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Abstract

The development of England's new Nature Recovery Network has been piloted in several counties in the country, but few has systematically mapped connectivity based on species dispersal. This study proposes and evaluates a novel modelling framework that integrates various layers of species information into a spatial conservation prioritization analysis. It aims to strategically identify optimal zones for nature recovery that can maximize species connectivity in Oxfordshire, using bats as a focal species. The framework was able to not only identify key landscape corridors but also stepping stone habitats for bats, and emphasized how well-placed, small-scale green and blue infrastructure, such as hedgerows and ponds, can be just as effective as larger reserves. It also found that the current coverage of protected areas may not adequately be protecting woodland habitat needed for connectivity. Next steps for Oxfordshire's NRN should scale up the application of this connectivity framework to address these areas of priority in the landscape.

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1. INTRODUCTION

Connectivity is at the core of the novel and ambitious Nature Recovery Network (NRN), a concerted effort to bridge the disjunct protected areas across England to restore and enhance the country's biodiverse zones. The implementation of the NRN is carried out through county-scale local nature recovery strategies (LNRS), a package policy that will include a list of priorities for habitat restoration, a map of existing restoration sites and areas of importance for biodiversity, and another map proposing locations for future habitat improvements, known as the local-scale NRN (Wentworth & Powell, 2021). Pilot LNRS projects carried out in 2020 trialled a variety of methodologies, but few integrated a data-driven, systematic framework that allows species connectivity to be appropriately represented in the final decision support maps (Cornwall Council, 2021; Wildlife and Countryside Link, 2021; Smith et al., 2021). This paper aims to address the evidence needed for establishing a NRN by taking a specific focus on prioritizing and optimizing species-based connectivity corridors through a proposed novel modelling framework. This framework was piloted in Oxfordshire, using bats as ecologically representative, bioindicator species. This novel methodology will aim to answer the following overarching research questions:

1. Where are priority zones for species-based connectivity to support the development of the local nature recovery network in Oxfordshire?
2. To what extent can a species-driven connectivity analysis effectively inform the pragmatic selection of a local nature recovery network in Oxfordshire?
3. What are the challenges and areas for further development in using connectivity modelling to help design nature recovery networks?

Through testing and evaluating this modelling framework, the goal of this paper is to produce a replicable and scalable methodology that can be integrated into the timely design of NRNs across counties in England and beyond.

1.1 Policy context

1.1.1 National NRN and LNRS policy context

The NRN was proposed in the 2018 25-Year Environment Plan (25YEP), an environmental strategic plan that set forth ten broad environmental goals and approaches on how to achieve them (Defra, 2018; UK Parliment, 2021). The 25YEP informed the 2020 Environment Bill, a landmark piece of legislation with the power to set legally binding environmental targets, which was enshrined and received Royal Assent in 2021, where it became the 2021 Environment Act. The Act builds upon and gives legal footing to the 25YEP, allowing the Secretary of State to set legally binding long-term targets on priority areas such as air quality and species abundance, as well as conform to five internationally recognized environmental principles (Dbouk, 2022). The 25YEP includes six policy areas that address how to act on the ten goals, from managing land (Chapter 1) to increasing resource efficiency (Chapter 4). One of these policy topics is the creation of a Nature Recovery Network (NRN), which was detailed in Chapter 2, but also mentioned in the "Thriving Plants and Wildlife" goal.

The goal of the NRN is to join existing protected sites through corridors and stepping stone habitats to enhance connectivity, allowing for landscape and climate change resilience and the preservation of England's historic nature (Defra & Natural England, 2020). The network will be based on the idea of "more habitat, in better condition; in bigger patches that are more closely connected", as proposed by Professor Sir John Lawton, a landmark report that arguably built the character of nature restoration and planning for England in the upcoming years (Lawton, 2010). This "Better", "Bigger", "More", and "Joined" (BBMJ) goal has gone on to define the mission of much of the UK's wildlife recovery initiatives, not just the nature recovery network (Rose et al., 2018; Clarke, 2015).

The NRN will also play into the wider "30 by 30" national agenda to protect 30% of terrestrial environments by 2030. In a report, the UK Department of Environment, Food and Rural Affairs (Defra) has identified that NRNs will be "crucial to the delivery of 30 by 30" (Defra, 2022b). The UK has employed landscape-scale restoration action in the past such as Nature Improvement Areas, the Countryside Stewardship Scheme, as well as the farmer cluster concept (UK Rural Payments Agency, 2020; Game and Wildlife Conservation Trust, 2015; Defra, 2022a). The NRN will draw on this existing work and expand the coverage to restore 75% of protected terrestrial and freshwater sites to favourable condition and 500 thousand hectares of habitats outside of existing protected sites, and recover threatened species, woodland cover, and ecosystem benefits by 2042 (Defra, 2022c).

In addition, with the legal footing of the Environment Act, there is now a mandatory system for creating spatial strategies at the local level – the LNRS. LNRS will provide the backbone and research behind a national high-level Nature Recovery Network (NRN), which will link biodiversity-rich areas across the country to increase connectivity and resilience (Ronish & Hilburn, 2022). There will be approximately 50 LNRS across England, produced through local knowledge and mapping, which will help inform and make up the national network (Defra, 2021a). LNRS will place heavy emphasis on local co-production and co-ownership, tailored to the locality (Wildlife and Countryside Link, 2021).

1.1.2 Existing work on LNRS and NRNs in the UK

Five pilot LNRS projects were initiated in 2020 in Buckinghamshire, Cornwall, Greater Manchester, Northumberland, and Cumbria (Defra, 2021a). The strategies were created through a stepwise process of engaging stakeholders and identifying existing conservation sites and opportunity regions for recovery. It involved reconciling the different stakeholder values on land to locate these new priority zones or conservation targets (Traill-Thompson, 2021). For instance, in Buckinghamshire, there was a total engagement of 358 stakeholders through a comprehensive workshop (Wildlife and Countryside Link, 2021; Buckinghamshire Council et al., 2021). The methodology to create a spatial plan varied between counties: Cumbria, Greater Manchester, and Northumberland used overlap mapping of existing protected areas with high-priority zones identified by stakeholders (Greater Manchester Council, 2021; Northumberland, 2021; Cumbria County Council, 2020). Buckinghamshire and Cornwall piloted systematic conservation planning strategies, which are more robust and evidence-based formulations of stakeholder engagement and landscape prioritization (Cornwall Council, 2021; Sutherland, 2021).

From these five pilot projects, several takeaway lessons identified the need for 1) robust leadership and governance to prepare the LNRS, 2) adequate resources and capacity to establish partnerships with experts, 3) access to data and evidence, 4) collaboration and transparent stakeholder engagement, and 5) prototypes that are user-friendly for end users (Defra, 2021b). The differences in the methodologies to arrive at a NRN map also allowed for comparative insight into the benefits and drawbacks of each approach.

Defra and Natural England aims for the LNRS to be complete and ready for its first phase of roll out by 2023 (Natural England, 2022). As such, many counties have begun the process, such as Oxfordshire county.

1.1.3 Oxfordshire LNRS

Oxfordshire is a hub for nature recovery work in the UK, with a portfolio of ecosystem restoration projections involving local NGOs, landowners, and researchers, such as but not limited to the Thames Valley Environmental Records Centre (TVERC), Wild Oxfordshire, Healthy Ecosystems Restoration in Oxfordshire (HERO), Treescapes, and Berks, Bucks, and Oxon Wildlife Trust (BBOWT). The passing of the Environment Bill and the new NRN policies has allowed the county to gain momentum to scale up nature recovery work, and as such, Oxfordshire provides a conducive sandbox for piloting a NRN modelling framework. Two main studies mapping the NRN have so far been conducted in Oxfordshire, as described below.

The first study was conducted by TVERC as commissioned by the County Council. Although formal guidance has not yet been issued by Defra, preparatory work for developing the LNRS is already underway in the county, involving Oxfordshire County Council in collaboration with the new Local Nature Partnership, a coalition of environmental NGOs, researchers, and community stakeholders (Oxfordshire County Council, 2021a). The county was also in the process of putting together Oxfordshire Plan 2050, a joint statutory spatial plan (JSSP) convening the six regional authorities in Oxfordshire - Cherwell District, South Oxfordshire, Vale of White Horse District, West Oxfordshire, Oxford City, and Oxfordshire County, primarily to set up new housing but also a strategic sustainable growth plan. An NRN map was included to inform this Oxfordshire Plan 2050 (TVERC, 2020). TVERC, the regional authority in terms of environmental data for Berkshire and Oxfordshire, and has an extensive species data and habitats repository, collected from citizen science recorders, NGOs, governmental agencies, and environmental consultants. With this data, they carried out preliminary habitat connectivity and landscape character analysis in order to identify a "recovery zone" to cover 50% of Oxfordshire for habitat restoration and creation. The connectivity component took a species-based approach by employing a focal woodland and grassland species to simulate dispersal through least-cost path analysis. The methodology used in the TVERC publication was based on the well-known cost-distance pathway by Roger Catchpole; however, the designation of the cost surface is somewhat arbitrary, and more importantly, the connectivity analysis was not used in the selection of the final network map (Catchpole, 2006). The final map was an overlay of existing core areas as the priority zone, and a combination of conservation target areas (CTAs) and important freshwater areas (IFAs) as the recovery zone, with adjustments informed by stakeholder input (TVERC, 2020).

The second central study was conducted by Smith et al. (2021) using a systematic conservation planning approach, a much more comprehensive and structured way of identifying ecological networks in the landscape. Bob Smith, the lead author, was the driving force behind the systematic conservation planning method used for the pilot Buckinghamshire LNRS. This decision-making method emphasizing representing diverse stakeholders, which is ideal for the UK landscape with its matrix of privately owned and public land, expansive agricultural cover, and existing conservation work (Smith et al., 2021). The study was conducted in partnership with BBOWT, and therefore the area of interest spanned across the three counties (Berks, Bucks, and Oxon), with the aim to pilot a systematic conservation planning methodology for nature recovery network design so it can be replicated in other counties across the UK. The paper prioritization models using expert opinion to identify priority conservation features and spatial data of existing recovery sites to make up the "core" zone. The analysis identified a recovery and wider landscape zone based on the best portfolio of sites that met a 30% conservation target while minimizing opportunity cost, calculated using land use criteria that identified the highest quality land with the lowest cost. However, Smith et al. (2021) discuss that the study had originally included species data to indicate habitat quality or functional connectivity but had purposefully left it out in the final analyses because the algorithms to predict the distribution of the species were not reliable enough due to the uncertainty of the input data quality. The two limitations discussed for future research were firstly, the lack of fine-scale species data to model species distributions, which would have been useful to act as proxies for habitat quality. Secondly, the 30% target set in the study was based on a national target, not a county-specific target (Prime Minister's Office, 2020; Garibaldi et al., 2021). As such, there needs to be more guidance and consultation with experts and stakeholders on setting priorities and conservation targets. Similarly, to TVERC's draft NRN, Smith et al. (2021) also did not include a connectivity analysis, justifying that setting a high conservation target (30%) would be able to include enough area to achieve the necessary level of connectivity in the landscape.

These two pieces of research set a strong foundation for establishing a robust, evidence based LNRS for Oxfordshire; however, the studies identified research gaps in integrating statistically based connectivity analysis into nature networks and species data into SCP analysis.

1.2 Research gap and theoretical framework

Connectivity has been addressed throughout the five pilot LNRS projects as well as the two central studies (TVERC, 2020; Smith et al., 2021) conducted for Oxfordshire, but they were often not integrated appropriately into the final map or include a robust ways of delineating connectivity corridors. Most of the work also focused on habitat connectivity, and not species connectivity. In order to answer the research questions, this analysis will build on TVERC's connectivity analysis (which was not used for final site selection in their NRN) and propose an approach that can integrate connectivity corridors into the final NRN output and select the optimal corridors using an SCP algorithm. Then to build on the limitations underlined by Smith et al. (2021), this study will also be using the rich species and habitat records from TVERC, with a subsidiary aim to also evaluate how bats serve as bioindicators for identifying connectivity corridors for nature recovery.

This paper will primarily take an umbrella landscape ecology theoretical approach to guide the configuration of the modelling framework. Landscape ecology theory studies the interactions between the spatially explicit heterogeneous matrix of the landscape - landscape structure - with biotic ecological processes – landscape functioning (Turner & Gardner, 2015; Wu & Hobbs, 2007; Kupfer, 1995). Applying landscape ecology theory to conservation planning began as early as 1991 in a seminal paper by Hansson & Angelstam (1991), highlighting how the understanding of the landscape from not just the human perceived biotopes but also to species perceived corridors (landscape functioning) are central to reserve selection (landscape structure). Its sub-fields in habitat fragmentation, patch dynamics, ecological corridors, and landscape resistance influencing species persistence and dispersal are also iterated as key considerations in the design of nature reserves and networks such as the NRN (Howell et al., 2018; Gergel & Turner, 2017; Wiens, 2009). Landscape ecology theories are also considered as an extension of the equilibrium theory of island biogeography (ETIB), an important contextual theory for understanding how landscape patches is populated (MacArthuer & Wilson, 1967; Urban, O'Neill & Shugart, 1987). ETIB postulates that species abundance and richness on an island are predictable given the dynamic colonization and extinction rates, which are dependent on the geographical isolation and size of the island (Ladle & Whittaker, 2011). The ETIB framework provides the theoretical framework for foundational reserve design principles, where reserves that are larger, unfragmented, connected, and with less edge effects are better than the opposite (Diamond, 1975; Wilson & Willis, 1975; Harris & Silva-Lopez, 1992; Margules, Higgs & Rafe, 1982; Shafer, 2008). These principles continue to be the basis of conservation planning today, exemplified by Lawton's BBMJ design for England (Daigle et al., 2020; Williams et al., 2020; Delmas et al., 2019). These two theories will postulate the motivations and configuration of the NRN on a broader level, but landscape connectivity, an important sub-discipline embedded within landscape ecology, will underpin how these networks can facilitate and improve species-level conservation.

1.2.1 Landscape connectivity and graph theory

The field of landscape connectivity studies how the landscape facilitates species movement between patches, or "islands" through dispersal, migration, or gene flow (Wiens & Moss, 2005; Mateo-Sánchez et al., 2015). Landscape ecology research typically focus on two main tools used in conservation for enhancing connectivity – corridors and stepping stones (Lynch, 2019; Baum et al., 2004; Wu, 2013). Stepping stones are refuges of optimal habitat patches protected and interspersed throughout the landscape, a concept based on ETIB, as stepping stones can act as refuges between core patches that are far away. Corridors on the other hand are continuous, mostly linear features that join two patches together (Stewart et al., 2019; Doerr et al., 2014). In addition, there are also two ecological concepts that show the different types of landscape connectivity – structural connectivity and functional connectivity (Baguette & van Dyck, 2007). Structural connectivity refers to the biophysical connections of two core patches, most seen through corridors, and functional connectivity is the actual degree in which the patches are connected, given limiting abiotic and biotic factors (Laliberté & St-Laurent, 2020). However, Calabrese & Fagan (2004) identifies a third type of connectivity in between structural and functional: potential connectivity, defined by predictions of connectivity not yet verified by actual species observances - most interpolative models of connectivity produce 'potential connectivity' pathways (Pietsch, 2018).

Over the years, multiple analytical tools and theoretical approaches have been developed to quantify connectivity indices to identify these 'potential connectivity' corridors. Modern theories articulating landscape connectivity are rooted in graph theory - the idea that the landscape can be represented through a series of nodes and links, with the connecting links representing the ability of species to move between the nodes, often defined as core habitat areas (Briers, 2012; Saura et al., 2011). Graph theory simplifies the landscape into a binary - core patches ("nodes") and links ("edges"). It is a powerful theoretic approach given its simplicity, but also for its focus on identifying the most efficient flow and connective pathways within a heterogenous landscape (Bunn, Urban & Keitt, 2000; Urban et al., 2009; Delmas et al., 2019).

1.3 Modelling landscape ecology and connectivity

Statistical models have been developed to simulate species movement and distribution through space based on how the overarching theoretical frameworks discussed above dictate ecological processes. As such, these models are ways that theory can be put into practice and inform on-the-ground conservation planning and policy. Several common tools used to model landscape ecology and connectivity are described below.

1.3.1 Species distribution models

Species distribution models are one of the most used tools to inform conservation planning (Franklin, 2010; Thorn et al., 2009; Kremen et al., 2008). The most basic form of SDMs is known as correlative models. They utilize a dataset of species observations – presences, and if available, absences – and a series of continuous environmental variables such as temperature or vegetation indices. By correlating the occurrence locations to the set of variable values they are found on, the models can extrapolate and predict the probability of species distribution across a landscape with those same variables (Guisan & Thuiller, 2005; Peterson et al., 2011). This described the simplest, correlative form of SDMs, while more complex variations are typically called mechanistic models, which use physiological information derived from typically lab-based studies to determine the range of environmental variables most optimal for a specific species (Tourinho & Vale, 2022).

