A spatial conservation plan for the UK

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Abstract

The current network of area-based conservation measures in the UK, and globally, is not delivering enough positive outcomes to prevent species declines. Systematic conservation planning can potentially assist in improving area-based conservation by providing a powerful tool for evaluating performance of protected areas. Here I use spatial prioritisation methods to evaluate protected area effectiveness within Britain over time; investigate the impact of a UK government pledge for biodiversity; and test how systematic approaches can be expanded to include restoration potential of landscapes, and different perspectives on conservation. I find although the existing protected area network is delivering some positive impacts on species persistence, it is not effectively buffering wider negative regional trends. I identify increasing topographic heterogeneity, as well as size and connectivity of sites, as key to improving the long-term effectiveness of the British protected area network. I also find that using British protected landscapes to meet area-based conservation targets does not deliver for nature efficiently. It is important to include a wide range of voices to make sure that area-based conservation delivers for everyone, and here I develop methods to reconcile different perspectives equitably. I find that both inclusive and pluralist approaches can deliver coherent spatial plans balancing a number of feature coverage trade-offs. Finally, I use the species pool concept to demonstrate that habitat restoration can be considered and balanced alongside existing priorities, and identify where landscape recovery can contribute most value to the existing network. Systematic conservation planning provides a powerful and, as I have shown here, versatile tool to assist policy makers to deliver effective area-based conservation. The UK, and the globe, need systematic conservation planning to efficiently deliver biodiversity outcomes. The sooner systematic conservation planning is more widely utilised in policy, the greater the benefit will be to the effectiveness of conservation efforts.

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Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

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View from Sutton Bank on the south-eastern edge of the North York Moors, looking towards the Yorkshire Dales National Park across the Vale of York

CHAPTER 1

General Introduction

1.1 What is Systematic Conservation Planning?

The need for carefully planned conservation

Global biodiversity is currently undergoing a period of acute and accelerating change (Daskalova et al. 2020) which is commonly described as a crisis of extreme biodiversity loss, or even a sixth mass extinction (Ceballos et al. 2015; Hallmann et al. 2017; WWF 2020). Recent global biodiversity change has also been interpreted as a period of increasing species turnover (Dornelas et al. 2019), and biotic homogenisation (Dornelas et al. 2014) resulting in both winners and losers, and suggesting that negative changes in biodiversity are often over-emphasised (Leung et al. 2020). Regardless of how global biodiversity change is viewed, it is clear that there will continue to be negative changes and it is crucial that conservation efforts are able to mitigate or minimise the worst of these where possible (Soulé 1985; Kareiva & Marvier 2012).

Against this background of accelerating global change, conservation targets are currently being set as part of the post-2020 global biodiversity framework which will seek to expand on the previous Aichi targets from 2010 (CBD 2021). These targets, and the conservation movement as a whole, often use area-based conservation measures as a tool for conservation; protecting or managing land to conserve species, habitats and ecosystems (Maxwell et al. 2020). However, protection and conservation targets set for 2020 as part of Aichi [17% global coverage from Biodiversity Target 11 (CBD 2010)] have not quite been reached, with the proportion of global land protected currently at approximately 16.6% (UNEP-WCMC & IUCN 2016; Stokstad 2020) and species continuing to be lost at a high rate (Pimm et al. 2014; Ceballos et al. 2015; Secretariat of the Convention on Biological Diversity 2020). Thus, conservation efforts have had limited success so far against threats from habitat loss and degradation (Hoffmann et al. 2010; Johnson et al. 2017).

Historically, protected areas (PA) have been considered one of the most important area-based tools to combat biodiversity decline by maintaining species diversity though protecting habitat integrity of the most important areas (Watson et al. 2014). Increasingly, other area-based conservation measures (OECM) are also considered appropriate conservation strategies to complement strictly protected areas in certain spatial, cultural or socioeconomic contexts (Maxwell et al. 2020). Regardless of the type of area-based conservation measure (PA or OECM), a crucial question is where to implement conservation strategies so that they maximise conservation outcomes.

Introducing systematic conservation planning

Considering the spatial component of area-based conservation measures is vital to ensure they are effective. Firstly, distributions of species and habitats (and all conservation features) are themselves spatial entities; and secondly any area-based conservation interventions need to be considered together so that species that are found in different locations are all catered for. For example, if a large protected area is designated in which a particular rare species is well represented, it would be sensible to concentrate further conservation effort on areas that ensure other threatened species are also adequately protected. Hence, site selection is a crucial element of conservation planning (Pressey et al. 2015), and poorly chosen sites will be unsuccessful in achieving conservation goals (Joppa & Pfaff 2009).

