Using Spatial Modelling to Inform a Strategic, Landscape-Level Approach to Bat Conservation

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For my Grandma, Joyce Dalzell

Abstract

Development is needed to meet housing demands and improve living standards globally. Land use change associated with development can, however, negatively impact many species through processes such as habitat loss and fragmentation. There is growing recognition that integrating landscape-level conservation plans into the planning process can help to alleviate the impact of development on wildlife populations. Using spatial modelling to better understand how species use the landscape can support intelligent, informed planning decisions that avoid negative impacts on biodiversity.

Focusing on the greater horseshoe bat (*Rhinolophus ferrumequinum*) in Somerset, UK, I explore how spatial modelling can be used to inform strategic conservation planning for bats at different scales. Chapter two is an acoustic study where I seek to identify the factors driving bat activity in an agricultural landscape around an important maternity roost, and use fine scale predictive modelling to map bat activity over the study area. In chapter three I develop a novel approach for validating a broad scale habitat suitability model and apply model findings to identify landscape-level conservation priorities. Looking back at a fine scale but over a broad extent, in chapter four I develop a novel framework for protecting bats in the planning system, using habitat suitability and landscape connectivity models to produce a number of high resolution mapping outputs that can be used to inform planning decisions.

Existing legal protection for habitat that supports *R. ferrumequinum* populations made Somerset an ideal study area for this work, although in most cases habitat that supports bats is not legally protected in the UK. There is a strong argument that frameworks protecting all bat species countrywide need to take a broader view that considers both bat populations and the habitat they depend on. This thesis demonstrates the value of spatial modelling as a tool for strategic, landscape-level conservation planning, and lays the groundwork for improving the frameworks that protect bats in the planning system.

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Chapter 1

General Introduction

We are living through a human-driven biodiversity crisis (Ceballos et al., 2017; Pimm et al., 2014). Human activities have far-reaching impacts in every ecosystem on earth and present major threats to biodiversity globally (Crutzen and Stoermer, 2000; Vitousek et al., 1997). Perhaps foremost among threats is conversion of natural land, which results in habitat loss and fragmentation for many species (Fischer and Lindenmayer, 2007). Land use change alters ecosystem function, causes changes to species assemblages and leads to genetic isolation, all of which leaves species more vulnerable to stochastic events, resulting in species declines, local extinctions and ultimately species loss (Meyer et al., 2016; Foley, 2005). Extensive habitat loss in Britain and intensification of agriculture since the green revolution is recognised as a major driver of species loss and declines (Oliver et al., 2015). Population growth (United Nations, 2019), demand for housing and climate change all have the potential to exacerbate this further.

Coincident with the current biodiversity crisis, there is a housing crisis in Britain (Bramley, 2019). A recent report estimated that 3.91 million new homes are needed to meet current housing requirements (Bramley, 2019). The latest land use change statistics (Department for Levelling Up, Housing and Communities, 2022) report that recent development in England had an average density of approximately 27.5 houses per hectare, so some back-of-the-envelope calculations suggest that 3.91 million new homes would require just under 142,000 hectares of land: an area larger than Greater Manchester. Based on current trends, about half of this new development could be expected to be built on currently undeveloped land. This is a huge amount of development. Associated infrastructure that comes with new housing such as roads, shops and schools, will significantly increase the total area of land needed (Kurvinen and Saari, 2020; Thacker et al., 2019). Clearly, if development is not well planned it is highly likely to have a negative impact on biodiversity that is already under immense pressure from human activities.

Bats are distributed globally and the majority of bat species are threatened, data deficient or have a declining population trend (Frick et al., 2020). Bats are often found in human-dominated landscapes where they deliver important ecosystem services (Kunz et al., 2011) such as pest control (Wanger et al., 2014; Williams-Guillen et al., 2008; Cleveland et al., 2006), pollination (Tremlett et al., 2020) and seed dispersal (Medellin and Gaona, 1999). Bats occupy a high trophic level meaning they can be used as bioindicators to reflect overall ecosystem health (Park, 2015; Jones et al., 2009). Conservation of bats can thus potentially have wider knock-on benefit for other species (Ardiantiono et al., 2024; Branton and Richardson, 2011; Lambeck, 1997).

Despite the services they provide, bats frequently come into conflict with humans and are threatened by human activities (Voigt and Kingston, 2016). Development is an area where this conflict frequently plays out (Cohen, 2011). Bats are threatened by development through habitat loss and fragmentation, loss of roosting sites, increased artificial light at night, pollution and energy demands (i.e. wind turbines; Browning et al., 2021; Frick et al., 2020).

1.1 Legal Frameworks Protecting Bats in the UK

As a result of declines seen in many species in the 20th century, in Europe all bats and their roosts are protected by law (Bern Convention, 1979; EUROBATS, 1991; Conservation of Natural Habitats and Wild Fauna and Flora, 1992). This is mirrored in UK law (The Conservation of Habitats and Species Regulations, 2017; Wildlife and Countryside Act, 1981), where most legal protection to bats is enacted through the planning system.

The National Planning Policy Framework (NPPF) requires local authorities in England to assess the potential of all planning applications to impact protected habitats and species, including bats (Department for Levelling Up, Housing and Communities, 2023). This puts a high onus on local authorities, who, in a time of chronic underfunding of public services (Mason, 2023; Royal Town Planning Institute, 2020; Knight-Lenihan, 2020), often do not have resources and knowledge to effectively assess the impact a development may have on bats (Cohen, 2011).

Developments that may impact bats are required to submit an ecological report as a supplement to their planning application. Ecological reports are produced using standard methodology (Collins, 2023) and detail if/how bats use the site and if/how the proposal could impact them (CIEEM, 2017). If works are likely to impact bats the applicant will be required to apply to Natural England for a protected species license. The application has to include a method statement that describes how the work will minimise impact on bats and detail mitigation measures to compensate for any loss caused by the development (Natural England, 2022a). Larger projects will need to complete an environmental impact assessment and projects that occur in the vicinity of a nationally or internationally designated site will also need to undergo a habitats regulations assessment. Additionally, as of 2024, biodiversity net gain (BNG) regulations in England require new developments to result in a 10% net gain for biodiversity (DEFRA, 2024).

The frameworks that protect bats in the UK have been criticised for being ineffective. Most noticeably lacking is legal protection of habitat: in most scenarios, only individuals and roosts are protected by law. The licensing system has been criticised for lacking strategic overview and for a lack of scientific evidence underpinning mitigation measures (Hunter et al., 2021; Stone et al., 2013). While BNG can be viewed as a positive step, it still operates very much on a site-by-site basis, and although biodiversity gains under BNG are permitted to be achieved off-site, there is not currently a systematic approach in place for choosing offsetting sites. Moreover, the effectiveness of no net loss policies and biodiversity offsetting have faced criticism similar to that of current mitigation practices: that robust evidence for their effectiveness is currently lacking (zu Ermgassen et al., 2021; Knight-Lenihan, 2020; Weissgerber et al., 2019; zu Ermgassen et al., 2019).

There is growing recognition that conservation needs to happen at the landscape-level and that the law needs to protect the habitat bats depend on, as well as roosts. In a review of England's wildlife sites and ecological networks, Lawton et al. (2010) recommended the creation of *'more, bigger, better, and joined up'* habitat networks. Natural England, the public body responsible for environmental regulation in England, have taken up this mantra (Natural England, 2014, 2022b). Around the same time as the Lawton report, a separate review of the Habitats Regulations concluded that, while the laws were fit for purpose, the way they are implemented could be improved (DEFRA, 2012). These events resulted in the creation of a new framework for enacting protection of the great crested newt (*Triturus cristatus*) in England (Natural England, 2019). Taking a science-led approach, the new scheme uses landscape-level modelling to identify the best habitat for newts and to focus conservation effort where it will have the greatest benefit for newt populations (Bormpoudakis et al., 2016). While this is encouraging, a later report highlighted that the same approach cannot be directly copied with bats, as bats are far more mobile than newts and number 18 species in Britain, all with varying requirements (Red Tape Initiative, 2018).

1.2 Spatial Modelling and Systematic Conservation Planning

Systematic conservation planning (Margules and Pressey, 2000) concerns the '*optimal application of spatially-explicit conservation management actions to promote the persistence of biodiversity and other natural features in situ*' (Watson et al., 2011). Although originally framed for design of protected areas, many of the principals of systematic conservation planning can be integrated into the planning system (Gordon et al., 2009; Rookwood, 1995). The goal is to minimise the impact of new development by taking a strategic approach in the planning process, siting development to minimise habitat loss and loss of landscape connectivity, and applying targetted mitigation in areas where it will be most effective (Kiesecker et al., 2010).

Obtaining information on the focal species' spatial occurrence, distribution and landscape use is the first step in conservation planning, only with this knowledge can one start to identify conservation actions and design spatially optimal conservation measures (Margules and Pressey, 2000). Spatial modelling is a powerful tool for achieving this (Babí Almenar et al., 2019). Spatial regression techniques seek to better understand species-environment relationships (Fortin and Dale, 2014; Fortin et al., 2012) and can support conservation decision-making by making spatially-explicit predictions about species' landscape use (Zurell et al., 2022). Both development and conservation planning are inherently spatial (Pressey et al., 2007), meaning spatial analyses can be vaulable tools for informing decision-making in the planning process (Jones et al., 2022; Bergès et al., 2020; Duflot et al., 2018; Bayliss et al., 2005). Assimilation of these approaches in the UK planning process has been restricted, however, as local authorities often do not have the resources or specialist knowledge required to apply spatial modelling techniques to the challenges they face (Bertuol-Garcia et al., 2018; Farwig et al., 2017).

1.2.1 Scale and Ecological Data

It is impossible to talk about spatial modelling in ecology without discussing scale. Wiens (1989) provides an illustrative example of the concept of scale: '*On the basis of experiments conducted at the scale of individual leaf surfaces, plant physiologists have concluded that stomatal mechanisms regulate transpiration, whereas meteorologists working at the broader scale of vegetation have concluded that climate is the principal control (Woodward, 1987; Jarvis and McNaughton, 1986)*'. While both views in this example can be considered correct, their differing findings highlight the need to consider the appropriate scale for the questions you are addressing. Some responses will only be apparent at certain scales and may not hold true at other scales (Schneider, 2001). For example, the effect of climate on species occurrence is only apparent at a broad scale, while land cover may be a better predictor at fine scale (Razgour et al., 2011).

There are two components to consider when talking about scale: grain and extent. Again, Wiens (1989) explains it aptly: *'Our ability to detect patterns is a function of both the extent and the grain of an investigation (O'Neill, 1986). Extent is the overall area encompassed by a study, what we often think of (imprecisely) as its scale or the population we wish to describe by sampling. Grain is the size of the individual units of observation, the quadrats of a field ecologist or the sample units of a statistician. Extent and grain define the upper and lower limits of resolution of a study; they are analogous to the overall size of a sieve and its mesh size, respectively'*. Thus, scale is facet of observation: the level at which you choose to observe something. By choosing a scale at which to run an analysis, the researcher inevitably introduces bias and places limits on the questions they are able to ask (Levin, 1992).

The chapters of this thesis vary in both grain and extent, also in the type of ecological data used. Different ecological data types are better suited to certain analyses than others, and, similarly to scale, the choice of ecological data will define the questions one is able to address. Acoustic data derived from passive acoustic monitoring, for example, are common in the study of bats (Sugai et al., 2019). These are usually point data consisting of recordings of the echolocation calls of all bats that pass by the sampling point. These data can tell you how an area is used by bats but will not provide information about how many bats are there, as individuals can not be distinguished by their echolocation calls, or what these bats do with their time when they are

Figure 1.1: The study species, the greater horseshoe bat (*Rhinolophus ferrumequinum*).

not at the point of sampling. Telemetry data, on the other hand, typically stem from a few individuals and (ideally) provide unbiased information on all the sites and habitats visited by the individual bat. What telemetry data do not tell you is how individual sites are used by the population as a whole. Both of these example data types contain information about how animals are interacting with the landscape but need to be treated in different ways. The appropriate scale and ecological data will thus be dictated by the questions you are trying to ask.

1.3 Study Species and Study Area

The greater horseshoe bat, *Rhinolophus ferrumequinum* (figure 1.1), despite having a large global distribution (figure 1.2) and a least concern (LC) rating by the IUCN (Piraccini, 2016), is a species of conservation concern in Britain (JNCC,

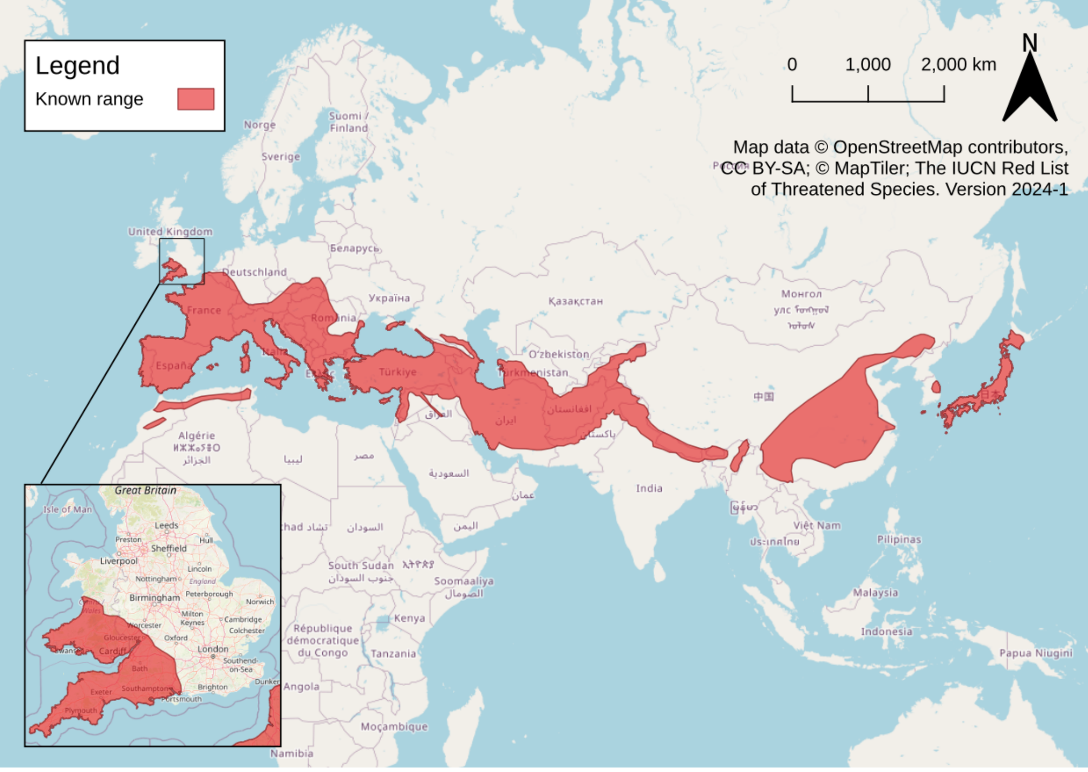

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Figure 1.2: Global distribution of *R. ferrumequinum*. Britain shown in inset map.

2007), the northern limit of its global distribution (Dietz and Kiefer, 2016). *R. ferrumequinum* suffered huge declines in the 20th century due to agricultural intensification, loss of roosts and increased use of insecticides (Mathews, 2018; Harris, 1995). Although *R. ferrumequinum* are still in decline globally (Piraccini, 2016), the population in Britain has increased since the 1990s (Mathews, 2018), partly due to intensive conservation efforts (e.g. Longley, 2003) but also due to a warming climate (Froidevaux et al., 2017).The species currently has a recovering population trend and in Britain is predominantly found in the south-west (figure 1.2), ranging from Cornwall to Dorset and South Wales, with isolated records from North Wales and as far east as Sussex (Mathews, 2018).

As a species on the northern edge of its global range, *R. ferrumequinum* is likely limited by climatic conditions in Britain. Long cold winters increase mortality, and breeding success is dependent upon warm spring temperatures (Ransome, 2020). Like many bat species, temperature is important for *R. ferrumequinum* in regulating its life history (Altringham, 2011). During hibernation, *R. ferrumequinum* require cool, stable climatic conditions to maximise time spent in torpor (Ransome, 2020). To meet these climatic demands, *R. ferrumequinum* roost in caves year-round through most of their range, as caves provide the required stable, predictable conditions. Caves are of high importance for *R. ferrumequinum*; availability of caves or other suitable underground sites likely limits species' distribution (Ransome, 2020).

Transitional roosts are used pre- and post-hibernation (Flanders and Jones, 2009). Mating occurs in autumn and spring, single males defend territorial roosts and are visited by multiple females (Rossiter et al., 2000). *R. ferrumequinum* use daily torpor to save energy, however, during the maternity period bats need to keep warm and active to maintain an increased metabolism for lactation and pup growth (Ransome, 1998). In Britain the species therefore usually breeds in disused buildings as mean ambient temperature in caves is too low (Ransome, 2020). Females gather at maternity colonies in large numbers from May-August to give birth, usually to a single pup (Dietz and Kiefer, 2016). Maternity roosts of this species are particularly vulnerable to threats as females concentrate in large numbers (up to 1,000; Dietz and Kiefer, 2016). Huge numbers of bats are known to have been lost through remedial timber woodworm treatment at maternity roosts (Mitchell-Jones et al., 1989; Stebbings and Arnold, 1987).

R. ferrumequinum are highly manoeuvrable aerial hawkers that use high frequency echolocation (~83kHz) for navigation and hunting (Jones and Rayner, 1989). When commuting from the roost they use distinct flight paths, almost always along woodland edges and mature hedgerows, as these likely offer cover from predators but also as they may provide foraging opportunities (Ransome, 1996; Jones et al., 1995). As high frequencies attenuate quickly in air (Altringham, 2011), *R. ferrumequinum* effectively have a very short field of vision and so are thought to use linear vegetation features to aid navigation (Ransome, 1997, 1996). Linear landscape features are thus extremely important for maintaining landscape connectivity for *R. ferrumequinum* (Finch et al., 2020b), and the species has been shown to be sensitive to landscape composition (Dietz et al., 2013). Agricultural intensification since the 1940s has resulted in the widespread removal of hedgerows (Robinson and Sutherland, 2002), to the detriment of *R. ferrumequinum* populations.

While in the past buildings may have facilitated the spread of *R. ferrumequinum* in Britain (Harris, 1995), new development does not lend itself to roosting and urban expansion poses a threat due to loss of foraging habitat. New development also has an impact through increased light pollution; *R. ferrumequinum* is a highly photosensitive species and is known to be negatively impacted by artificial light at night (ALAN) at a landscape-level (Froidevaux et al., 2017). Light pollution makes habitat unsuitable for bats, acting similarly to habitat loss, by increasing the risk of predation and reducing insect numbers (Voigt et al., 2021; Owens et al., 2020; Stone et al., 2015).

R. ferrumequinum takes prey on the wing and by perch-hunting (Jones and Rayner, 1989). It preys on large insects, primarily moths (Lepidoptera), beetles

(Coleoptera), particularly dung beetles (*Geotrupes* and *Aphodius* spp.) and cockchafers (*Melolontha melolontha*), and Diptera, including crane flies and caddis flies (Tournayre et al., 2021; Flanders and Jones, 2009; Ransome, 1997, 1996; Jones, 1990). *R. ferrumequinum* shows dietary plasticity (Tournayre et al., 2021; Whitaker and Karataş, 2009) and will vary its diet according to seasonal prey availability (Jones, 1990). Dung beetles have been highlighted as being particularly important for young during the maternity period (Jones et al., 1995), meaning grazed pasture is extremely valuable. The use of endectocides (anti-parasitic pesticides) is a threat, as these drugs are known to decrease insect numbers in animal dung, thus reducing the availability of an important food resource (Finch et al., 2020a; Ransome, 1996). *R. ferrumequinum* make greater use of woodland in the spring and open fields later in year, likely due to increased temperatures and prey abundance in woodland (Jones et al., 1995). It is a photosensitive species and is known to avoid well-lit areas (Zeale et al., 2018; Froidevaux et al., 2017; Stone et al., 2009, 2012).

All of the above mean that *R. ferrumequinum* favour a mosaicked landscape with grazed pasture inter-mixed with large, sheltered hedgerows, tree lines and natural deciduous woodland (Froidevaux et al., 2017; Flanders and Jones, 2009; Ransome, 1997, 1996), which is what is found in Somerset, UK, the focus of the majority of the work in this thesis (figure 1.3). Land cover in Somerset is dominated by agriculture (80% land cover), just over half of which is grazed pasture (Rae, 2017), and is littered with old growth woodland, mature hedgerows and an extensive network of limestone caves. Somerset is a stronghold for greater horseshoe bats: it is home to three special areas of conservation (SACs) designated for their important breeding populations of *R. ferrumequinum* (JNCC, 2015a,b,c) which together contain approximately 20% of

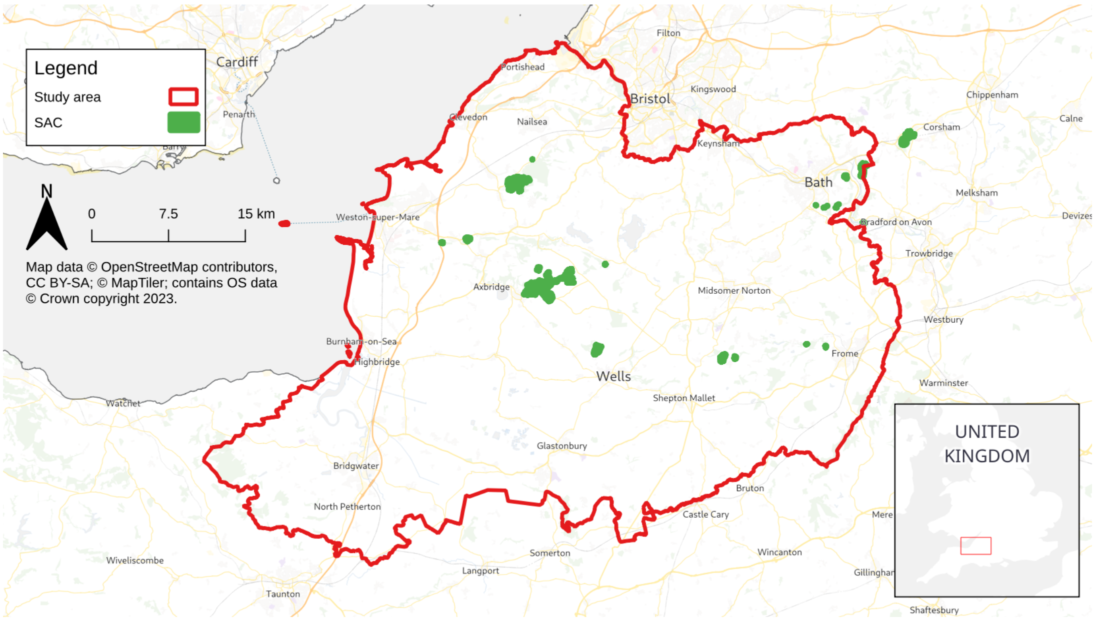

Figure 1.3: Study area in Somerset, UK, where the fieldwork for this thesis was focused. Britain shown in inset map.

the British population (calculated with total population estimate from Mathews, 2018, and roost counts from species records used in chapter 4, section 4.4.3). SACs are statutory designations created under the UK Habitats Regulations (2017) to protect species listed on annex II of the EU Habitats Directive (Conservation of Natural Habitats and Wild Fauna and Flora, 1992). Any new development that may impact an SAC needs to undergo a habitats regulations assessment (HRA), which in effect protects the habitat around the SAC, making this a rare example of a situation where habitat that supports bats is legally protected.

Development is a threat to *R. ferrumequinum* in Somerset. North Somerset's local plan, for example, requires 13,000 new homes to be built over the next 25 years, two-thirds of which are likely to be built within 4km of the SSSI units of the North Somerset and Mendip Bats SAC (North Somerset Council, 2020). As bats range over the whole county, new development in North Somerset frequently requires an HRA. Understanding how bats use landscape is of key importance to understanding the potential of development to impact the SAC, however this knowledge is hard to obtain in practice: bats are both volant and nocturnal, making it difficult to study their landscape ecology.

Previous studies of the SAC bat populations used radio telemetry to gather data on foraging areas and commuting routes around the SSSI units of the SACs (Jones and Billington, 1999; Billington, 2001, 2000). While these data were the best available at the time they were collected, as discussed above, all ecological data have limitations. The limitations of radio telemetry when working with a fast moving nocturnal species is that it is not very accurate at fine scales (i.e. <100m; e.g. Razgour et al., 2011) and it is prone to gaps in data collection, as tracking teams often struggle to keep up with tagged bats. This results in bias in radio telemetry datasets to areas near to the roost with good vantage points (required to pick up radio signal) that are easily accessible to trackers. Due to the high cost and intrusive nature of tagging bats, radio telemetry studies usually involve only a small subsample of the population under study, meaning data are used to extrapolate predicted behaviour of the study population, which is where the biases in radio telemetry can lead to inaccuracies in ecological inferences drawn from the data.

Current supplementary planning guidance for the Somerset SACs uses buffers based on radio telemetry findings and a habitat scoring system to estimate the impact of new development on SAC bat populations (Burrows, 2019, 2018). Spatial modelling approaches have potential to improve planning guidance by filling knowledge gaps, providing a robust evidence base that can support development and conservation decisions in Somerset.

1.4 Thesis Rationale, Aims and Outline

Natural England funded this work with the goal of developing an improved approach to protecting *R. ferrumequinum* in Somerset, due to the existing legal protection for this species here, but also with the notion that this work can act as proof-of-concept for an improved approach to all bat species nationwide. I have worked closely with both Natural England and North Somerset Council to address these aims:

- to apply spatial modelling techniques to better understand how *R. ferrumequinum* use the landscape;
- to create an evidence base that can be used to inform policy and planning.

The following chapters of this thesis consist of distinct projects that are united by this common theme. Chapter two is an acoustic study in which I use very high density sampling to model acoustic activity of *R. ferrumequinum* around the roosts at Brockley Hall SSSI and Kings and Urchin Wood SSSI in North Somerset. The main focus of the project was *R. ferrumequinum* but other species are also considered. Analysis is conducted at a fine scale in a relatively small study area. I look for associations between species activity and field boundary, field, and local landscape characteristics to identify the drivers of acoustic activity and to aid habitat management decisions in the areas surrounding the SSSIs. I use predictive modelling to map acoustic activity for three species, to better understand how bats use the landscape around these important roosts.