As with any model, SDMs have several key assumptions. Particularly for this study, a major assumption of correlative models is that species are at equilibrium with environmental conditions and thus can reach any area with favourable environments (Araújo, Marcondes-Machado & Costa, 2014; Richmond et al., 2010). Evidently this is not the case since behavioural factors are just as important in governing species movement and distribution. While this can be addressed with the integration of dispersal, competition, and other biotic variables, the ability to access this data and the understanding of specific species ecology are limited (Guisan & Thuiller, 2005). Another pertinent assumption is the selection of pseudo-absences in presence-only SDMs. Normally, absence points are meant to represent either locations the species are not able to reach due to unfavourable abiotic barriers or biotic limitations, but often absences are due to sampling bias where difficult-to-reach locations result in scarce data (Hortal, Lobo & Jiménez-Valverde, 2007; Soberón & Nakamura, 2009). Therefore, the selection of pseudo-absences at random locations where there are no presences often results in poor predictive models with low performance accuracy (Lobo, Jiménez-Valverde & Hortal, 2010; Pearce & Boyce, 2006).

Between the modelling complexity of correlative and mechanistic models, there is a realm of hybrid models that integrates more biological and spatially-explicit species information into a correlative model, such as dispersal patterns. Integrating SDMs and connectivity models is an early step towards a hybrid framework. One way this is done is using SDMs as a part of the "resistance surface" of a connectivity model. The "resistance surface" is a raster surface with values that represent how permeable each cell is to the study species depending on the environmental parameters present (Zeller et al., 2017). While these surfaces are frequently created through expert consultation where certain land classes are given a certain score of permeability, it is also recommended in literature to not entirely rely on expert opinion (Clevenger et al., 2002; Ofori et al., 2017; Shirk et al., 2010). Using the output of a species distribution model (SDM) is one of the more popular empirical data-based alternatives (Dutta et al., 2022). High values of probability of occurrence on the SDM output surface can equate to low resistance values, as it indicates the preferability of the habitat to species movement (Poor et al., 2012; Algeo et al., 2017).

1.3.1 Connectivity models

Connectivity models based in graph theory simulate pathways species would take across a landscape, given the understanding of dispersal distance and landscape permeability (as defined by the "resistance surface"). Statistical connectivity models produce metrics, such as probability of connectivity or current flow (Foltête et al., 2021), while other widely used tools produce geospatial raster grids to create more diffused and alternative paths (Grafius et al., 2017). For instance, least cost path models identify a surface of permeability, representing the ease with which species can travel across different types of land cover (Etherington, 2016). Circuit theory is another alternative, like least cost paths, but instead represents the land surface as an electrical field with each parcel having a 'conductance' based on its suitability for species of interest (McRae et al., 2008). One application by Isaac et al. (2018) develops a qualitative adaptive management framework for designing a resilient NRN in the UK using spatial network theory, which dictates that population persistence and resilience is determined by the connectivity between habitat patches. It is a call to action for more quantitative connectivity analyses for NRN design that takes into account spatial network theory.

For connectivity models, there are several limitations in the ability for resistance surfaces to represent the energetic cost of movement as well as accounting for the spatial autocorrelation of species dispersal (Cushman, 2010; Unnithan Kumar et al., 2022). Connectivity models also do not incorporate temporal variation. The high dispersal capacity of migratory birds and large mammals are contingent on a multitude of dynamic variables, such as in the paper by Kaszta et al. (2021) on African elephants, they found resistance surfaces are highly variable over seasons (Kaszta, Cushman & Slotow, 2021).

1.3.2 Systematic conservation planning and spatial conservation prioritization

SDMs and connectivity models set the value of the land – identifying zones or corridors of high connectivity and high probability of species occurrence. It takes further decision-making and conservation planning to decide how they can be refined down into target zones for nature restoration and habitat creation.

Sutherland et al. (2004)'s seminal paper on "The need for evidence-based conservation" highlighted conservation practitioners in the UK working on wetland management largely rely on anecdotal evidence (77%) and only 2% rely on scientific information. Systematic conservation planning is a paradigm built in response to the ad hoc process of decision-making in conservation in the late 20th to early 21st century. It delineates an interactive, step-based protocol for designing and implementing reserves and other conservation initiatives (Fig. 1) (McIntosh et al., 2018; Groves & Game, 2015:p.12). Several core concepts underpin systematic conservation planning: first, it aims to enhance complementarity, where many biodiversity features are represented in the final range of the protected area (PA) with minimal overlap. Second, the persistence of species in the long-term is prioritized, where good design, such as reserve size, come into play. Third, the irreplaceability of a site, defined by how unique the assemblage of conservation features or species are in the site, can also represent the flexibility and fragility of the PA as a whole (Moilanen, Wilson & Possingham, 2008; Margules & Sarkar, 2007).

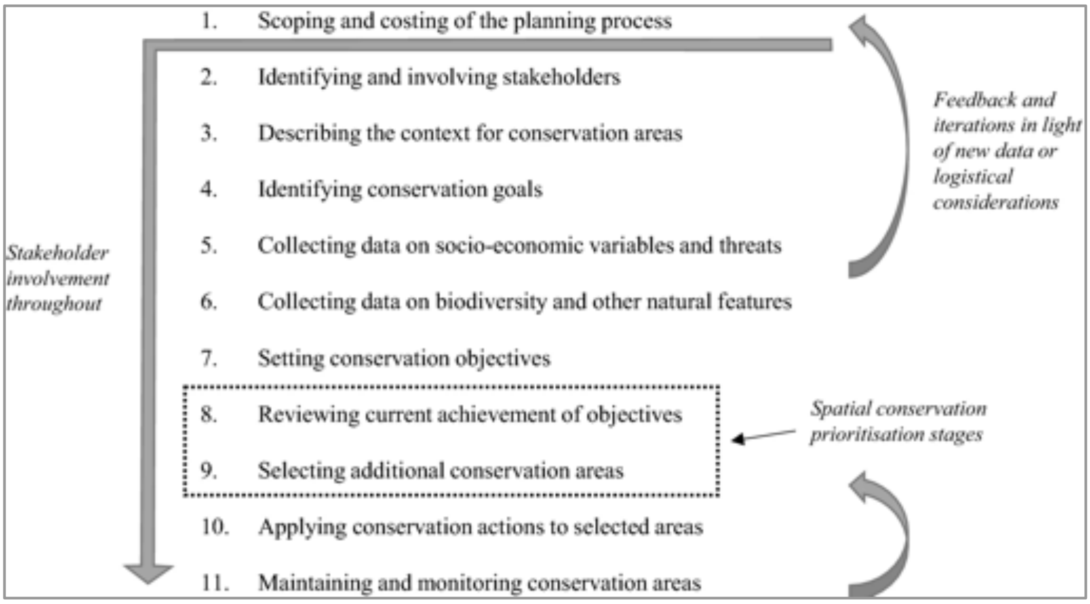

Figure 1. Stages of systematic conservation planning, from McIntosh et al., 2018.

The process itself is transparent, iterative, and consists of some general steps: scoping, stakeholder engagement, understanding the context, establishing conservation targets, compilation of relevant data, identifying biodiversity surrogates, reviewing existing conservation work, selecting, and refining new areas for conservation action, implementation, examining feasibility, and implication (Margules & Sarkar, 2007:p.10; Pressey & Bottrill, 2009). The steps that involve computational analyses are for the selection of new conservation sites, and this subset makes up strategic conservation prioritization (SCP[1]). Within SCP, there are two main problem configurations: the minimum set problem that identifies the best conservation portfolios with the least cost (typically conducted through a software called Marxan), and the maximum cover problem identifies the optimal, maximum coverage portfolios given a pre-set cost (through software called Zonation) (Delavenne et al., 2012; Kukkala & Moilanen, 2013).

The creators of systematic conservation planning particularly emphasized the need to adequately identify and engage all relevant stakeholders to address the common gap between expert-generated conservation plans and reality on the ground (Pressey et al., 1993). There is no superior algorithm to conduct site prioritization as it depends on stakeholder and interest group priorities; however, given that the scope and timeframe of this study constrains the feasibility of meaningful stakeholder engagement, the study will only utilize the computation-focused SCP steps. The SCP algorithm will be applied solely as an ecological prioritization model to select optimal conservation corridors.

[1] Note: SCP abbreviation stands for spatial conservation prioritization, not systematic conservation planning

Smith et al. (2021) paved the path for using systematic conservation planning for the designation of NRNs across the country. Bob Smith advocates that it is the best way to develop LNRS but acknowledges that there needs to be a cultural shift for this new framework and calls for national guidance on creating communities of practice to scale up this methodology (Smith, 2022).

1.4 Modelling framework

While the models described above are often operationalized in their own capacity, an integrated methodology that incorporates multiple models can allow a more nuanced simulation of ecological behaviour and processes. There is a robust body of literature that has also investigated how to best assemble two or more of the described independent conservation planning models to optimize the models and take advantage of their synergies. In 2006, the Biological and Environmental Evaluation Tools for Landscape Ecology (BEETLE) toolkit was created with the UK Wales Forestry Commission, which integrated a focal species concept and connectivity model to map habitat networks (Watts et al., 2005; Eycott et al., 2007). Although it has since been archived, this suite of tools laid the foundation for species-focused connectivity modelling. Even today, some of its tools have been modified and used for pilot LNRS (Cumbria County Council, 2020). More recent studies such as a paper by Wang et al. (2020) proposes a framework that integrates landscape theory with species distribution and connectivity modelling to suggest conservation zones, using Maxent outputs in Conefor and Fragstats, a spatial graph and landscape ecology statistical program, respectively. Alternatively, Fajardo et al. (2014) utilized a combined systematic conservation prioritization, species distribution model, and connectivity analysis to examine conservation gaps in Peru. The study highlighted how despite the increasing efforts towards area-based conservation, there are still large conservation gaps, and found that this integrated modelling approach can better optimize the selection of a more representative and connected network. Another notable study is by Jennings et al. (2020) on modelling and prioritizing connectivity pathways using ensemble SDMs, which were used for three different connectivity analyses, including Linkage Mapper, Circuitscape and a species-agnostic geodiversity analysis.

For this study, an integrated modelling framework will be adopted to drive a species-focused study and moving away from the existing habitat-based approaches in Oxfordshire, which may not account for the dynamic movement of species and therefore cannot adequately protect areas where species are traversing. This study will draw from the existing work of the three modelling tools described above - SDMs, connectivity analyses, and SCPs - and propose a flexible framework to incorporate species data and connectivity modelling to select sites that reduce habitat fragmentation and promote connectivity into the development of NRNs (Fig. 2).

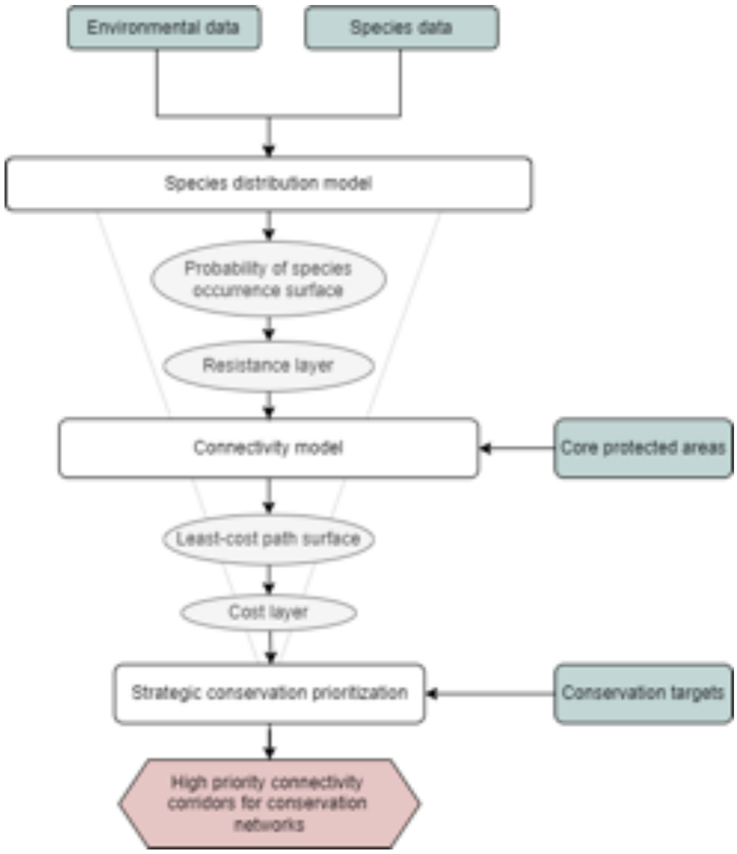

Figure 2: Modelling framework

The hierarchical framework uses easily accessible datasets including species occurrence points, environmental covariates, a map of existing protected areas, and conservation targets to build a series of models that will ultimately produce a map of the corridors of highest connectivity to inform the selection of the NRN. While this paper proposes several modelling tools and evaluative, the choice of modelling software remains customizable depending on the purposes of the end product.

For this study, an ensemble species distribution model will first be conducted using the extensive presence-only bat records from TVERC. TVERC validates their species data with a quality check process, so citizen science records are verified by experts in the field (TVERC, 2020). Using widely available presence-only data allows the tractable modelling framework to be more transferable and scalable to other counties with sparser species datasets. There is also uncertainty surrounding presence-absence datasets, where the detection of a true and significant "absence" requires high sampling effort and detectability (Lobo, Jiménez-Valverde & Hortal, 2010; Grimmett, Whitsed & Horta, 2020). The ensemble model will aim to address some of the limiting assumptions of correlative SDMs to create a reliable probability surface. The SDM output surface will then be transformed in ArcGIS into the resistance layer for a connectivity model. A least-cost path connectivity model will then measure structural/potential connectivity and identify the optimal paths between existing protected areas and produce a raster surface representing species movement and presence routes. This surface will be used as a "cost" surface in an optimization algorithm, which will be constructed with a SCP coding library. With bats as the focal species, the SCP algorithm will identify the bottlenecks of species movement and optimal zones for the focal species connectivity. Various previous studies have incorporated seascape connectivity metrics into SCP algorithms (largely using Marxan), but very little landscape studies have taken this approach. As such, this framework will further act as a proof of concept for integrating landscape connectivity metrics into conservation prioritization (Weeks, 2017; Beger et al., 2010; Engelhard et al., 2017).

1.5 Bats as focal indicator species

The focal species approach is based on the umbrella species concept, where the functional needs of the wider biodiversity can be encapsulated by one species (Lambeck, 1997). This differs from a single and narrow species approach which focuses more on species-specific preferences, but instead encapsulates an evaluation of the landscape based on realistic species movement and advocates high quality habitats for a whole suite of species (Lõhmus et al., 2020). In particular, this approach can benefit counties with a lack of species records and allow a more efficient modelling process that reduces the noise of individual species preferences. The Healthy Ecosystems Restoration Oxfordshire (HERO) network, a convening initiative that brings together the different nature recovery implementers and researchers across the county, also advocated for a species-targeted approach using a shortlist of keystone species to be selected as proxies for other ecologically similar species for nature recovery strategies (HERO, 2021).

Bats were chosen as the focus of this study as focal species. Their ecological preferences in or near woodlands, water bodies, and urban development allow them to share and represent a wide range of ecological niches in Oxfordshire, highlighting critical habitat and favouring connectivity features such as hedgerows (Lacoeuilhe et al., 2018; Altringham, 2014). As aerial species, bats have high mobility and are less constrained by terrestrial barriers, but due to their body sizes, their dispersal range is also small with relatively high home range fidelity (Hillen, Kiefer & Veith, 2009). This study benefits from bat ecology, as it simplifies the landscape from a high amount of connectivity barriers but also maintains small ranges, which are shared with various other small mammals common in Oxfordshire (Oxfordshire Mammal Group, 2017).

Bats are also a bioindicator species, which are species sensitive to environmental change, and as a result, changes in their population numbers or health can be indicative of the health of the ecosystem they live in. Indicator species typically have a widespread distribution, clear and distinguishable taxonomy, high on the trophic level, and sensitive to habitat loss (Spector & Forsyth, 1998; Jones et al., 2009; Li & Kalcounis-Rueppell, 2018). Jones et al. (2009) wrote one of the most comprehensive studies on bats as bioindicators, and the researchers argue that bats can exhibit all these traits well - bat taxonomy is largely stable except for the recent discovery of a few cryptic species, and the slow reproductive cycle allows bats to show clear population trends, including rapid declines. Bats in the UK are also insectivores, and this higher trophic level allows for interaction with a variety of other species as well (Alleva et al., 2006). Furthermore, the geographical distribution and the abundance of bats allow them to be bioindicators around the world (Kunz, 1982). As such, bats can fill a variety of ecological niches due to this high functional diversity.

For the policy context, all bat species in the UK are under national and international protection. Internationally, the UK is a signatory of the EUROBATs agreement (1994) where 51 bats and their roosts are protected by legislation (Joint Nature Conservation Committee, 2020), as well as the Convention on Migratory Species (1983) (Convention on the Conservation of Migratory Species of Wild Animals, 1979). Nationally, there has been a series of legislation, such as the Wildlife and Countryside Act (1981) and the Conservation of Habitats and Species Regulations (2017) that set out and enforce protection rules for bats (Bat Conservation Trust, 2016). In 2018, Defra published a list of indicator species to measure progress to combat biodiversity loss, and eleven bat species were listed in this catalogue: brown long-eared bat, common pipistrelle, Daubenton's bat, greater horseshoe bat, lesser horseshoe bat, Natterer’s bat, noctule, serotine, soprano pipistrelle and whiskered/Brandt’s bat (the latter two species cannot be separately distinguished during monitoring surveys and so are treated as one species group) (Joint Nature Conservation Committee, 2020).