When multiple area-based conservation measures are considered together, they can be viewed as a conservation (or specifically protected area) ‘network’. This allows new sites to be assessed on what they will contribute to the existing network, in terms of coverage or representation of conservation features. Although conservation areas are usually treated as though they are part of a collective strategy, in fact they are often selected and designated individually, and for a variety of different reasons (Geldmann et al. 2013). Hence, despite the name, these networks do not necessarily form a functional *ecological* network and do not reflect typical properties of networks such as resilience and connectivity (Isaac et al. 2018).

Even though an area-based conservation measure may be highly successful on a local, or even national, level for individual site-specific criteria, important areas may be missed if they are considered as individual sites rather than at the network-scale (Gaston et al. 2006). Hence, the global conservation network, resulting from decades of sequential conservation decision making, is not situated in the best locations to conserve the biological diversity it is designed to protect, a disparity that needs to be addressed if positive conservation outcomes are to be maximised (Brooks et al. 2004).

Systematic Conservation Planning (SCP) in its simplest form is conservation planning that explicitly takes into account the existing conservation system/estate (hereafter ‘network) in order to better sample and protect biodiversity (Margules & Pressey 2000). SCP facilitates the ‘evaluation’ of conservation networks, and therefore provides a powerful tool to improve their performance (Pressey & Bottrill 2008; Wilson et al. 2009). SCP uses network-scale criteria, such as the contribution of each site to the full set of species that is represented over the entire conservation network; rather than site-based criteria, such as species richness, to inform conservation decisions.

Using these types of criteria for area-based conservation measures results in better average species distribution protected (Veach et al. 2017a). SCP therefore provides a rigorous and accountable way to assess allocation of resources to maximise biodiversity conservation efficiency of the entire conservation network (Wilson et al. 2009).

SCP is an inherently applied process and typically progresses through a number of planning stages (Figure 1.1), starting with initial scoping of stakeholders, context and goals; to collecting data, setting goals and identifying priorities; to finally applying the conservation actions (Pressey & Bottrill 2009; McIntosh et al. 2017). Additionally, even after implementation, the stages should be repeated periodically so that the conservation network continues to deliver on conservation priorities (Cheok et al. 2018). The most important stage within, and fundamental to, SCP is the spatial prioritisation stage where (additional) conservation areas are selected. As a result SCP is sometimes used synonymously with spatial (conservation) prioritisation, but it is important to distinguish between spatial prioritisation and the entire planning process (Arponen 2012; McIntosh et al. 2017). Note that this thesis contains spatial prioritisations, not entire SCP applications, within Britain to test hypotheses in conservation planning.

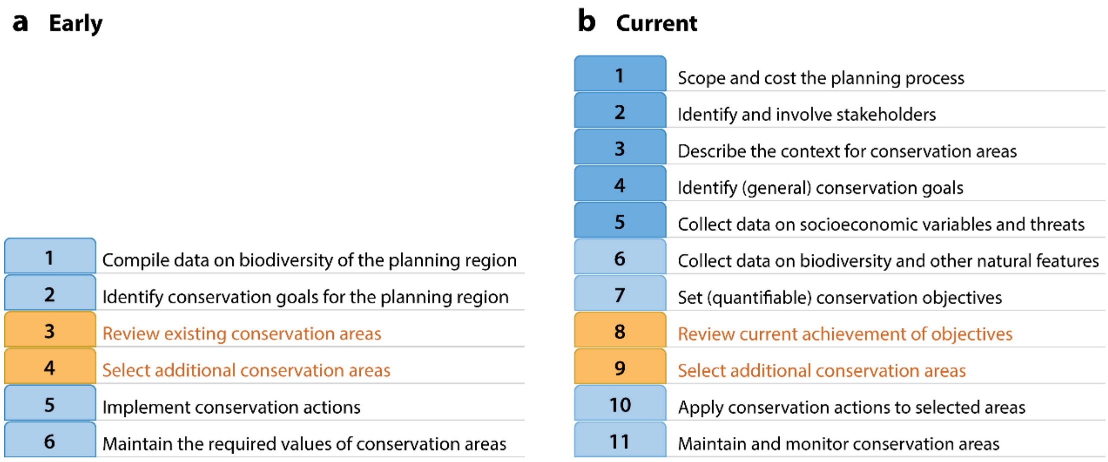


Figure 1.1 Outline of primary stages in systematic conservation planning (SCP) from McIntosh et al. (2017). (a) Early SCP framework from Margules and Pressey (2000) and (b) the current dominant framework from Pressey and Bottrill (2009). Spatial conservation prioritisation stages are presented in orange, light blue stages are conserved from the early framework.