In chapter three I develop a novel method for habitat suitability model validation using passive acoustic monitoring. I carry out an acoustic survey (distinct from the dataset gathered in chapter two) to measure a predicted habitat suitability gradient over a large part of Somerset, use a habitat suitability model to identify factors affecting *R. ferrumequinum* distribution in Britain at a broad scale, and apply this to landscape-level conservation challenges.

Chapter four focuses back at a fine scale but over a wide area. I use GPS telemetry to gather fine scale data on *R. ferrumequinum* habitat use, I then use these to build habitat suitability models to understand factors affecting foraging and commuting habitat suitability. I use habitat suitability model predictions as a basemap for high resolution connectivity modelling to predict bat movement in the landscape around the three Somerset bat SACs. From these models I produce easy-to-use mapping outputs, designed specifically for use in the planning process.

Chapter five is a general discussion where I bring together findings from previous chapters and examine them in light of the overall thesis narrative. I discuss strengths and applications of different modelling approaches, the impact of this work, and discuss how I would like to build on this in future.

1.5 Author Contributions

Contributions are for all data chapters unless noted otherwise. Thomas Foxley: conceptualisation (chapter three), methodology, investigation, project administration, data curation, formal analysis, validation, visualisation, funding acquisition (chapter four), writing - original draft; Paul Lintott: writing-reviewing and editing, supervision; Simon Stonehouse: funding acquisition, writing- reviewing and editing (chapter four); John Flannigan: funding acquisition, writing- reviewing and editing (chapter four); Emma Stone: conceptualisation, funding acquisition, methodology, writing- reviewing and editing, supervision.

Chapter 2

What Drives Bat Activity at Field Boundaries?

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2.1 Abstract

Field boundaries are important habitat for bats in agricultural landscapes, serving as commuting and foraging areas for many species. The goal of our study was to better understand the drivers of bat activity in agricultural landscapes to inform conservation policy and make specific recommendations for habitat management. We placed sixty-four full spectrum bat detectors at random recording locations, weekly, along field boundaries in North Somerset between July and October 2020. We used an automated classifier to analyse recordings and performed error rate modelling to account for and remove the majority of error in automated classifications. We used generalised additive models to explore bat response to recording location metrics, controlling for spatial-autocorrelation and temporal differences in sampling. We validated our models with k-fold cross-validation and explored the utility of our models for predicting bat activity at new sites. We found that field boundary characteristics better describe bat activity than adjacent field characteristics or measures of local landscape for the majority of species studied. Bat activity was higher along tall, wide, vegetated field boundaries containing trees; there was lower activity at arable recording locations. Still, bat activity was highly variable and predictive error was high. We found a large spatial effect driving activity patterns, meaning models are not able to predict activity beyond the extent of the study area. We recommend management strategies that give incentives to farmers for replacing fences with hedgerows, planting hedgerow trees, and maintaining tall and outgrown field boundaries.

2.2 Introduction

Modern intensive agriculture is a major driver of the current biodiversity crisis (e.g. Sánchez-Bayo and Wyckhuys, 2019). Low levels of habitat diversity associated with intensive farming are a primary cause of species declines (Benton et al., 2003; Robinson and Sutherland, 2002). As half of all habitable land globally has been converted to agriculture (UN Food and Agricultural Organization, 2021) there is a need to make agriculture compatible with biodiversity (in western Europe the proportion of land converted to agriculture is much higher: for example, in England 75% of land is used for agriculture; Rae 2017).

Increasing landscape heterogeneity has been proposed as a method to make agricultural landscapes functional for both wildlife and humanity, increasing the area of vegetated field boundaries is a key approach for achieving this (Benton et al., 2003; Kremen and Merenlender, 2018; Tscharntke et al., 2021). Hedgerows and woody field boundaries provide food, shelter and facilitate landscape connectivity for wildlife (Barr et al., 1999; Montgomery et al., 2020), while services provided by functional ecosystems, such as flood management, pollination, nutrient cycling, soil retention, windbreaks and pest control, can improve agricultural outputs (Bommarco et al., 2018; Fischer et al., 2008; Pereira et al., 2018).

Bats are valuable pest control agents (Kunz et al., 2011; Williams-Guillén and Perfecto, 2011) which benefit from vegetated field boundaries (Graham et al., 2018; Walsh and Harris, 1996b). Vegetated field boundaries support a diverse array of invertebrate prey items for bats (Froidevaux et al., 2019; Graham et al., 2018; Merckx et al., 2009), and vegetation offers shelter from wind and predators (Jones et al., 1995; Verboom and Spoelstra, 1999). Vegetated field boundaries could also act as navigational aids for species with quiet or high frequency echolocation calls that attenuate quickly in air (Altringham, 2011), for example *Rhinolophus spp*. Vegetated field boundaries are known to be of particular importance for *Rhinolophus ferrumequinum*, (Dietz et al., 2013; Ransome, 1996), as demonstrated by a study in southern England that found 71% of *R. ferrumequinum* activity to be in close proximity to field boundaries, compared to centres of fields (Finch et al., 2020b).

Although the importance of field boundaries is well known, the mechanisms by which field boundaries benefit bats are still being explored. Specific aspects of field boundary structure are important for different bat species, likely a function of how different species utilise field boundaries (Lacoeuilhe et al., 2018), based on their echolocation and morphological adaptations (Jacobs and Bastian, 2016). Species adapted to forage in cluttered environments (e.g. *Myotis bechsteinii*) will prefer large, overgrown field boundaries (Toffoli, 2016). Species that forage along edge habitats (e.g. *Pipistrellus* species) have not previously been found to respond to specific aspects of hedgerow structure, although *P. pygmaeus* may prefer boundaries with a greater number of trees (Boughey et al., 2011). In general, high numbers of trees in field boundaries has been found to promote activity of many species (Boughey et al., 2011; Finch et al., 2020b; Heim et al., 2015; Lacoeuilhe et al., 2018). Free-flying aerial hawkers such as *Nyctalus* spp. and *Eptesicus* spp. have not previously been found to associate with field boundary structure (Boughey et al., 2011; Finch et al., 2020b; Kelm et al., 2014; Toffoli, 2016; Verboom and Huitema, 1997) and instead are likely responding to characteristics of adjacent fields or local landscape.

Although some studies have investigated the relationship between specific field boundary measurements and bat activity (e.g. Boughey et al., 2011; Lacoeuilhe et al., 2018; Toffoli, 2016), the relationship remains unclear for many species (e.g. Rhinolophus spp.). Understanding how boundary features are important for bats is essential to inform recommendations for effective field boundary and habitat management that enhances biodiversity. In the UK, for example, best practice guidelines lack detail on the specific relationships different bat species have with field boundaries (Hedgelink, 2022), and further research into the link with bats and hedgerows has been recommended (ADAS UK Ltd., 2004). To our knowledge, no study has compared the relative importance of field boundaries with other landscape characteristics in driving bat activity, despite the importance of this information for informing evidence-based conservation strategies.

Here we investigate the relationship between field boundary structure, surrounding habitat and bat activity, with the aim of making specific recommendations for field boundary management. We predict that there will be high bat activity at vegetated field boundaries, vegetation biomass (as measured by height, width, tree content) will be positively associated with bat activity, and this association will be most pronounced in gleaning and edge-foraging species. We also explore the utility of our modelling approach for predictive modelling of bat activity across a wider landscape.

2.3 Methods

2.3.1 Study Site

Fieldwork was conducted over 12 weeks in North Somerset, UK, between 9th July and 1st October 2020. The target species was *R. ferrumequinum*, however, as our recording equipment picked up all bat species present in the study area the decision was made to include more species in our analysis. Fieldwork was carried out within 4 km of two *R. ferrumequinum* maternity roosts: Brockley Hall Stables SSSI (ST470669) and Kings & Urchin Woods SSSI (ST452647). The study site was chosen to comprise the main foraging areas around the roosts (Jones et al., 1995; Billington, 2001; Burrows, 2018; figure 2.1). This set up gave us the additional opportunity to investigate how much the spatial component of bat activity depends upon knowledge of where the bats are roosting.

At 51° latitude, the study area has a wet and mild marine climate (Köppen classification Cfb). The topography of the area is diverse, encompassing the coastal plains of the North Somerset levels and limestone hills of the Lulsgate Plateau. Land cover in the study area comprises 14.4% broadleaf woodland,

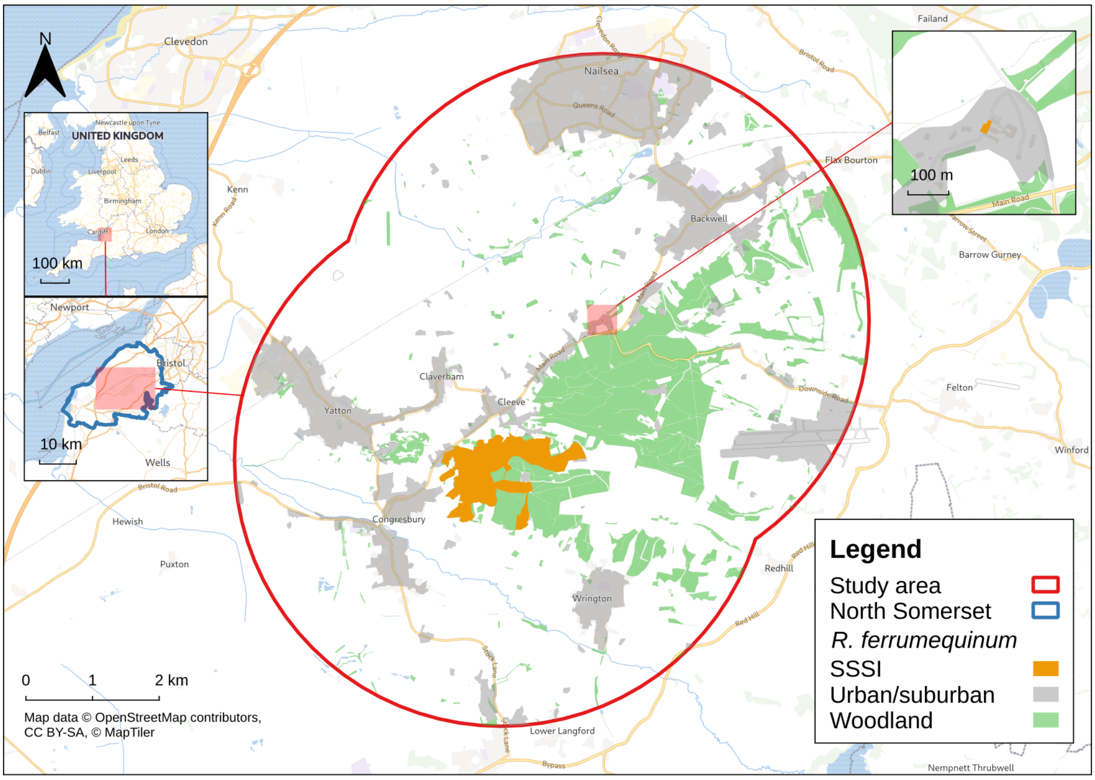

Figure 2.1: Map showing location of study site (main image) within North Somerset (inset, lower left, and North Somerset in the UK (inset, top left). *R. ferrumequinum* maternity roosts are located in the two SSSIs. The northernmost (inset, top right) is Brockley Hall SSSI, the southernmost is Kings and Urchin Woods SSSI.

0.8% coniferous woodland, 8.1% arable farmland, 58.9% grassland and 17.7% built-up areas and gardens (Morton et al., 2021). Arable crops include wheat and maize, while grassland is mainly grazed by cattle.

2.3.2 Recording Equipment

We monitored bat activity using passive ultrasound detectors (Song Meter Mini Bat, Wildlife Acoustics Ltd, Manyard USA) placed along field boundaries (hedgerows, lines of trees, fences and ditches) in the study area. All detectors were new from the manufacturer and microphones were manufacturer-calibrated. We attached detectors to fenceposts or branches 1-2m above the ground using cable ties, facing the length of the field boundary. We set detectors to record bat activity from 15 minutes before sunset to 15 minutes after sunrise, using a 20kHz minimum trigger threshold and a maximum recording length of one minute.

2.3.3 Sampling Design

A stratified random sampling approach was employed whereby 32 recording locations were generated randomly along field boundaries each week, with 50% of locations within a 2km buffer of the roosts and 50% between 2-4 km. This sampled the area closer to the roost at higher density and allowed for spatial stratification of detectors avoiding spatial temporal bias in sampling with regard to distance from the roost.

Detectors were moved to new recording locations every week after a minimum of six nights (figure 2.2), the minimum duration to ensure the detection of common species (Mathews et al., 2016). Different field boundary types (hedgerows, lines of trees, fences and ditches) were surveyed in proportion to their availability. We placed detectors in pairs where possible, one either side of each field boundary. An individual field boundary was defined as ending at the point of connection between two or more field boundaries, following DEFRA hedge survey guidelines 2007. Each recording location was surveyed only once. Spatial autocorrelation between recording locations was controlled for in the statistical analysis (section 2.3.6 below).

2.3.4 Recording Location Characteristics

Field boundary characteristics and habitats of adjacent fields were recorded at each recording location (table 2.1). A field was defined as adjacent if the detector was able to pick up bats in that field, e.g. a detector on a thickly vegetated field boundary would only pick up bats on the same side as the detector, whereas a detector placed on a bare fence would pick up bats in fields either side of the fence. Three adjacent field habitat types were surveyed: arable, improved grassland and road/track. Images of example recording locations are presented in figure 2.3.

To assess the impact of local landscape features on bat activity we created a 250 m buffer around each recording location and quantified local landscape metrics in QGIS (`http://www.qgis.org`, 2022; table 2.1). A number of different sized buffers (up to 4 km) were considered, at 500 m and above variables started to become collinear due to close proximity of recording locations. A 250 m buffer was the largest scale that was feasible to model and represents the immediate surroundings that may influence activity at the recording location.

2.3.5 Bat Activity

Acoustic Analysis and Error Rate Modelling

Automated species identification was necessary as manual classification would have been prohibitively time consuming. We used BatClassify (Scott, 2012) to classify bat calls by species or species groups. Consistent with recommendations (López-Baucells et al., 2019; Russo and Voigt, 2016; Rydell et al., 2017) we manually verified the automated analysis following Barré et al. (2019) to quantify classification error rates (see appendix A for detail of error rate modelling approach).

It was not possible to reliably differentiate *Myotis* spp. in the manual verification due to similarity in call structure between species in this genus, so these species were grouped. *Nyctalus* spp. and *Eptesicus* spp. are grouped by BatClassify, and *Pipistrellus nathusii* is grouped with *P. pipistrellus*. The decision was taken not to include *Plecotus* spp. in the statistical analyses on the basis that acoustic monitoring is not an effective survey method for these species, as their calls are often too quiet to be detected (Flaquer et al., 2007). *Barbastella barbastellus* was not included in statistical analyses due to low numbers of recordings.

Acoustic Activity Index

We quantified bat activity at recording locations according to Miller (2001). Every minute in which a bat species is present was counted as one occurrence, the total occurrences were then divided by the total time the detector was recording, creating an activity index (AI). The AI thus represents the rate of bat occurrences over the whole period the detector was recording (approximately one week, mean 6.8 nights). This allows us to account for variation in night length over the study period and to compare activity between recording locations with differing recording effort.

Rather than providing positive and negative classifications for recordings, error rate modelling returns a probability of a correct classification (by species). Following Barré et al. (2019) we excluded all classifications below a 50% probability. We then weighted classifications by their probability, so a classification with a 90% probability would count as an activity index of 0.9. This meant classifications with a higher probability contributed more towards the final analysis.

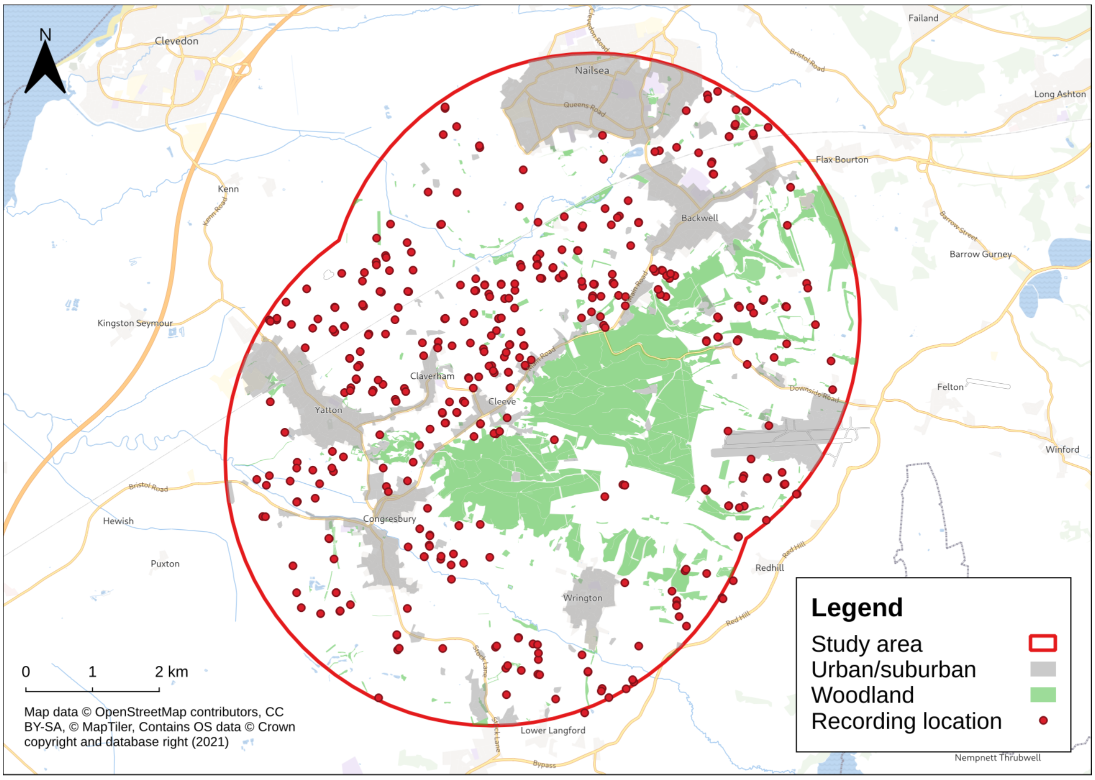

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Figure 2.2: Map of study area and recording locations in North Somerset, UK.

Figure 2.3: Photos of example recording locations

2.3.6 Statistical Analysis

We conducted statistical analyses in R (R Core Team, 2022). We fitted models for six different species/species groups using a generalised additive model (GAM) with a negative binomial error distribution in the *mgcv* package (Wood, 2011).

For each species we first fitted a global model to explore the relationship between predictors and bat activity (bat activity~predictors). We then assigned predictors from the global model to one of three 'scenario' models, dependent upon their scale of action (table 2.1). This allowed us to gauge the relative importance of different aspects of landscape structure (field boundaries, adjacent fields and local landscape) in driving bat activity. The first model contained descriptors of field boundary structure (field boundary model), the second contained descriptors of the field adjacent to the detector (adjacent field model). The third model contained descriptors of local landscape measured in GIS (local landscape model).

Continuous data were scaled and centred. Smooth terms were included for geographic coordinates (Duchon spline; bs=”ds”, k=250) and week of study (thin plate regression spline; bs="tp", k=12) to account for spatial autocorrelation and temporal differences in sampling, respectively. All other variables were included as linear predictors (table 2.1). Model fit was assessed by visual inspection of residuals and diagnostic plots. We tested all models for multicollinearity and concurvity (the equivalent of multicollinearity for GAMs) and we removed recording locations with less than four nights data.

We optimised global and scenario models by searching all possible combinations of variables using the *dredge* function from the *MuMIn* package (Bartoń, 2020), with the control variables fixed. AICc of the best model identified

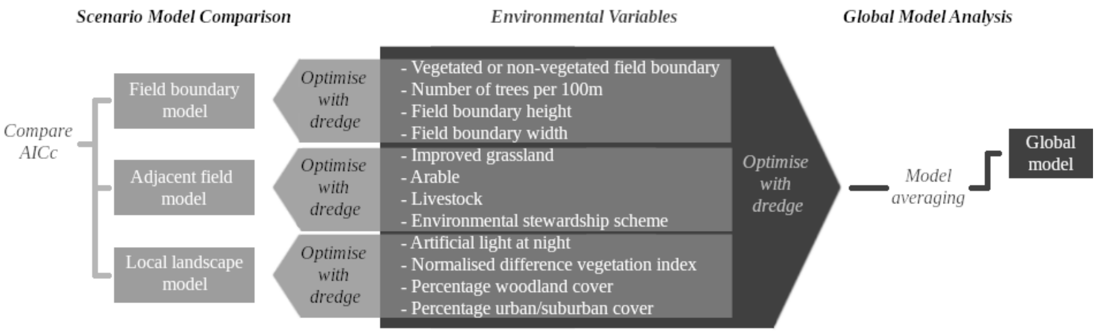

Figure 2.4: Graphical representation of the modelling procedure.

by *dredge* was used to compare competing scenario models. We performed model averaging on the global model, using all models <2 ΔAICc of the best model (Burnham and Anderson, 2002), calculating the model averaged coefficients and z-values in the *MuMIn* package. Effect size was assessed by calculating the percentage change in variables. The modelling procedure is summarised in figure 2.4.

2.3.7 Model Validation and Predictive Power

We tested the ability of models to predict bat activity at new sites. We performed 10-fold cross validation and fitted a GLM with predicted vs actual values, calculating McFadden's pseudo-R^2 to assess how well predictions match the actual data.

To assess the relative magnitude of the effect of predictor variables compared with the spatial component of the model, we also fitted models with 1) only control variables; 2) only control variables and no spatial smooth; 3) control variables, no spatial smooth, only one predictor variable, 'distance to *R. ferrumequinum* roosts at the centre of the study site'.

Predicted activity maps were made for three species at a 10 m resolution using three predictor variables: vegetated boundaries, habitat type (improved

Table 2.1: All variables included in analysis (global model). 'Scenario model' column shows which scenario model each variable was assigned to.

Variable	**Detail**	**Scenario model**
Vegetated field boundary	Hedge, lines of trees etc. = yes; fence, ditch etc. = no	Field boundary
Number of trees per 100 m	Only included trees above 15cm diameter at breast height	Field boundary
Field boundary height	Mean calculated from three representative points measured using either a tape measure or geometry (following West 2009), depending on height.	Field boundary
Field boundary width	Width was defined as the widest point of the boundary cross-section. Measured at three representative points along the field boundary with a tape measure and calculated the mean.	Field boundary
Improved grassland	Yes/no	Adjacent field
Arable	Yes/no	Adjacent field
Livestock (cows, sheep, horses)	Livestock present or evidence of recent livestock presence (fresh faeces)? Yes/no	Adjacent field
Environmental stewardship scheme	Yes/no – is the land managed under an environmental stewardship scheme?	Adjacent field
ALAN	Artificial light at night. Measured in 250 m buffer from satellite imagery (Earth Observation Group, NOAA/NCEI)	Local landscape
NDVI	Normalised difference vegetation index. Measured in a 250 m buffer from satellite imagery (LandSat 8) using imagery acquired during the study period (20/09/2020)	Local landscape
Woodland cover (%)	Percentage woodland cover calculated in a 250 m buffer from Ordnance Survey data (OS Open Map Local). Includes both coniferous and broadleaf (study area is 92% broadleaf) and any patch size	Local landscape
Urban land cover (%)	Percentage of land classified as urban/suburban in CEH Land Cover Map 2015 (Rowland et al., 2017b) calculated in a 250 m buffer	Local landscape
Easting and northing	British National Grid format	All
Week of study	1-12	All
Average nightly minimum temperature	Mean nightly minimum temperature for all nights the detector was recording (taken from detector internal thermometer or average of all other detectors out at the same time if not available)	All
Average nightly rainfall	Mean nightly rainfall (mm), obtained from the Environment Agency station no. 417635 (Barrow Gurney, grid ref. ST5377167950, 7.75km NEE from centre of study site)	All

Table 2.2: Mean activity index (AI) across recording locations. AI was calculated as the number of minutes in which a bat was recorded per hour of survey. Note that this is weighted by the confidence in the species classification, as described in section 2.3.5. Species not included in the statistical analysis are denoted with *.

Species	**Mean Activity Index**	**Standard Deviation**
*Barbastella barbastellus**	0.01	0.02
Nyctalus noctula/N. leisleri/Eptesicus serotinus	3	2.95
Plecotus spp.*	0.1	0.13
Pipistrellus pipistrellus	4.76	4.8
Pipistrellus pygmaeus	0.69	1.25
Rhinolophus ferrumequinum	0.65	1.04
Rhinolophus hipposideros	0.13	0.3
Myotis spp.	2.05	2.62
All species	11.39	8.19

grassland or arable). Within the study site most field boundaries represent the edge of a land parcel and can therefore be mapped with reasonable accuracy using OS Master Map land parcel boundaries. We used LIDAR data from the National LIDAR Programme (Environment Agency, 2022), masked with OS MasterMap boundaries, to map vegetated field boundaries. Arable sites were mapped from sites identified during the survey period.

2.4 Results

Detectors were deployed at 380 locations, which equated to 26,557 recording hours, or 2,656 10-hour nights (mean night length = 9.82 hours). In total over 1.6 million files were recorded, yielding 484,795 bat classifications. A total of eight species/species groups were identified (mean = 6.8 per site). Bats were detected on average just over 11 minutes (±8.2 s.d.) in every hour (table 2.2, figure 2.5).