2. METHODOLOGY

The study area is Oxfordshire County in Southeast England, with an area of 2,605 km^2 and a population of 725,300 in 2021 (Oxfordshire County Council, 2021b) (Fig. 3). All analyses were done in the OSGB36 British National Grid - EPSG:27700 projection. The Oxfordshire Wildlife and Landscape Study (OWLS) divided the county into several landscape character areas, which are used in reference to broad regional stretches throughout the rest of this paper.

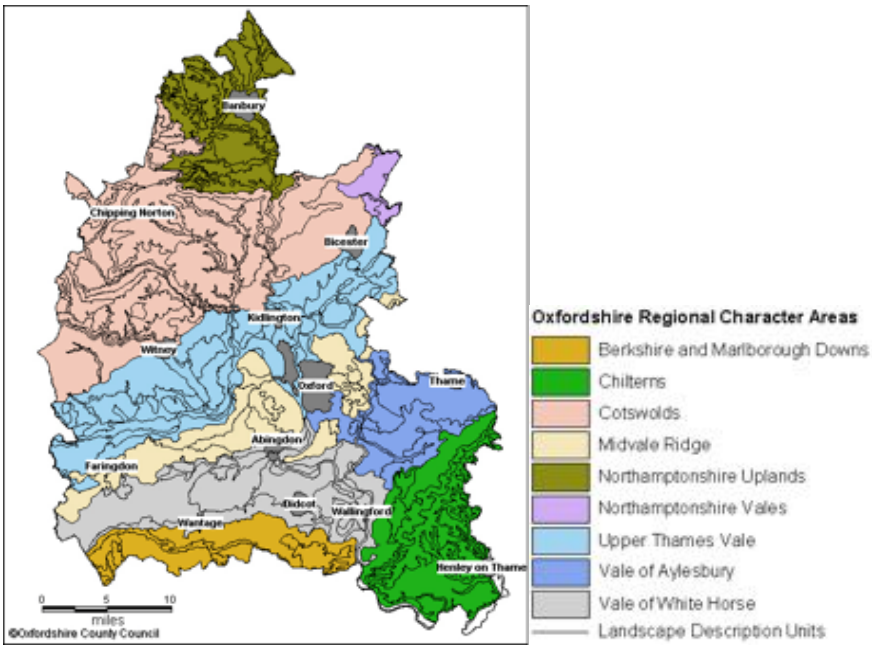

Figure 3: Map of Oxfordshire character zones (OWLS, 2004)

2.1 Data and preprocessing

The data needed for the three-step modelling process can be simply seen as three main components: the species data, the environmental covariates, and existing protected areas (cores). The full GIS workflow is detailed in Appendix 1.

2.1.1 Species data

Several data wrangling and cleaning steps were taken to ensure the dataset is relevant and scoped to fit well within the constraints of the study area and research period. The species records were extracted from 2019 to 2022 to maintain the relevance of current distributions, but also to take into account the impact COVID-19 has had on sampling effort by including a pre-pandemic year as well. The TVERC data also included values for abundance, but the data was not used for the scope of this paper as species abundance distribution requires absence data as well (Pearce & Boyce, 2006).

Eliminating spatial autocorrelation is also one of the main concerns of presence-only data, and there is no perfect methodology to address it (Franklin, 2010:p.139; F. Dormann et al., 2007). Studies agree that the best tools to use are to spatially filter (rarefy) the occurrence points and build a bias file, a raster surface that limits where background points are selected to limit them to locations closer to the rest of the distribution points (Fourcade et al., 2014; Brown, 2014; Hawkins et al., 2007). The species occurrence data were spatially rarefied in ArcGIS Pro using SDMToolbox (Brown, Bennett & French, 2017), a Python open-source toolbox for creating input files for SDM models. The rarefying tool used a distance parameter to remove points within a certain buffer zone. The distance value used for this analysis was 200 meters, which was chosen based on habitat heterogeneity - the recommended criteria by past literature, as well as average generalist dispersal distance (Boria et al., 2014; Anderson & Raza, 2010; Pearson et al., 2006; Mimet et al., 2020). The distance away from a habitat feature from a certain cell also tends to be approximately 200m according to histograms produced from the Euclidean distance analysis.

Eleven bat species were selected using the Defra biodiversity indicator guidelines: brown long-eared bat, common pipistrelle, Daubenton's bat, greater horseshoe bat, lesser horseshoe bat, Natterer’s bat, noctule, serotine, soprano pipistrelle, and whiskered/Brandt’s bat (Defra et al., 2021; Boughey & Langton, 2021). Due to high computational times of the modelling process (~5 hours per model), the species are then categorized into functional guilds representing two major specialist habitat types to use as surrogates for analysis. There is a lot of habitats overlap between the species as bats in the UK all tend to prefer similar habitat types - woodlands with accessible meadows and riparian zones, with linear features such as treelines and hedges to traverse (Walsh & Harris, 1996).

A literature review was conducted for the categorization but the Bat Conservation Trust guidelines on “woodland specialist” bat species were used to determine guild membership (Table 1). The average dispersal distances were also determined through several sources and was inputted into later steps of the analysis. Bat roosts alongside flight sightings were included as presences to consider the full home range, from foraging habitat to colonies.

Table 1: Literature review determining bat guild membership and dispersal distances

Functional guild	Species	Evidence for guild membership	Dispersal distance
Riparian specialists	Daubenton's bat *Myotis daubentonii*	Downs & Racey, 2006; Todd & Williamson, 2019	**2.3 km** (Dietz, Encarnacão & Kalko, 2006)
	Soprano pipistrelle *Pipistrellus pygmaeus*	Lundy & Montgomery, 2010; Rachwald et al., 2016; Todd & Williamson, 2019	**2 km** (Vaughan, 1997)
Woodland specialists	Natterer's bat *Myotis nattereri*	Bat Conservation Trust, 2010; Ciechanowski, 2015)	**3 - 5 km** (Smith & Racey, 2008)
	Noctule bat *Nyctalus noctula*	Bat Conservation Trust, 2010; Ducci et al., 2019; Mackie & Racey, 2007	**4 km** (Mackie & Racey, 2007)
	Lesser horseshoe bat *Rhinolophus hipposideros*	Bat Conservation Trust, 2010; Reiter et al., 2013	**1.5 - 6 km** (Billington & Rawlinson, 2006)
	Brown long-eared bat *Plecotus auritus*	Bat Conservation Trust, 2010; Murphy et al., 2012	**2.8 - 3.3 km** (Veith et al., 2004)
	Whiskered bat and Brandt's bat *Myotis mystacinus &*	Bat Conservation Trust, 2010; Kurek et al., 2020	**3.2 - 5 km** (Buckley et al., 2013; Dietz &

	Myotis brandti		Kiefer, 2016)
Generalist	Common pipistrelle *Pipistrellus pipistrellus*	Mimet et al., 2020; Rachwald et al., 2016; Regnery et al., 2013	**500m - 5 km** (Lacoeuilhe et al., 2018; Avery, 1985)
	Serotine bat *Eptesicus serotinus*	Ciechanowski, 2015; Tiede et al., 2020; Tink et al., 2014	**2 - 6.5 km** (Catto et al., 1996)

There are some elements that cannot be included in the scale of this multi-species analysis. For example, life stages, migratory paths, mating and breeding areas, and roost selection need to be taken into consideration to model functional connectivity and realized niches.

2.1.2 Environmental data

Environmental or explanatory variables were raster datasets obtained from a variety of different sources. Due to the small scope of the study area, using the classic bioclimatic variables from WorldClim often seen in species distributions models was not appropriate, as the highest publicly available resolution is 1 km^2 (Segal et al., 2021). Segal et al. (2021) also proved that downscaling the data to a finer resolution was also insufficient as there is minimal climatic variation across the county, and thus bioclimatic variables would not hold significant predictive potential. Oxfordshire currently does not have sufficient microclimate data that would have been able to replace the bioclimatic variables either. As a result, the most essential environmental variables were land use datasets, including a vector polygon land use map and linear hedgerow map which was then rasterized (Smith, 2021).

A digital elevation model (DEM) was obtained from the Japan Aerospace Exploration Agency using the ALOS satellite, which is available at a 30-meter resolution (JAXA, 2021). Aspect and slope were also variables that were extracted from the DEM using their respective tools in ArcMap Pro. An additional variable of a normalized difference vegetation index was also calculated from USGS Landsat 8 Collection 1 Tier 1 OLI raw scenes using the equation NDVI = (Near Infrared - Red) / (Near Infrared + Red), to identify areas of high vegetation coverage and urban extent (USGS, 2022).

Lastly, depending on the species guild, different Euclidean distance rasters were also added to selectively weight preferential habitat. This data was derived from the land use polygon feature class, with the relevant features selected by attribute and exported. A Euclidean distance tool was run on the exported features, a commonly used methodology including categorical data in species distribution models (Hollings et al., 2017; Rainho & Palmeirim, 2011). For water-biased species which are observed near a diversity of different water bodies including running and still, the included environmental variable was 'distance to water', with features that include "water", "canal", "fen, marsh, and swamp", "reedbed", "reservoir", "running water", and "standing water". For woodland-biased species, the only feature selected was "woodland: broadleaved", as Ciechanowski (2015) found that many of the selected species for this study avoided coniferous and mixed forests (Ciechanowski, 2015). A multicollinearity test on all environmental covariates was run using the SDMToolbox, and the aspect layer was removed. None of the other environmental variables were highly autocorrelated.

2.1.3 Core areas - existing protected areas

The core zone of the TVERC draft NRN was used as the existing protected area polygon, or the main nodes in the connectivity analysis. It covers approximately 11% of Oxfordshire and includes existing protected sites such as Special Protection Areas, Sites of Special Scientific Interest, Ramsar sites, local nature reserves, Woodland Trust reserves, and more (TVERC, 2020). The AONBs are not included as a part of the core protected areas, because they cover such large areas and are thus managed as landscape characters and include large areas of intensive farmland. Due to the extensive processing time of the connectivity analysis and the complexity of the core polygon edges, the core areas are selected based on their proximity to bat observances and size. Taking into consideration the dispersal distance of bats (Table 1), a two-kilometre buffer was set around each occurrence point, and core areas were selected based on their intersection with the buffer distance. Sites that are larger than 10 hectares were filtered and selected, with a focus on assessing "bigger" reserves (BBMJ) and to manage runtime.

2.2 Modelling

2.2.1 Species distribution modelling using BIOMOD2

The species distribution modelling was done in R using the 'BIOMOD2' package for ensemble modelling (Thuiller et al., 2009) (Appendix 2). In order to increase the robustness of the model given only presence-only data, which is often the case of environmental records for counties in the UK, the BIOMOD2 package was chosen for its ability to conduct several different SDM algorithms, identify the best model results, merge them with a weighted means algorithm and create ensemble model results. Ensemble forecasting is an increasingly popular SDM methodology as it can combat some of the limitations of individual algorithms but allow for comparison between the performance of various algorithms and explore a range of distribution predictions (Aguirre-Gutiérrez et al., 2013; Araújo & New, 2007; Hao et al., 2019). An increasing number of studies have also found that ensembles have better predictive power as well (Friedman & Popescu, 2008; Seni & Elder, 2010). Though it is also important to address the limitations, as seen by a study by Hannemann et al. (2015), which found that unstable species responses to environmental covariates can still limit the ability for ensemble algorithms to rectify the faults of individual models (Hannemann, Willis & Macias-Fauria, 2016).

The algorithms chosen for the ensemble analysis were the generalized linear model (GLM), generalized additive model (GAM), generalized boosted model (GBM), random forest (RF), and maximum entropy (MAXENT). These models were selected for their complementarity in creating a hybrid of two regression-based (GLM and GAM), two tree-based (RF and GBM), and other models (MAXENT), also with varying parametric and non-parametric classifiers for computation (Valavi et al., 2022; Aguirre-Gutiérrez et al., 2013). The ensemble model selected was a weighted means calculation, which preferentially weighs the individual models that have the best performing results before merging. Studies have found that weighted means is able to significantly improve model predictive power and forecasting compared to other popular methods such as committee averaging (Marmion et al., 2009; Jinga, Liao & Nobis, 2021). A 0.6 threshold was also used to filter out models that performed below a TSS score of 0.6 in order to optimize the ensemble model performance (Thuiller et al., 2009).

In order to optimize the algorithm performance, modelling options and parameters were carefully chosen. Merow et al. (2013) emphasizes the drawbacks of using default Maxent parameters and instead, demonstrates the importance of setting locally specific input parameters for MAXENT in determining model outputs and accuracy (Merow, Smith & Silander, 2013). For MAXENT, an additional analysis was coded in R using the ENMeval package (Appendix 3), which produced a bias file using two-dimensional kernel density estimation. The analysis also identified the best feature classes and regularization multiplier parameters for each individual species guild, selecting the parameters that had the lowest delta Akaike Information Criterion (AIC) score (Appendix 5) (Kass et al., 2021). Features are mathematical transformations of the environmental covariates, and the regularization parameter works to limit the fit of the model distribution to avoid overfitting - a smaller multiplier will produce a localized fit, while a larger multiplier can result in a more distributed fit (Phillips, Anderson & Schapire, 2006). Bias files were not yet supported with the BIOMOD2 package, but a comparison was run using the BIOMOD Maxent results and the Maxent results from the standalone interface, and there was little difference in the AUC/ROC scores. The package also checked for potential background points and as there were 4,400,405, the library and literature recommended 10,000 background points (Kass et al., 2021; Barbet-Massin et al., 2012). 1000 trees were selected for the RF (Valavi et al., 2021), and for GLM, an interaction level of 1 and a quadratic formula were specified. A mixed GAM computation vehicle algorithm (mgcv) was used for the GAM analysis for a more robust smoothing parameter (Zurell et al., 2020; Larson, 2015). The models were run with 10,000 pseudo-absence points using a random selection strategy, two selection iterations were run to account for variability (Descombes et al., 2018; Barbet-Massin et al., 2012).

For model evaluation, ten evaluation runs were conducted; 80% of the data was partitioned to train and calibrate models, with 20% used for testing. The evaluation of SDM models is also a critical consideration of the analysis, and thus, another benefit of choosing the BIOMOD2 library was its ability to calculate true skill statistics (TSS) scores. TSS can compensate for the reliance on prevalence from the kappa statistic and when compared to AUC, specificity, and sensitivity scores, TSS was able to produce more realistic results (Allouche, Tsoar & Kadmon, 2006; Somodi, Lepesi & Botta-Dukát, 2017; Shabani, Kumar & Ahmadi, 2018).

2.2.2 Connectivity modelling using Linkage Mapper

The connectivity model was conducted in Linkage Mapper, a least cost path (LCP) tool built in Python and operated in ArcMap 10.8 (McRae & Kavangh, 2011). The TVERC draft NRN similarly used a least-cost approach, using expert opinion to assign a cost value for each land use type to represent how permeable the landscape is to the focal species, and using a QGIS cost-distance tool to identify the pathways. LCPs are based on network theory and uses Euclidean distance and cost allocation calculations to construct pathways between core areas. It uses Voronoi polygons to divide the core area into different vertices to connect to other polygons, which means edge complexity is an important variable. Linkage Mapper expands upon least cost paths by producing multigraph pathways instead of a singular least cost link connecting nodes (Walker et al., 2019).

In Raster Calculator, the SDM surfaces were normalized to a scale of 0 to 1 and inverted to create the resistance raster. This is done so the highest probabilities of presence were represented as 0 instead of 1, to reflect high permeability (low cost) instead of high resistance for the least cost path analysis.

The pairwise analysis was selected to find connection of each core to any other potential reachable core. The model then located adjacent cores using a cost and Euclidean allocation method, and a network of core areas constructed using a cost-weighted and Euclidean network adjacency method. The dispersal distance for each species guild was taken into consideration in parsing the corridors, where the 5 km was inputted as the maximum corridor distance (Altringham & Kerth, 2016; Davidson-Watts, Walls & Jones, 2006; Bontadina, Schofield & Naef-Daenzer, 2002; Rainho & Palmeirim, 2011). For an exploratory evaluation, the corridors were ground-truthed with remote sensing imagery to see if existing bat occurrences are captured by the corridors.

Several metrics were calculated to quantify the importance of the cores and links for connectivity. The ratio of the cost-weighted distance (CWD) to the Euclidean (CWD:Euc) and least-cost path (CWD:LCP) were calculated to evaluate linkage quality. CWD:Euc represents the resistance of the corridor relative to their distance to the core node, with a higher ratio indicating that the two distances are similar, and thus a lower resistance for travel while CWD:LCP measures the resistance along the path of least resistance (Qiangqiang et al., 2019; Feng et al., 2021; Dutta et al., 2022). Additionally, the current flow betweenness centrality was calculated to evaluate the importance of the cores (nodes) for connectivity. Betweenness centrality was identified in the literature as the most useful in the suite of centrality metrics for determining how each node contributes to the conductance of the landscape (Estrada & Bodin, 2008; Poodat et al., 2015). This was calculated through a separate Centrality Mapper tool, which was run using the same Python toolbox as Linkage Mapper, but it integrates Circuitscape algorithms to deduce how topologically important a node is within a graph network (Pereira, Saura & Jordán, 2017; Brodie, Mohd-Azlan & Schnell, 2016; McRae & Kavangh, 2011). Using circuit theory, each link is assigned a resistance value determined by the cost-weighted distance, and 1 Amp of electric current is injected into each core and adds the current flow out of each core to evaluate its importance (Carroll, McRae & Brookes, 2012; Keeley, Beier & Jenness, 2021).