The first spatial prioritisation conservation algorithm in 1983 iteratively assigned reserve selection priorities (Kirkpatrick 1983; Pressey 2002). Higher priorities identified at the start of the analysis were considered protected and taken into account when lower priorities were assigned and, crucially, this allowed sites to be valued on their contribution to the existing conservation network rather than individually. Since then SCP has grown as a subject exponentially over the last forty years, with numerous examples of policy implementation (Fernandes et al. 2005; Knight et al. 2006). Associated concepts and terminology have developed within the field (Kukkala & Moilanen 2013) as well as sophisticated computational tools (Moilanen et al. 2009), but fundamental SCP concepts have remained unchanged.

Core concepts within systematic conservation planning

The fundamental characteristic of spatial conservation prioritisation is *complementarity*, meaning that conservation areas complement others in achieving objectives (Watson et al. 2011). Conservation networks are not equal to the sum of their individual sites and must be considered together as networks for evaluation. Along with this defining characteristic (Margules & Pressey 2000), other core concepts and principles have developed around SCP since it’s conception. Another important SCP concept is *representation*, which is the extent of occurrence of a conservation ‘feature’ within an area, i.e. usually the proportion of a specific species’ distribution that falls within a set of conservation areas (Cabeza & Moilanen 2001). Similarly, *representativeness* is the representation across all considered features within a conservation network, i.e. the extent to which a conservation network represents biodiversity as a whole (Margules & Pressey 2000). *Efficiency* is the degree to which conservation goals (usually representativeness) are achieved, compared to the amount of land (or monetary costs) required to achieve them, i.e. greater conservation return on less land/cost is a more efficient conservation network (Rodrigues et al. 1999; Naidoo et al. 2006). *Adequacy* relates to the persistence of species; a conservation network is adequate for a species if it ensures the persistence of that species through time (Wilson et al. 2009). Finally, *effectiveness* is a more holistic concept determined by the extent to which the long-term conservation of nature is achieved (Rodrigues & Cazalis 2020) although this term is perhaps the most vague term within the literature.

These terms are sometimes loosely defined, and there are also additional concepts such as comprehensiveness, vulnerability, irreplaceability, and flexibility (Table 1.1).

Table 1.1 Brief definitions of core concepts within systematic conservation planning, summarised from Kukkala and Moilanen (2013) if not directly quoted.

Concept	*Definition*
Adequacy	An adequate network is one that is sufficient to ensure that biotic features persist in the long-term.
Complementarity	"... a measure of the extent to which an area, or set of areas, contributes unrepresented features to an existing area or set of areas" (Margules & Pressey 2000).
Comprehensiveness	A fully comprehensive network is one that samples every biodiversity feature. Somewhat overlaps with the concept of representativeness, which is preferentially used within this thesis.
Effectiveness	Broad concept describing the extent to which conservation goals are achieved in the long term.
Efficiency	An efficient conservation plan is one which maximises conservation objectives while minimising cost or area, which is likely to be easier to implement.
Feature (layer)	Species or other resource of interest to include within conservation plan using spatial distribution data, including habitat type, ecosystem service, ecosystem process, gene, surrogate data etc. May be additionally weighted according to importance.
Flexibility	The extent to which sites within conservation plans can be replaced with other potential sites to fulfil conservation objectives; the opposite of irreplaceability.
Irreplaceability	The importance of an area to meeting conservation objectives, can be interpreted differently depending on SCP approach
Representation	The occurrence of a single feature, i.e. species, within the conservation network or other area.

Representativeness	The degree to which a conservation network represents the breadth of biodiversity features; representation across all biodiversity features.
Vulnerability	The potential loss of value at a site caused by presence of threats, as such it allows incorporation of human impacts into evaluation of site importance.