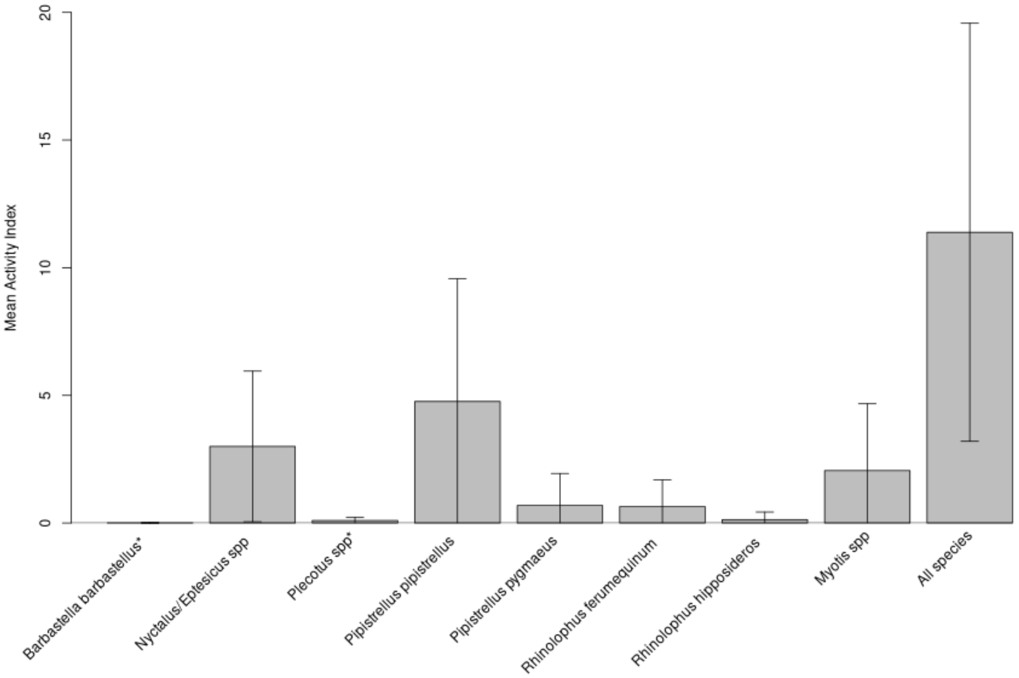

Figure 2.5: Mean activity index (AI) across recording locations in North Somerset, UK, showing standard deviation. AI was calculated as the number of minutes in which a bat was recorded per hour of survey. Note that this is weighted by the confidence in the species classification, as described in section 2.3.5. Species not included in the statistical analysis are denoted with *.

Table 2.3: Model ranking of competing scenario models. Units are ΔAICc between models, meaning the best performing scenario model has the lowest ΔAICc. Models with ΔAICc <10 (i.e. all models with some level of empirical support; Burnham and Anderson 2002, pg. 70) are highlighted in bold

Species/species group	**Field boundary**	**Adjacent field**	**Local landscape**
Rhinolophus ferrumequinum	**0.00**	15.83	24.40
Rhinolophus hipposideros	**0.00**	12.21	20.87
Pipistrellus pipistrellus	**0.00**	18.62	41.32
Pipistrellus pygmaeus	**0.00**	67.02	69.93
Myotis spp.	**0.74**	**0.09**	**0.00**
Nyctalus spp./*Eptesicus serotinus*	17.47	**5.54**	**0.00**

2.4.1 Scenario Model Comparison

The field boundary model was best supported for *P. pipistrellus*, *P. pygmaeus*, *R. ferrumequinum* and *R. hipposideros* (table 2.3). The local landscape model was best supported for *N. noctula/N. leisleri/E. serotinus* while the adjacent field model received some support for this species group. All three models were highly supported for *Myotis* spp.

2.4.2 Global Model

A total of 4,095 models were examined by dredge for each species. The number of models ranked in the top model set (<2 ΔAICc) for each species were as follows: *Myotis* spp. n = 15, *N.* spp./*E. serotinus* n = 2, *P. pipistrellus* n = 2, *P. pygmaeus* n = 5, *R. ferrumequinum* n = 5, *R. hipposideros* n = 13.

Field Boundary Characteristics

Activity of *R. ferrumequinum*, *R. hipposideros*, *P. pipistrellus* and *N.* spp./*E. serotinus* was higher along vegetated field boundaries, compared to non-

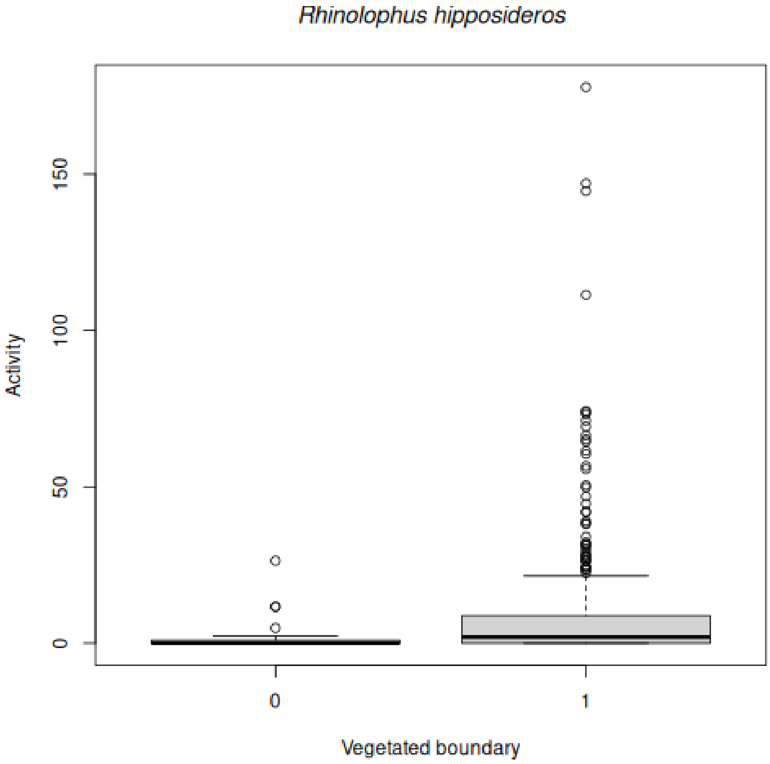

Figure 2.6: Boxplot showing *Rhinolophus hipposideros* activity at vegetated/non-vegetated field boundaries in North Somerset, UK. Activity is the summed number of minutes in which bats were recorded.

vegetated field boundaries (145%, 307%, 123% and 33% higher, respectively; p<0.001, p<0.001, p<0.001, p=0.01 ; table 2.6-2.7, figure 2.6). *R. ferrumequinum* and *P. pygmaeus* activity was higher at boundaries with trees (2% and 3% increase in activity per tree per 100 m; p<0.001 and p=0.01, respectively). *P. pipistrellus* and *P. pygmaeus* activity was higher at field boundaries with tall vegetation (a 9% and 15% increase in activity for every extra metre of height, respectively; both p<0.001, figure 2.7). *Myotis* spp. activity was higher at wide boundaries (4% increase in activity for every extra metre of width; p<0.001).

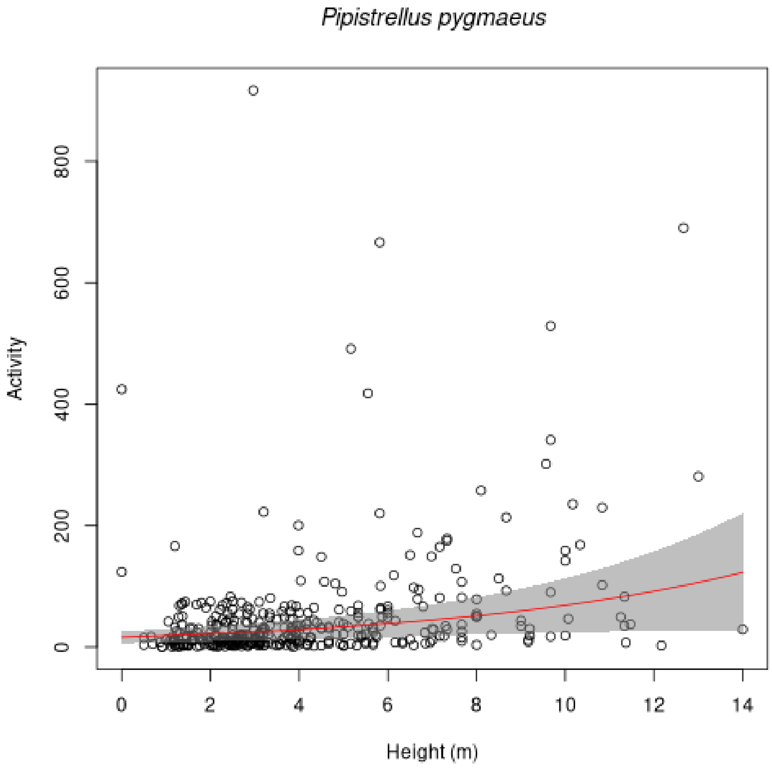

Figure 2.7: Partial effects plot showing the effect of field boundary height on *Pipistrellus pygmaeus* activity (red line, 95% confidence intervals shaded) in North Somerset, UK. Activity is the summed number of minutes in which bats were recorded.

Adjacent Field Characteristics

R. hipposideros activity was 149% higher at field boundaries bounded by improved grassland ($p<0.001$, table 2.6-2.7), whereas *P. pipistrellus* activity was lower (42%; $p<0.001$). *R. ferrumequinum* and *P. pipistrellus* activity was lower at field boundaries bounded by arable land (46% and 48%; both $p<0.001$, figure 2.8). *Myotis* spp. activity was lower at recording locations managed under an environmental stewardship scheme (39%; $p=0.01$). *P. pipistrellus*, *P. pygmaeus* and *N. noctula/N. leisleri/E. serotinus* activity was higher at recording locations with livestock, compared to recording locations without (26%, 34% and 26% respectively; $p=0.02$, $p=0.03$ and $p<0.001$; table 2.6-2.7, figure 2.9).

Local Landscape Characteristics

R. hipposideros and *N.* spp./*E. serotinus* activity was higher with greater woodland cover in a 250 m buffer (both 2% higher activity for every 1% increase in woodland cover; $p=0.004$ and $p<0.001$ respectively; table 2.6-2.7). *N.* spp./*E. serotinus* activity was higher with greater urban/suburban cover in a 250 m buffer (1.4% higher activity for every 1% increase in urban/suburban cover; $p<0.001$). *P. pygmaeus* and *Myotis* spp. activity was lower with higher levels of ALAN in a 250 m buffer of the recording site (8% and 5% lower activity for every 1 increase in radiance; $p=0.01$, $p=0.03$, respectively).

2.4.3 Model Validation and Predictive Power

We found a large spatial component explaining activity patterns: removing predictor variables did relatively little to reduce the deviance explained (table 2.4) or the predictive power of the models (table 2.5) when compared with the effect of removing the spatial smooth. For *R. ferrumequinum*, part of this

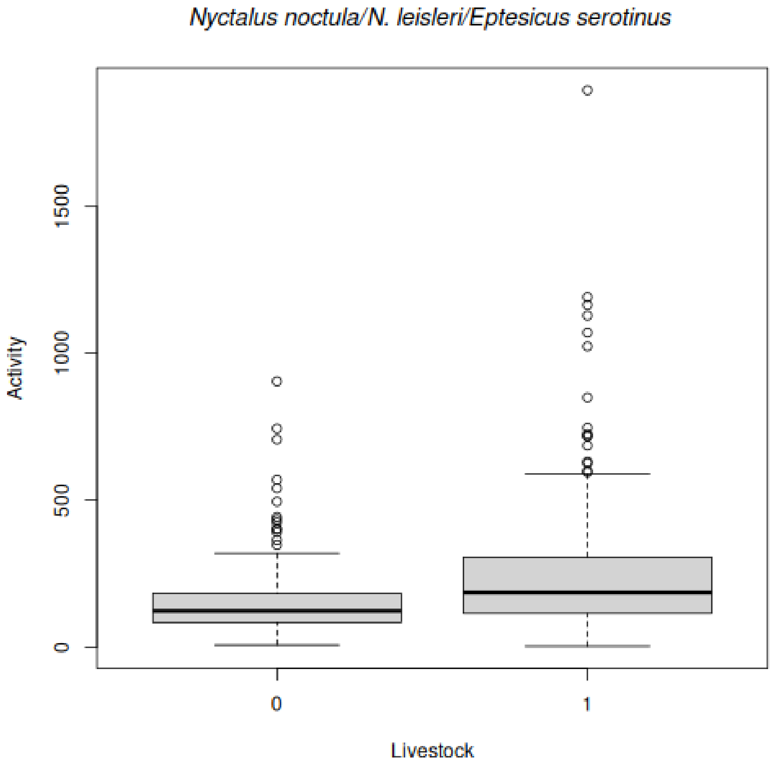

Figure 2.8: Boxplot showing *Nyctalus* spp./*Eptesicus serotinus* activity at recording locations with/without livestock in North Somerset, UK. Activity is the summed number of minutes in which bats were recorded.

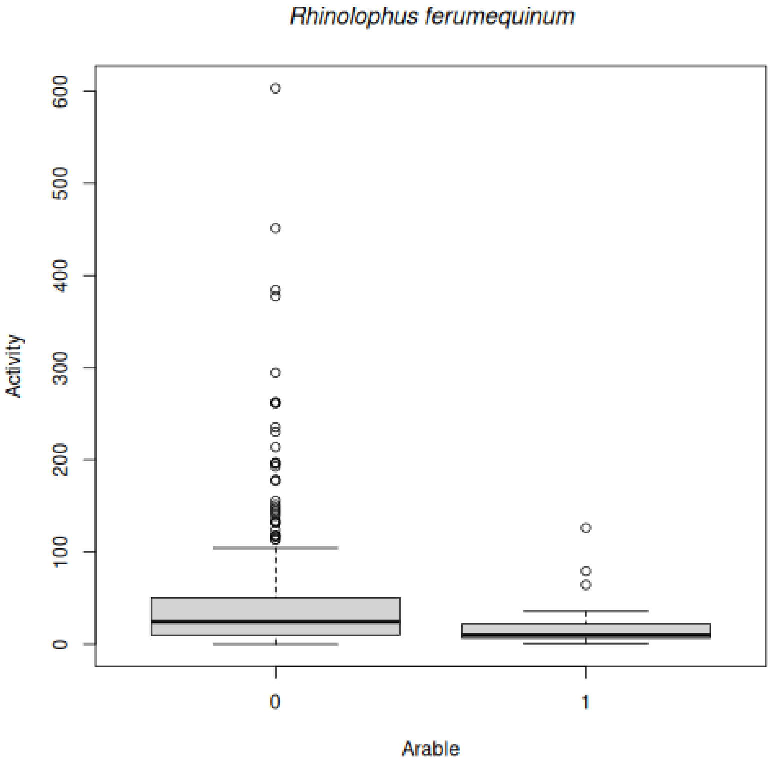

Figure 2.9: Boxplot showing *Rhinolophus ferrumequinum* activity at arable/non-arable recording locations in North Somerset, UK. Activity is the summed number of minutes in which bats were recorded.

Table 2.4: Percentage deviance explained by models. Comparison between the global model with all predictor variables (global), a model with only control variables (control only), a model with only control variables but lacking the spatial control (control nonspatial), and a model with only control variables, no spatial control but with the variable 'distance to the roost' added (control nonspatial with roost).

Species	**Global**	**Control only**	**Control nonspatial**	**Control nonspatial with roost**
Rhinolophus ferrumequinum	85.07	79.50	18.19	35.51
Rhinolophus hipposideros	39.79	34.95	8.98	9.06
Pipistrellus pipistrellus	77.06	63.11	14.09	14.84
Pipistrellus pygmaeus	67.09	62.64	4.19	4.60
Myotis spp.	55.47	48.69	7.09	8.00
Nyctalus spp./*Eptesicus serotinus*	81.36	83.00	23.77	23.84

was explained by proximity to the roost (tables 2.4 and 2.5). Predicted activity maps for *Nyctalus* spp./*E. serotinus*, *P. pipistrellus* and *R. ferrumequinum* (figure 2.10) show spatial activity patterns recorded in the study period. There is a clear concentration of *R. ferrumequinum* activity around the roost at Brockley Hall, while *Nyctalus* spp./*E. serotinus* and *P. pipistrellus* activity hotspots are more dispersed (location of roosts for these species in the study area are unknown).

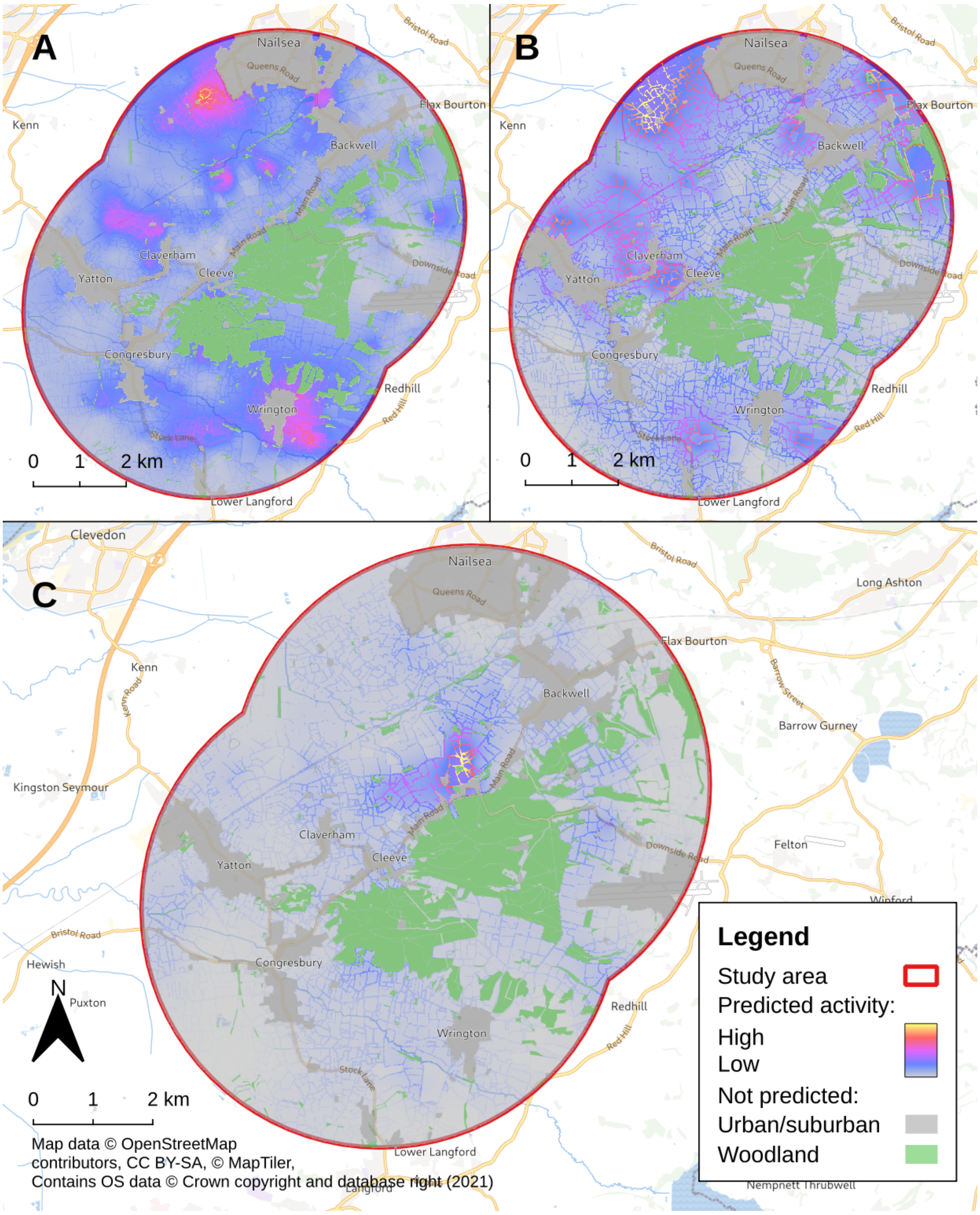

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Figure 2.10: Predicted activity outside woodland and urban areas in North Somerset, UK for A) *Nyctalus* spp./*Eptesicus serotinus*, B) *Pipistrellus pipistrellus*, C) *Rhinolophus ferrumequinum*.

Table 2.5: McFadden's pseudo-R^2 of predicted vs actual values from cross validation, measuring how well model predictions match the actual data. Comparison between the global model with all predictor variables (global), a model with only control variables (control only), a model with only control variables but lacking the spatial control (control nonspatial), and a model with only control variables, no spatial control but with the variable 'distance to the roost' added (control nonspatial with roost).

Species	**Global**	**Control only**	**Control nonspatial**	**Control nonspatial with roost**
Rhinolophus ferrumequinum	0.42	0.39	0.07	0.26
Rhinolophus hipposideros	0.15	0.13	0.05	0.05
Pipistrellus pipistrellus	0.31	0.25	0.09	0.10
Pipistrellus pygmaeus	0.25	0.23	0.02	0.02
Myotis spp.	0.13	0.09	0.01	0.02
Nyctalus spp./*Eptesicus serotinus*	0.46	0.42	0.17	0.17

Table 2.6: Estimates, (adjusted) standard errors and p-values for all variables in global model. Variables not included in the final optimised models are denoted with -. Statistically significant relationships highlighted.

	R. ferrumequinum	***R. hipposideros***	***P. pipistrellus***	***P. pygmaeus***	***Myotis* spp.**	***N.* spp./*E. serotinus***
Vegetated/non-veg. field boundary	**0.894 (±0.159), <0.001***	**1.402 (±0.337), <0.001***	**0.8 (±0.158), <0.001***	0.109 (±0.241), 0.65	-	**0.285 (±0.109), 0.01***
Trees per 100 m	**0.149 (±0.047), <0.001***	0.149 (±0.14), 0.29	-	**0.169 (±0.067), 0.01***	0.036 (±0.054), 0.51	-
Height	-	-0.112 (±0.167), 0.5	**0.234 (±0.05), <0.001***	**0.374 (±0.081), <0.001***	-	-
Width	-	0.208 (±0.123), 0.09	-	-	**0.165 (±0.056), <0.001***	-
Improved grassland	0.079 (±0.158), 0.62	**0.914 (±0.262), <0.001***	**-0.542 (±0.152), <0.001***	-0.419 (±0.249), 0.09	-0.022 (±0.085), 0.79	-
Arable	**-0.624 (±0.202), <0.001***	-	**-0.656 (±0.187), <0.001***	-0.479 (±0.298), 0.11	-0.039 (±0.125), 0.76	-
Livestock	-	-0.381 (±0.222), 0.09	**0.231 (±0.1), 0.02***	**0.29 (±0.134), 0.03***	-0.082 (±0.108), 0.45	**0.232 (±0.068), <0.001***
ESS	-	-0.091 (±0.2), 0.65	-	-0.065 (±0.168), 0.7	**-0.499 (±0.178), 0.01***	-
ALAN	-	-0.023 (±0.07), 0.74	-0.132 (±0.08), 0.1	**-0.262 (±0.093), 0.01***	**-0.174 (±0.082), 0.03***	-0.031 (±0.056), 0.59
NDVI	-	0.003 (±0.027), 0.91	0.083 (±0.084), 0.32	0.011 (±0.04), 0.79	0.02 (±0.052), 0.7	0.098 (±0.058), 0.09
Woodland cover	-0.031 (±0.06), 0.6	**0.199 (±0.097), 0.04***	-0.023 (±0.049), 0.64	-0.008 (±0.035), 0.82	-	**0.156 (±0.053), <0.001***
Urban/suburban cover	-0.081 (±0.07), 0.25	-	0.098 (±0.086), 0.25	-	0.075 (±0.078), 0.34	**0.143 (±0.051), <0.001***

Table 2.7: Percentage change in activity for every one unit of predictor in global model. For binary variables this is the difference between true/false (e.g. arable/not arable). Note NDVI is very high because it is calculated on a scale of -1 to 1, so an increase in one unit represents a large change, i.e. equivalent to the difference between bare rock and tropical rainforest.

	R. ferrumequinum	***R. hipposideros***	***P. pipistrellus***	***P. pygmaeus***	***Myotis* spp.**	***N.* spp./*E. serotinus***
Vegetated/non-veg. field boundary	144.58	306.52	122.57	11.52	-	32.94
Trees per 100 m	2.45	2.45	-	2.79	0.58	-
Height	-	-4.22	9.43	15.45	-	-
Width	-	5.23	-	-	4.14	-
Improved grassland	8.22	149.38	-41.82	-34.26	-2.22	-
Arable	-46.41	-	-48.09	-38.05	-3.79	-
Livestock	-	-31.70	26.01	33.65	-7.86	26.17
ESS	-	-8.67	-	-6.27	-39.29	-
ALAN	-	-0.73	-4.07	-7.92	-5.33	-0.96
NDVI	-	7.34	599.94	27.96	60.46	890.30
Woodland cover	-0.33	2.16	-0.24	-0.09	-	1.69
Urban/suburban cover	-0.78	-	0.95	-	0.73	1.40

2.5 Discussion

For many animal species, field boundaries represent important slivers of habitat in an otherwise inhospitable agricultural landscape. Here, we demonstrate the value of field boundaries for bats and identify specific characteristics of agricultural landscapes that are associated with bat activity in six species/species groups. Our results have direct application in landscape management and for the specification of Environmental Stewardship Schemes.

We show that field boundary characteristics are better than local landscape or adjacent field characteristics at describing activity patterns in four of the six species studied (*P. pipistrellus*, *P. pygmaeus*, *R. hipposideros* and *R. ferrumequinum*) and that vegetated field boundaries are associated with significantly higher activity than non-vegetated boundaries (*P. pipistrellus*, *N.* spp./*E. serotinus*, *R. hipposideros* and *R. ferrumequinum*). Our results reiterate the importance of vegetated field boundaries for bats in agricultural landscapes – increasing activity by over 300% for *R. hipposideros* – and demonstrate that increasing the area of vegetated field boundaries can enhance the biodiversity value of farmland.

The importance of tall, overgrown hedgerows for *R. ferrumequinum* was previously known (Ransome, 1996), however, here we provide new evidence that the number of field boundary trees is the most important aspect of field boundary structure for this species. This builds on previous research that found high *R. ferrumequinum* activity along tree lines (Finch et al., 2020b) and affords an easily-implemented approach to improving habitat quality for *R. ferrumequinum*. We also found trees to be important for *P. pygmaeus*, a finding reported previously (Boughey et al., 2011). Coupled with the finding that

Myotis spp. activity was higher at wide field boundaries and *P. pipistrellus* and *P. pygmaeus* activity was higher at tall field boundaries, our results add to the body of evidence that planting field boundary trees and allowing existing hedgerows to outgrow will benefit a number of bat species (Boughey et al., 2011; Heim et al., 2015; Lacoeuilhe et al., 2018; Toffoli, 2016; Wickramasinghe et al., 2003).