2.2.3 Spatial conservation prioritization using prioritizr with the Gurobi optimizer

The SCP analysis was conducted in R using the Gurobi optimizer integrated into the ‘prioritizr’ package (Gurobi Optimization, 2022; Hanson et al., 2022) (Appendix 4). It is a multiple integer linear programming (MILP) solver and is currently the fastest solver available as it was found to outperform Marxan, a simulated annealing heuristic solver, in identifying the least cost solutions with the fastest calculation time (Schuster et al., 2020; Beyer et al., 2016). Integer programming solvers are the basis of prioritization solvers and has been used for reserve selection before heuristic algorithms like Marxan (Underhill, 1994). In brief, they are designed to minimize the cost value of establishing reserves given a set of constraints and a target – either reserve size or conservation feature representation (Moilanen, Wilson & Possingham, 2008).

The data inputs for an SCP algorithm includes three key components: planning units, conservation features, and conservation targets. Oxfordshire was first divided into 66,364 square

200m^2 planning units, which are gridded spatial units used to determine the cost value of each parcel and implement action (Daigle et al., 2020). The resolution was scaled up from the 30m resolution of the SDM and connectivity analysis given the computing intensity of the models. 200m^2 was carefully chosen after trialing planning unit sizes with 50m, 100m, 300m, 500m, and 1km, and was selected for its computing efficiency (~20-30-minute processing time) and high enough resolution to allow for habitat heterogeneity to be represented (Mo et al., 2019). Furthermore, planning units that are too small are 1) computationally intensive and 2) reduced efficiency with too small planning units (Ball, Possingham & Watts, 2009).The cost values were derived from the connectivity raster, which represents both species distribution and movement. The connectivity raster was converted into points and spatially joined to the planning units using the mean connectivity value for each. The existing core areas were also spatially joined with the planning units to identify which planning units are already protected. The conservation features are rasterized habitat files of woodland and freshwater bodies. Hedgerows were not included in the SCP analysis because they are too fine scale, and if the hedgerows raster was resampled to 200m, it would cover nearly the entirety of the county, as if there are any hedgerow coverage in the 200m planning unit, it would be considered a full hedgerow site because of the binary character of the hedgerow raster. SCP modelling requires "targets" to be set, representing the proportion of a conservation feature that should be protected. For instance, a meadow feature of 20 planning units with a 50% target means 10 planning units will be selected for conservation. This is often determined through iterative discussions with local stakeholders such as environmental NGOs, farmers, landowners, parish, and town councillors, and more. Given the scope of this study, it was impractical to conduct stakeholder engagement, and as such, two proxy targets of 50% from TVERC's Draft Nature Recovery Strategy and 30% from Smith et al. (2021)'s analysis will be used to allow for comparison (Ferrier, Pressey & Barrett, 2000). The 50% target will also provide more leeway for integrating stakeholder engagement in future research,

The problem formulation was designed using a minimum set objective, which aims to minimize cost during the design of the solution, where the cost value can be anything such as land cost or species dispersal cost. A low boundary penalty parameter was also included to slightly favour spatial clumping.

Lastly, the two statistical metrics were calculated to evaluate the performance of the prioritization solution. The irreplaceability of selected planning units was first evaluated using Ferrier's score (2000), a metric to evaluate the importance of a site in helping achieve the pre-set conservation target (Ferrier, Pressey & Barrett, 2000). Irreplaceability as defined by Pressey et al. (1993), is how important is a planning unit in achieving the target, or the lost cost if the site is not protected. The Ferrier's score can be a complex calculation given different SCP scenarios, but for this analysis, the Ferrier's score indicates how frequently a planning unit with a certain set of conservation features is selected given all possible site selection iterations (Ferrier, Pressey & Barrett, 2000). It is a calculation of how representative a site is for conservation features. A representation statistic was also calculated using a *prioritizr* package function to see how well conservation feature is currently protected by existing core areas, and how well the new proposed network protected it.

3. RESULTS

3.1 Species distribution models

As expected, the species distribution models between the bat guilds are similar given their widespread distribution and similarity in habitat, despite having specialist habitat types. There was also a high preference for population centres, as seen with the high probability of occurrence in Oxford City, Witney, Abingdon, Wallingford, Henley-on-Thames, Bicester, Banbury, and many others. This is highly likely due to the skewed citizen science recording effort that favours locations that are easily reachable. It could also likely that bats also prefer population dense centres given their urban ecologies - there are typically high invertebrate populations and many high potential roosting sites in older infrastructure and green spaces with street trees (Altringham, 2014).

An interesting phenomenon can also be observed where the middle of city centres typically has a lower probability of occurrence for riparian specialists than the margins of the city or town, often with a stark delineation. This is most easily seen in Carterton, Banbury, Bicester, Oxford, and Didcot. Wildlife avoiding areas of high human density may seem intuitive, but for synanthropic species such as bats, there is fairly little evidence that states bats avoid centres of high human activity (Li et al., 2020; Lehrer et al., 2021). Lehrer et al. (2021) was the first study to provide evidence that bats avoided areas of urban noise. It is likely that for the riparian species model, these are areas far from aquatic bodies, which was a preferentially added environmental variable, indicating the habitat specialism of the two species in the guild (Fig. 4c). Woodland specialists and generalist guilds do not show the same behaviour (Fig. 4b).

The high resolution of the environmental data also allows a clear designation of land units to be visualized even in the model outputs, with the preferential selection of hedgerows and rivers showing particularly clear delineations of borders between arable land parcels. The environmental variable response curves also indicated that the most important variable was the habitat and distance to habitat raster for all three guilds. These linear features on the landscape of not just hedgerows but also rivers have been found to be highly important for bats, a well-studied habitat feature for bat movement (Boughey & Langton, 2021; Lacoeuilhe et al., 2018).

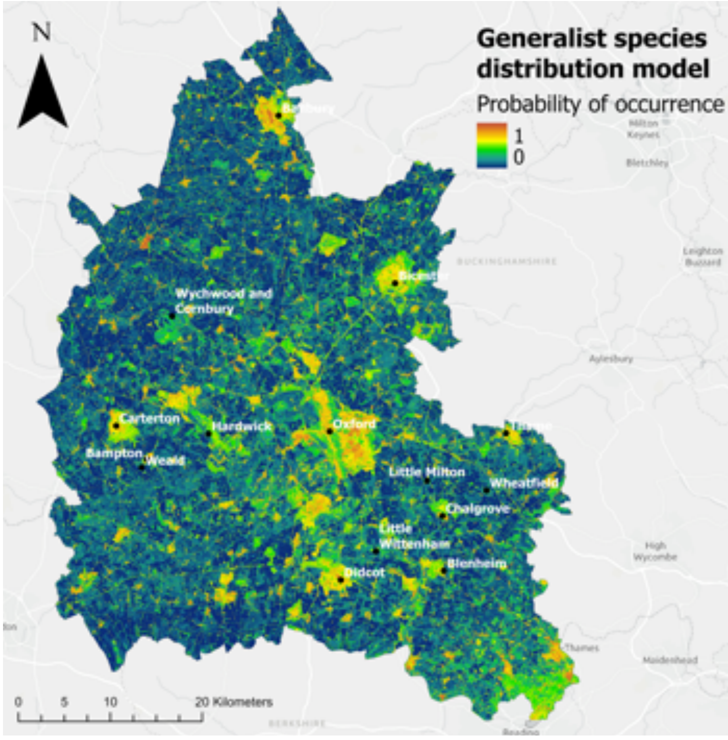

Figure 4a: Generalist species SDM

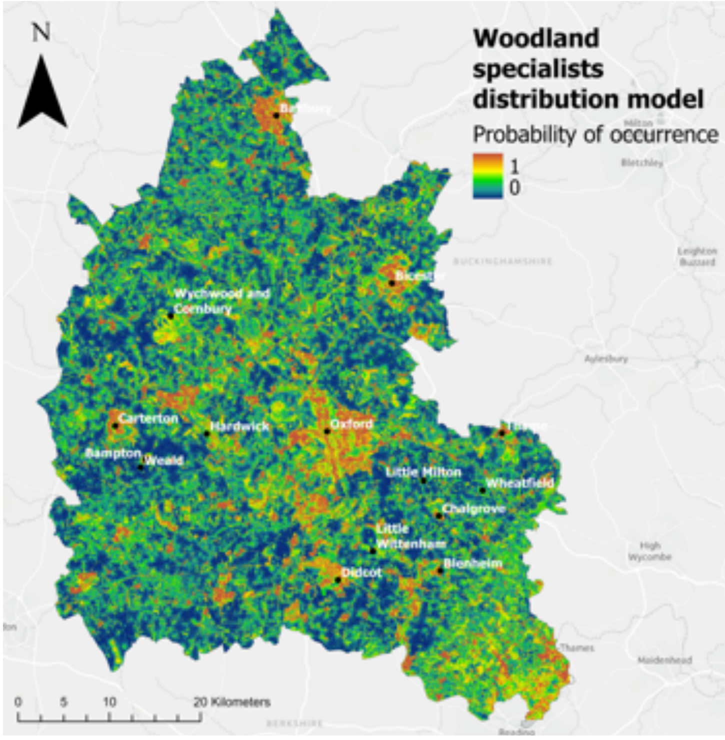

Figure 4b: Woodland specialists SDM

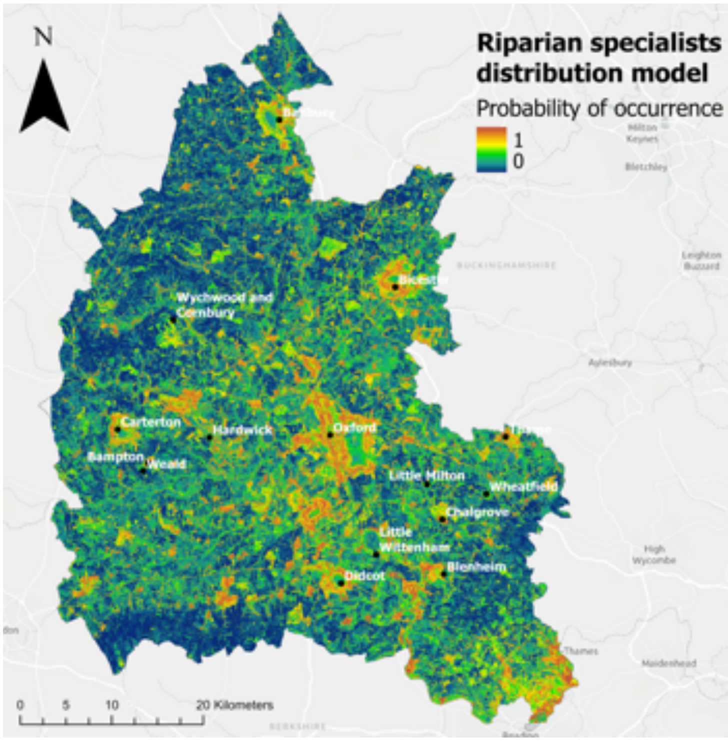

Figure 4c: Riparian specialists SDM

Figure 4: Ensemble species distribution models for three bat species guilds in Oxfordshire merged with weighted means algorithm

Data: NDVI (USGS), DEM (JAXA ALOS), Natural Capital habitat map, species occurrences (TVERC)

CRS: OSGB36 British National Grid - EPSG:27700

Riparian specialists saw proportionally higher predicted occurrences around the Tar Lakes and other surrounding water bodies near Hardwick village. The River Thames can also be traced with areas of high probability of occurrence as well, showing almost a linear feature. There is also a relatively high preference for middle and lower regions of Oxfordshire, as there are relatively fewer water features towards the northwest in the Cotswolds and low woodland coverage in the Cherwell District. Riparian specialists showed the most restricted range of the three guilds – with high regions of potential occurrence focused on the Upper Thames Vale and Midvale Ridge character areas (OWLS, 2004).

In comparison to riparian species, woodland specialists found much higher preference for habitat in the Chilterns Area of Outstanding Natural Beauty (AONB), given its higher density of continuous woodlands. Wychwood Forest was also highlighted as an area with high probability of occurrence.

The generalist species results (Fig 4a) provide a perspective into the distributions of species with a widespread range. The city centres can be seen to be slightly more preferred in comparison to the two habitat specialist guilds, potentially due to the inclusion of serotine bat within this guild, which is known to be a synanthropic species (Ciechanowski, 2015). In particular, the generalist model can highlight some of the limitations of SDMs - the spatial autocorrelation of sampling efforts, which tend to be highest near population centres, are brought to the forefront, showing disproportionately high presence around major cities and towns in the county.

The minimum TSS score threshold for reliable models was determined to be 0.4 by Thuiller et al., 2019) and all models were above the threshold, but only models above 0.6 were selected (Table 2). Random forest algorithms consistently performed better than other algorithms, followed by the generalized boosted model, except for generalist species where the generalized linear model did better. RF and GBM are non-parametric models, which do not assume normal distribution of data unlike parametric classifiers (Gislason, Benediktsson & Sveinsson, 2006; Waske & Braun, 2009). Given the skewed unimodal curves of the SDM values, non-parametric models will likely perform better (Franklin, 2010). The high TSS scores for the ensemble model were also expected as evidenced in Jinga et al. (2021), where a weighted means algorithm can dramatically improve model accuracy. However, generalist species show the greatest distribution of occurrence probability lower than 50% (Appendix 6), which is reasonable given the widespread distributions capturing an equally wide range of environmental covariates often resulting in lower predictive accuracy of SDMs (Evangelista et al., 2008; Goedecke et al., 2020). The weighted means TSS scores for generalists; however, are unexpectedly high for the species guild. Potential underlying reasons could be due to low-pass filtering, which is when the average function of ensemble models result in a "cleaning effect" - as where isolated predicted occurrences are removed (Marmion et al., 2009; Grenouillet et al., 2011). This allows a more accurate fit and a reduction of overfitted models. The AUC scores are included as well as it provides an indicator for the sensitivity of the models, but not the specificity or accuracy of its predictions (Lobo, Jiménez-Valverde & Real, 2008; Ruete & Leynaud, 2015).

Table 2: TSS and AUC scores of individual and ensemble SDM models averaged between runs

	Generalists		Woodland specialists		Riparian specialists	
	TSS	AUC	TSS	AUC	TSS	AUC
Generalized additive model	0.535	0.799	0.587	0.855	0.5613	0.838
Generalized boosted model	0.659	0.819	0.619	0.878	0.640	0.863
Generalized linear model	0.530	0.803	0.555	0.858	0.607	0.860
Maximum entropy	0.375	0.700	0.595	0.877	0.627	0.858
Random forest	0.642	0.770	0.793	0.903	0.709	0.841
Weighted means ensemble	0.938	0.996	0.938	0.969	0.721	0.933

3.2 Connectivity models

Since the model outputs for the least-cost path analysis represent potential or structural connectivity, there is a high density of corridors across the Oxfordshire landscape as there is no representation of true barriers. Since there is no information on the locations of source and sink patches, omnidirectional least cost analyses are best able to represent corridors. The pathways are also relatively linear, which is expected of a least cost path model (Laliberté & St-Laurent, 2020). Gangadharan et al. (2017) found that least-cost paths (LCP) are preferred for finer scale analysis in comparison to other algorithms such as ones based on circuit theory, which allows LCPs to be better suited to the higher resolution analysis in this study. Similarly, to SDMs, the generalist species show the most diffuse pathways while specialists, especially riparian species, show the best delineated paths.

