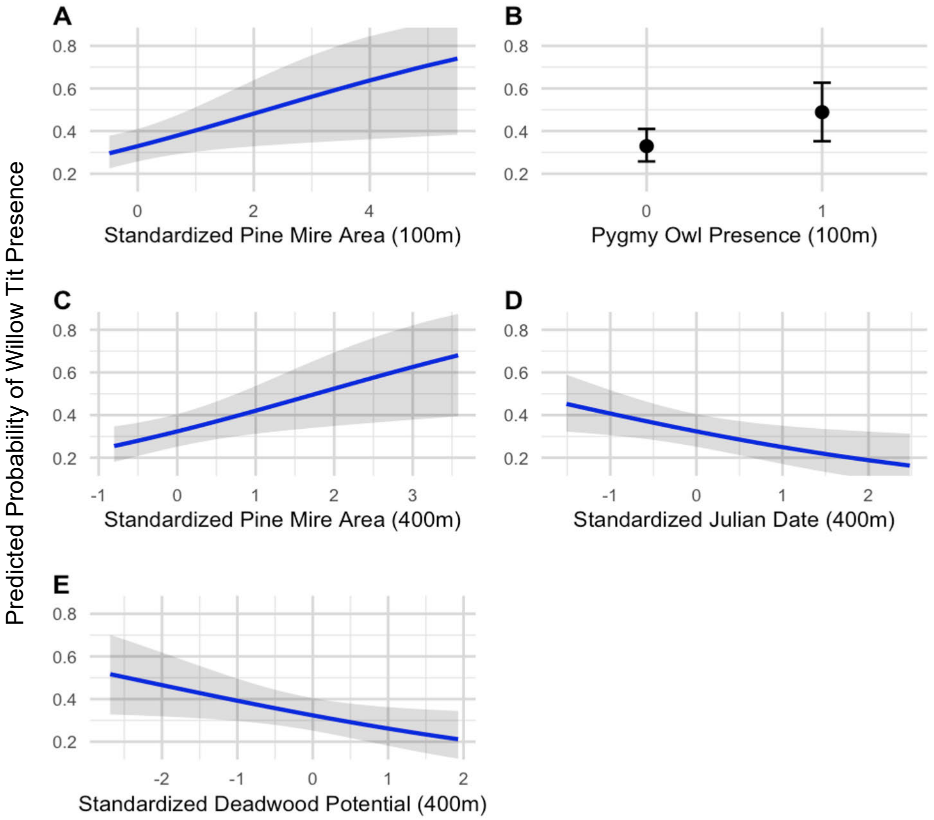


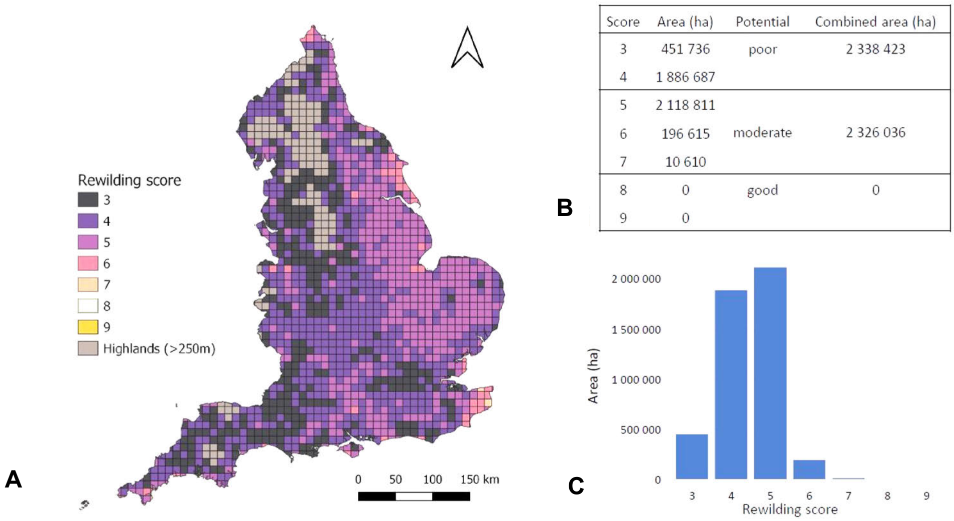
Figure 6. Predicted probability of Willow Tit presence in relation to key habitat variables at two spatial scales, based on Generalized Linear Mixed Model (GLMM). Panels A and B show 100 m buffer results: A: standardized pine mire area (only non-zero values shown), and B: Pygmy Owl presence. Panels C–E show 400 m buffer variables: C: standardized pine mire area, D: standardized Julian date, and E: standardized mean deadwood potential. All predictors were standardized (mean = 0, SD = 1) for effect size comparison. Solid lines represent model predictions with 95% confidence intervals (shaded ribbons or error bars). Figure issued from Hamedani Raja *et al.* (Manuscript), **Chapter II**.