Nyctalus spp./*E. serotinus* activity was better explained by local landscape characteristics than field boundary or adjacent field characteristics. These species forage above the height of vegetated field boundaries or at pace over open areas, targeting large free-flying prey items using loud, low-frequency echolocation (Jones, 1995; Waters et al., 1999). *Nyctalus* spp./*E. serotinus* would not therefore be expected to interact with field boundaries the same way as gleaning bats, or species with low-intensity or high-frequency echolocation calls that attenuate quickly in air. In this respect, our findings support previous studies (Boughey et al., 2011; Finch et al., 2020b; Kelm et al., 2014; Toffoli, 2016; Verboom and Huitema, 1997). In contrast, we found higher *Nyctalus* spp./*E. serotinus* activity along vegetated field boundaries than non-vegetated boundaries, although the effect size is small compared to that of other species (table 2.7). Our interpretation of this is that while *Nyctalus* spp./*E. serotinus* are not selecting for field boundary characteristics directly, they may still benefit from the increased landscape heterogeneity provided by vegetated field boundaries. This view is supported as both increased woodland and urban/suburban cover had a positive impact on activity for this species group.

Activity of *Nyctalus* spp./*E. serotinus* was higher in fields with livestock. Dung beetles (Geotrupidae, Scarabaeidae) comprise a significant portion of the diet of this group, which likely explains this finding (Jones, 1995; Shiel et al., 1998; Waters et al., 1999; Whitaker and Karataş, 2009). Activity of both *Pipistrellus* species was also higher in fields with livestock, likely because livestock attract prey items such as midges and mosquitoes that are important for *Pipistrellus* species (Ancillotto et al., 2021, 2017).

Activity of *R. ferrumequinum* and *P. pipistrellus* activity was negatively associated with arable fields (either in current crop production or fallow), a finding reported in previous studies (Dietz et al., 2013; Flanders and Jones, 2009; Walsh and Harris, 1996a; Wickramasinghe et al., 2003). Additionally, *R. hipposideros* activity was higher in improved grassland. Arable farming requires a greater amounts of agrochemicals than pasture, which have been shown to negatively impact bat activity (Kahnonitch *et al.*, 2018; Wickramasinghe *et al.*, 2003), while traditionally managed semi-natural grassland can support relatively high insect diversity (Green, 1990). Encouraging the establishment of species rich, permanent pasture with low-intensity management would be beneficial for these species.

P. pipistrellus activity was negatively associated with improved grassland, in comparison to the reference group, roads. While roads have been shown to have a negative effect on bat activity, in our study area roads comprise small country lanes or farm tracks, rather than major roads that have been the focus of previous studies (motorways, Berthinussen and Altringham 2012; dual carriageways, Claireau et al. 2019). The benefit of roads for bats our study was likely that there was almost always a hedgerow and/or tree line either side of the road. Hedgerows and tree lines are important for edge-foraging *Pipistrellus* species, as they provide shelter from wind and predators, high surface area of vegetation and high densities of insects (Froidevaux et al., 2019; Oakeley and Jones, 1998; Verboom and Huitema, 1997). Our findings corroborate this as the field boundary model best explained activity in both *Pipistrellus* species, and vegetated boundaries had significantly higher *P. pipistrellus* activity. Our results further highlight the value of vegetated field boundaries for *Pipistrellus* species.

Environmental stewardship schemes (ESS) award a subsidy to landowners for managing their land for the benefit of wildlife and the environment. ESS were not positively associated with bat activity in our study. Instead, we found reduced *Myotis* activity at recording locations managed under ESS. It may be that survey locations under ESS are unsuitable for *Myotis* spp. for unmeasured reasons, however this requires further investigation.

Assessing the frequency of feeding buzzes (increased repetition rate of echolocation calls associated with the bat honing in on a prey item) was beyond the scope of this study, however future work would benefit from the extra insight this would provide into how bats are using field boundaries.

2.5.1 Using Models for Prediction

We found a large spatial effect driving activity patterns, which would make models unsuitable for predicting outside the study area where the spatial component is unknown. We found that part of the spatial effect for *R. ferrumequinum* was explained by proximity to known roosts, demonstrating that location of species-centric landmarks in the landscape plays a large part in dictating spatial activity patterns.

Bat activity is known to be highly variable and difficult to predict (Langton et al., 2010; Richardson et al., 2019; Silva et al., 2017). High variation in activity levels meant that predictions at best had an R^2 value of 0.45 when regressed with the actual values (for *Nyctalus* spp./*E. serotinus*), but for most species this was considerably less (table 2.5).

The predicted activity maps generated in this study (figure 2.10) describe spatial activity patterns during our study period, albeit a smoothed-over version of true activity. It is unclear whether this would be representative of activity at the same sites in subsequent years, although there is evidence to suggest that activity hotspots change over time (Medinas et al., 2021). Border et al. (2022) used a similar modelling and mapping approach to ours, but treated bat activity as a proxy of habitat suitability. While there almost certainly is a link between habitat suitability and bat activity levels, based on our findings we would not recommend using predictive modelling of bat activity as a substitute for habitat suitability until the relationship between the two has been better characterised.

2.5.2 Conclusions

Our results add to a growing understanding of the value of field boundaries for bats. We shed new light on the specific aspects of field boundary structure that benefit bats and identify a number of measures that could be used for habitat restoration and species conservation. We show that increasing the area of vegetated field boundaries, planting hedgerow trees and developing tall and outgrown hedgerows will enhance agricultural landscapes for many species. Our results show how field boundaries can be a valuable tool in developing biodiversity-friendly agricultural landscapes.

Chapter 3

Habitat Suitability is Correlated with Acoustic Activity Measured by Passive Acoustic Monitoring: a Novel Method for Model Validation and Applications for Landscape-Level Conservation

3.1 Abstract

Habitat suitability models (HSMs) are a powerful tool for estimating species occurrence and contribute to evidence-based conservation planning. It is important to verify HSM predictions with ground validation but this is not always carried out, partly because habitat suitability cannot be measured dir-

ectly. The emergence of passive acoustic monitoring (PAM) as an inexpensive tool for obtaining ecological data over a wide area provides an opportunity to relate habitat suitability predictions to a physical measure of species activity on the ground.

The aims of this study were to investigate the relationship between acoustic activity measured by PAM and habitat suitability predictions, test the utility of PAM for HSM validation, and apply a ground validated HSM to landscape-level conservation. We illustrate this approach with a species of conservation concern in Britain, the greater horseshoe bat (*Rhinolophus ferrumequinum*).

We built a 1 km resolution HSM for *R. ferrumequinum* and used PAM to record acoustic activity across a predicted habitat suitability gradient. We looked for correlation between acoustic activity and habitat suitability, and performed a post-hoc power analysis to determine the minimum sample size needed to detect a habitat suitability signal in our acoustic data.

We found a statistically significant positive correlation between acoustic activity and predicted habitat suitability, losing power below about 50 sampling points. Our results indicate that climate change could have a positive effect on *R. ferrumequinum* distribution in Britain, whereas cave availability is a limitation. We predict a negative effect of urban expansion, driven by urban sprawl rather than urban densification.

Our study demonstrates the huge potential of PAM as a tool for model validation as part of robust, evidence-based species conservation planning.

3.2 Introduction

Habitat suitability models (HSMs; also known as species distribution models or environmental niche models) use species occurrence records to estimate the suitability of a given area as a function of local environmental conditions (Hirzel and Lay, 2008). By improving understanding of species' spatial ecology and identifying factors affecting species' distribution, HSMs can be a valuable tool for strategic conservation planning (Guisan et al., 2013). The development of open source, presence-only approaches for estimating habitat suitability models (e.g. Royle et al., 2012; Phillips et al., 2006; Hirzel et al., 2002) coupled with freely available occurrence data from online repositories (e.g. NBN Atlas, `https://nbnatlas.org/`; GBIF, `https://www.gbif.org/`) has increased the accessibility of HSMs (Bellamy and Altringham, 2015), which are now widely used in conservation (Pecchi et al., 2019; Guisan et al., 2013).

Broad scale HSMs are a valuable landscape-level tool that can be used to identify the spatial distribution of threats, factors affecting species distribution, as well as potential range contractions/expansions and approaches to improving habitat. HSMs can be used to predict the impact of dynamic threatening processes such as climate change (Ahmed et al., 2023; Guan et al., 2021; Graham et al., 2011) and land use change (Poor et al., 2020; Trisurat and Duengkae, 2011; Ficetola et al., 2010). Predictions from HSMs are spatially explicit, so can be used to identify areas where conservation effort is needed or sites where mitigation will have the biggest impact (Duflot et al., 2018; Bayliss et al., 2005).

The effectiveness of HSMs is reliant on effective validation. Many studies rely on statistical metrics to assess model performance (Qazi et al., 2022;

Hao et al., 2019; Robinson et al., 2017), however ground validation with an independent dataset is regarded as the gold standard (Greaves et al., 2006). Ground validation can be difficult to achieve in practice as habitat suitability is not a substance or phenomena that can be measured directly, and validation of HSMs is often restricted to the simple confirmation of species presence/absence (e.g. West et al., 2016; Rebelo and Jones, 2010), while the habitat suitability index (HSI) estimated by an HSM is continuous (normally between 0 and 1), meaning information is lost on the relative suitability of habitat.

HSI has been shown to be correlated with abundance in many species (Weber et al., 2017), meaning a measure of abundance could be a good test of model predictions, although measuring abundance can be challenging for many species (Bonar et al., 2011). A lack of detailed abundance data is indeed often a motive for using an HSM, and is why many methods for HSMs have been developed for presence-only data (Pearce and Boyce, 2006). An additional complication is that full occupancy/abundance may not always be realised at every locality (VanDerWal et al., 2009), and the positive correlation between HSI and abundance may not be true for every study group and/or every measure of abundance (Dallas and Hastings, 2018).

Passive acoustic monitoring (PAM) is increasingly used for studying and monitoring wildlife populations (Sugai et al., 2019) and can be applied to answer fundamental questions in ecology (Ross et al., 2023). As an emerging area of interest, more work is needed to understand how to fully utilise acoustics in ecological research (Gibb et al., 2019). Acoustic activity recorded by PAM is not a true measure of abundance, as individuals can not be distinguished from recordings: one individual making extensive use of an area can generate similar activity to many individuals using an area a little (Ross et al., 2023). Although there are approaches for estimating abundance from acoustics (e.g. Pérez-Granados and Traba, 2021; Marques et al., 2013), acoustic activity should be viewed as a measure of habitat use rather than abundance.

Acoustic activity has been used as a proxy for habitat suitability in recent studies (Border et al., 2022; Newson et al., 2015), although the exact relationship between habitat suitability and acoustic activity is not currently well understood. Habitat suitability can be expected to be an important factor in driving acoustic activity, as individuals are likely to spend more time in areas of highly suitable habitat, although there will be many factors affecting acoustic activity levels. Foxley et al. (2023), for example, found a significant spatial effect driving acoustic activity in bats that was largely explained by the distance to known roosts. Furthermore, count data like those from PAM are inherently stochastic, leading to a lot of unexplained variance (Milne et al., 2005; Broders, 2003; Hayes, 1997). Therefore, while acoustic activity measured by PAM is likely correlated with habitat suitability, it is not currently clear how well PAM is suited to HSM validation. Although a limited number of studies have used acoustics to validate HSMs before (Hintze et al., 2021; Brookes et al., 2013), to our knowledge no studies have used PAM to test continuous habitat suitability predictions in a terrestrial setting.

Between 1992 and 2018, 50% of PAM studies focused on bats (Sugai et al., 2019). Bats are often found in human-dominated landscapes and are vulnerable anthropogenic threats (Voigt and Kingston, 2016), however, being volant, nocturnal and cryptic, studying the distribution and abundance of bats can be challenging. HSMs made with presence-only data have thus become a valuable tool for bat conservation (e.g. Bellamy and Altringham, 2015; Bellamy et al., 2013; Razgour et al., 2011). PAM has also proven invaluable for studying bats, as many echolocating bat species can be identified from their distinctive echolocation calls (Jones et al., 2000). Bats are therefore an ideal study group to test the relationship between habitat suitability and acoustic activity measured by PAM.

3.3 Aims

The aims of this study were to investigate the relationship between acoustic activity measured by PAM and habitat suitability predictions, test the utility of PAM for HSM validation, and demonstrate the power of ground validated HSMs for landscape-level conservation. We illustrate this approach with the greater horseshoe bat (*Rhinolophus ferrumequinum*), a species of conservation concern in Britain (JNCC, 2007). We aimed to accomplish this through a number of objectives:

- build a broad scale HSM for *R. ferrumequinum* in Britain with freely-available presence-only data;
- ground validate habitat suitability predictions using PAM and investigate the utility of PAM for model validation;
- identify factors affecting *R. ferrumequinum* distribution and run simulations to identify areas where threats may impact the species, where conservation action may be of benefit, and where changes to distribution are likely to happen in future.

We expect to find a positive correlation between acoustic activity measured by PAM and predicted habitat suitability. We do not expect a perfect correlation, but that relationship will be wedge-shaped, per VanDerWal et al. (2009):

high habitat suitability will have either high or low acoustic activity, while low habitat suitability will only have low acoustic activity.

3.4 Methods

All statistical analysis and data processing was conducted in R (R Core Team, 2022); spatial data manipulation was completed using the *terra* package (Hijmans, 2022).

3.4.1 Habitat Suitability Model

We built HSMs using MaxEnt (Phillips et al., 2006) for the whole of Britain at a 1 km resolution. We downloaded occurrence records for all bat species from the year 2000 to 2020 from the NBN Atlas (`https://nbnatlas.org/`). We removed records with less than 1 km spatial resolution and added additional records from a recently discovered *R. ferrumequinum* roost in Sussex (Vincent Wildlife Trust, personal correspondence) and incidental records collected over the course of the study.

We chose appropriate environmental variables based on a literature review of *R. ferrumequinum* ecology (table 3.1). These included variables that were likely to affect *R. ferrumequinum* distribution at a broad scale, such as climate, land use and topography. Environmental data was downloaded or generated at a 1 km resolution. Raster data were generally available projected in Ordnance Survey National Grid (OSGB36) reference system, if spatial data were available in a different projection they were resampled to a 1 km OSGB36 grid by bilinear interpolation. Environmental rasters were checked for multicol-

Table 3.1: Environmental variables included in the models.

Variable	**Statistic**	**Source**
Annual precipitation (mm)	2000-2021 mean	Met Office et al., 2022
Arable/horticulture	% cover	Rowland et al., 2017a
Broadleaf woodland	% cover	Rowland et al., 2017a
Caves and mines	Distance to	Openstreetmap, Mendip Caves Registry (`http://www.mcra.org.uk/`)
Elevation (m)	Mean	OS Terrain 50 (Ordnance Survey, 2017)
Grassland (improved and semi-natural)	% cover	Rowland et al., 2017a
Night light pollution nanoWatts/cm^2/sr)	Mean	Falchi et al., 2016 (Earth Observation Group, NOAA/NCEI)
Summer maximum temperature (°C)	2000-2021 mean	Met Office et al., 2022
Urban and suburban	% cover	Rowland et al., 2017a
Winter minimum temperature (°C)	2000- 2021 mean	Met Office et al., 2022

linearity with the *usdm* R package (Naimi et al., 2014) and occurrence records were thinned to a maximum of one record per 1 km grid square.

We used ENMEval (Muscarella et al., 2014) to determine the optimal feature classes and regularisation multiplier for MaxEnt. We generated 10,000 background points weighted by the kernel density estimate of all bat species records (i.e. the target group; Phillips et al., 2009) to account for bias in survey effort. The bandwidth of the kernel density estimate was set to 10,000. Model fit was assessed with area under the receiver operating characteristic curve (AUC), calculated with 5-fold cross validation. Additionally, we calculated model sensitivity according to Bellamy et al. (2020) and tested whether there were more species records in habitat predicted to be above the maximum test sensitivity and specificity (MTSS) threshold (Liu et al., 2005) than by chance.

3.4.2 Acoustic Validation

Acoustic Survey Design

We conducted an acoustic survey of bats in North Somerset, Bath and North-East Somerset, and the former Mendip and Sedgemoor districts between July and September 2022 (figure 3.1). The study area is a regional stronghold for horseshoe bats containing a number of protected sites for *R. ferrumequinum* (JNCC, 2015a,b,c; English Nature, 1996). The study area has a wet and mild marine climate (Köppen classification *Cfb*) with diverse topography encompassing the coastal plains of the Somerset levels and the limestone Mendip hills. Land use in the study area is typical of the known range of *R. ferrumequinum* in Britain, comprising 8.7% broadleaf woodland, 19.7% arable farmland, 52.8% grassland and 15% built-up areas and gardens (Marston et al., 2022a).

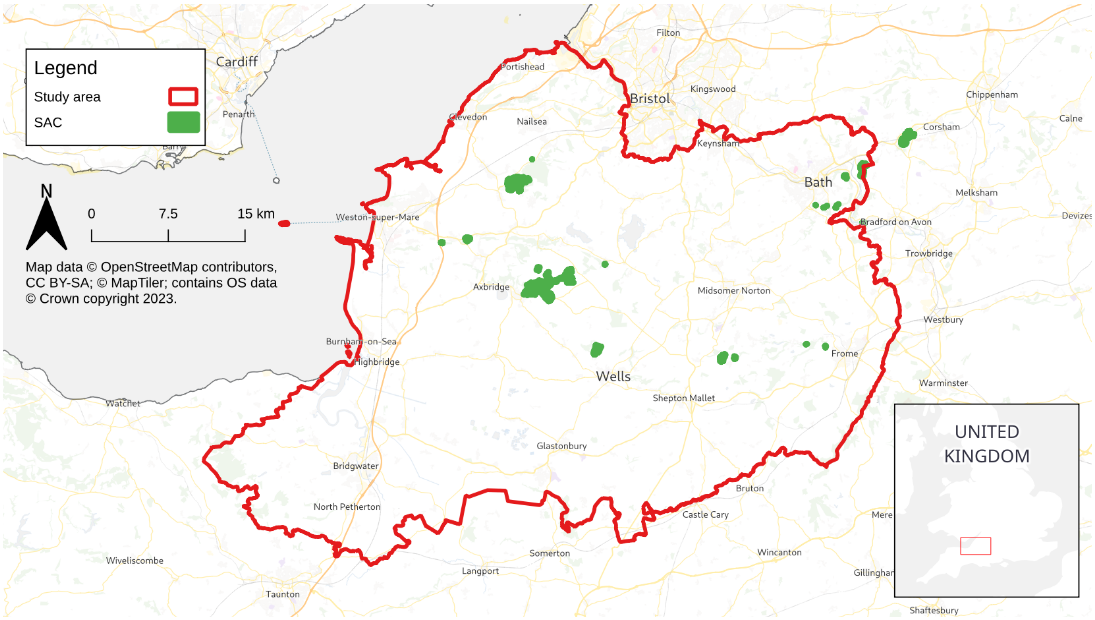


Figure 3.1: Study area for acoustic validation.

To determine survey locations we trimmed the HSM to the extent of the study area and split it into habitat suitability quartiles. We then identified 96 random 1 km sample squares, split evenly across quantiles (i.e. twenty four 1 km squares per quantile; figure 3.3). Where access could not be obtained the nearest 1 km square of the same quantile was used. We placed ultrasonic detectors (Song Meter Mini Bat, Wildlife Acoustics, Inc) along hedgerows and woodland edges to maximise detections, as *R. ferrumequinum* activity has been shown to be highest along vegetated field boundaries with trees (Foxley et al., 2023). In total sixteen detectors were deployed at any one time, these were moved on a 10-night per site rotation. The proportion of detectors in each quantile was kept the same throughout the study period. We placed detectors in similar habitat at all sites, always on a vegetated field boundary bounded by grassland, away from roads, houses and other light sources. We recorded additional environmental characteristics to control for factors that may affect bat activity (Ransome, 1996; Jones et al., 1995), including the presence of livestock when deploying/collecting detectors, temperature (recorded internally by the bat detectors), and mean rainfall from the nearest weather station to each detector (mean 6 km ± s.d. 3 km; Environment Agency).

Species Classification and Quantification

Bat species were identified using BatClassify (Scott, 2012). Error in automated classification was classified according to Barré et al. (2019), discarding classifications below a false positive rate of 50%.

We calculated a bat activity index by counting every one-minute block in which a bat species was present as one occurrence and dividing total occurrences by total recording time (AI; Miller, 2001). The AI allows comparison of activity between sites with varying recording effort, accounting for mechanical issues (e.g. battery failure) and variation in night length over the study period.

Statistical Analysis

We used a generalised additive model with a negative binomial error structure in the *mgcv* R package (Wood, 2011) to assess the relationship between bat activity and predicted habitat suitability. Acoustic activity (represented by AI) was the dependent variable and habitat suitability, temperature, rainfall and presence of livestock were explanatory variables. We included latitude and longitude as a smooth term (Duchon spline, k=25) to account for spatial autocorrelation between sites and week of the year as a smooth term (thin plate regression spline, k=9) to account for temporal differences in sampling. Model residuals were checked using the *DHARMa* R package (Hartig, 2021). We also used *DHARMa* to test for residual spatial autocorrelation. Additionally, we tested for over- and under-dispersion, and multicollinearity by calculating variance inflation factor in the *mgcv.helper* R package (Clifford, 2022).

We conducted a post-hoc power analysis to determine the minimum sample size required to detect a significant effect of broad scale habitat suitability in our acoustic dataset, as a reference for future studies. We took a random subsample of the main dataset and refitted the model 100 times. We performed model averaging using the *MuMIn* R package (Bartoń, 2020) to calculate average coefficients, giving each model an even weighting. This process was repeated at different sample sizes (*n*), decreasing *n* iteratively at intervals of 10% of the full dataset. Power was calculated as the fraction of subsampled models that achieved statistical significance.

3.4.3 Climate Change, Artificial Hibernacula and Urban Expansion Simulations

To apply the findings of our HSM to landscape-level conservation, we ran three simulations that address different conservation challenges: we simulated the impact of climate change, the threat of urban expansion, and the provision of artificial hibernacula on the predicted distribution of *R. ferrumequinum* in Britain. For the climate change simulation, we refitted the HSM after adding 2°C to minimum winter temperature, that being the projected change by 2100 under RCP4.5 climate change scenario (Lowe et al., 2018). We used MTSS (Cao et al., 2013; Liu et al., 2005) to define suitable/not suitable habitat under current conditions and under projected climate change, and we calculated the percentage change in area between current and projected conditions.

We simulated the provision of artificial hibernacula by refitting the HSM with an altered ′distance to caves′ variable, setting the maximum distance to caves as 20 km over the whole of Britain (but allowing shorter distances). We chose 20 km based on distances species may be expected to travel for hibernation reported from a long-term ringing study (Ransome, 1980). This analysis was designed to highlight areas where the species might be constrained by a lack of caves in an otherwise hospitable landscape and to identify areas that would benefit from the provision of artificial hibernacula.

We simulated an increase in the proportion of urban land cover (percentage in each 1 km square) by adding an additional 50% land cover to the existing urban cover (i.e. a grid square with 10% urban cover becomes 60%), with an upper limit of 100%. Such a large increase in urban land cover may not be realistic in many locations but was designed to identify areas where

R. ferrumequinum would be impacted by urban expansion. Part of the threat of urban expansion for *R. ferrumequinum* comes with the associated increase in artificial light at night (ALAN). We found our urban land cover and night light pollution variables to be highly correlated (Pearson's correlation coefficient = 0.75). To account for this, we fitted a simple linear model to estimate the relationship between urban cover and light pollution. We then estimated the predicted increase in light pollution associated with an additional 50% urban cover, and added this to the light pollution layer. We then refitted the model per above simulations and calculated the predicted change in habitat suitability. For realism, we removed any areas with existing land cover <5%. The aim of this was to exclude areas where new urban development is unlikely to occur, such as green belt, national parks, and extensive farmland. We also constrained the simulation to areas currently predicted to be suitable habitat, as estimated with the HSM using the MTSS threshold.

3.5 Results

3.5.1 Habitat Suitability Model

After thinning, a total of 389 species occurrence records were used in model training. Optimal features identified by ENMeval were linear, quadratic, hinge and product, with a betamultiplier of five. The HSM achieved an independent AUC of 0.9, with a sensitivity of 0.91 (i.e. 91% of occurrence points were predicted to be in suitable habitat above the MTSS threshold; $p<0.001$).

The HSM predicts suitable habitat in the West Midlands, Surrey, Sussex and Kent, which are currently outside the current known *R. ferrumequinum*

Table 3.2: Measures of predictor performance in HSMs. For details of calculation method see Phillips (2017). Training gain from jackknife test is given as a percentage of the full model.

Predictor	**Percentage contribution**	**Permutation importance**	**Training gain without variable**	**Training gain with only variable**
Annual precipitation (mm)	12.3	12.4	96.3	23.1
Arable/horticulture (% cover)	1.5	0.4	99.8	7.6
Broadleaf woodland (% cover)	1.4	2.5	97.6	8.1
Caves and mines (distance to)	36.2	25.8	83.2	43.9
Elevation (m)	0.9	1.3	99.3	4.1
Grassland (improved and semi-natural; % cover)	1.4	3.1	98.1	7.9
Night light pollution (nanoWatts/cm^2/sr)	4.5	6.3	98.5	4.1
Summer maximum temperature (°C)	2.7	11.2	95.8	14
Urban and suburban (% cover)	2.4	1.8	98.7	3.1
Winter minimum temperature (°C)	36.6	35.3	84.8	46.2

distribution in Britain (figure 3.3). The model predicted uplands such as Dartmoor, Exmoor and much of central Wales to be unsuitable. Distance to caves, minimum winter temperature and mean annual precipitation were the most important predictors of habitat suitability (36.2%, 36.6% and 12.3% contribution, respectively; table 3.2).