Different SCP prioritisation algorithms

There are a number of potential spatial analytical tools which can be used to quantitatively carry out the spatial prioritisation stage of SCP, depending upon the planning context and any identified conservation goals (Moilanen et al. 2009). All spatial prioritisation software seeks to find an optimal solution to a given conservation planning problem. These are usually either a variation on meeting conservation objectives while minimising area or costs needed (basic minimum set problem, i.e. *Marxan* software), or maximising representation of conservation features in the presence of other constraints (maximum representation problem, i.e. *Zonation* software) (Ciarleglio et al. 2009). It is also important to remember that spatial prioritisation tools support and inform conservation policy makers to make planning decisions, they do not actually make decisions, as there will always be additional economic, and political, considerations and constraints involved in the planning process (Pressey & Bottrill 2008). Four spatial conservation prioritisation software products (approaches) are briefly described below.

Marxan software uses a simulated annealing metaheuristic to solve ‘minimum set problems’. *Marxan* is a high-profile spatial prioritisation tool, possibly most famous for informing the rezoning of the Great Barrier Reef (Fernandes et al. 2005). The goal in Marxan is to meet a set of conservation targets, i.e. ‘protect X percent of priority species distributions’, while minimising reserve network cost and boundary length (total edge length of the solution). A smaller total conservation network boundary is preferable as it equates to larger, more connected sites that improve connectivity and reduce management costs and edge effects (Ball et al. 2009). The software runs the same randomised simulated annealing heuristic many times, and this allows an output of the best solution but also the selection frequency of sites (a measure of irreplaceability). Very simply, sites are randomly added and removed from the solution, and kept if the new configuration is improved, until targets are met. This is then repeated many times so that selection frequency (site irreplaceability) can be calculated. The setting of conservation targets is core to running a *Marxan* spatial prioritisation and, although at the heart of good conservation planning, a potential critique of *Marxan* is that these can be of a somewhat arbitrary nature for some planning scenarios (Ball et al. 2009).

Another spatial prioritisation approach is *Zonation* which differs from *Marxan* primarily in that it does not require specific a priori targets to run, rather trade-offs are implicitly defined through weightings (Moilanen 2007). The *Zonation* algorithm is an example of a maximum representation problem, unlike the minimum set problem that *Marxan* solves. *Zonation* works by a reverse stepwise heuristic; beginning with the entire focal area, planning units are removed which contribute the lowest conservation value to the remaining area and in this way complementarity of the solution is ensured. Different cell removal rules can be used depending upon the planning objectives, and additional weightings and cost layers can be included (Lehtomäki & Moilanen 2013). As targets are not explicitly set within *Zonation*, there may be uncertainty whether solutions are adequate to conserve the currently protected biodiversity in the long term.

Alternatively *C-Plan* can be used, which uses a heuristic algorithm that estimates site importance based upon irreplaceability, similar to *Marxan*, specifically the likelihood a site is required to meet a conservation objective (Vanderkam et al. 2007). *C-plan* also optionally incorporates ‘summed irreplaceability’ which is the number of features for which the site is irreplaceable. This allows conservation planners to distinguish between sites that are irreplaceable to meet every conservation objective, but cannot all be incorporated due to other constraints (Pressey et al. 2009). *C-Plan* also dynamically updates spatial options so that conservation planning can be carried out in real time (Pressey et al. 2009).

ConsNet comprises a wide suite of software packages that run separately and have different objectives. The main package is *ResNet* which solves either a minimum area problem (representation targets must be set) or maximum representation problem (up to an a priori cost or area budget), using a heuristic algorithm (Sarkar et al. 2009). *Consnet* also includes *Surrogacy* which tests the performance of feature surrogates, *MultCSync* which balances different land uses with biodiversity representation using a number of methods, and *LQGraph* which optimises improving connectivity within the conservation network (Sarkar et al. 2009).

Each spatial conservation prioritisation approach has benefits as well as challenges, but note that spatial prioritisations within this thesis use *Zonation* software due the flexibility of investigating conservation planning hypotheses through maximum representation problems. Additionally, the 10x10 km resolution of much of the analysis meant the boundary length penalty used in *Marxan* to improve solution connectivity would have been less meaningful in a planning context at that scale. However, as well as those listed above, many other approaches to prioritisation exist, and could also be used to investigate the research questions, such as the recent *prioritizr* R package, which uses integer linear programming to find guaranteed optimal solutions (Hanson et al. 2017).