Together, these results highlight the strong role of pine-dominated peatlands in shaping early-season Willow Tit distributions, while also revealing scale-dependent responses to foraging resources, predation risk, and seasonal variation in detection.

3.3 Rewilding Potential in Temperate Agricultural Landscapes (Chapter III)

3.3.1 Rewilding Potential and Biodiversity Units

The rewilding potential analysis for lowland agricultural areas of England, developed in the context of the Biodiversity Net Gain (BNG) framework, showed that the highest potential is concentrated in the southeast, with eastern regions generally offering more opportunities than the west (Figure 7). Converting rewilding potential into habitat condition using the Biodiversity Metric 3.1 indicated that most sites could only be restored to poor or moderate condition, with only one scenario producing areas that reached good condition (**Chapter III**, Table 2).



Score	Area (ha)	Potential	Combined area (ha)
3	451 736	poor	2 338 423
4	1 886 687		
5	2 118 811	moderate	2 326 036
6	196 615		
7	10 610		
8	0	good	0
9	0		

Figure 7. A: Map of England showing the rewilding potential as scores across the country. B: Table with area (ha) of different rewilding potential scores from 3 (poor potential) to 9 (good potential). C: Figure of rewilding scores and associated areas (ha). Highlands are marked separately as our analysis is based on lowland agricultural land. Figure issued from Kalliolevo *et al*. (2025), **Chapter III**.

Calculations of biodiversity units using the Biodiversity Metric 3.1, under different woodland habitat types and assumptions about condition, time to target, and locality, produced outcomes ranging from 3,650,856 to 32,562,736 units, or 0.78–7.34 units per hectare. Given that annual development in England is estimated to require about 38,000 biodiversity units (Ministry of Housing, Communities and Local Government 2020), restoring between 0.15% and 1.06% of agricultural land annually could in principle compensate for ongoing development losses.

Rewilding could therefore provide a significant contribution to BNG, though adjustments may be required to current calculation practices, since natural regeneration does not always lead to predictable habitat outcomes. This may necessitate restoration guidance or post-establishment evaluation before biodiversity units are formally accounted (Maron et al. 2012; zu Ermgassen et al. 2019).

3.3.2 Sensitivity Analysis

The sensitivity analysis revealed that varying the forest and arable thresholds produced noticeable numerical shifts in the total area assigned to each suitability score (**Chapter III**, Table 3). However, these shifts did not translate into major changes in the overall classification of rewilding potential.

Across all eight tested versions, the landscape was consistently dominated by two classes—Poor and Moderate potential. The Good category appeared only in one extreme scenario (Version 5: forest −5%, arable +10%), and even then, it represented a very small area (6,221 ha), indicating that the classification rarely escalates areas to the highest suitability simply through moderate threshold adjustments.

Although the absolute area within each score (3–7) varied across versions, the relative pattern remained similar:

- Scores 4 and 5 consistently covered the largest areas,
- Scores 7–8 remained very limited under all conditions,
- No version produced any areas in score 9.

Importantly, the redistribution of area between classes did not alter the spatial identity of the top-ranked regions: geographic locations classified as highest potential remained stable across nearly all versions. This indicates that while threshold adjustments modify area totals, they do not fundamentally change which areas are identified as suitable.

Overall, the analysis shows that the rewilding index is robust to moderate uncertainty in input thresholds. The general structure of suitability classes, the dominance of Moderate–Poor categories, and the identity of high-potential areas remain consistent across all threshold variations.