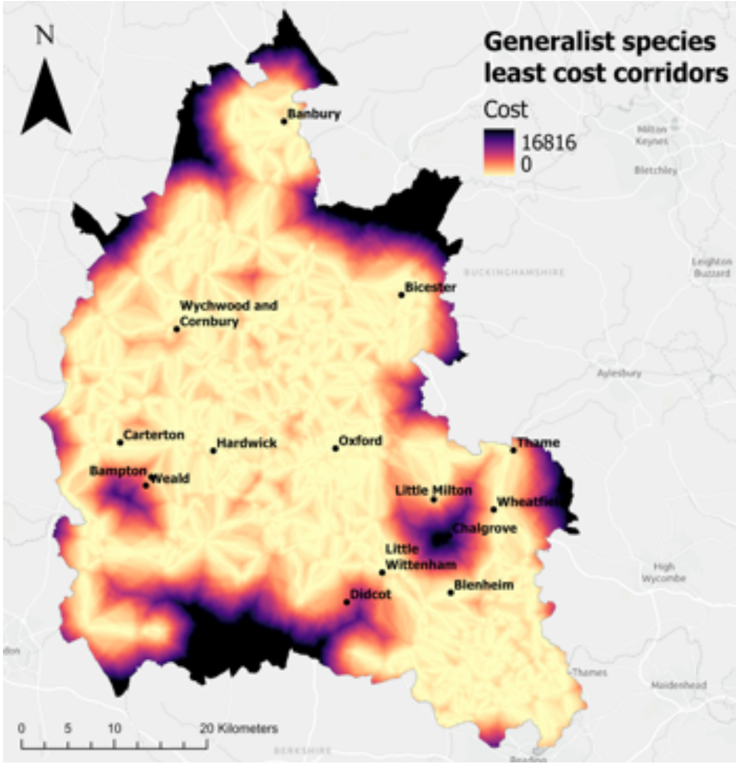

Figure 5a: Generalist species least cost corridors

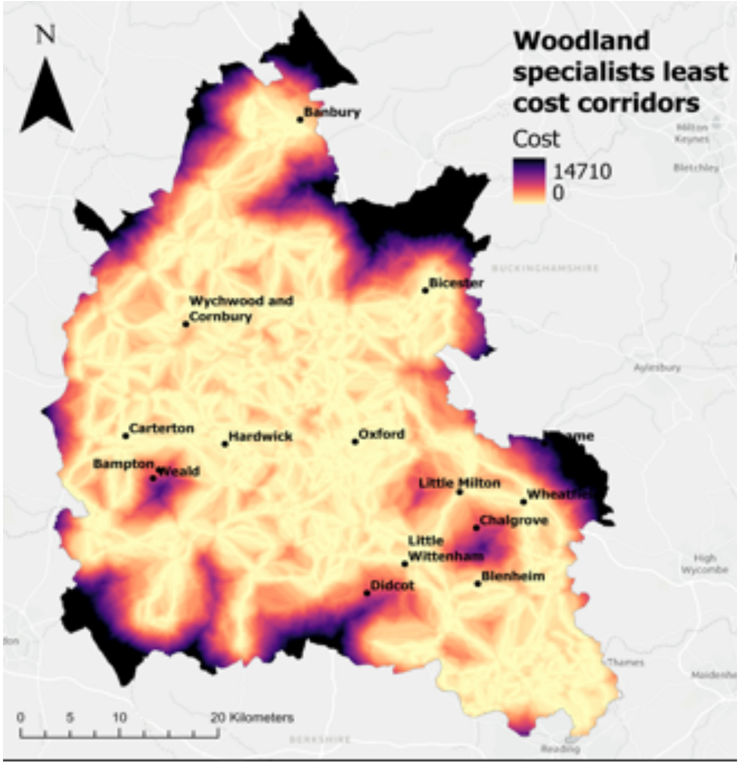

Figure 5b: Woodland specialist species least cost corridors

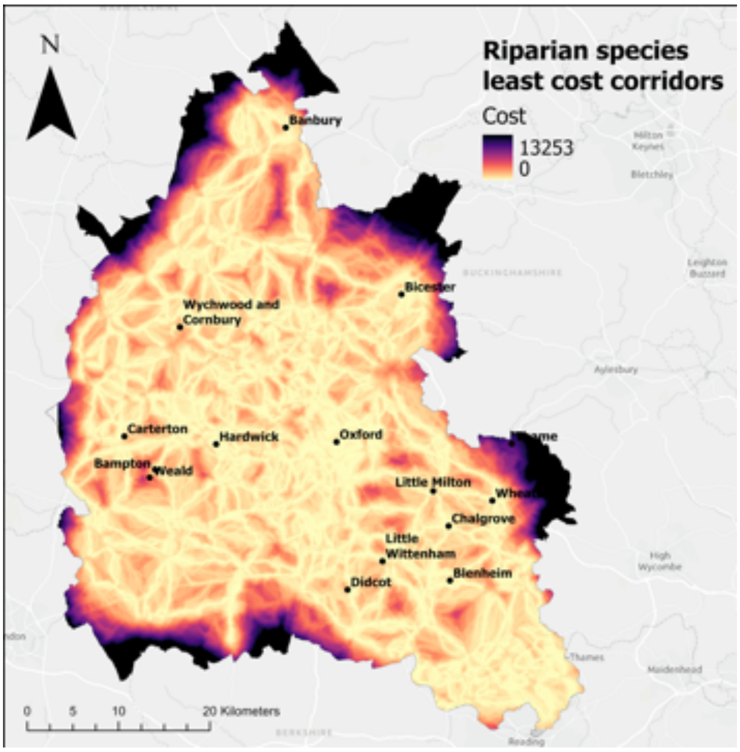

Figure 5c: Riparian specialist species least cost corridors

Figure 5: Linkage Mapper models for three bat species guilds in Oxfordshire

Data: Species distribution model raster surface, core nature recovery areas (TVERC)

CRS: OSGB36 British National Grid - EPSG:27700

For riparian species, zones of low connectivity (high-cost areas) tend to overlap with large and continuous patches of arable land, indicating low preference of passage over likely uncovered fields, regardless of the hedgerows. On the other hand, woodland specialists have a much higher avoidance of larger open areas, seen by two notable regions of low connectivity in Chalgrove, a village with an airfield, and Weald, a hamlet in Bampton parish. While the airfield likely removed the connectivity corridors through Chalgrove, Weald and Bampton have normal to high habitat suitability. It is likely that due to the connectivity pathways being truncated to 5 km and as there are no existing protected areas within or near the two towns, connecting corridors would exceed the maximum dispersal distance. The black edges (indicating the highest costs) are likely an artefact of the county borders, as there are no protected areas outside of Oxfordshire that were in the input core areas shapefile. As such, because there were no linkages outbounds, the peripheries of the county are not well represented for connectivity, which is likely not realistic.

The metrics calculated to evaluate the quality of links were CWD:Euc and CWD:LCP (Fig. 6), and for quality of cores, a centrality metric was calculated. High quality links means low cost of travel along the least cost path, meaning a lower ratio, indicating lower resistance along the path of movement (Feng et al., 2021). The high-quality linkages do not have a strong spatial pattern for generalists, as expected from their wide-ranging tolerance to environmental conditions. Similarly, woodland specialists also do not show a strong spatial preference, but there is a slight lean of strong linkages towards South Oxfordshire, where there are prevalent forest patches in the Chiltern AONB. For riparian specialists, the best linkages can also see in the Chiltern AONB and city centre.

The Centrality Mapper was another metric calculated, which evaluates the importance of the nodes in the graph. Centrality values can also indicate which smaller patches have a high connectivity value that might have been overlooked due to their size. These smaller patches are thus important for building stepping stone corridors between larger patches (Mallory & Boyce, 2019; Greenspan et al., 2021). As expected, the best cores are larger in size and closer to the centre of the county, but smaller cores in notably in Wheatfield, Little Wittenham, Cholsey, Little Milton, and Thame (all guilds) has centrality values rivalling cores eight times its size.

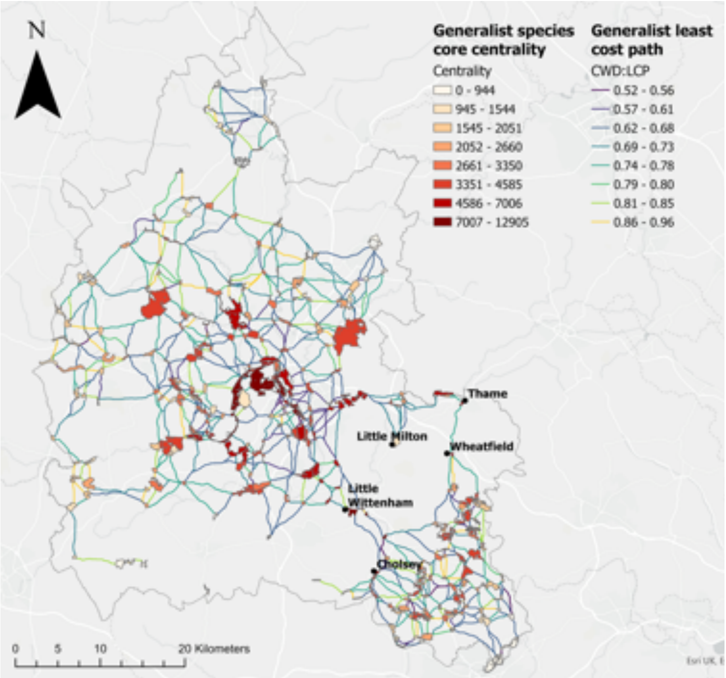

Figure 6a: Generalist species node centrality and link metrics

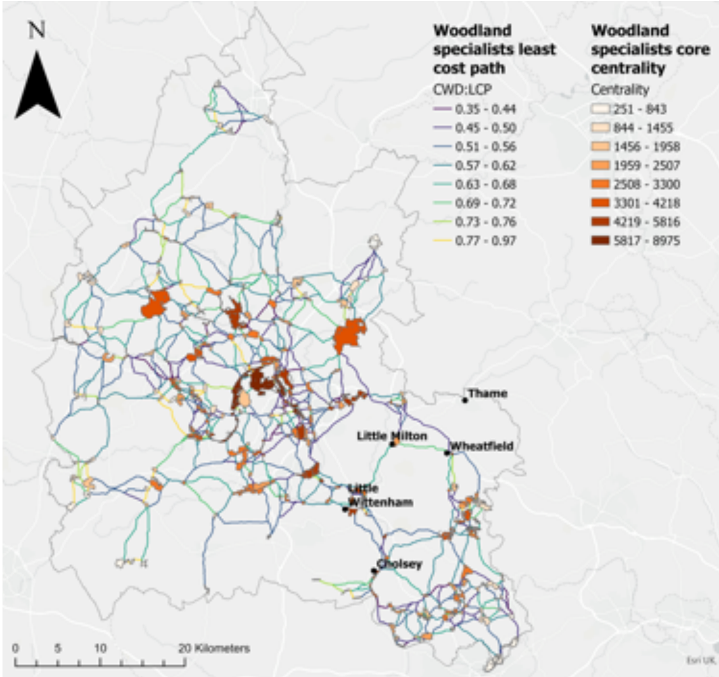

Figure 6b: Woodland specialists node centrality and link metrics

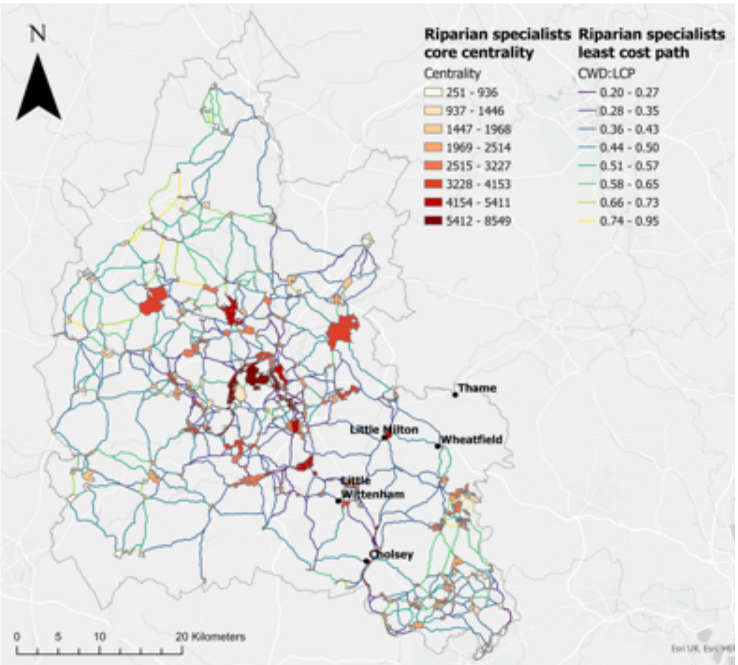

Figure 6c: Riparian specialists node centrality and link metrics

Figure 6: Current flow centrality metrics and cost-weighted distance to least-cost path ratio for three bat species guilds in Oxfordshire

Data: Least-cost path from Linkage Mapper, core nature recovery areas (TVERC)

CRS: OSGB36 British National Grid - EPSG:27700

3.3 Spatial conservation prioritization

The selected zones for recovery that maximizes connectivity are the pinch points, or bottlenecks, on the landscape for conservation. Other tools such as Pinchpoint Mapper, part of the Linkage Mapper toolset, was not used for this selection as it did not allow conservation targets to be set as a target feature for how much area to select. Within the SCP model outputs, the linear connectivity corridors from the Linkage Mapper model are clearly reflected (Fig 7), highlighting the best zones for establishing new conservation core areas. Most of the zones with high importance (Fig. 7b) are in the Upper Thames Vale and Midvale Ridge character zones, and a large part also overlaps with the Chilterns AONB. Feedback for TVERC's draft NRN also identified the need to increase connectivity between patches within the Cotswolds AONB.

While the selected corridors have a large degree of similarity between the three species guilds, there are significant differences between the area of corridors present, where the woodland specialist species have much stronger preference for certain pathways as seen by clearly delineated and wider but fewer corridors, while riparian species have many narrower, more disconnected corridors. The areas of high importance for both present and future conservation action is calculated by the Ferrier's score (Figs. 7b, 7d); however, are largely the same across the guilds. It is notable that the areas of high importance, or irreplaceability, largely overlap water features, including the Otmoor lake reserve, the private lakes around Hardwick, the Farmoor reservoir, the three adjoining Cresswell, Peninsula, and Oxey Mead Lakes, the lakes by Dorchester, the River Glyme dammed by Blenheim, and the Caversham Lakes bordering Reading. The preference for water features across all species is appropriate as UK bat ecologists identified that standing water (seen the lake preference from the Ferrier scores) results in high invertebrate populations, and the complex habitat assemblages of wetlands and riparian woodlands provide ample foraging and roosting grounds (Dietz & Kiefer, 2016).

While freshwater features are ecologically important and prioritized for connectivity, the representation of waterbodies in existing protected areas are already high, where ~50% of water features were already covered by core areas (Appendix 7). Woodland features were much more poorly represented, where only 22.7% were represented for generalist species (Appendix 7). This can indicate to the importance of focusing on protecting more areas of woodlands, while enhancing the habitat quality of existing protected water features.

Compared with the previous nature recovery networks conducted for Oxfordshire by both Smith et al. (2021) and TVERC, there are many overlapping areas of similarity (TVERC, 2020; Smith et al., 2021). Most importantly, all three analyses proposed recovery zones concentrated in the south-eastern Chilterns AONB, the horizontal stretch of the Midvale Ridge and the Upper

Thames character area, as well as patches in the Cotswolds AONB, above the Upper Thames strip. These are zones that already have a high number of protected reserves, which indicates the accuracy of the models that identified high ecological priority zones but also highlight that these areas will particularly benefit from corridors to connect the individual core patches.

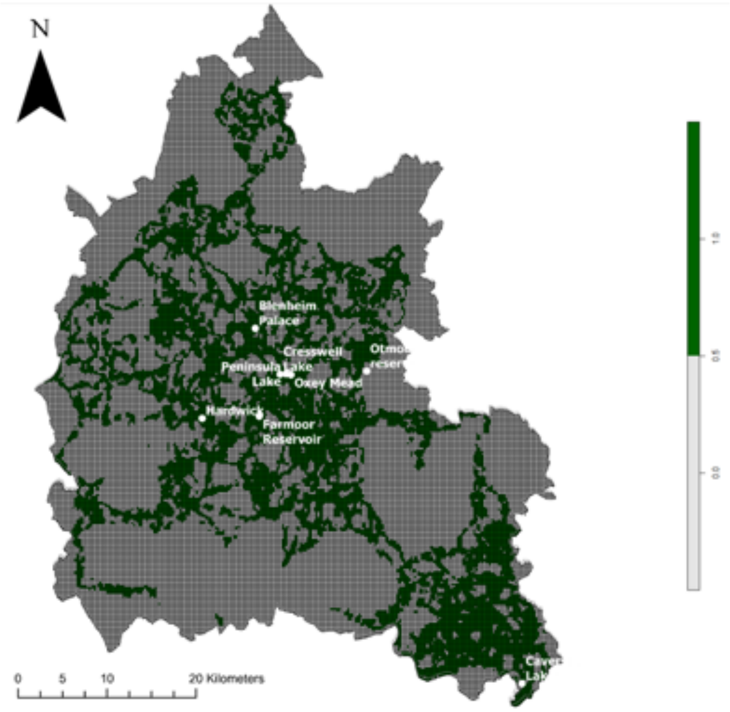

Figure 7a: Proposed nature recovery network for generalist bat guild in Oxfordshire with a 50% conservation target

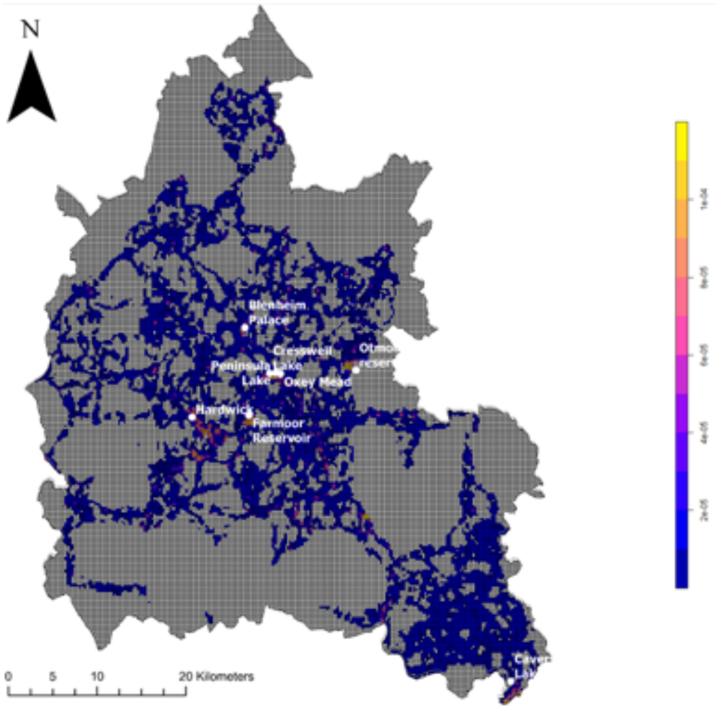

Figure 7b: Importance of selected nature recovery network for generalist bat guild in Oxfordshire with a 50% conservation target