Feature layers

When undertaking a spatial prioritisation as part of SCP, there are many considerations in addition to the prioritisation method, depending upon the aims of the planning and the spatial context. One of the most important of these is deciding and collecting which feature layers to use, and how to include them within the analysis (Kujala et al. 2018). Feature layers typically constitute biological data (especially distribution or population data), but ecosystem service, economic, environmental and social data can also be used (Ferrier 2002; Knight et al. 2010). However, a common prioritisation problem is that distributional data for many taxa are sparse. In this instance, spatial interpolation can be used to fill in the gaps or, alternatively, surrogate data (correlated variables) can be used within the spatial prioritisation. The efficacy of the latter method will depend on the congruence of the surrogate data with the actual biological distributions of interest (Ferrier 2002). Surrogate data can constitute any spatial information that explains variation in biodiversity, from abiotic environmental data to the distributions of well-studied umbrella species (Lewandowski et al. 2010). Cross-taxon surrogates generally outperform those based on environmental data (Rodrigues & Brooks 2007). However, surrogate performance will depend upon spatial context, and surrogates that function well for one measure of network performance may not function well for another (Grantham et al. 2010).

Costs and threats

In addition to including feature layers that conservation planners are interested in protecting, there are other spatial factors that can be taken into account within SCP, such as costs and threats (Kujala et al. 2018). Costs can be quantified in different ways within SCP, for example; initial site acquisition costs; ongoing management costs; or opportunity costs of not using an area for other land uses, such as agriculture (Naidoo et al. 2006). Incorporating costs into conservation plans ensures increased efficiency in implementation, but will necessarily result in trade-offs against overall conservation network representativeness. Systematic planning is able to minimise these trade-offs, but care must be taken when weighting costs for maximum representation approaches. Allowing costs to have too great a leverage in these would result in selecting areas with low biodiversity value simply because they are inexpensive, and could generate plans that are similar to the opportunistic approaches that SCP was designed to avoid (Arponen et al. 2010).

Conservation areas are globally currently biased towards low cost areas that are generally high, steep, and far from residential and transport infrastructure (Joppa & Pfaff 2009). These are locations that are often less exposed to threats anyway, and protection here is likely to have less positive conservation impact than in more vulnerable areas. Threats to biodiversity can also be included within prioritisations, such as threat from development, agricultural expansion or habitat loss (Veach et al. 2017b). Incorporating both costs and threats can further improve conservation efficiency, as they are not necessarily correlated (Sacre et al. 2019).

Connectivity, habitat size/quality

Once the method and feature layers have been selected, there are then further considerations involving how to carry out the prioritisation, such as the degree to which connectivity, habitat size, and site 'quality' should be considered in spatial prioritisation. Ensuring connectivity within a conservation network can ensure greater species persistence (Magris et al. 2018), as well as facilitating range shifts (Hiley et al. 2013; Saura et al. 2014). It can also potentially increase opportunities for the spread of invasive species and disease (Beger et al. 2010), but this is not seen for introduced species (Hiley et al. 2014). It is important not to conflate *functional* connectivity, i.e. realised dispersal rate, with *structural* (or *landscape*) connectivity, i.e. the distance between habitat patches. Structural connectivity is fixed whereas functional connectivity is species-dependent and determined by; population size and dynamics, structural connectivity, and habitat size/quality (Doerr et al. 2011).

Although it can easily be calculated, structural landscape connectivity can be a poor predictor of immigration rate when the land between local populations is heterogeneous (Bender & Fahrig 2005). Similarly, although it is relatively straightforward to incorporate functional connectivity information from a single species into spatial prioritisation (Isaak et al. 2007; Minor & Urban 2007); it becomes increasingly complex when considering the multiple species necessary for a systematic plan, and there is some uncertainty about the conservation benefit of including this information (Hodgson et al. 2009; Hanson et al. 2019; but see Doerr et al. 2011). Although incorporating connectivity into conservation plans will result in trade-offs with other objectives, these can be greatly minimised through systematic planning (Williams et al. 2020) and some spatial prioritisation software includes structural connectivity by default, i.e. *Marxan*, or have in-built options for inclusion, i.e. the boundary-quality penalty in *Zonation* (Moilanen & Wintle 2007).

Reducing habitat size (Marini et al. 2012) or habitat quality (Hodgson et al. 2011) can also result in decreases in occupancy by individual species, normally greater than the effect of reducing connectivity. Larger habitats generally have higher habitat heterogeneity, as well as greater species richness and source populations (Kallimanis et al. 2008; Hodgson et al. 2011). Responses to both connectivity (Uezu et al. 2005), habitat quality (Doerr et al. 2011) and their interaction (Visconti & Elkin 2009) are species-specific, further complicating their usefulness as metrics of conservation adequacy. The relative importance of connectivity, habitat size and quality is somewhat contentious (Hodgson et al. 2009; Doerr et al. 2011), however it is likely that a product of all three is needed to produce an efficient and robust protected area network (Saura et al. 2014); prioritising size and quality first, and spatial configuration second (Moilanen 2011).