4 Discussion

This thesis explored how spatial ecological analyses can enhance our understanding of species–habitat relationships and guide both conservation and restoration planning. It brought together three case studies linked by a common framework: assessing habitat suitability across taxa, forest types, and spatial scales. The studies move from fine-scale, species-specific analyses in boreal forests (Crested Tit and Willow Tit) to a national-scale prioritisation of passive rewilding in agricultural landscapes in England. Below, each aim is revisited considering the findings from the respective manuscripts.

4.1 Habitat Selection and Anthropogenic Responses in the Crested Tit

The Crested Tit study used passive acoustic monitoring across a 285-site grid in southern Finland to assess habitat preferences during early spring, just before the breeding season. Results showed that Crested Tits were positively associated with higher pine foliage biomass within 100 m but not at 400 m, suggesting that foraging habitat selection occurs at fine spatial scales. This supports previous findings on the species' reliance on coniferous habitat and insect-rich pine canopies (Lens & Dhondt 1993; Summers *et al*. 1999; Berlusconi *et al*. 2022).

Conversely, there was no observed preference for mature forest (>80 years), which challenges assumptions about old-growth reliance during this season (Berlusconi *et al*. 2022). While the species is known to nest in decaying trees, our results suggest that nesting microhabitats may be more widespread or that requirements for old forests intensify later in the season. It is also possible that the structural characteristics of forests aged over 80 years in our dataset do not correspond with the habitat complexity typically expected in old-growth systems. Previous studies reporting positive associations between Crested Tits and old forests have largely focused on protected or near-natural stands, where forest age coincides with high availability of decaying wood and nesting cavities (Virkkala *et al*. 1994; Pakkala *et al.* 2024). In intensively managed boreal landscapes, forest age alone may therefore be a poor proxy for habitat quality during the early season.

Avoidance of human settlements was consistent at both scales, reinforcing sensitivity to anthropogenic disturbance (Marzluff 2001; McKinney 2008). Interestingly, sites near houses may also experience increased competition from generalist species such as Great Tits (*Parus major*) or Blue Tits (*Cyanistes caeruleus*) (Solonen & Hildén 2014), further reducing habitat suitability for Crested Tits. These patterns highlight the need to maintain structurally rich pine habitats and reduce urban encroachment near forests. Overall, the limited number of statistically strong associations likely reflects the high prevalence of Crested Tits across the study area during early spring, resulting in widespread habitat suitability and reduced contrast between occupied and unoccupied sites, rather than absence of habitat selection. This pattern may also indicate a broader habitat use during the pre-breeding period, when Crested Tits may behave more generally than during later breeding stages. Longer-term passive acoustic monitoring extending into the main breeding season would provide an important opportunity to evaluate whether these patterns persist across different behavioural stages and to better disentangle early-season habitat use from breeding-period habitat associations.

The analyses focused on a relatively short early-season window, spanning mid-March to late April, which likely overlaps with territory establishment and the onset of early breeding activity in southern Finland. While this period does not capture the full breeding season, it represents a biologically important phase during which habitat selection and territory settlement occur and can strongly influence subsequent reproductive outcomes. Declining detection rates toward the end of the sampling period likely reflect seasonal changes in vocal activity rather than true absence and therefore limit inference on habitat use later in the breeding season (Lindbladh *et al.* 2019). Passive acoustic monitoring was also validated as a useful and scalable method for detecting fine-scale habitat associations in forest birds. The results reinforce its potential as a low-impact, high-coverage tool for long-term ecological monitoring. At the same time, passive acoustic monitoring relies on species-specific vocal behaviour, which varies among taxa, individuals, and environmental conditions, and is further influenced by habitat structure and seasonal timing (Marques *et al.* 2013; Darras *et al.* 2018; Sugai *et al.* 2020). Consequently, acoustic detections reflect detectability during the sampling period rather than true occupancy, and non-detection does not necessarily indicate true absence, particularly when vocal activity is low or temporally constrained (Furnas & Callas 2015).

Detection distance in acoustic monitoring is species-specific and strongly influenced by habitat structure, vegetation density, and meteorological conditions (Marques *et al.* 2013; Darras *et al.* 2016). Experimental sound propagation studies have shown that for many small forest passerines, including species with vocal characteristics similar to Crested Tit and Willow Tit, detection probabilities typically decline rapidly beyond 100–150 m, although audible detections may occasionally occur at greater distances under favourable conditions (Winiarska *et al.* 2024). Consequently, habitat variables quantified within the 100 m radius likely provide a closer approximation of the habitat occupied at the time of detection, whereas the 400 m radius reflects broader landscape context rather than precise bird location.