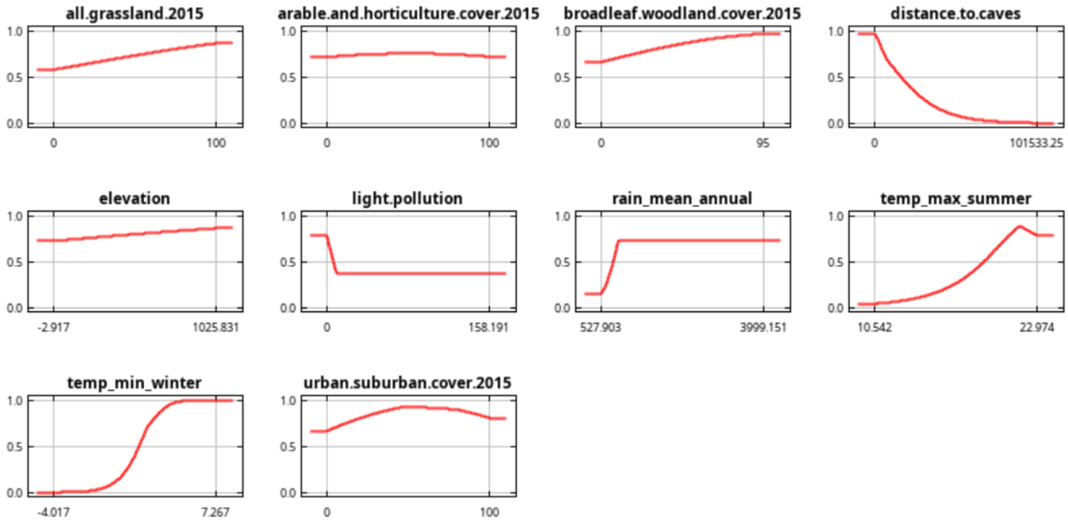


Figure 3.2: HSM response curves.

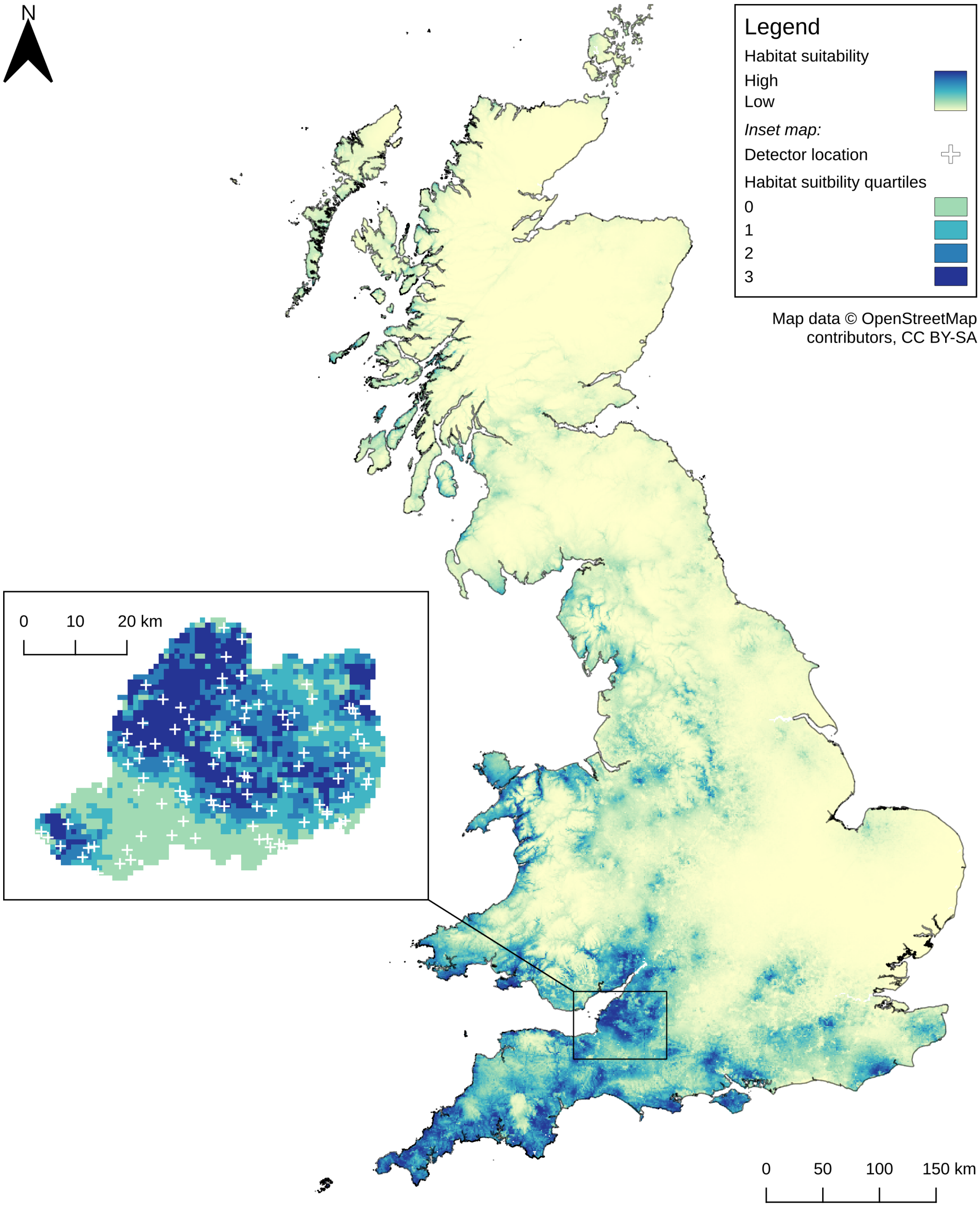
Table 3.3: Estimates, standard errors and p-values for all variables in acoustic analysis with HSM. Statistical significance denoted with *.

Predictor	Estimate	Std. Error	z-value	p-value
HSM	2.621	0.682	3.845	<0.001*
Presence of livestock (0/1)	0.092	0.276	0.334	0.738
Mean minimum temperature (°C)	-0.041	0.125	-0.329	0.742
Mean nightly rainfall (mm)	-0.162	0.160	-1.012	0.311

3.5.2 Acoustic Validation

One detector failed to record, therefore 95 sites were included in the in final analysis (figure 3.3). We conducted a total of 8,908 hours recording and detected *R. ferrumequinum* at 89% of recording locations (85 sites). On average *R. ferrumequinum* were recorded in two one-minute blocks every 12 hours (i.e. per standardised night; ± s.d. 3.5; range 0-26).

There was a significant positive relationship between predicted habitat suitability and *R. ferrumequinum* activity (p<0.001; table 3.3, figure 3.4) and the model explained 57.1% of deviance. The relationship is wedge-shaped:



Map data © OpenStreetMap contributors, CC BY-SA

Figure 3.3: Predicted habitat suitability for *R. ferrumequinum* in Britain at 1 km resolution. Habitat suitability quartiles in validation study area and detector locations for acoustic validation are shown inset.

low activity was only recorded at low suitability sites, while high suitability sites had either high or low activity.

Table 3.4: Model-averaged results from power analysis of acoustic validation, showing changes in estimates, standard errors and p-values as sample size is decreased. Statistical significance of averaged models denoted with *.

Sample size (n)	Estimate	Std. Error	Adjusted SE	z-value	p-value	Power
95	2.621	0.682	0.693	3.782	0.000*	1
86	2.615	0.762	0.775	3.376	0.001*	1
76	2.706	0.891	0.905	2.990	0.003*	1
66	2.578	1.042	1.059	2.435	0.015*	0.95
57	2.536	1.271	1.291	1.965	0.049*	0.82
48	2.568	1.278	1.306	1.966	0.049*	0.77
38	2.308	1.847	1.882	1.226	0.220	0.53
28	2.219	2.278	2.345	0.946	0.344	0.39
19	1.613	2.995	3.190	0.505	0.613	0.25

Power analysis found a loss of power below a sample size of 57 (i.e. a power of <0.8) and a loss of statistical significance below a sample size of 48 (table 3.4).

3.5.3 Climate Change, Artificial Hibernacula and Urban Expansion Simulations

Our climate change projection predicts a 153% range expansion for *R. ferrumequinum* in Britain by 2100 under RCP4.5, with the largest expansions predicted in southern England and the West Midlands (figure 3.5A).

The artificial hibernacula simulation highlights large areas in southern England where *R. ferrumequinum* distribution may be constrained by a lack of hibernation sites (figure 3.5B). Affected areas are identified in North Devon, Dorset, Hampshire, Sussex and Kent.

The urban expansion simulation identifies sites where new development may impact *R. ferrumequinum*. Impact in existing urban centres was generally

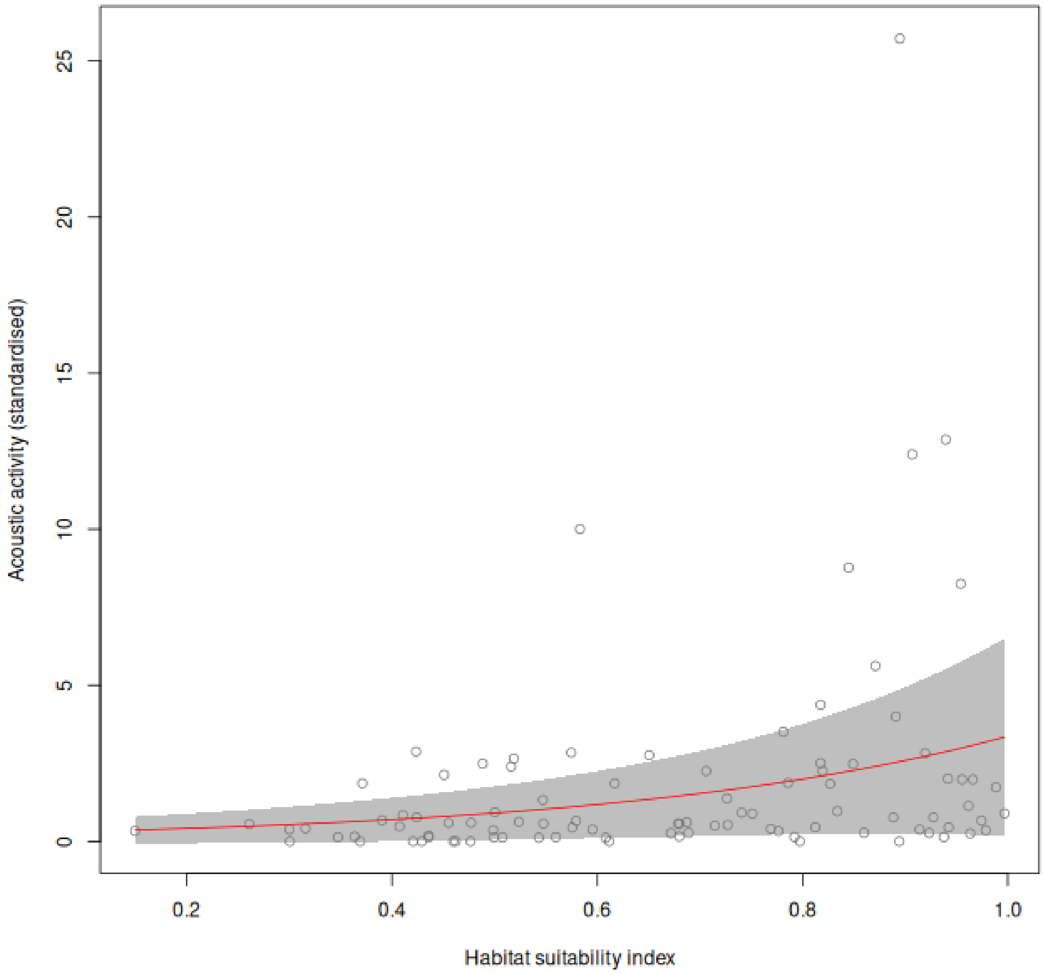


Figure 3.4: Partial effects plot showing the relationship between *R. ferrumequinum* activity (x axis) and habitat suitability index (y axis). Showing 95% confidence intervals (grey shaded). Activity is measured as the number of one-minute blocks in which a bat was recorded and has been standardised to one 12-hour night.

much lower than in suburban areas (figure 3.6). Some of the areas of highest impact are around Swansea and the Gower peninsular in South Wales, in the surrounds of Bristol up to the Forest of Dean, and in the suburbs of Southampton and Portsmouth.

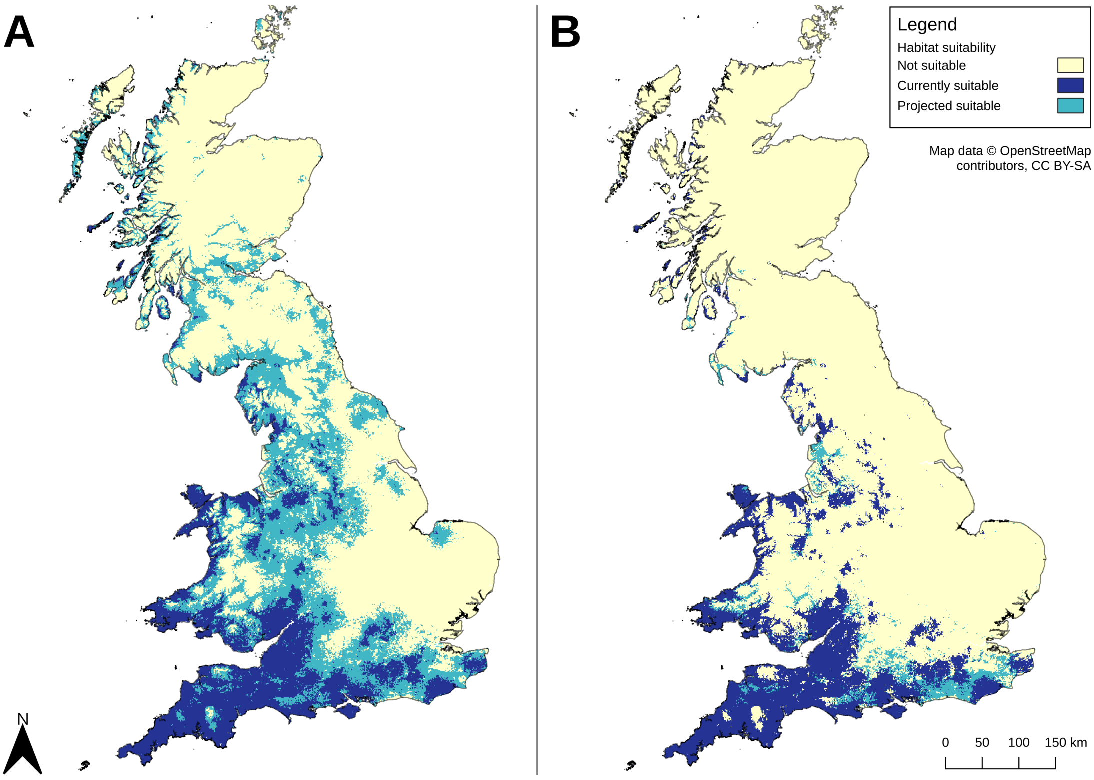


Figure 3.5: Projected range expansion for *R. ferrumequinum* in Britain: (A) by 2100 under RCP4.5 climate change scenario (2°C rise in minimum winter temperature); (B) under current climatic conditions given the provision of artificial hibernacula. MTSS used to define suitable/not suitable.

3.6 Discussion

We found PAM to be a useful tool for validating our HSM, observing a highly significant relationship between predicted habitat suitability and bat activity. This relationship was wedge-shaped: only low activity was recorded in low habitat suitability, while either high or low activity was recorded in high suitability. This relationship has been described previously for numerous measures of abundance (VanDerWal et al., 2009) and is explained by the fact that maximum abundance may not be realised at all sites, due to factors not accounted for in modelling. While not a true measure of abundance (Ross et al.,

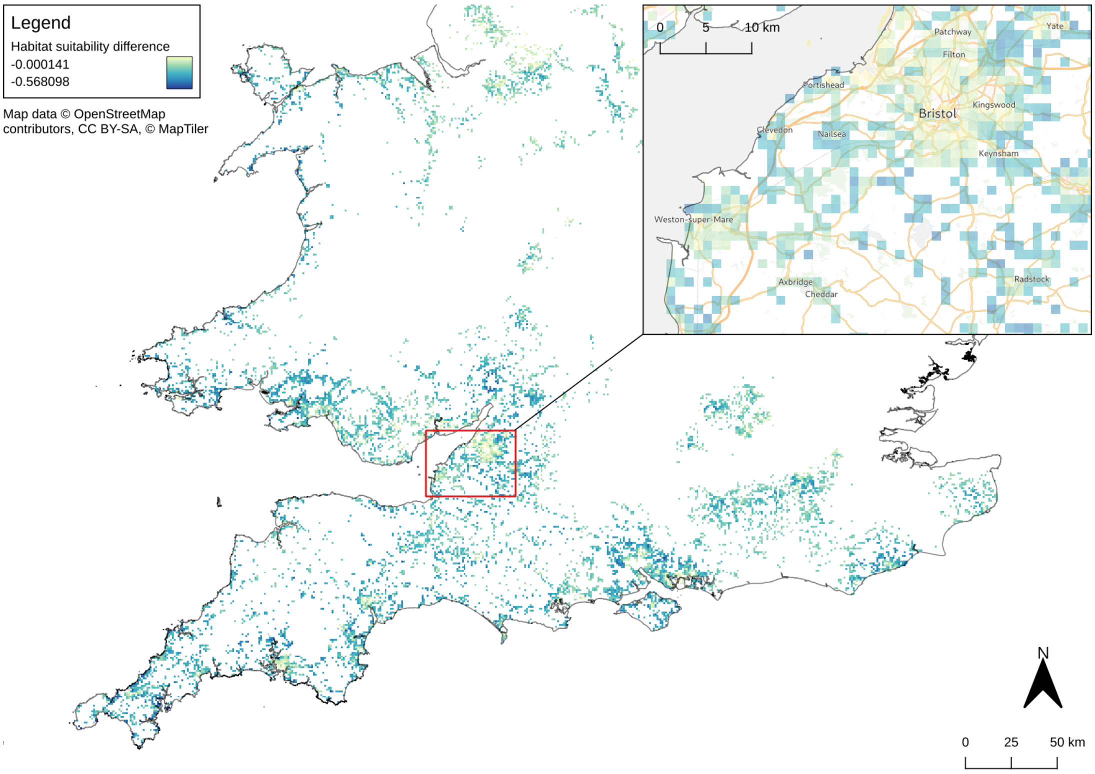


Figure 3.6: Urban expansion simulation showing projected change in habitat suitability from increased urban cover and associated increase in night light pollution. Only showing change in suitable habitat with existing urban land cover >5%. Inset map shows Bristol and North Somerset, existing urban areas are visibly less impacted than suburban areas.

2023), it is informative to see that acoustic activity had a similar relationship with habitat suitability in our study.

Abundance certainly explains a large component of acoustic activity, but there are many other factors affecting recorded activity levels. Inherent variability found in any sort of ecological sampling can result in high variability in acoustic data (e.g. Milne et al., 2005; Broders, 2003; Hayes, 1997). The relatively short sampling period used in most acoustic studies, owing to limitations of both battery and storage capacity (Ross et al., 2023), means that sampling may miss key times of year a site is in use. Density of prey, for example, will be a key driver of acoustic activity (Bhalla et al., 2023; Froidevaux et al., 2021;

Kolkert et al., 2020; Hałat et al., 2018) but will vary seasonally as prey species progress through their annual cycles (e.g. Gittings and Giller, 1997).

Foxley et al. (2023) found a large spatial effect driving bat activity, partly explained by distance to known roosts, highlighting how chance placement of recording equipment in relation to species-specific landmarks can impact recorded acoustic activity. A demonstration of chance placement of recording equipment is found in the outlier in figure 3.4. On inspection of the sound files we found evidence of extensive perch feeding at this site. This is a well-documented behaviour in *R. ferrumequinum* (Jones and Rayner, 1989) where bats perch under overhanging vegetation and catch prey that flies past, much like a flycatcher. This behaviour produces recordings of echolocation calls at a consistent amplitude. Given the acoustic detection range of *R. ferrumequinum* is <20 m (Kerbiriou et al., 2019), the chance of placing a detector to capture this behaviour is low. This outlier was found not to have undue influence on results and was included in the analysis as it is a genuine measure of habitat use, however, had the detector been placed 50 m further down the hedgerow, recorded activity may have been very different at this site. On the same logic, chance placement of detectors at other sites may have caused us to miss perch feeding behaviour, resulting in lower recorded activity.

While we found that acoustic activity certainly contains information about habitat suitability, it is far from a direct measure. This has implications for how we can use acoustic data, which is highly topical at a time when large scale acoustic datasets, for example from citizen science projects (e.g. Newson et al., 2015) are becoming common, and the applications of such data are still being explored (e.g. Border et al., 2022). We would not recommend using acoustic activity as a substitute for habitat suitability in these cases.

We would recommend a large sample size in future studies that seek to identify broad scale trends in acoustic data. Our detector placement was designed to maximise chances of detecting a trend using *a priori* knowledge of the signal we were trying to measure, therefore without this knowledge a higher sample size might be needed. We show that a minimum of 50 recording locations were required across our study area to identify a statistically significant link between habitat suitability and acoustic activity.

3.6.1 Climate Change, Artificial Hibernacula and Urban Expansion Simulations

Despite the fact that models are always a simplification of reality (Box, 1976), our models show great utility for addressing landscape-level conservation challenges, and are supported in a number of respects by current species trend data.

As a species on the northern edge of its range, *R. ferrumequinum* is likely constrained by climatic conditions in Britain (Ransome, 2020). Confirming this, we found minimum winter temperature to be an important predictor of habitat suitability for *R. ferrumequinum*; although note that as an edge-of-range study, our HSM might not have captured the full extent of the species' responses to environmental conditions it experiences elsewhere in its range.

Climate change encompasses a wide range of environmental changes, including extreme weather events and warmer winters. Each of these climatic changes will have differing impacts on wildlife and their habitats. There is evidence that climate change may be having a positive impact on *R. ferrumequinum* populations in Britain (Froidevaux et al., 2017), our projection supports this view and predicted a substantial range expansion with increased minimum winter temperature. There are, however, countless potential effects climate change may have on ecosystems that are complex and interconnected (Urban et al., 2016; Garcia et al., 2014). There are many ways climate change could have a negative impact on *R. ferrumequinum* that we were not able to model here, for example by reduction of prey items: many studies predict that climate change will have a negative impact on insects (e.g. Filazzola et al., 2021; Halsch et al., 2021; Gely et al., 2020).

Caves and underground structures are of high importance to *R. ferrumequinum* (Ransome, 2020). We found distance to caves to be an important predictor and our simulation highlights areas where *R. ferrumequinum* is potentially constrained by a lack of caves. Caves are used by *R. ferrumequinum* year-round but in Britain have particular value for hibernation. Ransome (2020) prescribes that *R. ferrumequinum* need to be within 40 km of a cave or suitable underground site for a population to persist. Man-made substitutes such as mines, cellars and abandoned buildings can be used instead of caves, where suitable structures exist in suitable habitat (Ransome, 2020; Winter et al., 2020).

An example of man-made structures being used by *R. ferrumequinum* is Bryanston SSSI and the Shaftesbury Estate in Dorset, where there are no caves but bats use man-made structures for breeding and hibernation (KP Ecology, 2022; English Nature, 1977). Our model predicted large areas around Bryanston and the Shaftesbury Estate to be unsuitable, as the locations of man-made roosts and hibernacula were not included in the modelling. This area is predicted to be suitable under the artificial hibernacula simulation as the constraint of caves is removed; the fact that there are healthy bat populations using an artificial hibernacula in this location can thus be viewed as validation of the simulation. Our simulation results highlight areas where the creation of artificial hibernacula would be beneficial or areas where existing artificial hibernacula are already having an impact.

Urban expansion was found to have a negative impact on habitat suitability predictions, although the extent of the impact was dependent upon the mode of urban expansion. The largest impact is predicted in suburban areas, while urban areas such as city centres are impacted much less, likely because urban centres already have a high degree of urbanisation that makes them poor habitat. Thus we find that *R. ferrumequinum* would be impacted much less by urban densification than by urban sprawl.

Mapping HSM predictions (figure 3.3) hints that *R. ferrumequinum* may be constrained by habitat discontinuity in Britain, for example between north and south Wales and along the south-east coast of England. The species was distributed as far as Kent in south-east England until around 1900 (Harris, 1995); recolonisation may be prevented by patchiness of suitable habitat along the south coast. Habitat along the south coast is improved in both the climate change and artificial hibernacula simulations (figure 3.5), suggesting that this colonisation may happen in future with increasing winter temperatures and could be aided by the provision of artificial hibernacula. A recently discovered roost in a building in Sussex may hint that this is already underway (BBC News, 2022).

3.6.2 Conclusions

We identify a link between habitat suitability predictions and a measure of habitat use. We demonstrate PAM to be a valuable tool for model validation and we highlight the value of HSMs and predictive modelling for landscape-level spatial conservation planning. Our findings provide novel insight into the nature of acoustic data recorded by PAM that will add to understanding in the burgeoning field of bioacoustic research. Our validation approach is not only relevant for acoustics, but for any remote sensing approach that monitors species activity, and can be applied to many species.

Our HSM has direct application in addressing landscape-level conservation challenges for a species of conservation concern in Britain. We show that *R. ferrumequinum* may experience future range expansion under climate change, identify regions where provision of artificial hibernacula would benefit the species, and highlight areas where the biggest threat is faced from urban expansion. We find that urban densification to be preferable to urban sprawl for *R. ferrumequinum*.

By providing a simple but powerful method for ground validation of HSMs, our approach will increase confidence in HSM predictions and will have practical application for conversation NGOs and local councils undertaking species conservation management.

Chapter 4

A High Resolution Spatial Modelling Framework for Landscape-Level, Strategic Conservation Planning

4.1 Abstract

Habitat loss and fragmentation are among the greatest threats to biodiversity globally. Development is needed to tackle the housing crisis in the UK but poses a threat to many species through habitat loss and fragmentation. There is a legal requirement to ensure that new development does not negatively impact protected species and the habitats they depend on, however planners and local authorities are unable to make informed decisions without a detailed understanding of how species use the landscape. Modern spatial modelling approaches can fill this knowledge gap by providing detailed information on the location of important habitat and an understanding of how it connects.

The aim of this study was to develop a spatial modelling framework for protecting biodiversity in the planning process. Using habitat suitability and

landscape connectivity modelling we aimed to produce high resolution mapping outputs that can inform development and planning decisions. We illustrate our approach with a species of conservation concern, the greater horseshoe bat (*Rhinolophus ferrumequinum*), in Somerset, UK.