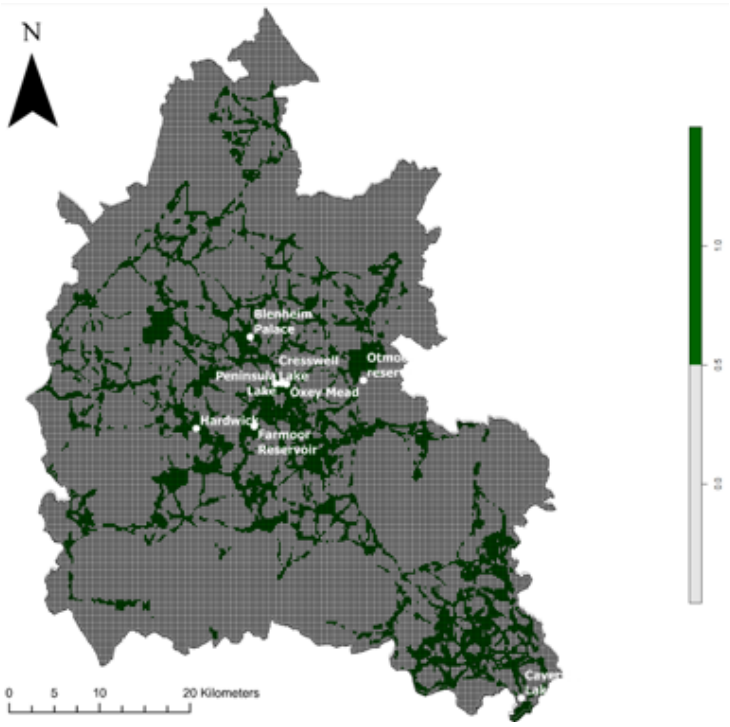

Figure 7c: Proposed nature recovery network for generalist bat guild in Oxfordshire with a 30% conservation target

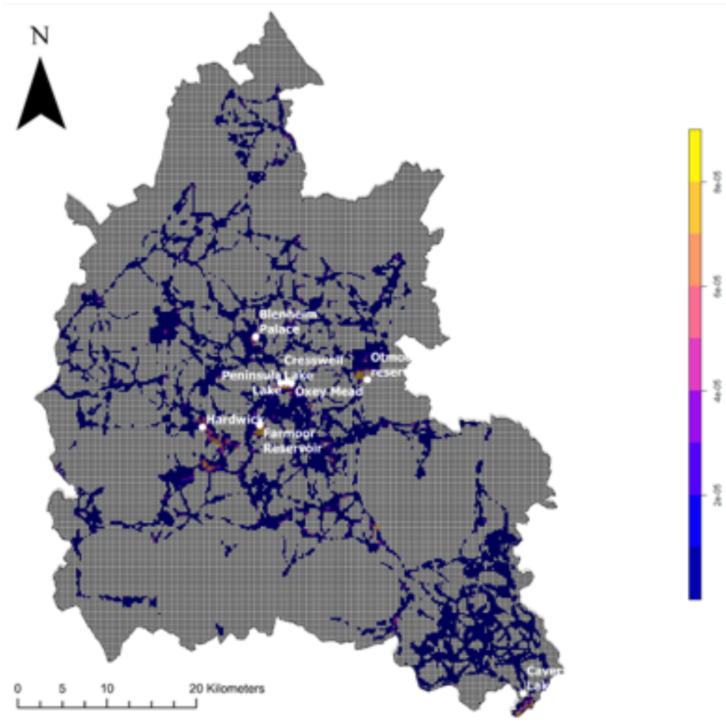

Figure 7d: Importance of selected nature recovery network for generalist bat guild in Oxfordshire with a 30% conservation target

See Appendix 5 for SCP maps for woodland and riparian specialists

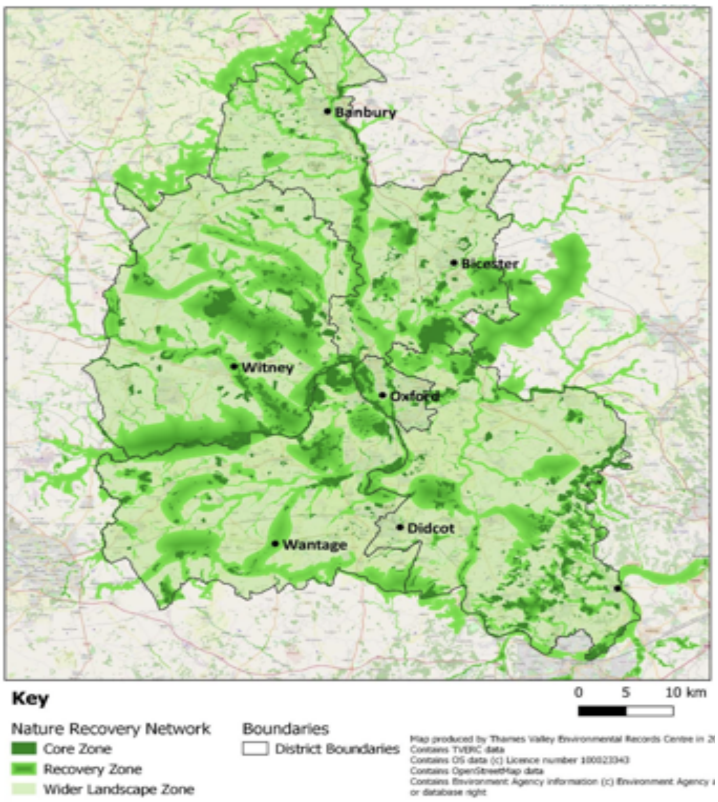

Figure 8a: TVERC draft NRN map (TVERC, 2020)

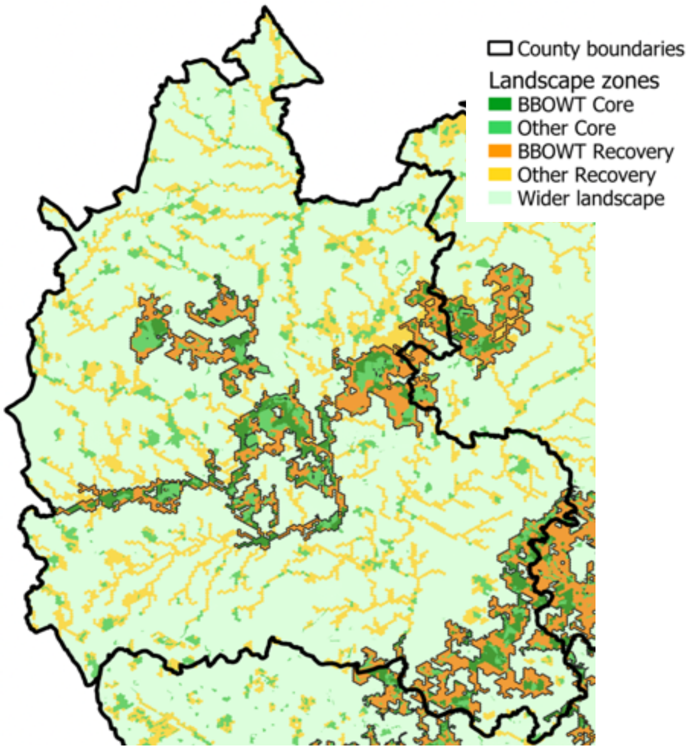

Figure 8b: Reformatted Smith et al. (2021) map (Smith et al., 2021)

4. DISCUSSION

4.1 Key findings

Counties across the UK are devising methods to design local nature recovery strategies for implementation to meet the scheduled 2023 LNRS completion date. While past UK environmental initiatives have taken into consideration connectivity, they were still heavily reliant on expert opinion and simplistic buffer and overlay analyses (Cunningham et al., 2021; Smith et al., 2021). Smith et al. (2021) emphasized the need for a transparent and precise methodology to identify and map NRN priority areas through tools such as systematic conservation planning, made increasingly accessible with new modelling software and data availability. This analysis aimed to respond to Smith et al. (2021)'s call for using SCP as the main instrument for the designation of the NRN; however, this analysis centres species connectivity, and pilots a novel modelling framework where ecological corridors are selected using a high-performance SCP solver. The findings reinforce the need for but also underscore the caveats of a connectivity-integrated SCP approach for designing an NRN.

The integrated framework allows a look into separate components within landscape connectivity, and it found that for bats, habitat suitability largely favours not only preferential habitat but also highly localized structures of existing connectivity, such as hedgerows and rivers. The least cost path model accentuated larger landscape-scale corridors of potential and structural connectivity based on graph theory, which took into account the resistance to travel given by the SDM surface. These routes were then prioritized using an SCP algorithm to identify the best areas for bat conservation that simultaneously meets two conservation targets – 30% and 50%. The performance of this modelling framework is best demonstrated by the triangulation of the final SCP maps with previous work by TVERC and Smith et al. (2021), which saw high degree of agreement and overlap over the selected areas. All three studies identify the main priority zones for nature recovery as being improvements of the links across the Upper Thames Vale character zone following the Thames from Kelmscott to Oxford city, and then out to Bicester along the Ray, and reduction of habitat fragmentation in the Chilterns AONBs. Other key zones also identified by either Smith et al. (2021) or TVERC include the connectivity corridor between Oxford City district and South Oxfordshire, and the larger patch of important zones in Cornbury and Wychwood. There are several additional sites identified in this analysis not seen in the other two maps, such as linkages identified in Linkage Mapper through Wheatley and Albury, and more connectivity around and towards Banbury from the city centre. These are areas for potential future research as they have been identified as important sites for connectivity in this analysis. This model formulation not only corroborated previous SCP-centred and expert-created maps, but it was able to do so with accessible and simple data inputs, which is an important implication for reproducibility in regions even with low data.

Furthermore, the high level of overlap with previous literature also provides evidence for the importance of bat species as bioindicators. The study results bring new focus and insight for the restoration and creation of woodlands and riparian zones, but future research would be needed to expand the functional niches represented by focal species. Thus, returning to the first initial research question of where priority zones for bat connectivity are located to support nature recovery and landscape connectivity, this analysis was able to map and identify the best corridors to achieve both goals.

In addition to being a modelling methodology, this stepwise framework is a way to structure the way conservation organizations bring together data and participants for the creation of a transparent and community-based nature recovery strategy. It highlights the importance of a species-targeted approach in identifying landscape corridors through the SDM and connectivity analyses, and how organizations and representatives can come together with the focus of defining and reconciling conservation objectives and targets for the SCP prioritization analysis. This is particularly relevant for the LNRS, which has a mandatory reporting period every five years. This allows the LNRS to remain dynamic and adaptable policies that can learn from previous years and change with the environment. The iterative nature of SCP therefore allows for these processes to remain streamlined. As such, this study strongly advocates for the use of SCP with connectivity integrated for the formulation of future LNRS and the scaling up to join local strategies to create the nationwide strategic NRN.

4.2 Recommendations for Oxfordshire's NRN

The decision-support maps produced through this analysis was created with the purpose of recommending new or reinforcing evidence for existing areas of restoration. It is done by systematically selecting habitat patches to reduce fragmentation and increase connectivity, aiming to achieve the landscape and linear corridors recommended by the Lawton Review (Fig. 9). These recommendations address the second research question on the practical ability of this modelling methodology to inform a NRN for Oxfordshire.

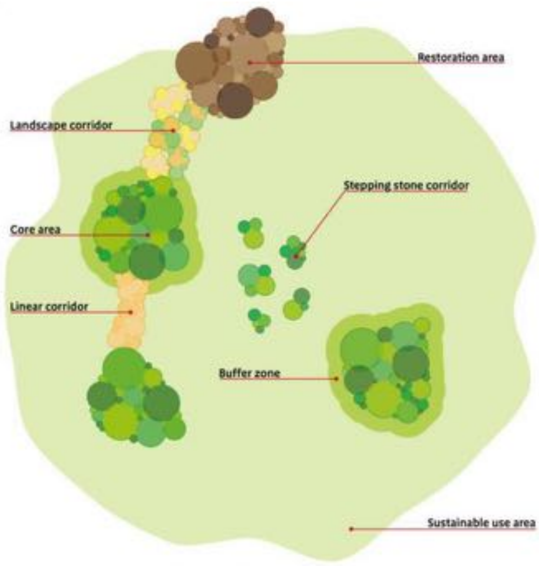

Figure 9: Components from ecological networks, from (Lawton, 2010)

The Ferrier's score highlighted the importance of water features not just for riparian specialist bats but for species across guilds. Existing work by the Freshwater Habitats Trust (FHT) has brought together conservation and community stakeholders to work to build and restore fens, meadows, and other small-scale waterbodies, identifying Important Freshwater Areas (IFAs) for ecological benefits. TVERC's Draft NRN used a modified IFA as a part of the proposed recovery zone, but the terrestrial habitats of the IFA were excluded to reduce overlap with a separate terrestrial analysis TVERC had conducted. This meant the upper river catchments and riparian woodlands identified in the IFA may not be well represented in the draft NRN. Potential next steps can focus on reinforcing these river and lakeside zones in future NRNs, as the habitat assemblages next to water features, in particular lakes, have been identified as highly important through the Ferrier's metric.

While freshwater habitat was identified as irreplaceable in the final prioritization solution, the representation statistics also revealed that most water features are fairly well protected under existing core patches, but only a low percentage of woodlands are represented, even for core areas selected for the woodland specialists (Appendix 7). As such, the network identified in this analysis will provide broad insight into where to target tree planting for habitat connectivity, and a recommendation for the NRN would be to use SCP with more detailed woodland environmental information to select optimal areas for treescapes. Similar to the FHT, the Oxfordshire Treescapes Project has been leading initiatives in this field and have produced an opportunity map for establishing treescapes in the county. They have also identified that 36% of Oxfordshire is not suitable for woodlands (Oxfordshire Treescape Project, 2021). Next steps can be to establish an SCP methodology with Treescapes to identify these opportunity areas with more conservation features (such as connectivity) and constraints (such as land ownership).

The importance of core area placement was also found to be critical, as demonstrated by the small core (eg. in Wheatfield) with similar centrality values to significantly larger core areas, indicating that while bigger cores with more complex edges are likely to be the most important for connectivity, cores that are smaller but well placed to act as stepping stones can be equally as important. While this deviates from ETIB's thesis of the species-area relationship where larger areas equate to more species diversity and abundance, it reinforces landscape connectivity theories around minimizing cost distances. This is an important finding as it indicates stepping stone corridors can be highly efficient while also being easier to implement as they can have lower levels of protection, increasing their widespread adoption and applicability even for private land (Lynch, 2019; Riggio & Caro, 2017). However, it should be considered that while stepping stones are easier to establish given their smaller size, corridors are often considered more ecologically important, because the surrounding landscape matrix around stepping stones needs to be favourable for the species in order for dispersal to happen (Baum et al., 2004; Lynch, 2019). Stepping stones often preferentially benefit highly mobile species as well (Pedley & Dolman, 2020; Mony et al., 2022). It is important to note that cores below 10ha were removed in the methodology due to high computational runtime and the focus on assessing "bigger" reserves (BBMJ), but these findings shows that an area of improvement would be to also assess these smaller patches. The focus of future NRNs would be an interspersed landscape of stepping stone corridors, potentially with ponds or urban forests, and small-scale linear features such as hedgerows as evidenced by the SDMs, and larger contiguous tracts of nature recovery to act as corridors. The FHT has also previously facilitated pondscape conservation initiatives, emphasizing the significance of creating small-scale riparian habitats that act as stepping stone patches for landscape connectivity (Freshwater Habitats Trust, 2012; Ponderful, 2020). For smaller linear habitats, existing work by the Countryside Charity (CPRE) aims to increase hedgerows by 40% by 2050, a target also echoed by Wild Oxfordshire (Wild Oxfordshire, 2020; The Countryside Charity, 2022). Hedgerows are also under council protection as it is considered an offense to remove hedgerows more than 20 meters long unless for a housing or infrastructure development, though unfortunately this only applies to farmers and certain landowners (Oxford City Council, 2015).

Regardless of quantitative metrics, how well this modelling framework performs will ultimately depend on its operationalization for conservationists and landowners. To gain a better understanding of usability of this analysis, several informal discussions on the applicability of the results of this modelling analysis were conducted with directors and researchers from Wild Oxfordshire, BBOWT, TVERC, and the Wild Oxfordshire, and the Durrell Institute of Conservation and Ecology. Key takeaways from these discussions highlighted the benefit of this framework to provide a statistically robust methodology to verify existing work and create decision-support maps that target reducing habitat fragmentation. They also touched on unreported weaknesses in previous Oxfordshire datasets, in particular the Conservation Target Areas that informed the TVERC draft NRN, which were outdated and did not sufficiently consider the wider catchment of freshwater habitats or connectivity. Lastly but most importantly, all discussions touched on the importance of stakeholder and local engagement, the lack of which was a key caveat of this modelling process. It was noted that while strategic level maps are important to direct focus on priority zones, they neglect the land tenure challenges and fragmentation of the Oxfordshire landscape. For NRNs to achieve rapid and significant results of nature recovery, private landowners must be involved in its implementation. Half of Oxfordshire is owned by 172 landowners, with 26 owning around a quarter of the county. This disproportionate land ownership results in highly influential voices governing large tracts of land (HERO, 2022). This is particularly important for potentially creating more small-scale stepping stone green and blue infrastructure such as hedgerows and ponds as identified in this analysis, as they can be more easily implemented on private estates. While more ambitious, restoration for wetlands, meadows, and woodlands identified in the Ferrier's irreplaceability score and representation statistics are also critical. Engagement with landowners for nature recovery is underway with the Oxfordshire Treescapes Project, which has mapped several estates. Many of the priority regions identified not only in this paper but also in the draft NRNs by TVERC and Smith et al. (2021) overlap with these estates, and while there are environmental payment schemes for incentivizing nature recovery action and funding, a more sustainable solution is needed to bring key landowners on board.