Importantly, detection distances have been shown to differ between forest types, with higher detection probabilities and longer maximum detection distances often observed in coniferous forests compared to denser deciduous stands (Winiarska *et al.* 2024).

Such habitat-dependent variation implies that acoustic detections reflect a combination of species presence and detectability, and results should therefore be interpreted as relative habitat associations rather than precise spatial locations of individuals.

4.2 Habitat Preferences and Resource Use in the Willow Tit

The Willow Tit study also used passive acoustic methods during early spring to assess species occurrence across pine-dominated boreal forests. A strong and consistent association was found with pine mires at both 100 m and 400 m scales, highlighting the importance of moist pine-mire habitats during early territory establishment. While Willow Tits rarely nest in pine trees (Cramp & Perrins 1993; Parry & Broughton 2018), pine mires may still be important early-season habitats by providing moist conditions and suitable nesting substrates at forest–mire edges, where birch, alder, and goat willow are commonly present. In addition to structural characteristics, the observed association with pine mires may reflect seasonal variation in resource use during early spring. Previous studies have shown that Willow Tits use pine-dominated habitats outside the breeding season (Siffczyk *et al.* 2003), suggesting that habitat associations during this period may be influenced by foraging opportunities rather than nesting requirements alone. Such seasonal shifts in habitat use across the annual cycle may help explain differences between early-season and breeding-period habitat associations. Acoustic detections during early spring likely reflect territorial presence rather than precise nest locations. While singing activity is often associated with territory establishment and may occur near future nesting areas, autonomous recordings do not allow direct inference about nest placement. Consequently, associations with pine mires should be interpreted as reflecting habitat use within the broader landscape context, potentially integrating both foraging areas and nearby nesting substrates.

Spruce mires and mature forest (>80 years) did not show similar associations. This may be due to limitations in coarse habitat classifications, which fail to capture critical features such as snag softness or understory density (Lehikoinen *et al.* 2024;

Milner *et al.* 2024). The absence of a positive association with mature forest during early spring may also reflect seasonal shifts in habitat use across the annual cycle. Willow Tits occupy larger winter territories that may encompass a wider range of forest types, including older stands used for food caching, whereas habitat use in spring may shift toward areas offering readily available food resources (Siffczyk *et al.* 2003). Consequently, early-season habitat associations may differ from those observed during winter or the core breeding period, and negative associations with old forest in spring do not necessarily contradict the importance of such habitats at other times of the year. Future acoustic monitoring during the winter period could help clarify how seasonal changes in habitat use influence detectability and habitat associations. A surprising finding was the negative association with modelled deadwood potential—a landscape-scale index derived from forest inventory data. This suggests that such proxies do not reliably reflect the fine-scale nesting suitability needed by cavity-nesting species, supporting earlier concerns about overreliance on broad-scale metrics. The negative association with modelled deadwood potential should be interpreted cautiously. Dead wood potential represents a broad, quantity-based proxy and does not capture the quality or suitability of individual snags, such as the presence of soft wood affected by white rot fungi, which are particularly important for Willow Tit cavity excavation (Cramp & Perrins 1993; Parry & Broughton 2018). Moreover, early spring detections likely precede active nest excavation, such that dead wood availability may not yet strongly influence habitat use during this period (Cramp & Perrins 1993). Importantly, these results do not imply that old forests or dead wood are unimportant for Willow Tits; rather, they highlight that fine-scale structural characteristics and seasonal timing are not well captured by coarse landscape-level indices.

Differences in responses between local (100 m) and broader (400 m) spatial scales further emphasize that habitat associations are scale-dependent, and that conclusions about suitability may vary depending on the spatial extent at which variables are quantified. As discussed above for Crested Tit, the effective detection range of passive acoustic monitoring suggests that habitat variables within the 100 m radius more closely represent the immediate environment of detected individuals, whereas the 400 m scale primarily reflects broader landscape context rather than precise bird location.