We gathered fine scale data on *R. ferrumequinum* habitat use with GPS telemetry, mapped habitat using a high resolution, satellite derived land classification, and built a detailed vegetation map with LIDAR. With these data we built models of habitat suitability and landscape connectivity, validated model predictions with an independent dataset, and generated a number of high resolution maps. We present a detailed case study to explore how different mapping outputs can guide development decisions.

We propose that robust tools such as integrated spatial modelling should be central to the planning process both in local planning departments and at a national level; our framework can act as a template for implementing this.

4.2 Introduction

Development, in the form of new housing and infrastructure, is crucial to improve living standards globally (Shackleton, 2021; Thacker et al., 2019; Thomson et al., 2013). Land use change and increased urbanisation associated with development can, however, negatively impact biodiversity through habitat loss and fragmentation, processes that are among the leading causes of global species declines (Jung and Threlfall, 2016; Haddad et al., 2015; Newbold et al., 2015; Fischer and Lindenmayer, 2007). Habitat loss results in diminution of foraging resources, shelter and mating opportunities; fragmentation and loss of functional landscape connectivity can act similarly by cutting individuals off from these same resources (Fahrig, 2003). Minimising the impact of habitat loss and fragmentation in the planning process should therefore be a high priority (Rookwood, 1995).

There is currently a housing crisis in the UK (Bramley, 2019). To meet housing needs, local authorities in England are legally obliged to facilitate house building by identifying land that can be used for new development (Department for Levelling Up, Housing and Communities, 2023). At the same time local authorities have a legal responsibility to ensure new development does not negatively impact wildlife and delivers biodiversity net gain (DEFRA, 2024; The Conservation of Habitats and Species Regulations, 2017; Wildlife and Countryside Act, 1981). In practice, it can be difficult for planners to know where to allow development to meet these aims. With increasing awareness of the importance of landscape-scale approaches to conservation in England, there is growing recognition of the need to adopt a strategic overview in planning processes to meet conservation objectives (Natural England, 2022b).

Systematic conservation planning (Margules and Pressey, 2000) offers a potential solution to meet the conflicting challenges of providing housing and protecting wildlife. Although much of the literature in this field is framed with design of protected areas in mind (Watson et al., 2011), many of the same principals can be built into the planning process: applying the mitigation hierarchy, avoiding development in key areas and offsetting the impact when avoidance is not possible (Barbé and Frascaria-Lacoste, 2021; Phalan et al., 2018; Coralie et al., 2015; Kiesecker et al., 2010). Offsetting can be achieved by making enhancements in strategic areas where restoration will have the biggest conservation impact (Kujala et al., 2015).

Some species' life histories bring them into conflict with humans more frequently than others (Soulsbury and White, 2015). Bats are one such group

(Voigt and Kingston, 2016) as they are often found in human-dominated landscapes and frequently come into conflict with humans during the planning process (Cohen, 2011). In the UK all bats and their roosts are protected by law (The Conservation of Habitats and Species Regulations, 2017; Wildlife and Countryside Act, 1981) and special areas of conservation (SACs) have been established to protect bat species listed on annex II of the European Council Directive 92/43/EEC (Conservation of Natural Habitats and Wild Fauna and Flora, 1992). It is a legal obligation for developments to consider their potential impact on nearby SACs; when an SAC has been established for a highly mobile species such as bats this effectively offers protection to large areas of habitat surrounding the SAC. Implementing this protection is challenging, however, without a detailed understanding of how species use the landscape. A robust, landscape-level, strategic approach is needed to enable local authorities to effectively protect wildlife and comply with legal obligations for protecting biodiversity.

4.3 Aims

The aim of the study was to develop an integrated framework to map and model landscape use of protected species. Illustrating our approach with the greater horseshoe bat (*Rhinolophus ferrumequinum*) in Somerset, UK, we aimed to develop a robust framework for informing development and planning decisions. We broke this down into four tasks:

- gather fine scale data on the study species' habitat use;
- identify habitat preferences and map important habitat using habitat suitability models;

- predict landscape movement using connectivity modelling;
- develop novel habitat and connectivity indices that aid interpretation of habitat suitability and connectivity predictions for planners.

4.4 Methods

All statistical analysis and data processing was conducted in R (R Core Team, 2022) and all spatial data manipulation was completed using the *terra* package (Hijmans, 2022), except where otherwise noted.

4.4.1 Study Area

Research was completed in North Somerset, Bath and North East Somerset, and the former Mendip and Sedgemoor Districts (figure 4.1). This area contains three SACs designated for *R. ferrumequinum* (JNCC, 2015a,b,c) which together contain approximately 20% of the British population (Mathews, 2018), and cannot be considered in isolation due to movement of bats between roosts (Ransome, 1980). A 10 km buffer around the study area was included to avoid edge effects during connectivity modelling.

The study area has a wet and mild marine climate (Köppen classification *Cfb*). The diverse topography of the area encompasses the coastal plains of the Somerset levels and the limestone uplands of the Mendip hills. The dominant land cover classes in the study area are grassland (both semi-natural and improved; 52.8%), arable farmland (19.7%), built-up areas and gardens (15%), and broadleaf woodland (8.7%; Marston et al. 2022a).

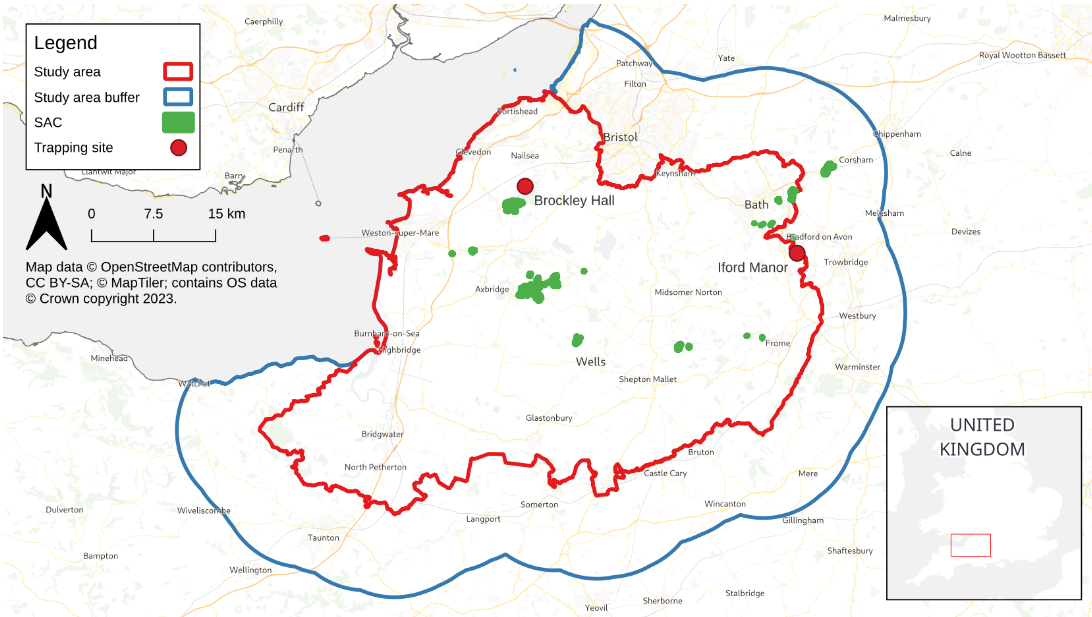


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Figure 4.1: Study area in South West England.

4.4.2 Habitat Suitability Models

We built habitat suitability models with MaxEnt (Phillips et al., 2006). We chose appropriate environmental variables based on a literature review of *R. ferrumequinum* ecology (table 4.1, figure 4.2*i*). We obtained high resolution (10 m) land cover data from Marston et al. (2022a) and included the four most prominent land cover classes in the study area: arable farmland, broadleaf woodland, grassland (including both improved and semi-natural) and built-up areas and gardens, all coded in a binary format (0/1). We generated vegetation maps with LIDAR point cloud data from the National LIDAR Programme (Environment Agency, 2022), using all point cloud data labelled as vegetation to build a digital surface model with the *lidR* package (Roussel and Auty, 2023; Roussel et al., 2020) and from this calculating the mean height of vegetation at a 10 m resolution. We also generated a 'distance to vegetation' layer in QGIS (QGIS.org, 2023) by calculating Euclidean distance to vegetation for every 10 m grid square. Normalised difference vegetation index (NDVI) was calculated for all available LandSat 8 imagery captured between July and September in the last 5 years (imagery from 18th September 2019, 21st July 2021, 07th September 2021, 16th July 2022, 18th August 2022; excludes available images with partial cloud cover). To estimate accurately the relationship between habitat use and NDVI, during model building we matched individual GPS fixes with the NDVI image captured closest in time to the GPS fix. Then for predictive mapping we calculated mean late summer NDVI using all imagery. NDVI was only available at an approximately 30 m resolution and so was disaggregated to a 10 m resolution by bilinear interpolation. Street light location data were obtained from local councils and Highways England (table 4.1) and used to make a 'distance to street lighting' layer in QGIS by calculating Euclidean distance to street lights for every 10 m grid square, up to a maximum of 100 m, as the effect of street lighting on bat activity is likely to be restricted to the immediate vicinity of the light source (Pauwels et al., 2021; Azam et al., 2018). We checked all environmental rasters for multicollinearity with the *usdm* package (Naimi et al., 2014) prior to model fitting, ensuring rasters did not exceed a variance inflation factor of 5.

We used GPS telemetry data gathered from *R. ferrumequinum* in Somerset as species occurrence records (for detailed methodology see appendix B). We categorised each GPS fix as either foraging, roosting or commuting behaviour by identifying clusters of fixes with the approach proposed by Birant and Kut (2007). Clusters were defined as two or more fixes that occurred within 1 km and 30 minutes of each other. Fixes in clusters were categorised as foraging behaviour, excluding clusters that were located in buildings (identified using satellite imagery), which we categorised as roosting behaviour. *R. fer-*

Table 4.1: Environmental variables included in habitat suitability models.

Variable	**Source**
Arable/horticulture (binary 0/1)	Marston et al. 2022a
Broadleaf woodland, minimum 5ha (binary 0/1)	Marston et al. 2022a
Built-up areas and gardens (binary 0/1)	Marston et al. 2022a
Euclidean distance to street lights, up to 100 m maximum (m)	North Somerset Council, Somerset Council, Bath and north-east Somerset Council, Highways England, Bristol City Council
Euclidean distance to vegetation (m)	National LIDAR Programme, Environment Agency
Grassland (semi-natural and improved; binary 0/1)	Marston et al. 2022a
Mean height of vegetation (m)	National LIDAR Programme, Environment Agency
NDVI	Landsat 8

rumequinum are able to fly 21-25 km per night (Ransome, 2020), so staying in a relatively small area for a long period is indicative of foraging or roosting (figure 4.2*ii*). Remaining fixes were categorised as commuting behaviour. We thinned occurrence data to one record per grid square prior to modelling. We modelled foraging habitat and commuting habitat separately (figure 4.2*iii*) in two HSMs, one built with foraging fixes (henceforth ′foraging HSM′) and one built with commuting fixes (henceforth ′commuting HSM′). The same environmental variables were used in both the foraging HSM and the commuting HSM.

GPS data came from two roosts; for model building we only used GPS data from bats tagged at Brockley Hall, withholding data from Iford Manor for later validation. We generated 10,000 background points within 13 km of Brockley Hall (the maximum distance a bat was recorded from the roost, i.e. the area available to the bats) to ensure background points had the same bias as the occurrence data (Phillips et al., 2009). We used ENMEval (Muscarella et al., 2014) with 5-fold cross-validation to identify the optimal regularisation multiplier and feature classes for MaxEnt. We then built a full MaxEnt model to predict habitat suitability over the whole study area (figure 4.2*iii*).

We calculated model sensitivity according to Bellamy et al. (2020), testing whether there were more occurrence data in suitable habitat, defined as a habitat suitability index above the maximum test sensitivity and specificity (MTSS) threshold (Liu et al., 2005), than would be expected by chance. We validated HSMs using data from bats tagged at Iford Manor, comparing the habitat suitability index at GPS fixes (either foraging or commuting fixes, respective of model; used) with predicted habitat suitability at an equal number of randomly generated fixes within 10 km of the roost (the maximum distance a bat was recorded from the roost at Iford; available). In a valid model we would expect to see higher habitat suitability scores at GPS fixes than at random points, as bats should use suitable habitat more frequently than in proportion to its availability. For this comparison we fitted a binomial generalised linear mixed-model with the *lme4* package (Bates et al., 2015), with bat ID as a random factor to avoid pseudoreplication from repeated sampling of the same bats.

4.4.3 Connectivity

We used Circuitscape (McRae, 2006; McRae et al., 2008) to model connectivity between known *R. ferrumequinum* roosts and the surrounding habitat, taking an approach similar to McRae et al. 2016 (see also Landau, 2020). This analysis was conducted in the Julia programming language (Anantharaman et al., 2019).

Circuitscape uses circuit theory, borrowed from electrical modelling, to simulate the movement of wildlife across a landscape. A current, representing the movement of wildlife, is allowed to pass over a circuit board, representing the landscape. The resulting current flow is then taken to represent commuting routes the study species is likely to take. The components of the connectivity analysis include 1) a resistance surface: a map of the landscape that defines cost of movement, with higher resistance values indicating higher cost of movement; 2) a source: the location the study species is coming from; 3) a ground point: the destination that the study species is travelling to. For the resistance surface we used the inverse of the commuting HSM, meaning areas of high commuting habitat suitability had low resistance (i.e. had a lower cost of movement) and areas of low commuting habitat suitability had high resistance (i.e. had a higher cost of movement). To create a realistic model of bat movement in the landscape we used predicted foraging habitat suitability to define source values and known roosts as ground points (explained in more detail below). We obtained roost records from the Bat Conservation Trust's National Bat Monitoring Programme (both summer and winter monitoring), Bristol Regional Environmental Records Centre, Somerset Environmental Records Centre and L. Burrows (unpublished). Roosts with a spatial accuracy lower than 10 m were removed.

The analysis started by focusing on a known roost. The resistance surface was trimmed to a buffer around the roost. The size of the buffer was determined by fitting a polynomial linear model to estimate the relationship between the number of bats using the roost and the maximum distance travelled from the roost, using data from the GPS study and historical radio tracking studies (Billington, 2001; Jones and Billington, 1999). This was based on the observation that bats at large roosts need to travel further to access foraging grounds, likely because territories close to the roost fill up (similar conceptually to the 'halo of depletion' observed in colonial seabirds; Weber et al., 2021). Buffer sizes varied from 12 km for high count roosts (650 bats) to 7 km for low count roosts (one bat). The roost was then set as the ground point and the source value of the roost (defined as the most recent bat count at the roost) was split among all surrounding cells in the buffer in proportion to habitat quality, as estimated by the foraging habitat suitability model. This meant higher quality foraging habitat was assigned more current than lower quality foraging habitat. This was repeated for every roost and the outputs were summed to produce a map of cumulative current flow across the study site (figure 4.2*iv*).

We also produced a normalised version of the connectivity map following McRae et al. (2016). First we produced a null model connectivity map using the same source values as the first connectivity map but with every resistance value set to zero, i.e. as if there were no barriers to movement. We then divided the cumulative current flow map by the null model to produce a normalised map. The normalised connectivity map highlights areas where barriers are channelling current flow and areas where current flow is impeded, irrespective of total current flow (figure 4.2*v*).

We validated the connectivity model by comparing normalised connectivity values at used versus available locations with commuting fixes of Iford bats, taking the same approach used to validate the HSMs (section 4.4.2). In a valid model we would expect to find higher connectivity values at GPS fixes than at random points, as bats would be more likely to use areas where current is channelled and less likely to use areas where current flow is impeded.

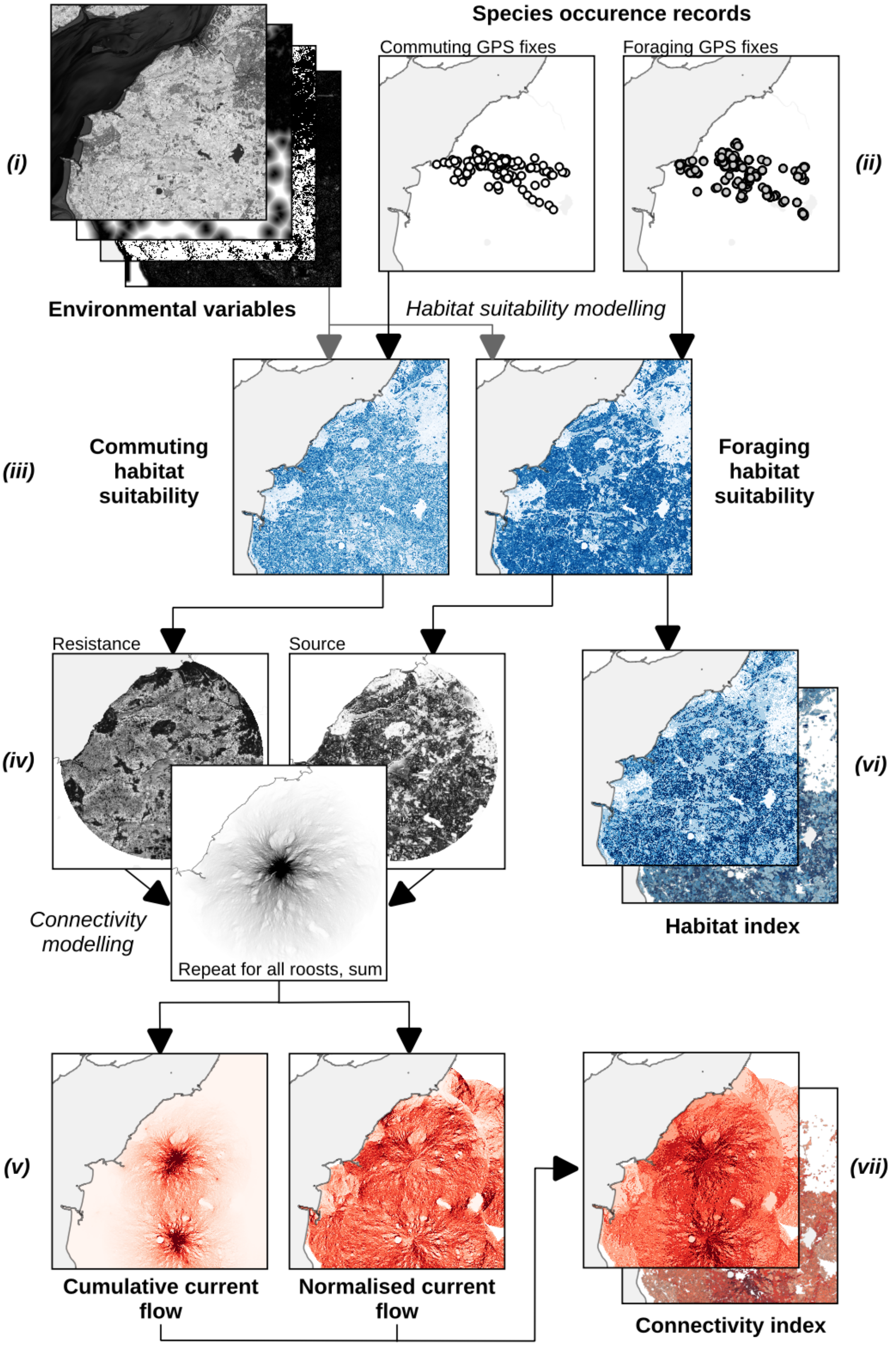


Figure 4.2: Graphical representation of the modelling framework.

4.4.4 Indices

We propose a habitat index and a connectivity index that summarise the results of the habitat suitability and connectivity modelling, respectively. The aim is to simplify the continuous predictions of the habitat suitability and connectivity models to aid interpretation and facilitate comparison of different locations in the landscape. To create the habitat index, we split the HSM into tertiles based on habitat suitability values at GPS fixes (i.e. split the HSM into three categories, high, medium and low, based on observed usage patterns in tagged bats; figure 4.2*vi*). To derive the connectivity index, we split the cumulative connectivity map into tertiles using the same approach used to derive the habitat index. We split the normalised connectivity map into quartiles, grouping the middle two quartiles to result in three categories. We then summed the categorised connectivity and normalised connectivity maps (figure 4.2*vii*).

To further aid interpretation, we summarised the habitat index and connectivity index by land parcels. The land parcel is the unit of currency in the planning process as land parcels are usually bought, sold and developed as a whole; each land parcel can be considered a potential development site. We obtained OS MasterMap land parcel polygons from Marston et al. (2022b) and removed land parcels identified as woodland, inland water or built-up areas and gardens. We then calculated the modal average of both the habitat index and the connectivity index in each land parcel (figure 4.2*vi* and 4.2*vii*).

4.4.5 Nailsea and Backwell Case Study

To explore the utility of mapping outputs and to examine how maps can be used, we looked in detail at a number of proposed development sites in the

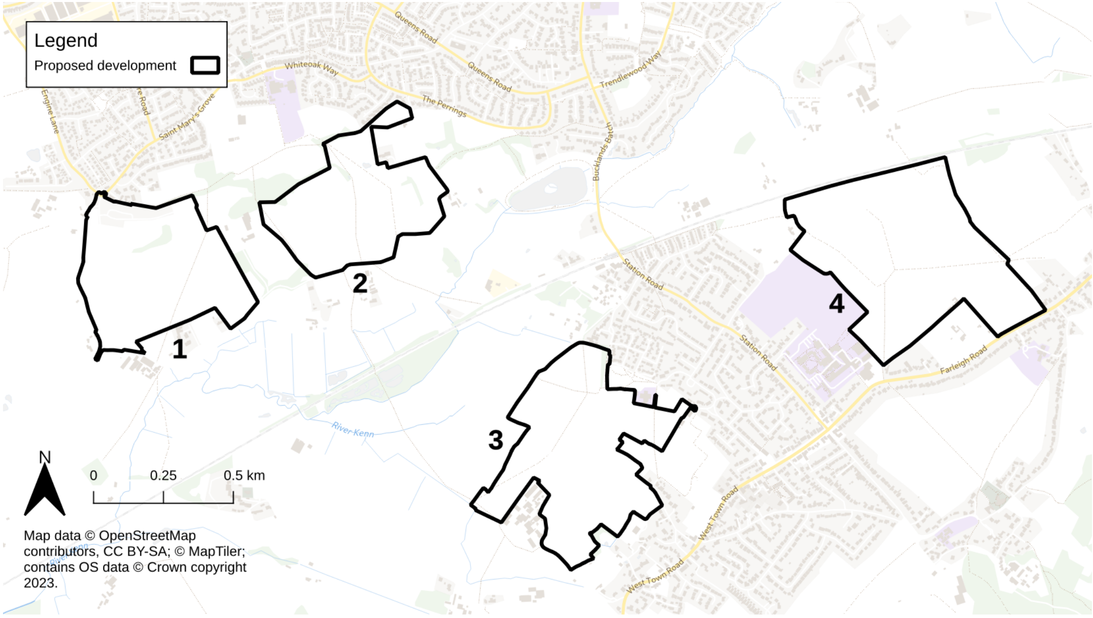


Figure 4.3: Case study sites between Nailsea and Backwell.

county of North Somerset. We plotted mapping outputs at each development site to assess the sites importance for and impact on *R. ferrumequinum*, and to consider potential habitat enhancements or mitigation strategies. This process was used to assess if maps were useful for applied planning and management, as such the results of this section are more qualitative than quantitative. We used this process to refine our methodology and maximise the utility of mapping outputs.

Shapefiles of proposed housing development sites were obtained from North Somerset Council. We selected four sites around the towns of Nailsea and Backwell as there is a concentration of proposed development in this area and the proximity to the Brockley Hall bat roost means development could have a significant impact on bats roosting and with foraging within the SAC (figure 4.3).

Table 4.2: Habitat suitability model tuning parameters and validation results. 'FC' = optimal feature classes identified by ENMeval, 'RM' = optimal regularisation multiplier identified by ENMeval, 'AUC ind.' = independent AUC, 'AUC n.ind.' = non-independent AUC, 'Sensitivity' = model sensitivity measured as the proportion of training data that fall within suitable habitat, defined with MTSS threshold (see section 4.4.2), 'Validation' = p-value of validation with independent dataset (see section 4.4.2).

Model	**FC**	**RM**	**AUC ind.**	**AUC n.ind.**	**Sensitivity**	**Validation**
Foraging HSM	LQHP	2.5	0.71	0.73	0.83	<0.001
Commuting HSM	LQ	0.5	0.73	0.75	0.86	0.0182

4.5 Results

Detailed results of GPS telemetry are presented in appendix B.

4.5.1 Habitat Suitability Models

Habitat suitability model tuning parameters and validation results are shown in table 4.2. Both models received strong support from validation with the independent (Iford) dataset.

Foraging Habitat Suitability

Variables that had the greatest influence on foraging habitat suitability included distance to street lighting, NDVI, grassland cover, height of and distance to vegetation (table 4.3, figure 4.4). This is visible in map predictions: there is a halo of low habitat suitability around street lights, grassland is predicted to have much higher habitat suitability than arable fields and urban areas, roads and railways stand out as areas of low suitability, and vegetated field boundaries show as high suitability (figure 4.5a).