Ecosystem services

As well as conserving biodiversity, area-based conservation measures can also protect and manage functions or processes that contribute to human well-being: ecosystem services (ES) (Costanza et al. 2017). ES can be classified into four broad categories of benefits people receive from ecological systems: *provisioning services* are products derived from ecosystems such as fresh water supply and agricultural output; *regulating services* are ecosystem benefits resulting from ecosystem regulation such as carbon storage and sequestration, and flood regulation; *cultural services* are the intangible benefits people obtain from ecosystems, including recreational, spiritual and educational benefits; and *supporting services* are those which are needed for ecosystems to produce all other ES, such as soil formation and oxygen production (Millennium Ecosystem Assessment 2005). ES will be an important component within the post-2020 global biodiversity framework, as the Convention on Biological Diversity has incorporated areas of importance for ‘contributions to people’ within its 30% protection targets (Table 1.2).

ES can be incorporated into SCP, but how this is undertaken will depend upon the stakeholders involved and the planning objectives. Incorporating ES into spatial prioritisations is different from incorporating species distributions as they depend on both service supply (presence of the service) and service demand (people’s needs). Hence, it is the flow between these that must be considered in spatial allocation of conservation resources to avoid severing the connection of ES supply and demand (Villarreal-Rosas et al. 2020). Although including ES within spatial prioritisation is complex, in the last decade there has been extensive research on both how to apply SCP to ES (Kukkala & Moilanen 2017; Verhagen et al. 2017; Mitchell et al. 2021), and how to balance ES and biodiversity priorities (Anderson et al. 2009; Bai et al. 2011; Fastré et al. 2020). The main restriction to utilisation of ES within SCP may be simply the accuracy and resolution of spatial ES data available to planners (Costanza et al. 2017).

Climate change

Although protecting current distributions of threatened species is the priority of conservation, it is now also important to consider potential impacts of climate change to species distributions, habitats and land use within conservation planning (Groves et al. 2012). In order to deliver better conservation outcomes in the long term, SCP can incorporate climate change information through a variety of mechanisms (Jones et al. 2016). Conservation planners can consider climate *refugia* which are areas that species can persist in, and potentially expand from, under changing abiotic conditions (Keppel et al. 2012). Although climate refugia for one taxonomic group may not be suitable for another, the refugia potential of an area is generally dependent on microclimate heterogeneity (Suggitt et al. 2018). Hence incorporating refugial habitat potential into spatial prioritisation is relatively straightforward, although defining it for specific species is much more difficult (Jones et al. 2016). Climate change is most often incorporated into spatial prioritisation through considering direct effects, i.e. predicting future distributions based on changes to climatic variables (Jones et al. 2016). Conservation network connectivity can also be evaluated with direct effects, to consider whether existing conservation areas are able to act as 'dispersal corridors' in facilitating expected range shifts (Lemes & Loyola 2013; Stralberg et al. 2020).

Although most work focuses on direct effects of climate change, it is also possible to predict the indirect effects of human responses to climate change. Indirect effects include changes to land use and threats due to a variety of factors including; changes in crop suitability, population change, and resource utilisation patterns (Turner et al. 2010), and these effects can also interact with direct effects to produce combined effects (Oliver & Morecroft 2014). However, human impacts resulting from changes in climate are complex to model and thus rarely incorporated into spatial prioritisation analyses (Chapman et al. 2014; Jones et al. 2016; but see Jetz et al. 2007; Faleiro et al. 2013; Albert et al. 2017). Indirect effects are usually easier to mitigate than direct effects, so incorporating them into SCP may offer more efficient planning solutions (Lehsten et al. 2015) Finally, as conservation budgets are limited, spatial prioritisation methods can also be used to identify conservation areas that will decline in importance with climate change, and potentially inform redirection of funding from these to enhance or designate others which will increase in importance (Alagador et al. 2014).

1.2 Challenges remaining in systematic conservation planning

What constitutes conservation value?