More generally, the use of remotely sensed or modelled habitat proxies may obscure fine-scale structural features, such as snag quality or microhabitat conditions, that are critical for some forest specialists (Lehikoinen *et al.* 2024). This highlights the need to complement large-scale spatial data with targeted field-based measurements where possible. Co-occurrence with Pygmy Owls also suggests that both species may use high-quality patches not easily defined by conventional habitat variables. Seasonal detection trends confirmed that vocal activity declines through spring, emphasizing the need for early-season monitoring.

Although Willow Tit is often associated with mature or structurally complex forests, some studies suggest that the species may exhibit a broader habitat amplitude than traditionally assumed, including use of managed or relatively young forest stands under certain conditions (Lindbladh *et al.* 2020). The observed associations in this study may therefore reflect early-season habitat use and detectability rather than strict breeding habitat requirements. Consequently, declines in Willow Tit populations are likely driven by multiple interacting factors, of which forest management practices represent only one component (Lehikoinen *et al.* 2024). Together, the findings call for more nuanced habitat modelling and protection of pine mires, which are increasingly threatened by changes in forest management and climate. They also underscore the risks of using generalized metrics in conservation targeting.

4.3 Passive Rewilding Potential in Agricultural Landscapes

The third study applied a spatial modelling framework to identify rewilding potential in lowland agricultural areas of England, in the context of delivering biodiversity gains under the Biodiversity Net Gain (BNG) policy. BNG mandates that all new developments in England result in at least a 10% net gain in biodiversity, calculated using standardized biodiversity units (DEFRA 2020).

Our analysis estimated the area of arable land required to be restored to meet this annual demand. Depending on habitat type and condition, between 0.27% and 0.90% of lowland agricultural land would need to be rewilded each year to offset losses from development (zu Ermgassen *et al.* 2019; Rampling *et al.* 2023). While passive restoration is cost-effective, it may require initial interventions such as planting or seeding to meet policy timeframes or achieve desired habitat conditions (Harmer *et al.* 2001; Fuentes-Montemayor *et al.* 2022).

Sensitivity analysis confirmed the robustness of the rewilding index to threshold changes, but outcomes still depend on site-level variables such as browsing pressure, seed source proximity, and soil type (Harmer *et al.* 2001; Forestry Commission 2020). These factors influence both the speed and success of woodland development and should be addressed in site-specific planning. The model provides a coarse national overview, but local feasibility assessments will be necessary for implementation. The rewilding index is therefore best interpreted as a strategic screening tool rather than a site-level prescription. Its reliance on aggregated spatial data and simplified scoring necessarily abstracts complex ecological processes, which should be evaluated in more detail during local planning and implementation.

Critically, this study shows that rewilding could play a meaningful role in achieving BNG targets and supporting strategic restoration at scale, especially when offsetting low-distinctiveness habitats. However, ensuring ecological outcomes will require appropriate monitoring, stakeholder engagement, and integration with broader landscape connectivity (Carver *et al.* 2021).

5 Summary/Conclusions

Together, these three studies demonstrate how spatial ecological analyses can inform species-specific conservation and landscape-scale restoration. Several key messages emerge:

Fine-scale habitat features (pine foliage, decaying wood, peatland structure) are critical for forest bird specialists and are not always reflected in general habitat classifications like forest age.

Anthropogenic pressures (urban proximity, land-use change) reduce habitat suitability but also highlight areas where targeted interventions—from managing forest edges to rewilding marginal farmland—can deliver conservation gains.

Spatial ecological tools, including passive acoustic monitoring and national-scale habitat modelling, provide scalable, transferable approaches for biodiversity planning.

In forest contexts, protecting and restoring structurally diverse pine- and peatland habitats is vital for species such as Crested and Willow Tits. In agricultural settings, passive rewilding offers a practical mechanism for achieving biodiversity goals under BNG, but success depends on careful matching of site conditions, timelines, and policy requirements.

Overall, this thesis illustrates how spatial ecology can bridge the gap between ecological knowledge and applied conservation. By aligning field-based data, modelling frameworks, and policy targets, it contributes to the development of more effective, evidence-based strategies for biodiversity protection and restoration. Future research would benefit from combining passive acoustic monitoring with repeated seasonal surveys and finer-scale habitat measurements to strengthen inference on habitat quality and demographic processes. Integrating spatial models with long-term monitoring and experimental management interventions would further improve the ability to translate habitat associations into effective conservation and restoration actions.

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