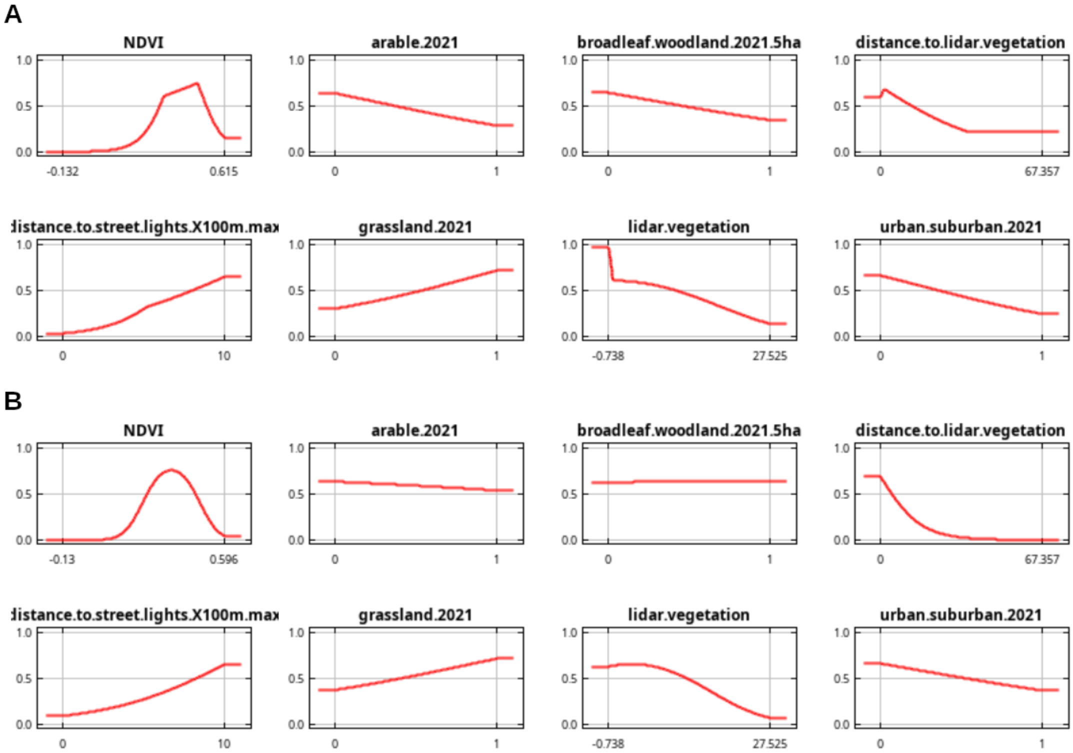


Figure 4.4: MaxEnt response curves for models containing only the variable of interest, from (a) foraging and (b) commuting habitat suitability models. The variable 'lidar.vegetation' refers to mean height of vegetation (m), as measured by LIDAR.

Commuting Habitat Suitability

The same variables were found to influence commuting habitat, although the relative impact of variables differed (table 4.3, figure 4.4). Distance to vegetation had a higher percentage contribution compared to the foraging model, and resulted in a higher drop in gain when removed in the jackknife test. Grassland had higher permutation importance compared to the foraging model, but comparatively lower gain in the jackknife test when it was the only variable.

The relative contribution of variables is clearest in model predictions. Distance to vegetation clearly had a large influence on commuting habitat predictions as vegetated field boundaries are predicted to be highly suitable, and

Table 4.3: Measures of predictor variable performance identified by MaxEnt in habitat suitability models. For details of how each is calculated see Phillips (2017). 'F.' = foraging HSM, 'C.' = commuting HSM, '% ct.' = percentage contribution, 'pm. imp.' = permutation importance, '% gain w/o' = jackknife test training gain without variable, '% gain only' = jackknife test training gain with only variable. Jackknife test gain is given as a percentage of the full model.

Predictor	**F. % ct.**	**F. pm. imp**	**F. % gain w/o**	**F. % gain w/ only**	**C. % ct.**	**C. pm. imp**	**C. % gain w/o**	**C. % gain w/ only**
Arable farmland (0/1)	0.4	0.8	99.5	6.3	1.8	4.5	93.8	0.4
Broadleaf woodland (0/1)	2.5	9.2	94.7	7.9	4.3	5.8	89.9	0
Built-up areas and gardens (0/1)	4.8	0.8	99.8	28.6	1.7	7.7	95	10
Distance to vegetation (m)	3.5	18.3	94.4	2.3	24.9	17.3	83.1	8.5
Distance to street lights (m)	33.2	13.6	93.7	32.7	13.6	10.9	89.4	18.7
Grassland (0/1)	25.6	4.4	98.4	53.1	28	39.1	78.3	24.2
Mean height of vegetation (m)	0.7	19.1	99.1	5.6	1.9	1.4	98.4	2.8
NDVI	29.3	33.8	76.5	58.9	23.8	13.2	69.9	39.3

centres of fields are less suitable than in the foraging model. This is especially apparent in large fields (figure 4.5b). The influence of land cover variables (grassland, arable, built-up areas and gardens, broadleaf woodland) and NDVI are less visible than in the foraging model.

4.5.2 Connectivity models

Normalised connectivity was significantly higher at GPS fixes in the Iford dataset than at random fixes (p<0.001), providing strong independent validation of model predictions. The cumulative current flow map shows total predicted movement of bats in the landscape (figure 4.5c); this is dominated by the main maternity and hibernation roosts, as they have the highest num-

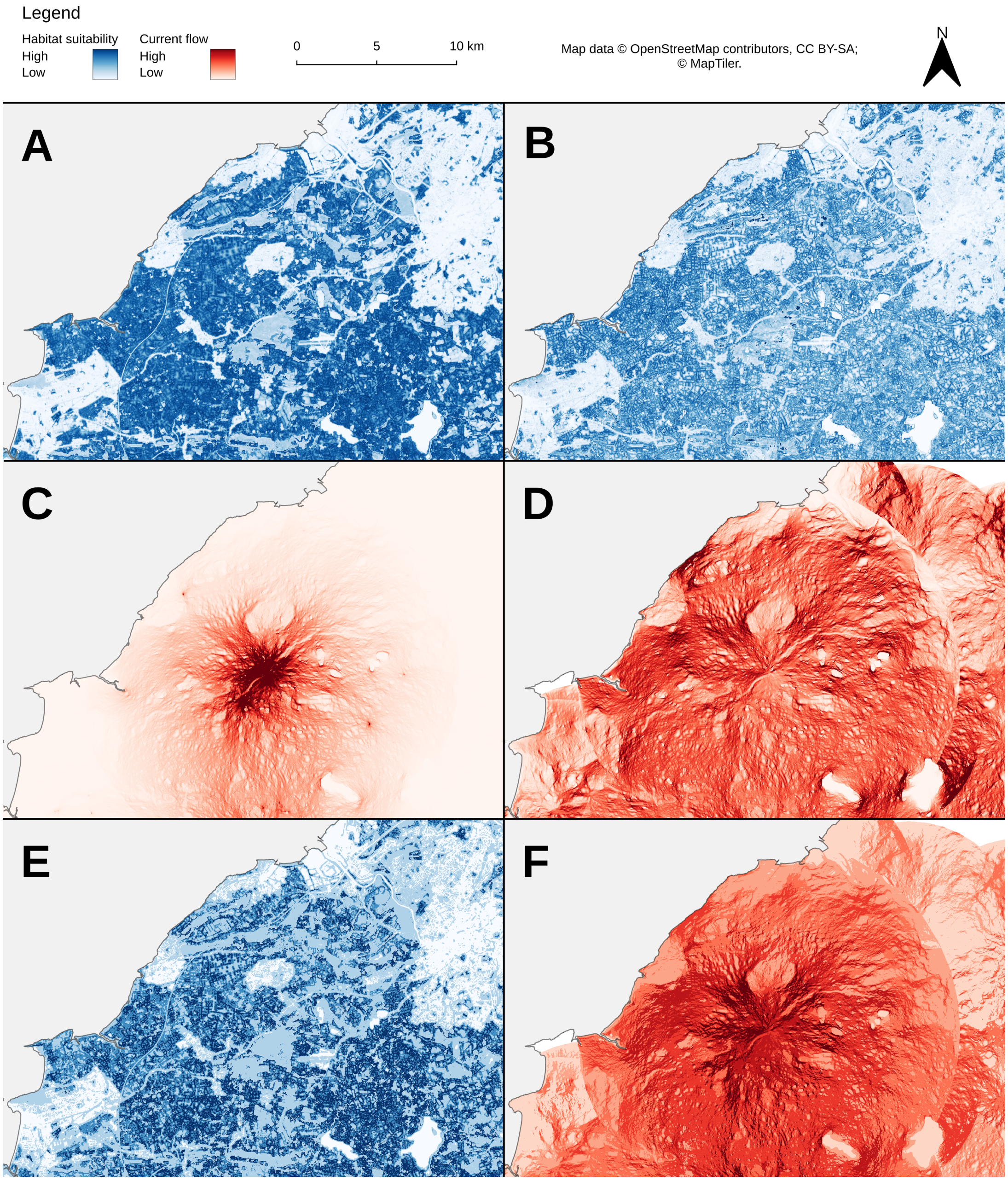


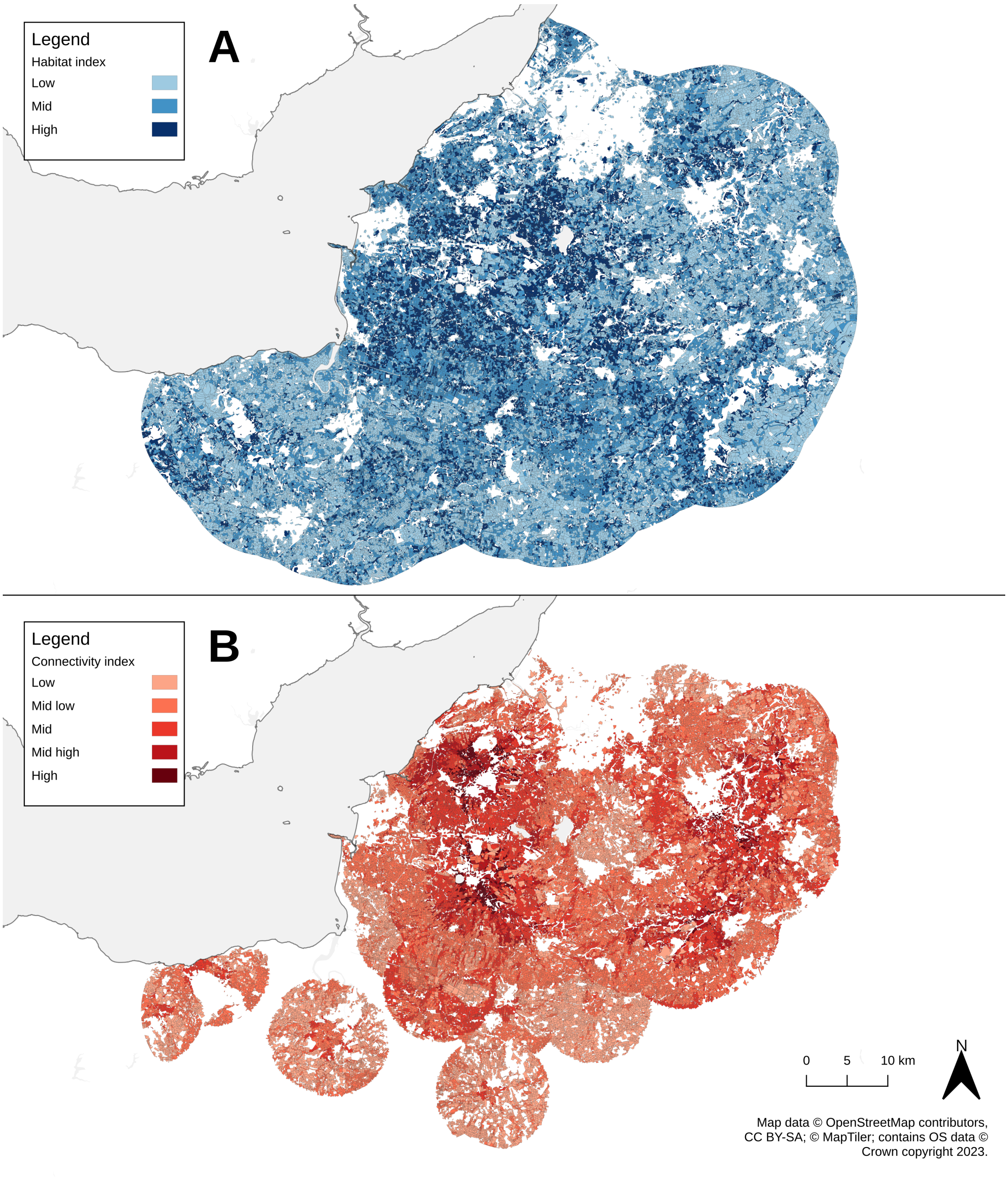
Figure 4.5: Habitat suitability, landscape connectivity and indices for *R. ferrumequinum* at a 10 m resolution. Predicted foraging (a) and commuting (b) habitat suitability; cumulative (c) and normalised (d) current flow from connectivity analysis; habitat (e) and connectivity index (f). Cumulative current flow represents the movement of all bats in the landscape, while the normalised map highlights areas where current is concentrated or obstructed, irrespective of total current flow.

bers of bats. The normalised map, meanwhile, highlights pinch points and barriers to connectivity irrespective of the total number of bats predicted to use that area (figure 4.5d).

The connectivity maps mirror the predictions of the underlying commuting habitat suitability model. Current tends to be channelled along vegetated field boundaries, while the middle of large fields that are far from vegetation are avoided. Current is channelled around edges of towns, lakes and large areas lacking tall vegetation such as heathland, as these represent barriers to movement. Similarly, roads with street lights show reduced current flow and in places disrupt landscape connectivity.

4.5.3 Indices

The habitat and connectivity index simplify the habitat suitability and connectivity maps to aid interpretation (figures 4.5e, 4.5f and 4.6). As with the foraging habitat suitability model, the habitat index identifies small pastures with well-developed hedgerow networks as having high suitability, while arable fields have lower suitability. The habitat index also makes clear the large scale trends (figure 4.6): the highest concentration of good habitat lies in the north-west of the study area, in approximately the area between Nailsea, Burnham-on-Sea, Glastonbury and Midsomer Norton. To the east of this, the habitat around the large maternity roost at Iford Manor is predicted to be lower suitability. Reference to the raw habitat suitability predictions around Iford reveals that there is a lot of good habitat woven into a mix of less suitable habitat, due in part to higher proportion of arable fields in this region, which is obscured somewhat when categorised.



Map data © OpenStreetMap contributors, CC BY-SA; © MapTiler; contains OS data © Crown copyright 2023.

Figure 4.6: Habitat index (a) and connectivity index (b), summarised by land parcels.

The large maternity roosts stand out in the connectivity index, although less so than the raw cumulative connectivity map. The connectivity index highlights features that are important for connectivity away from large roosts, while still placing high importance on immediate roost surroundings. Thus, areas of concentrated current flow close to large roosts are ranked highest, then diffuse flow close to large roosts and concentrated current flow at mid-distance. The further from a large roost the lower the ranking; areas of less concentrated current and at greater distances to large roosts are ranked the lowest. As in the raw connectivity map, the highest current flow is visible along vegetated field boundaries. When summarised by land parcel, this results in fields with well-developed vegetated boundaries near to large roosts and on the edge of barriers being highlighted.

4.5.4 Nailsea and Backwell Case Study

High resolution mapping means that habitat suitability and connectivity maps (figures 4.7a and 4.7b, respectively) highlight features such as hedgerows and individual fields that are high quality habitat or important for connectivity. Street lights are visible in the HSM (figure 4.7a), individual hedgerows are visible in the connectivity map (figure 4.7b).

The habitat suitability map (figure 4.7a) shows that all proposed developments contain areas of good habitat, although site four possibly less than the others. Comparison between sites is made clearer in the habitat index (figure 4.7c). It is apparent from the connectivity map (figure 4.7b) that site three is important for connectivity; the Brockley Hall roost (of approximately 650 bats) is just off the map to the south of site three, so this was to be expected. The connectivity index (figure 4.7d) highlights linear features along the south-western portion of site one as being important for connectivity; connectivity here could be retained or redirected around the perimeter of the site as part of on-site mitigation, perhaps with vegetated a dark corridor.

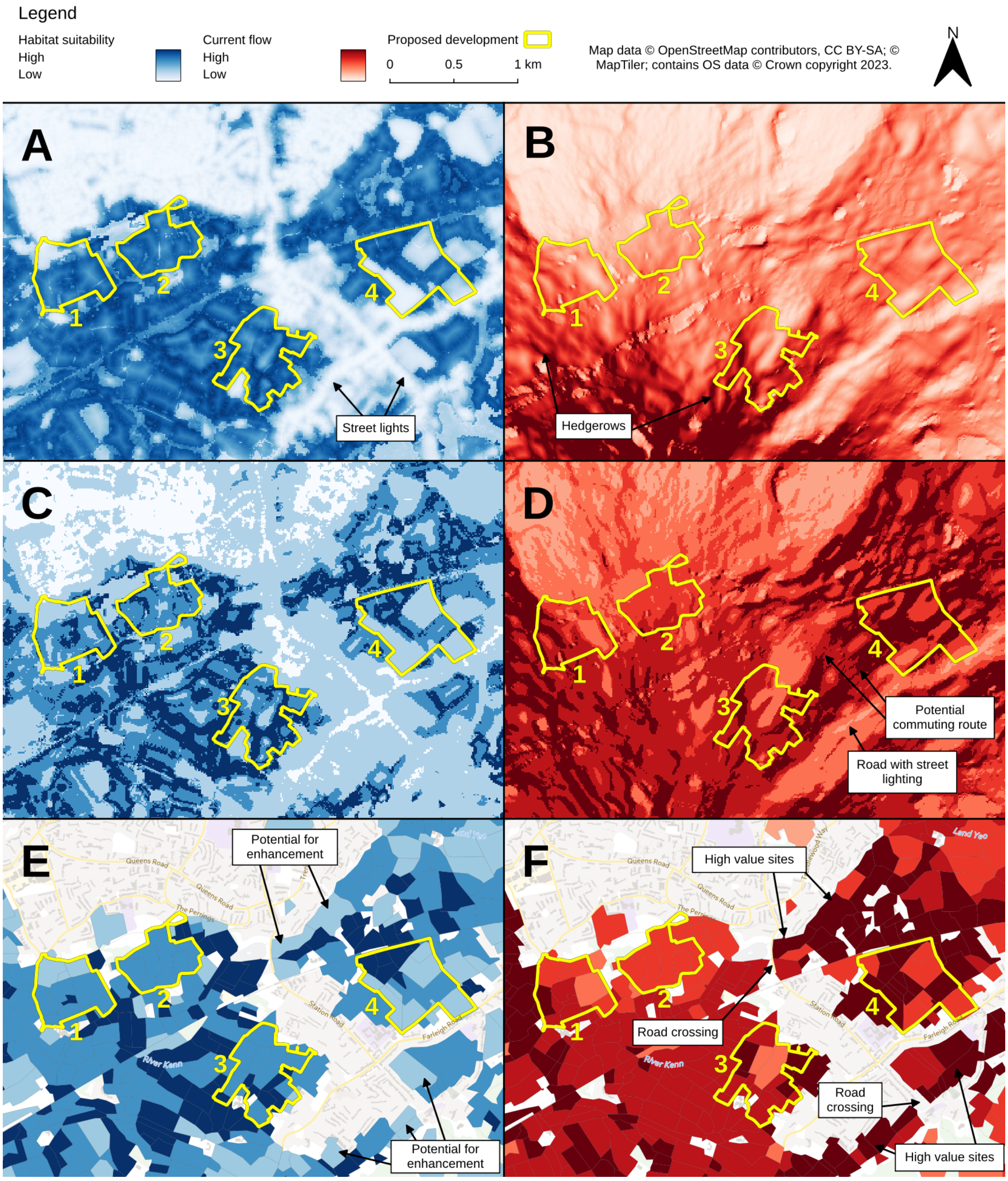


Figure 4.7: Case study of mapping outputs showing proposed development sites around Nailsea and Backwell. Predicted foraging habitat suitability (a); cumulative current flow (b); habitat (c) and connectivity index (d); habitat (e) and connectivity index (f) summarised by land parcels. Points of consideration highlighted.

The connectivity index (figure 4.7d) highlights a potential crossing route through Backwell between sites three and four. This is a residential area of leafy gardens with no street lighting that might not have been highlighted as an obvious commuting route without modelling; having been identified, this area can be targeted for on-site surveys. The proposed developments of site three and four in combination could sever this potential commuting route as bats are hemmed in by a road with street lighting to the south. Careful consideration would need to be given to avoid impacting landscape connectivity here.

The connectivity index (figure 4.7f) shows that there are sites that would be valuable for off-site mitigation to the north and south of Backwell, as there is channelled connectivity here. Protecting these areas and improving habitat would strengthen landscape connectivity. At both these points bats need to cross a road, so habitat enhancements might include a green bridge or an underpass (Ramalho and Aguiar, 2020; Davies, 2019). Reducing lighting in these areas would also be of benefit; street lights are evident at both these locations in the HSM (figure 4.7a). The habitat index (figure 4.7e) shows that there are low suitability fields in both these areas, meaning habitat enhancements could have a large impact and deliver good value for money.

Of all these developments site two is possibly the most favourable, as although it contains good habitat it will have limited impact on landscape connectivity and there are many opportunities nearby for off-site mitigation that would strengthen connectivity.

4.6 Discussion

We have developed a framework to generate a number of mapping outputs that can inform development decision-making. The maps generated by our approach can be used when considering a planning application or the potential of a development site at the pre-application stage. Equally, our maps can be used in designing mitigation and for biodiversity net gain; high resolution enables users to pick out individual fields and hedgerows of value. Additionally, modelling results provide insight into the factors affecting habitat suitability and their relative importance, which can guide habitat enhancement strategies.

We have illustrated the utility of the different maps in the case study (section 4.5.4), both for gauging impact, planning habitat enhancements and designing mitigation. Different maps have their own strengths and limitations. While the cumulative connectivity map provides a realistic estimate of landscape use, the map is dominated by large roosts making it hard to identify landscape features that are valuable for connectivity away from big roosts. Individual landscape features can be better discerned in the normalised connectivity map, however this is not representative of actual predicted site usage (a commuting route used by one bat gets same weighting as a route used by 100); the connectivity index combines the best of both. Habitat suitability and connectivity maps provide continuous predictions in great detail, but this can make it difficult to compare different locations or sites. Categorising predictions into indices aids interpretation and makes it easier to compare sites, summarising by land parcel further still, but at the expense of detail. Used in combination, however, our maps can be a valuable tool for guiding development decisions and planning conservation measures.

Our findings corroborate many aspects of *R. ferrumequinum* ecology that are documented in the literature, but our novel approach provides a powerful application of this knowledge through spatial visualisation. We found grassland cover, distance to street lighting, NDVI, height of and distance to vegetation to be important predictors of foraging habitat suitability. Habitat enhancements could thus involve creation of permanent pasture, allowing vegetated field boundaries to grow tall and planting more field boundary trees (Foxley et al., 2023; Ransome, 1996, 1997).

We found that while *R. ferrumequinum* foraging habitat would benefit from reduced street lighting (Stone et al., 2015), in our study area the actual area of foraging habitat affected by lighting is very small relative to the total available foraging habitat. Street lighting may, however, act as an insect sink, reducing quality of foraging habitat over a larger area than our model predicts (Tielens et al., 2021; Desouhant et al., 2019; Macgregor et al., 2015). We found street lighting to negatively impact commuting habitat, with knock-on effects for landscape connectivity. Our work further highlights the need for careful design of street lighting strategies to avoid impacting landscape connectivity for photosensitive species (Laforge et al., 2019; Zeale et al., 2018; Stone et al., 2009).

We found that the same habitat enhancements aimed at improving foraging habitat would also improve connectivity, but more emphasis would need to be given to improving vegetated field boundaries for connectivity, as our findings suggest land cover is less important for commuting than for foraging. Dividing large fields into smaller compartments by creation of new hedgerows would improve commuting habitat (Foxley et al., 2023; Finch et al., 2020b).

4.6.1 Future Work and Limitations

Our approach could be further developed by altering the basemap (e.g. simulating the conversion of grassland to housing) to model different development scenarios, looking at the effect on landscape connectivity. Similarly, it could be used for testing mitigation designs, for example by testing if current flow can be diffused by improving habitat adjacent to a proposed development, or modelling how planned habitat improvements influence landscape connectivity.

It is worth highlighting that habitat suitability is not static, but changes seasonally (Franklin, 2010; Zurell et al., 2009), and species' habitat use will reflect this. The importance of woodland for *R. ferrumequinum*, particularly in the spring, is documented extensively in the literature (e.g. Flanders and Jones, 2009; Duverge, 1996; Jones et al., 1995). All our field work was carried out in late summer when bats are more likely to forage in open habitats, meaning the overall importance of woodland was likely under-estimated, reflecting this seasonal bias. To add to this, we suspect that GPS data were under-represented in woodland due to difficulty of obtaining a GPS fix under dense canopy (Jiang et al., 2008; Moen et al., 1996). Models would be improved by accounting for seasonal changes in environmental variables and habitat use (Smeraldo et al., 2018).

Being able to change maps is important as models should be considered to be dynamic (Pressey et al., 2007) and should be updated when more data has been gathered (e.g. new roosts discovered) or when the landscape is altered (e.g. with a new development). We are working with local authorities in our study area to enable this.

Note that the approach presented here was designed for a communally roosting bat species with well-documented roosts. A lack of information on roost locations would be an impediment to modelling and a different approach might be needed for a species with more dispersed roosting habits (e.g. Omniscape; Landau, 2020).

At present, the lightest GPS tags available weigh around 1 g, which restricts their use to bat species >20 g (Aldridge and Brigham, 1988). This is an obvious limitation; a different approach to gather data on habitat use would be needed for smaller species. Radio tracking is not a viable option at such high resolution as it lacks accuracy. Acoustic monitoring is a good option but would require a careful sampling design.

Finally, it is important to note that the habitat index and the connectivity index are not intended to replace field surveys. Our mapping does not necessarily take into account the many additional factors on the ground, such as habitat management (e.g. pesticide use), that may affect habitat suitability (Ransome, 1996).

4.6.2 Conclusions

Our novel approach provides an evidence-based tool to be used by local authorities, ecological consultants, planners and conservationists, helping them reverse species declines and achieve legal requirements for biodiversity net gain. While the present study focused on bats in an SAC, with small modifications to account for differences in species' life history, our modelling framework could be used to inform strategic conservation planning for many protected species.

We propose that our modelling framework should be used as part of an evidenced-based, applied approach to protecting wildlife in the planning system, and that integrated spatial modelling should be central to the planning process at both national and local levels. Habitat loss and fragmentation are among the greatest threats to biodiversity; an integrated approach that informs intelligent, considerate planning with targeted mitigation could alleviate a lot of pressure on wildlife populations.

Chapter 5

General Discussion

Spatial modelling is a valuable tool for applied conservation. Spatial modelling helps to better understand species-environment relationships (Fortin et al., 2012) and can be used to make spatially explicit predictions of species' landscape use to support informed conservation decision-making (Zurell et al., 2022). In this thesis I explored a number of different spatial modelling techniques and their use in applied conservation.