A recurring question within conservation planning is how to reach consensus over priorities when individual conservationists and stakeholders have differing perceptions of conservation value. Conservationists may place importance upon different landscape features and, over time, the overall community focus may shift from one framing of conservation value to another (Mace 2014; Sandbrook et al. 2019). The two main characterisations of conservation value are ‘traditional’ and ‘new’ conservation. ‘Traditional’ focuses on the inherent value of nature, i.e. species and ecosystem diversity, and values ‘wild’ places with lower anthropogenic impact (Soulé 1985). Conversely, ‘new’ conservation places importance upon services to people; preserving biodiversity while also maximising human well-being (Kareiva & Marvier 2012). These two perspectives can seem irreconcilable, and how value is determined will affect conservation planning priorities. However, conservation is likely to be more successful if united and focused on joint priorities (Hunter Jr et al. 2014), and there have been numerous calls for consensus in conservation implementation (Marvier 2014a; Tallis & Lubchenco 2014; Matulis & Moyer 2017).

As part of a full SCP implementation, there are opportunities to build consensus between different stakeholders’ perspectives within the different planning stages, primarily when conservation goals are being set (Pressey & Bottrill 2009). At this stage iterative decision tools can be used to facilitate consensus-building; including interviews (Young et al. 2018), focus group discussion (Nyumba et al. 2018), nominal group technique (Hugé & Mukherjee 2018), multi-criteria decision analysis (MCDA) (Esmail & Geneletti 2018), Q methodology (Sandbrook et al. 2019), and Delphi technique (Mukherjee et al. 2015). The best method to use will depend upon the level of conflict between the perspectives and the nature of the decision(s) to be made, and a combination of approaches can be used at various steps of this decision-making process. For the decision-*making* step, as opposed to framing the problem and eliciting judgement steps, the Delphi technique and MCDA methods are most appropriate (Mukherjee et al. 2018). When any of these approaches are used, social biases can occur that are extremely difficult to control for, such as group think (individuals reducing independent thinking to support majority decision and avoid group disunity), or the dominance effect (disproportionate influence of individuals perceived to be dominant) (Mukherjee et al. 2018). In this thesis, I develop methods to create 'consensus' conservation plans, incorporating different viewpoints equitably into integrated spatial approaches, while also controlling for social biases that are often introduced at the decision-making stage.

Measuring success

Equally, measuring conservation value itself is problematic as there are many different approaches which will result in different indicators of conservation network performance (Rodrigues et al. 1999); from representativeness (Araújo et al. 2007), to feature coverage (Rodrigues et al. 2004), to the success of a priori targets (Kapos et al. 2008). Even if only considering biological diversity, there are multiple facets that can be used to measure it, such as taxonomic, functional, or phylogenetic diversity, and each will produce a different set of optimal conservation areas when used within spatial prioritisation (Pollock et al. 2017). Most approaches focus on current performance, even though conservation interventions generate long-term impacts. However, these are difficult to measure within most project timeframes and intrinsically difficult to incorporate into spatial prioritisation at the beginning of a project (Kapos et al. 2008).

Ultimately, whatever conservation values are decided upon, and whichever approaches used to quantify area-based conservation performance in delivering these, overall conservation ‘success’ depends on whether conservation objectives are delivered in the long-term. Within SCP terminology, effectiveness is perhaps the term that best aligns with the broad concept of conservation ‘success’. Effectiveness depends on an interaction of decisions made at the time of establishment, such as locations and network design, and subsequent decisions over time, such as management and changes to the network configuration (Rodrigues & Cazalis 2020). However, many measures of network performance only focus on the time of the analysis, i.e. representativeness, but whether that is what will be observed in the long-term remains largely unknown; the network may not be adequate to facilitate species persistence and biodiversity may decline significantly over time. Quantifying the long-term effectiveness of entire conservation networks is rarely undertaken, despite its potential to provide invaluable information for policy makers (Bottrill & Pressey 2012; Geldmann et al. 2013).

There are practical difficulties in assessing long-term performance of conservation networks, as high quality, long-term ecological datasets are needed. As a result there is uncertainty over how well conservation networks perform in delivering conservation outcomes in the long-term, i.e. how effective they are. Although PAs successfully conserve forest habitat (Geldmann et al. 2013), there is mixed evidence that they reduce human pressure (Geldmann et al. 2019), or mitigate species declines (Geldmann et al. 2013; Virkkala et al. 2018; Rada et al. 2019). In this thesis I analyse species representation over four decades, as well as initial representativeness, in order to robustly evaluate PA network effectiveness.