4.3 Areas for improvement and future research

As this study piloted a new modelling framework, there are several areas of improvement for improving the nuance of the models. These recommendations aim to answer the last research question, and sets guidelines for how future research can be directed.

4.3.1 Modelling framework

Primarily, it is important to reiterate that this analysis proposes a species-focused decision-support methodology for selecting high priority connectivity corridors. As such, the study framework is deliberately focused on ecological data and theory, as such a socioeconomic dimension was out of the scope of this project, with recognition for its importance in terms of the praxis of the nature recovery network. It would not be appropriate to apply the proposed framework to draft a full NRN, as it is meant to inform the selection of key conservation features such as connectivity. However, in order to move forward to drafting a holistic NRN, future work should focus on gaining insight from expert and local collaborators especially for the resistance raster inputted into the connectivity model, which does not have to just be specific species movement resistance but can also incorporate socioeconomic values (Whitehead et al., 2014). The cost surface, which was a connectivity raster for this analysis, should also be consulted to incorporate other values such as the opportunity cost for nature recovery. A future analysis can potentially examine opportunity cost through quantifying ecosystem services and natural capital assets (Lin et al., 2017). This would align with the natural capital approach of the 25YEP and help indicate that landowners can see the ecological value of their land for the network through the economic terms they are familiar with (Lü et al., 2017; Dempsey, 2021).

While socioeconomic and human dimensions of nature recovery are additional components to be incorporated into the framework, there are several areas where the modelling methodology can be enhanced to optimize its accuracy. In particular, it is important to note the hierarchical nature of the modelling process can result in a common modelling problem of "garbage-in-garbage-out" (GIGO), where the input data and modelling limitations are carried through to the next model. These areas for improvement are best discussed by addressing the individual steps of the framework.

4.3.2 Models

As the modelling framework proposes the steps to be taken, the models themselves can be purposefully chosen to suit the needs of the county. To inform future selection of models, there are several notable lessons learnt from the specific algorithms used in this analysis.

4.3.2.1 Species distribution models

SDMs are a good example of the GIGO concept, because while the widely accessible presence-only species records were intentionally selected for this study for their tractability, they are also known for their coarse and potential unreliability when inferring species occurrences (Peterson & Soberón, 2012; Franklin, 2010). This can be further exacerbated by the inherent limitations of models themselves. The models for this analysis are based on landscape ecology theory and graph theory using habitat variables to simplify the landscape to estimate species presence and movement. While efforts to enhance modelling accuracy were taken for each step of the framework, such as deliberately using ensemble models and careful consideration of model parameters, the models are ultimately still correlative. Future analyses would benefit from a better understanding of the biological processes contributing to dispersal beyond least-cost paths and taking into consideration the theoretical underpinnings of ecological connectivity at the individual species scale, which postulates behavioural and foraging ecology as its main concepts (Fletcher et al., 2016). As such, these hybrid-oriented models would need more detailed and mechanistic species records to be included, and the existing protected area dataset should be updated to include source and sink species population dynamics. Fortunately, there are existing tools such as spatially explicit population models (Paquet et al., 2020), species abundance distributions (Baldridge et al., 2016), joint species distribution modelling (Wilkinson et al., 2021; Escamilla Molgora et al., 2022), or metapopulation models (Donaldson et al., 2021).

4.3.2.2 Connectivity model

The intention of LNRS is to produce a county, local-scale analysis; but evidently, ecology is not limited by county borders. As seen in the connectivity models (Fig. 5), the artefacts of Oxfordshire's borders result in unrepresentative resistance values around the county edges. While the national NRN is meant to coalesce local scale LNRSs, they should still be designed with the wider landscape in mind, such as a buffer around the county to avoid any potential edge effects.

Additionally, Linkage Mapper is a cost-weighted distance analysis, which implicitly indicates that species have an understanding of the entire landscape and therefore are able to identify the least cost paths (McClure, Hansen & Inman, 2016; Palmer, Coulon & Travis, 2011). It has often been critiqued to be sensitive to over-generalization and overfitting due to low resistance between patches, resulting in straight line corridors (Rayfield, Fortin & Fall, 2011; Koenig & Bender, 2018; Laliberté & St-Laurent, 2020). Additionally, future analyses would benefit from additional manipulation of the SDM surface before using it as a resistance raster, as species are still able to traverse sub-optimal (low probability of occurrence) habitats (Elliot et al., 2014). A solution would be to use a non-linear transformation to account for species responses to resistance values (Jennings et al., 2020).

While least-cost path is considered a fairly early and rudimentary version of connectivity modelling, its applicability is dependent on the species, as McClure et al. (2016) found that it outperformed the more popular circuit theory models for elk, due to the generational transfer of migratory routes. As such, the most important step to ensure connectivity analyses in future research is optimized is the selection of the appropriate model, and with the rapid development of new tools, there is a much more diversified selection to choose from (Dutta et al., 2022).

4.3.2.3 Spatial conservation prioritization

Through informal discussions with Oxfordshire conservationists working with the city council to formulate a county LNRS, the SCP process advocated by this study and Smith et al. (2021) was noted to be considered computationally difficult to understand and politically contentious, which may undermine the transparent process that SCP champions (Margules & Sarkar, 2007:p.9). Unlike the consultation often conducted for LNRS that tend to focus on conservationists and experts, the SCP process involves bringing together stakeholders with a variety of conflicting interests (TVERC, 2020; Wildlife and Countryside Link, 2021). As a result, the selection of targets for SCP can be highly debated. This is a prime instance where there needs to be a bridge between science and policy through a co-designed, co-productive process to allow for effective decision-making to fill a "usability gap" between strategic maps and users on the ground. However, this may require a shift in the way conservation planning is conceptualized in the country. Previously, protected areas in England were designated through expert opinion (Janssen & Knippenberg, 2012:p.241). In recent years, a study by Dempsey (2021) reviewed conflicting perspectives of conservationists in the UK, which noted that while there is a shift towards having more human-integrated conservation areas. However, it also found that "wild nature" untouched by conservationists is considered the best management choice. The implications of these perspectives mean that the voices of farmers and local parishes can be potentially undervalued in LNRS consultation. Furthermore, a recent environmental policy development in England is the new focus on natural assets and capital through the 25YEP - the financial quantification of ecosystem services. A natural capital perspective that holistically integrates a diversity of values can inform the selection of targets for prioritization, but in the same paper by Dempsey (2021), it was shown that most conservationists are opposed to this economic-centric policy perspective.

4.3.3 Scalability

In terms of scalability of this project, two important considerations should be addressed for future studies. The first consideration is how the high computational intensity can limit how modifiable the modelling framework is for different counties. Due to the resolution of the dataset and the modelling algorithms, runtimes for each SDM exceeded 5 hours and for each connectivity model, each runtime exceeded 7 hours. While the Gurobi software for SCP is the fastest optimizer in the world, free licenses are only available for academic purposes. Fortunately, there are multiple ways that this can be streamlined and made open source for counties to benefit from this approach. To reduce computation time, the 30-meter input raster data (habitat layer, NDVI) can be resampled, but to change the 200m planning unit size, there needs to be consultation on what is the area of land that should be used to target action. There are also new SCP models that can streamline the connectivity analysis into the prioritization problem - the new Marxan Connect model (still under development) is one of the first SCP algorithms to foreground connectivity into the selection of new sites (Daigle et al., 2020).

The second consideration is the choice of focal species. Using focal species can be limited depending on how representative they are for other species habitats. While bats are found throughout the Oxfordshire landscape and share a high degree of functional niches with many other common woodland species, there are still several unique characteristics that limit their generalizability, such as the nocturnalism and their dwelling preferences in abandoned infrastructure and caves. Furthermore, using generalist bioindicator species for SDMs can potentially reduce accuracy. Generalists are noted to be challenging to model given their wide-ranging habitat preferences, which can result in model overfitting and creating a non-discriminate surface for all high probability of all low probability (Goedecke et al., 2020; Evangelista et al., 2008; Grenouillet et al., 2011). Future work can incorporate a multiple focal species approach instead with joint species distribution modelling to encapsulate more ecological processes more accurately (Wilkinson et al., 2021; Escamilla Molgora et al., 2022).

Summary of key takeaways and next steps for designing NRNs in Oxfordshire:

- While Smith et al. (2021) did not include species distribution models in their analysis as it was considered to not be representative of habitat quality, this study has found that they are still valuable, especially for connectivity modelling. However, more robust data such as abundances, spatiotemporal information to inform movement ecology, and the selection of other species representing other habitat niches would increase the ecological accuracy to future analysis.
- Connectivity modelling is an ever-changing field, and future research can work to compare different modelling methodologies or attribute nodes with information based on whether they are “sources” or “sinks” of genes and populations, taking more of a metapopulation theory approach.
- To encapsulate the full socioecological underpinnings of conservation planning, SCPs need to integrate human dimensions, either by including natural capital information, or through the careful selection of targets and land use cost - which is not limited to monetary units but could be values representing the likelihood of bringing onboard private landowners.
- The creation of the network should focus on a well-balanced mix of longer, contiguous corridors between large but far patches, but a series of interspersed small stepping stone refuges that can be less maintenance and with lower protection to incentivize and streamline implementation.

5. CONCLUSION

The nature recovery networks for the county LNRS have the potential to be a powerful policy tool to drive data-driven and integrative landscape-scale conservation in the UK in the upcoming years. The selection of these networks will be the priority of many decision-makers and conservationists as the first LNRS for each county is scheduled to be rolled out in 2023, but every five years thereafter. Connectivity modelling and spatial prioritization will be key in the creation of decision support outputs, but as this study has found, there needs to be a careful and purposeful selection and operationalization of the models and input data. The future also holds opportunities to scale up this methodology in multiple ways - expanding the network beyond county boundaries, enhancing the robustness of model predictions, and the inclusion of more open-source data as they are being published.

This novel modelling framework untethers the potential to leverage the rich local ecological data into delineating emergent corridors and new habitat patches - the pillars of a resilient nature recovery network. With future work to embed this framework in meaningful and inclusive stakeholder engagement, it can begin to disassemble the siloes of science and community, moving away from expert-driven conservation to identifying bottom-up and socio-ecological connections.

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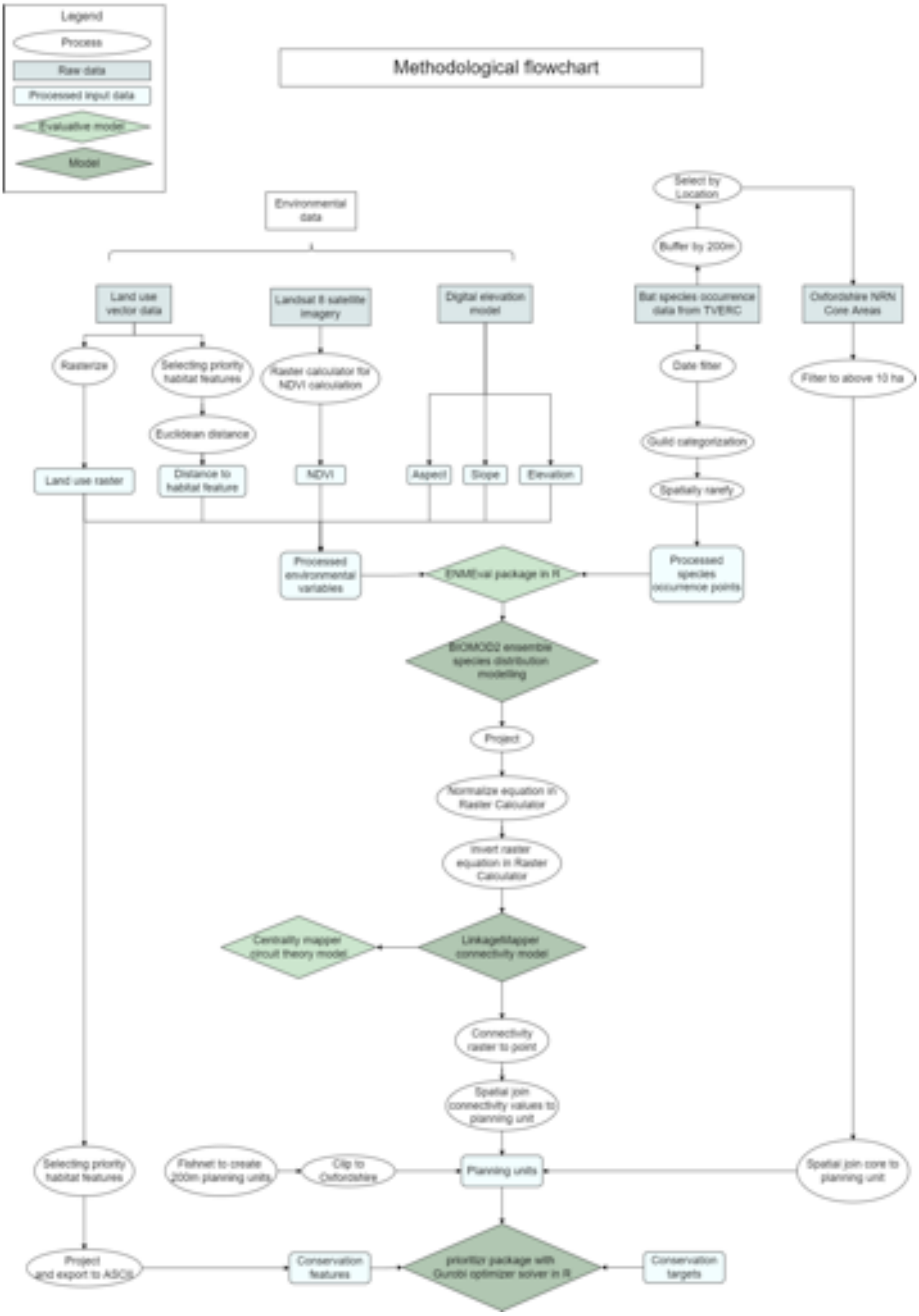
APPENDICES

Appendix 1:



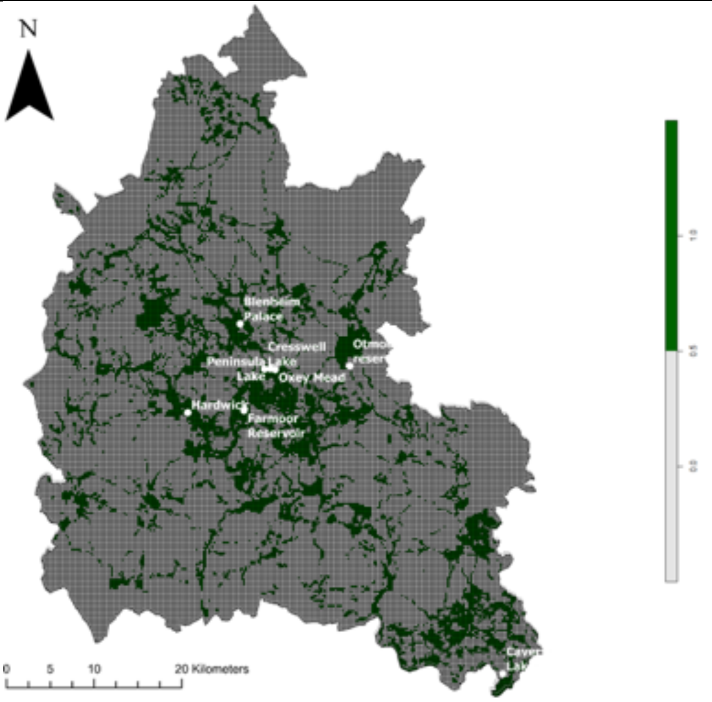
Appendix 2 – 4: Github R code repository (anonymized):
https://github.com/dissertationrepository/BCMdissertation

- **Appendix 2**: Biomod code https://github.com/dissertationrepository/BCMdissertation/blob/main/appdx2-biomod2.R
- **Appendix 3**: ENMeval code https://github.com/dissertationrepository/BCMdissertation/blob/main/appdx3-enmevaluate.R
- **Appendix 4**: prioritizr code https://github.com/dissertationrepository/BCMdissertation/blob/main/appdx4-prioritizr.R

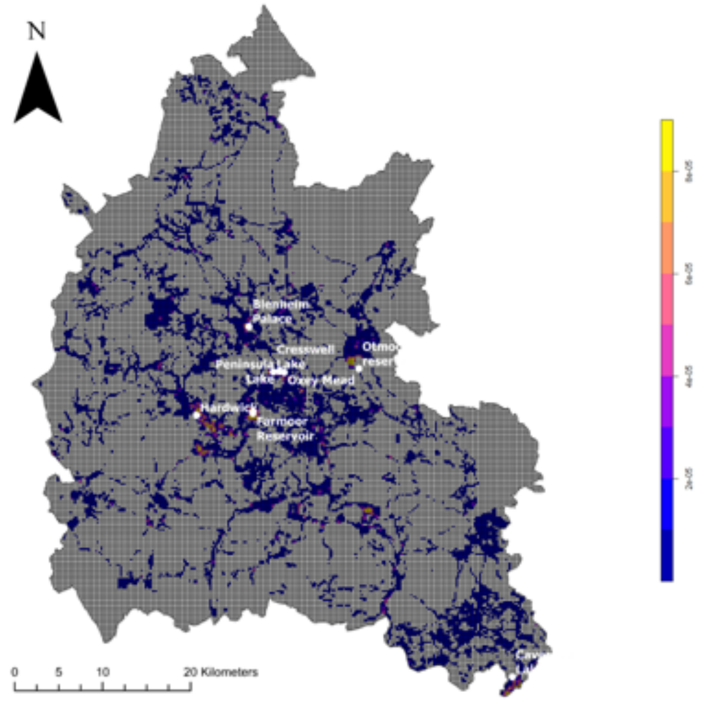
Appendix 5: ENMeval results, parsed to selected parameters