In chapter one I identified the drivers of *R. ferrumequinum* activity in an agricultural landscape. I found low activity over arable farmland and high activity along vegetated field boundaries with lots of trees. The acoustic approach I used enabled the study to extend to species other than just *R. ferrumequinum*. I identified a strong spatial component driving bat activity in all species, which in *R. ferrumequinum* was partially explained by distance to the roost. The study was centred around the large *R. ferrumequinum* maternity roost at Brockley Hall SSSI, so it should be expected that this would have a strong impact on activity levels, nevertheless, this is an interesting insight into the nature of acoustic data. I expanded on this theme in chapter three, where I identified that a broad scale habitat suitability trend can be picked out in acoustic data. This is particularly interesting because the main finding of chapter one was that fine scale characteristics of field boundaries were better descriptors of acoustic activity than the characteristics of the adjacent fields or the local landscape. Together, these findings help to better understand the information contained within acoustic data and thus its potential applications.

The above insights tell us that the predicted activity maps in chapter one contain information both on bat movement in the landscape and habitat use. This type of mapping clearly has value for local planning and habitat management around important roost sites as it gives the user an idea of the importance of different sites for the study species, at a very high resolution. The model could also be used to simulate the effect of a change in land use or farming practice, for example. The main challenge involved in mapping predicted activity is that acoustic activity is liable to change over the year and over the course of years, making it difficult to make accurate predictions. Data from a longer study period would provide extra information for more robust predictive modelling. Sadly, it was not feasible to extend my survey period in the time-frame of my PhD, and it would have been incredibly labour-intensive to do so using the same methodology.

The key takeaway from chapter one surely must be to avoid building close to big roosts: predicted activity maps (figure 2.10) for *R. ferrumequinum* show the highest activity up to 3 km from the roost. This is clearly an important area, and development should be avoided here.

The value of acoustic approaches is further demonstrated in chapter three, where I used passive acoustic monitoring for validation of a broad scale habitat suitability model (HSM). HSMs are widely used in conservation (Guisan et al., 2013). By providing a simple approach for HSM validation, this work will increase confidence in HSM predictions and have great value in conservation management. Interestingly, this approach worked well despite the potential mismatch in scale: acoustic activity is inherently measured at a fine scale (most bat calls will not be detected at distance >40 m; Adams et al. 2012), while the model being validated was broad scale, both in grain and extent.

The broad scale models used in chapter three have a different kind of value to fine scale predictions from chapters one and four, and can be used to address different issues. The HSM identified factors affecting *R. ferrumequinum* distribution, finding climatic variables and availability of caves to be important predictors at this scale. I used this model to identify landscape-level conservation priorities and to suggest approaches to mitigation. The climate change simulation predicted a future range expansion for *R. ferrumequinum*, which is valuable information that enables forward planning (Cook et al., 2014; Pressey et al., 2007). The development simulation identified areas where development would have a negative impact and how this could potentially hinder colonisation of new areas. Additionally, the artificial hibernacula simulation identified areas where provision of hibernacula would benefit *R. ferrumequinum*. This chapter demonstrates the power of spatial approaches for targetted conservation at a broad scale and identifies a clear rule of thumb for developers: build up, not out, to avoid impacting bats.

Models in chapter four identified a number of factors affecting *R. ferrumequinum* habitat suitability that corroborate the results of previous chapters, finding hedges and vegetation to be important for foraging habitat suitability, grassland to be better than arable, and finding street lighting to have a negative impact on habitat suitability. A rule of thumb here is that greener is better: bats are more likely to use natural areas with more vegetation and higher landscape heterogeneity. These findings can be used to direct mitigation measures, spatially explicit modelling can then say where mitigation measures would be most effective. This chapter again highlights the value of spatial modelling by producing a number of mapping outputs that can support conservation decision-making in the planning process. It would be possible to build on this further by using chapter four models to simulate the impact of different proposed development scenarios, which would have great application in local planning departments.

Collecting data on the study species is just the first step in systematic conservation planning (Margules and Pressey, 2000). This first step is what I aimed to achieve in this thesis: to provide a better understanding of how *R. ferrumequinum* use the landscape, creating a robust evidence base that can be used to inform conservation decisions (section 1.4). This work focused on the greater horseshoe bat, however, the approaches developed here can easily be applied to other bat species and other regions. Differences in species' life history and knowledge base may affect the details of the modelling: for example, a lack of data on location of roosts would require a different approach to connectivity modelling in chapter four (see chapter discussion, section 4.6), but the principals remain the same.

The next steps in systematic conservation planning include identifying conservation goals and implementing them; the drive for this needs to come from regulators and local authorities.

5.1 Impact

It has been argued that there is a science-practice gap in ecology and conservation (also referred to as a research-implementation gap or a knowledge-action gap): that research is seldom used to drive policy and that decisions are not always made using the latest scientific knowledge (Sutherland et al., 2004). Multiple causes have been suggested, these are analysed in depth by Bertuol-Garcia et al. (2018). Pertinent among these are (*i*) that research often does not address the issues conservation practitioners and policymakers face on the ground (Laurance et al., 2012; Griffiths, 2004), and (*ii*) that research papers make recommendations for their approaches to be used in conservation but do not make the techniques they develop accessible for a non-technical audience. To address this gap, many authors recommend dialogue between policymakers and scientists, and that requirements of decision makers should be used to drive conservation research questions (Anderson, 2014; Bainbridge, 2014; Cook et al., 2013). Toomey et al. (2017) put it aptly: '*...conservation [should be] a social process that engages science, not a scientific process that engages society*'. For conservation research to truly have impact, there is a clear need to address the science-practice gap.

To this end, my PhD was designed to receive as much input as possible from local stakeholder groups. We held regular 'steering group' meetings over the course of the project that included representatives from Natural England, North Somerset Council, Somerset Council, Avon Wildlife Trust and the Vincent Wildlife Trust. Separate from the steering group meetings, I held meetings with ecologists from Bath & Northeast Somerset and South Gloucestershire. We also held regular meetings with North Somerset Council that were integral in developing applied aspects of the work and ensuring results have practical application. There are already positive signs that the modelling approaches I developed in this thesis are being incorporated into local planning: mapping outputs generated in chapter four have been used to inform North

Somerset Council's new local plan, for habitats regulations assessments, and in developing the West of England Local Nature Recovery Strategy. I would like to keep working with North Somerset Council and Natural England to make sure this trend continues.

5.2 Future Work

Eventually it will become necessary to update chapter four models. GPS telemetry produces fantastic data, however comes with high costs financially, in terms of training and experience required, and in terms of disturbance when trapping and tagging bats. An approach based on acoustics would have a number of advantages: it is considerably less intrusive, cheaper, requires no specialist training, and captures data on all bat species (as well as other non-bat species e.g. Newson et al. 2020, 2017).

Deploying passive acoustic detectors and analysing the data as I did in chapters two and three is, however, labour-intensive. Citizen science offers a potential solution; harnessing the power of citizen scientists can enable researchers to generate large-scale datasets that would otherwise be impossible (Brown and Williams, 2019; Kosmala et al., 2016). Following on from the work in chapter two, the North Somerset Bat Survey (NSBS; `https://www.batconservationresearchlab.co.uk/north-somerset-bat-survey`) launched in 2021 and has been collecting acoustic data from over Somerset every summer since. The NSBS definitely has a role to play in the future of planning in North Somerset.

While citizen science data tends to be biased to urban and easily accessible areas (Tang et al., 2021; Johnston et al., 2020), if supplemented with additional targetted surveys (Krabbenhoft and Kashian, 2020) these data could potentially be used instead of GPS telemetry for the fine resolution habitat suitability modelling used in chapter four. Supplementary surveys could use permanent static detectors that upload their results automatically to a central server for real-time analysis (e.g. Gallacher et al., 2021; Sethi et al., 2020). This would enable long-term data to be gathered over seasons and years, and is an area I would like to explore further.

I would like to keep working with NSC to make sure spatial modelling retains a central role in planning throughout the county. The goal would be to develop an automated modelling workflow that can be managed in-house, with the ultimate aim of expanding this framework beyond North Somerset.

5.3 Concluding Remarks

This thesis showcases the power of spatial modelling for landscape-level conservation. My work focused on the greater horseshoe bat, however, the approaches developed here can be applied to any other bat species. Spatial modelling should be integral to planning, although there remain some challenges for modelling to be assimilated into planning at a national level. Huge investment is needed both in applied research and in building technical capacity at local authorities and planning departments. Ultimately, the initiative needs to come from policy: it needs to be a legal requirement that spatial modelling and landscape-level approaches to conservation become part of the planning process.

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Appendix A

Error Rate Modelling

A.1 Methods

Recordings were analysed an automatically assigned a species classification with BatClassify (Scott, 2012). BatClassify provides a confidence score for every species/species group's presence in each recording, it is then down to the user to set a threshold above which to consider a recording to contain a positive species ID (e.g. accepting all scores above 0.8 as positive IDs). Following Barré et al. (2019), we manually analysed 2,400 random recordings, 25 recordings for every confidence score value at 0.1 intervals (0.1, 0.2, 0.3 etc) for every species/species group, and recorded the result (0/1, incorrect/correct ID). If less than 25 recordings were available then all files were used (e.g. *Myotis alcathoe*). We then performed a logistic regression (correct/incorrect ID $\sim$ confidence score) to estimate the probability of a given confidence score containing a correct identification.

All manual sound analysis was conducted blind whereby the confidence score was hidden when performing manual ID. It was not possible to differentiate *Myotis* species manually, so all *Myotis* calls were merged, keeping the highest confidence score. *Pipistrellus* calls =<48kHz were classified as *P. pipistrellus*, calls >=52kHz were classified as *P. pygmaeus*, pipistrelle calls between these two thresholds were recorded as *Pipistrellus* spp.

At a 50% probability of a correct ID it is expected that the results will contain approximately the same number of false positives as false negatives, meaning that the results for the entire dataset will be accurate (Barré et al., 2019), although errors will not necessarily be evenly distributed across recording locations. Calls with a probability >0.5 were therefore weighted according to their confidence score (i.e. a file with 0.9 probability of correct identification will count as an occurrence of 0.9), meaning that files with greater certainty contribute more to the results.

Correlation between error rate and environmental variables was investigated. Using the manual ID set, the number of false positives and false negatives were calculated at a 50% probability cut off. A mixed model was fit (false positive/negative $\sim$ environmental variable) with recording location as a random effect to control for differences between recording locations, using the *lme4* R package (Bates et al., 2015). All environmental variables that may affect the acoustic properties of the environment or the ability of the detector to record were individually tested. It was not possible to test species separately as there were too few data points in random effect groups, causing singular fits, so errors for all species were included in a single analysis.

A.2 Results

It was not possible to calculate error rates over 70% and 50% for *P. pipistrellus* and *P. pygmaeus* respectively (figure A.1) due to a large number of false positives in the manual ID set it. As the 50% threshold corresponded with a

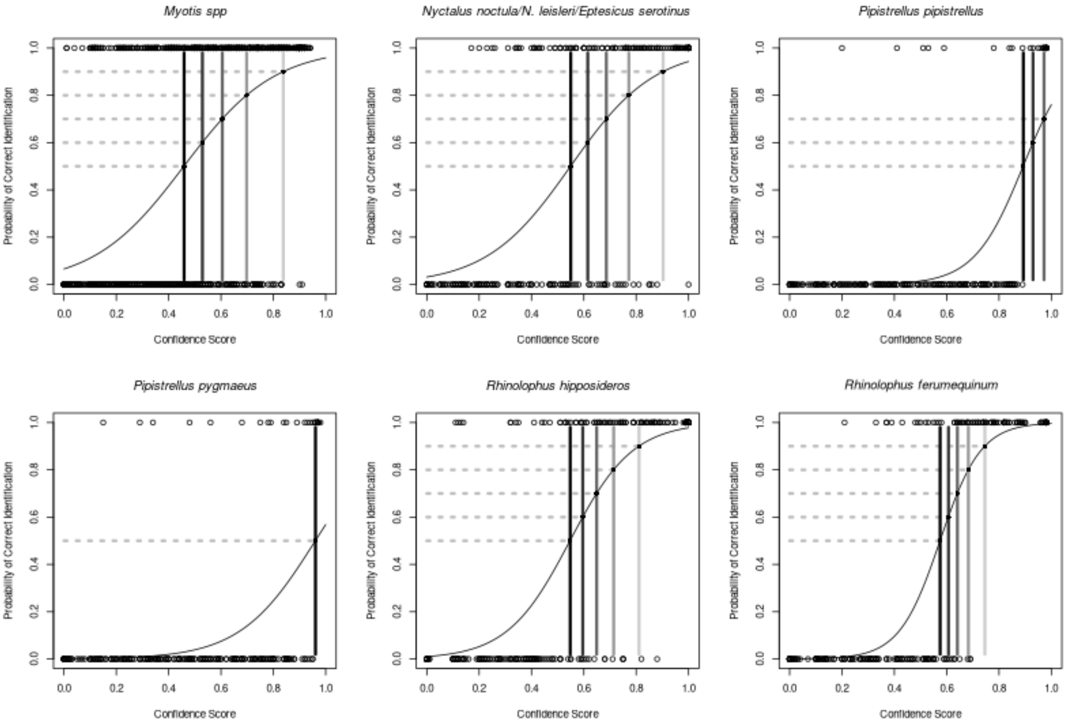

Figure A.1: Predicted curve of logistic regression, showing probability of correct ID at different confidence levels (False Positive Tolerances)

high confidence score for both species, the occurrence (weighted probability) would never be much above 0.5 for *P. pygmaeus* and 0.7 for *P. pipistrellus*. This may have resulted in lower estimates of activity for both species.

We found error in auto-ID to correlate with some habitat types (table A.1) but the effect was generally very small (figure A.2). Most noteworthy was that the probability of false positives at vegetated field boundaries was 20% lower than at non-vegetated field boundaries.

Table A.1: Effect of environmental variables on error rate in automatic classification at 50% FPT. Showing Nakagawa pseudo-R^2 Nakagawa et al. 2017

	False Negatives			False Positives		
	P-value	Estimate	R^2	P-value	Estimate	R^2
vegetated_boundary	0.06	0.744	0.01	0.00	-1.567	0.04
trees_per_100m	0.01	0.029	0.01	0.02	-0.049	0.03
fence	0.41	-0.353	0.00	0.00	1.118	0.01
improved_grassland	0.55	0.130	0.00	0.07	0.557	0.01
road	0.61	-0.157	0.00	0.05	-0.927	0.02
arable	0.08	-0.625	0.01	0.66	-0.175	0.00
stream	0.19	0.365	0.00	0.01	0.938	0.02
percentage_gaps	0.03	-0.063	0.02	0.83	0.005	0.00
height	0.05	0.058	0.01	0.01	-0.116	0.02
overhang_height	0.07	0.106	0.01	0.15	-0.121	0.01
overhang_width	0.14	0.055	0.00	0.26	-0.063	0.00
slope	0.20	2.859	0.00	0.01	-8.770	0.02
mean_nightly_rainfall	0.66	0.032	0.00	0.03	0.191	0.01
mean_min_temp	0.40	0.027	0.00	0.23	-0.048	0.00
mean_nightly_humidity	NA	NA	NA	NA	NA	NA
mean_nightly_wind.speed	0.91	-0.010	0.00	0.07	0.205	0.01

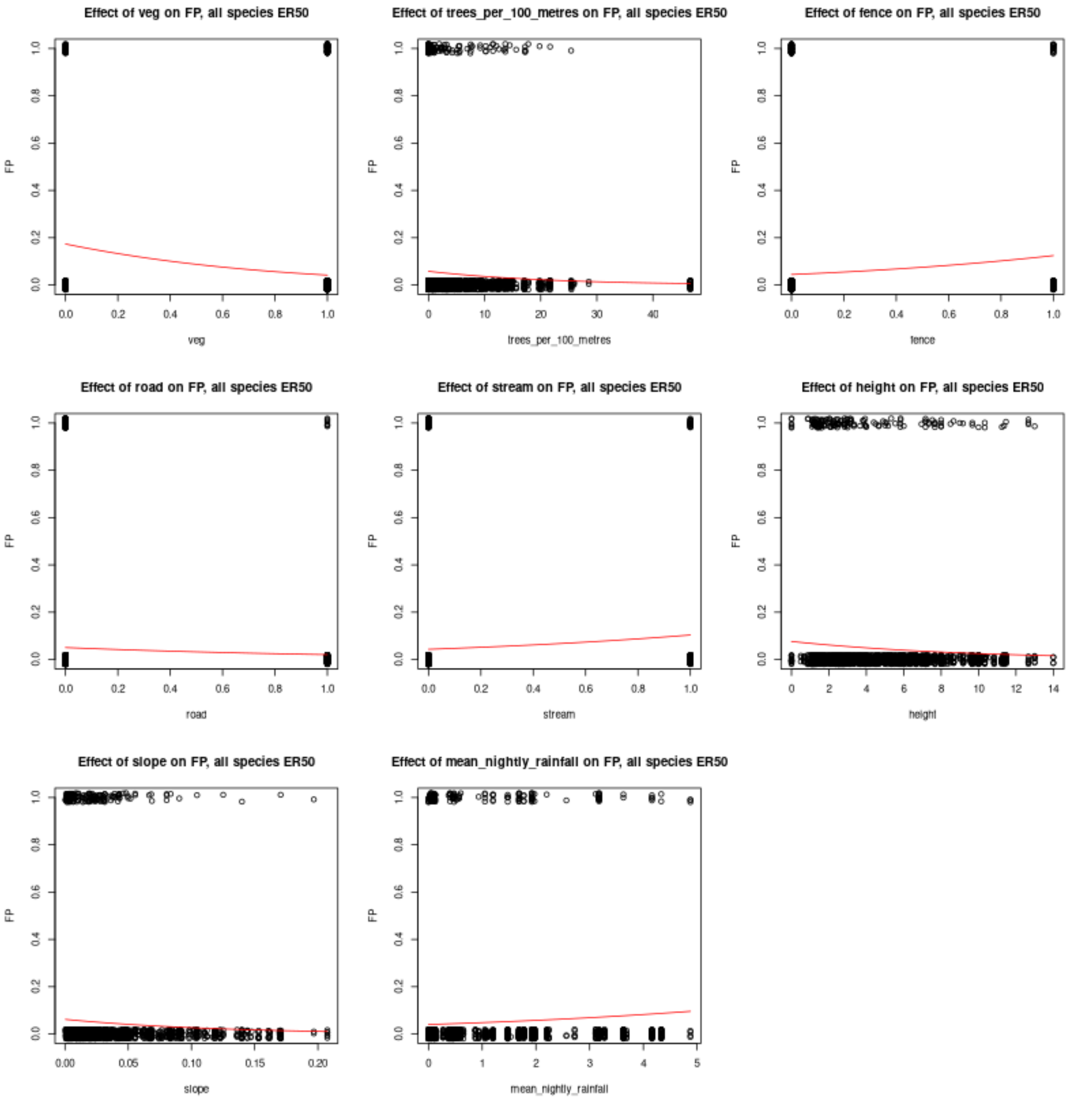

Figure A.2: Effect of environmental variables on error of automatic classification (significant effects only)

Appendix B

GPS Telemetry

B.1 Methods

We conducted a GPS telemetry study on *R. ferrumequinum* to gather high resolution habitat use data, using two types of GPS tag: PinPoint 10 (Lotek UK Ltd., Wareham, Dorset, UK) and nanoFix GEO MINI (Pathtrack, Otley, Yorkshire, UK). Both tags weighed approximately 1 g and were therefore suitable for bats weighing >20 g (Aldridge and Brigham, 1988). We also used PicoPip Ag337 VHF tags (Lotek UK Ltd., Wareham, Dorset, UK) for tag retrieval. We programmed GPS tags to obtain a locational fix every 15 minutes between sunset and sunrise.

We trapped bats under license from Natural England (license number 2021-54190-SCI-SCI and 2022-60583-SCI-SCI-1) at *R. ferrumequinum* maternity roosts located in Brockley Hall SSSI and Iford Manor SSSI, with permission from the Vincent Wildlife Trust who manage the roosts. Trapping took place in August-September 2021 and August 2022. All trapping was carried out in compliance with the Bat Conservation Trust Bat Survey Good Practice

Guidelines (Collins, 2016) while observing guidance relating to SARS-CoV-2 (Kingston et al., 2021).

We caught bats with a harp trap (Faunatech Austbat, Australia) located on flight lines 10-50 m away from the roost. Trapped bats were extracted promptly and juveniles, males and pregnant or lactating females were released immediately. Females that were not pregnant or lactating were placed into cloth holding bags and a provisional weight was recorded. Bats >20 g that appeared to be in good health were kept for tagging. We fitted combined GPS/VHF tags (in 2021) or GPS tags only (in 2022) to each bat below the scapulae by trimming the fur and fixing the tag with surgical adhesive. Tags attached in this way have been shown to remain attached to the bat for an average of 10 days (O'Mara et al., 2014). We recorded weight and forearm length and then released bats where they were caught.

GPS tags were retrieved either by: a) recapturing bats using the same methodology outlined above or with a hand net (n = 3 tags), b) collecting from the floor of the roost in the autumn having been groomed off by the bat (n = 10 tags), or c) locating them where they had fallen in the field via radio telemetry (n = 1 tag). GPS data were downloaded from retrieved tags. To ensure accuracy of the data we removed a small number of isolated erroneous fixes that were >20 km from the roost site (n = 5 fixes). We conducted tests with the tags prior to tagging bats to determine tag accuracy. Based on our findings we removed fixes recorded by Lotek tags with an HDOP >5 (n = 32 fixes, 6% of total) and fixes recorded by Pathtrack tags that used fewer than 5 satellites (n = 114 fixes, 16% of total).

B.2 Results

In total 34 bats were tagged and 14 tags were retrieved (41% recovery rate). Bats were tracked for an average of four nights each (±2 s.d.; table B.1). We recorded an average of 66 locational fixes per bat (±24 s.d.), of which through cluster analysis 64% were classified as foraging, 25% as commuting and 11% as roosting (figure B.1). We recorded an average of 11 foraging clusters per bat (±5 s.d.) and identified 16 new roosts through GPS tracking, plus an additional four through radio tracking.

Tag performance differed between brands. Lotek tags lasted on average 3 nights (mean, ±1 s.d.) and took 50 usable locational fixes per bat (±17 s.d.), while Pathtrack tags lasted an average of 7 nights (±1 s.d.) and took 88 usable locational fixes per bat (±12 s.d.).

B.2.1 Bat Dispersal and Colony Size

The maximum distance bats were recorded from the roost was 12.5 km at Brockley (roost size ~800 bats) and 9.8 km at Iford (roost size ~400 bats), while the mean maximum distance from the roost was 8.9 km (±3 km s.d.) at Brockley and 7.2 km (±2.2 km s.d.) at Iford (table B.1).

Table B.1: GPS tracking statistics.

Bat #	**Tag type**	**Site**	**Max. dist. from roost (m)**	**Fixes**	**Foraging fixes**	**Commuting fixes**	**Clusters**	**Nights tracked**
1	Pathtrack	Brockley	9,985	81	46	33	14	8
2	Pathtrack	Brockley	11,577	97	53	31	16	8
3	Pathtrack	Brockley	10,212	101	65	34	14	7
4	Pathtrack	Brockley	9,871	79	54	24	12	6
5	Pathtrack	Iford	9,350	72	52	20	5	5
6	Pathtrack	Iford	9,812	95	71	23	15	7
7	Lotek	Brockley	3,491	54	37	7	8	3
8	Lotek	Brockley	6,224	48	45	3	6	2
9	Lotek	Iford	6,124	44	26	5	12	3
10	Lotek	Iford	3,765	25	19	0	6	2
11	Lotek	Brockley	7,117	39	15	5	6	2
12	Lotek	Brockley	12,532	68	43	15	14	3
13	Lotek	Iford	7,520	64	31	14	19	3
14	Lotek	Iford	6,919	34	23	11	4	2
-	-	**Mean (±s.d.)**	8,178 (±2,738)	64 (±25)	41 (±17)	16 (±12)	11 (±5)	4 (±2)

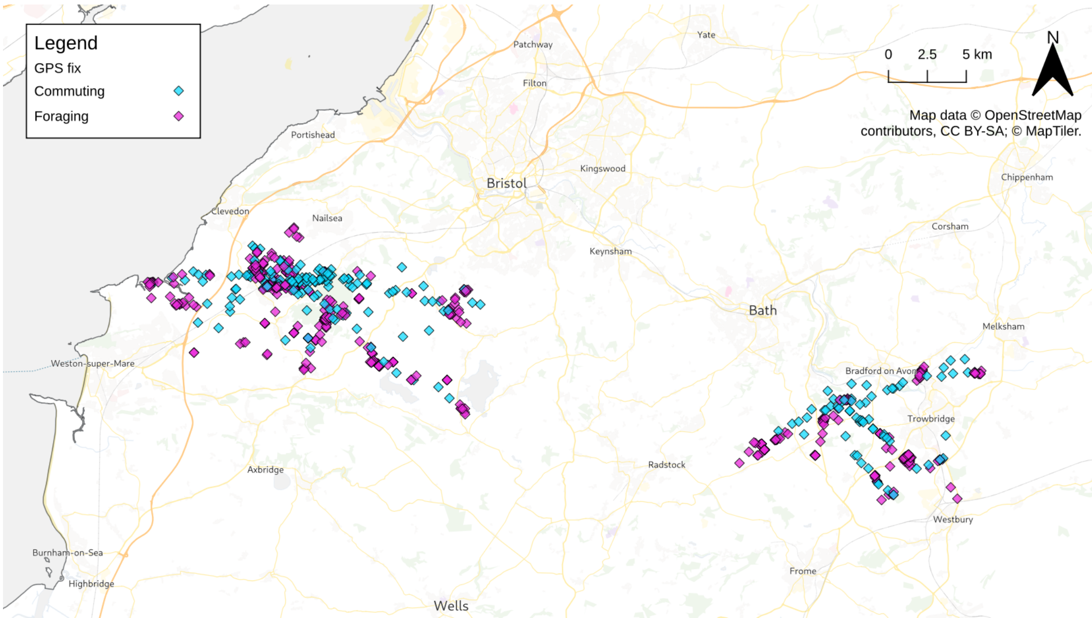

Figure B.1: Locational fixes from GPS tracking at Brockley Hall, North Somerset and Iford Manor, Bath and Northeast Somerset, 2021-22. Fixes are categorised as either commuting or foraging behaviour. Roosting fixes not shown for sensitivity.