	Feature type	Regularization multiplier	AICc	delta.AICc
Generalist	L	2	1578.361	13.81656876
	LQ	2	1861.673	297.1288549
	H	2	1641.116	76.57200414
	L	3	1564.544	0
	LQ	3	1812.99	248.4461614
	H	3	1573.125	8.580689281
Woodland	L	1	7642.757	292.2310258
	LQ	1	7469.21	118.6844383
	H	1	7417.677	67.1510036
	LQH	1	7417.718	67.1924739
	LQHP	1	7406.844	56.31864685
	LQHPT	1	7350.526	0
Riparian	L	3	5665.652	187.5903135
	LQ	3	5517.721	39.65960896
	H	3	5478.061	0
	LQH	3	5484.221	6.159709545
	LQHP	3	5491.705	13.64344477
	LQHPT	3	5495.773	17.71124162

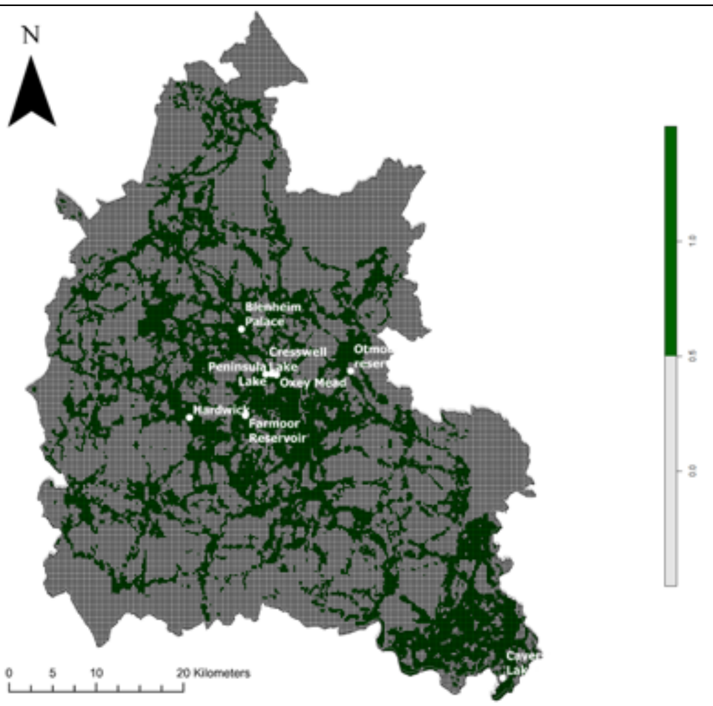
Appendix 5: Spatial conservation prioritization maps



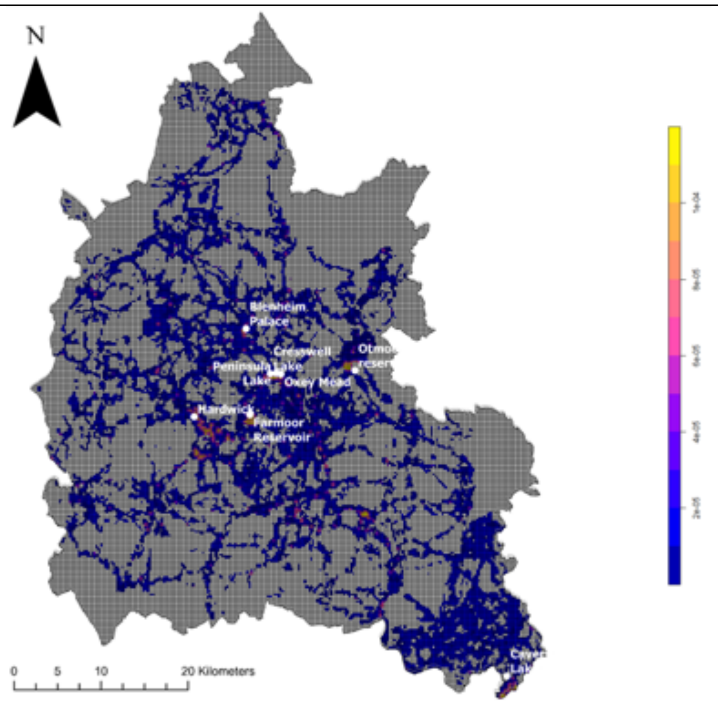
5A: SCP map for riparian specialists for a 30% target



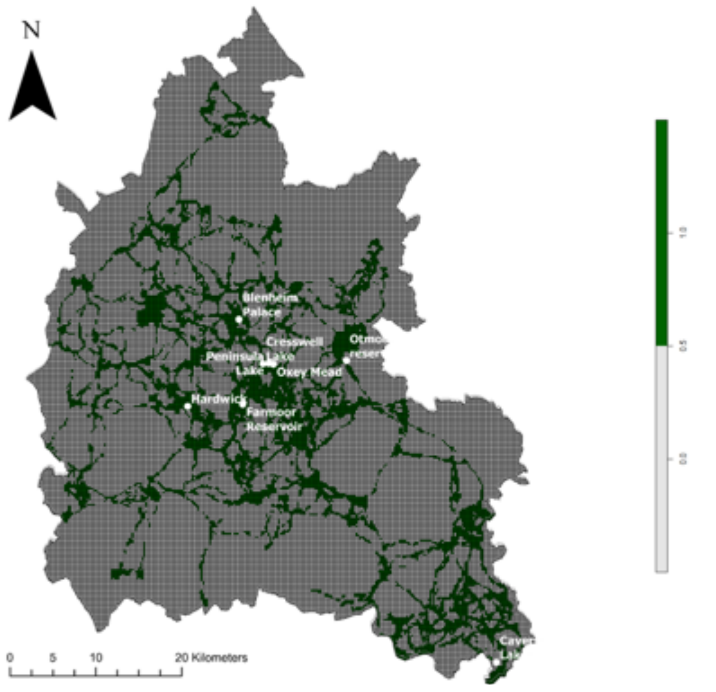
5B: Site irreplaceability map for riparian specialists for a 30% target



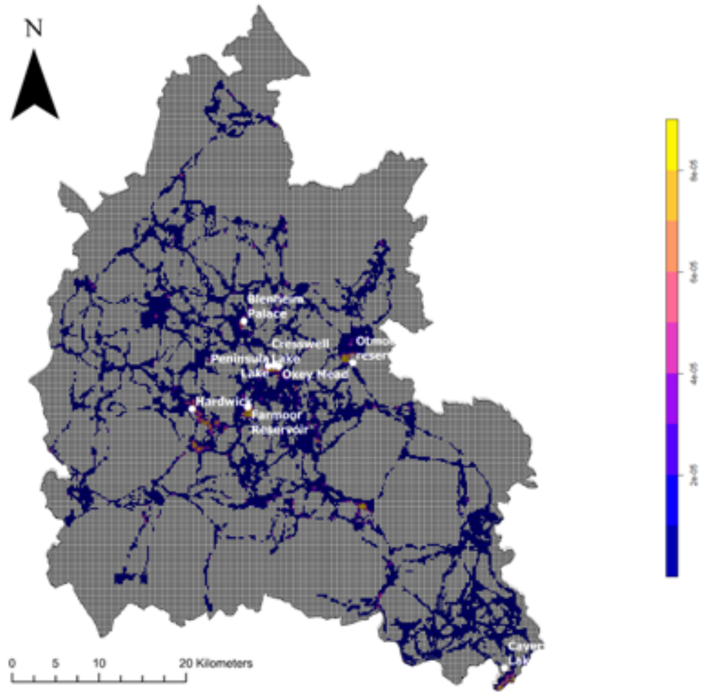
5C: SCP map for riparian specialists for a 50% target



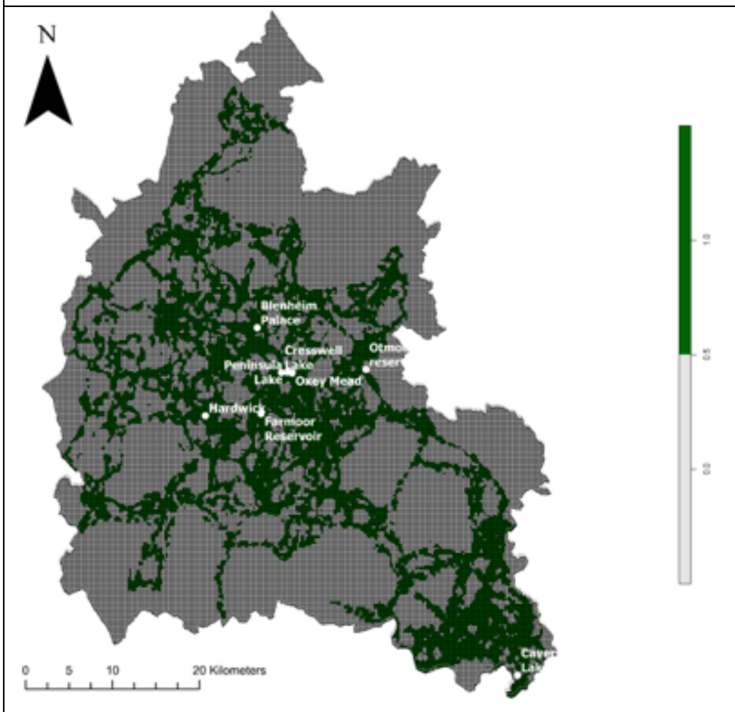
5D: Site irreplaceability map for riparian specialists for a 50% target



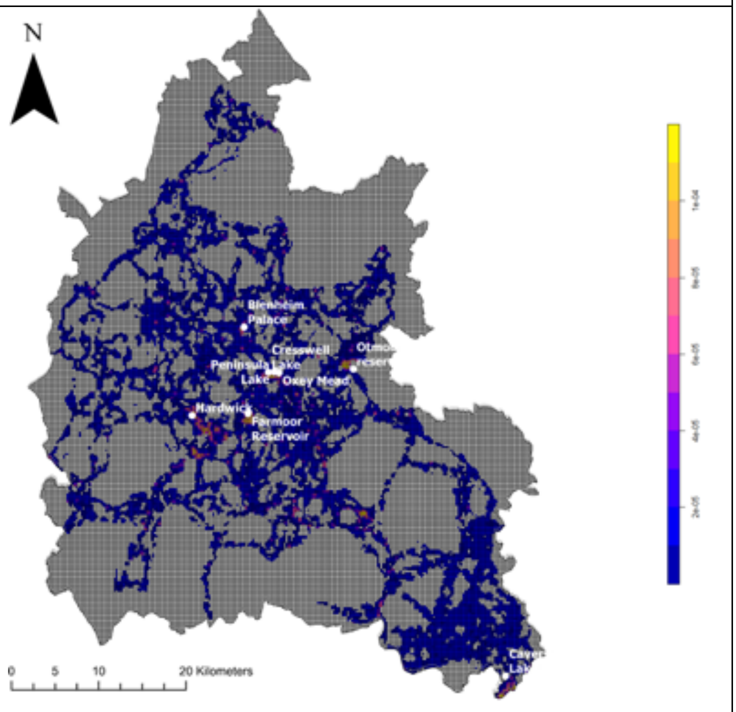
5E: SCP map for woodland specialists for a 30% target



5F: Site irreplaceability map for woodland specialists for a 30% target

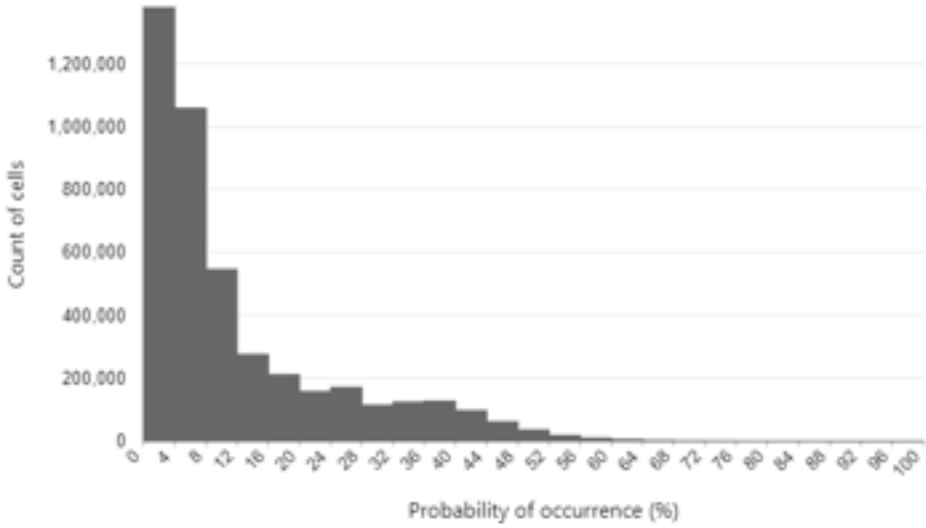


5G: SCP map for woodland specialists for a 50% target

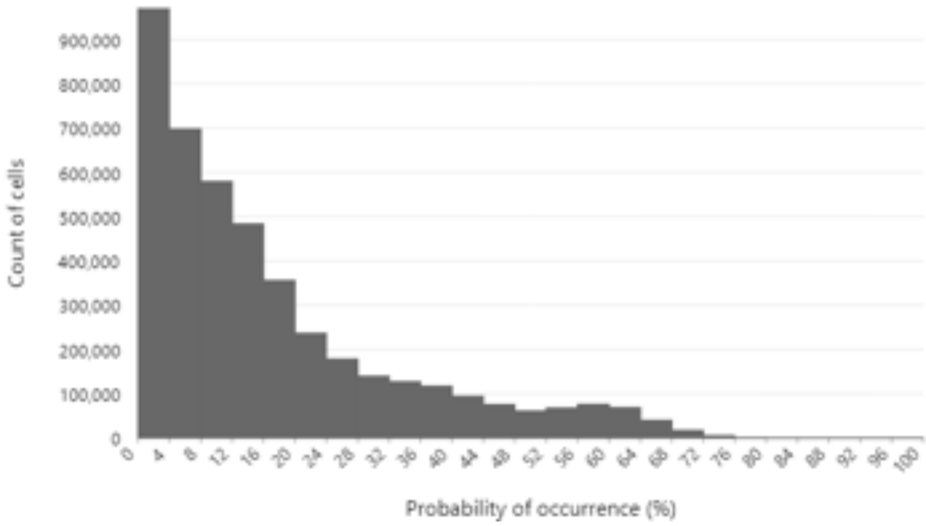


5H: Site irreplaceability map for woodland specialists for a 50% target

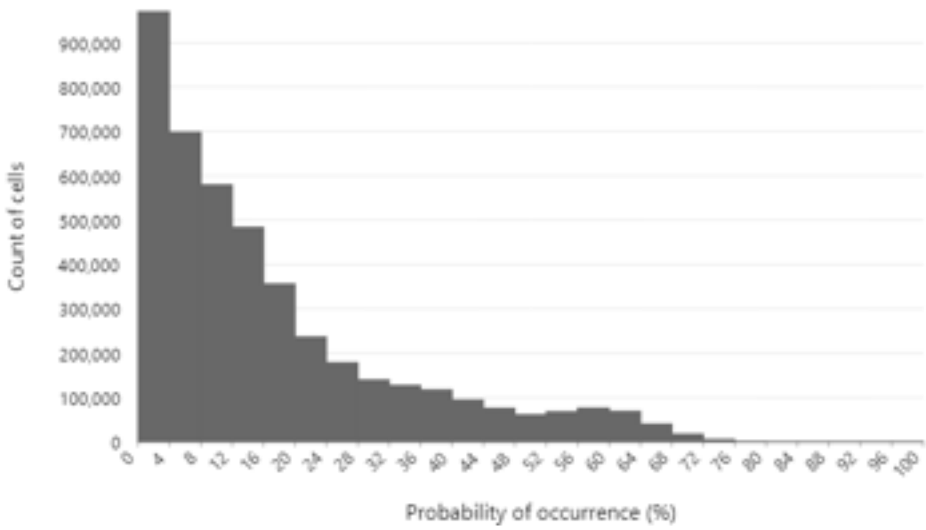
Appendix 6: Histograms of species distribution model probabilities



6A: Generalist species distribution model probability distribution



6B: Riparian specialist species distribution model probability distribution



6C: Woodland specialist species distribution model probability distribution

Appendix 7: Representation statistics from SCP model

	Generalist		
	Already protected	Proposed NRN	
		30%	50%
Woodlands	15.3%	30%	50%
Riparian zones	39.3%	49.7%	62.9%
	Woodland specialist		
	Already protected	Proposed NRN	
		30%	50%
Woodlands	13.6%	30%	50%
Riparian zones	39.8%	51.8%	64%
	Riparian specialist		
	Already protected	Proposed NRN	
		30%	50%
Woodlands	22.7%	30%	50%
Riparian zones	50.7%	54.8%	67.5%