As well as ‘effectiveness’, we can also talk about conservation success in terms of ‘impact’, which is the difference that conservation interventions have made over time (Rodrigues 2006). However, quantifying conservation impact of entire conservation networks in the absence of comparable no-protection counterfactuals is inherently difficult and rarely undertaken (Pressey et al. 2015; McIntosh et al. 2017), but also has potential to offer insight into network performance. As well as evaluating overall network effectiveness, I also compare different regions within the network to test PA impact, and whether other regional characteristics can predict long-term effectiveness.

Restoration

Another understudied question within conservation planning is how best to incorporate landscape 'recovery' into systematic plans (Ockendon et al. 2018). As well as protecting existing high quality landscape features, the focus of the UK conservation community has moved towards enabling landscape-scale conservation outside of protected areas (Donaldson et al. 2017; Crick et al. 2020), along many other countries which have highly modified landscapes with limited semi-natural habitat. Much of the high-quality habitat is already protected (Müller et al. 2020) but this protection may not be adequate to conserve protected species (Gaston et al. 2008), and therefore a mix of protecting existing high-quality sites and landscape-scale recovery more broadly is needed to deliver conservation commitments (Rappaport et al. 2015; Mikusiński et al. 2021). In practice, this 'recovery' consists of habitat restoration using a mix of enhancement of degraded habitat and habitat creation at the landscape-scale, usually outside existing protected areas (Adams et al. 2016).

Incorporating systematic approaches to landscape recovery has the potential to deliver large increases in cost-effectiveness (Arponen 2019). However, quantifying this is inherently difficult. In order to assess potential future ecological return, you need to quantify the relative benefits of taking recovery action for particular habitats in different areas (Wilson et al. 2011). This has been undertaken in several ways, including using existing environmental conditions and species distributions (Crossman & Bryan 2006), habitat suitability (Thomson et al. 2009), modelled return on restoration investment (Wilson et al. 2011), historic species distributions (Yoshioka et al. 2014), and reduction in projected extinctions (Strassburg et al. 2019). However, as well as prioritising recovery, this must also be balanced against protecting existing natural habitat, and how to reconcile these separate conservation goals is still a priority question in conservation (Ockendon et al. 2018). I approach this question by incorporating potential complementarity of 'recovered' landscapes to existing conservation value to select areas that can deliver efficiently for biodiversity in joint conservation/recovery plans.

1.3 Area-based conservation in the UK

The development of the UK protected areas network

The protected area network of Great Britain (GB) is extensive, with over 10 000 terrestrial statutory designated sites (Gaston et al. 2006). The first *national* protected areas, aside from individual patches of land managed for wildlife by local trusts and non-governmental organisations, were National Parks (NP) legislated for in the National Parks and Access to the Countryside Act 1949. This gave powers to a National Parks Commission to designate National Parks in England and Wales, but not Scotland or Northern Ireland. However, NPs were not originally chosen, or managed for, biodiversity and are now recognised as IUCN category V protection (Crofts & Phillips 2013) denoting ‘protected landscape/seascape’ which does not offer additional protection for biodiversity. The other IUCN V landscape designation that can be designated by the National Parks Commission within the UK are Areas of Outstanding Natural Beauty (AONB) (Starnes et al. 2021).

Within the 1949 Act another land designation was created for the whole of Britain: National Nature Reserves (NNR) that *were* chosen for their biodiversity (and sometimes geological) value. These sites offered a higher level of protection, now comparable to IUCN category IV (Crofts & Phillips 2013), and were protected sites selected by the then newly created Nature Conservancy. Sites were selected that covered the most important land for biological or geographic features. Land covered by NNRs could either be bought by the Nature Conservancy, leased, or held under agreement with landowners. The Nature Conservancy, which later became the Nature Conservancy Council before separating into devolved national organisations, could also designate Sites of Special Scientific Interest (SSSI), which were typically smaller than NNRs and designated on private land with management agreements (Adams 2003).

Northern Ireland has a slightly different conservation designation structure. There are NNR and AONB, but no SSSI or NP, designations. There is a legislative equivalent land designation to SSSI, which are Areas of Special Scientific Interest (ASSI) which were created under the Nature Conservation and Amenity Lands Order 1985. Likewise Scotland does not have AONBs, but it has comparable National Scenic Areas (NSA) (Adams 2003). There are currently 15 NPs within GB (10 in England, 3 in Wales, and 2 in Scotland), 348 NNRs (approximately 224 in England, 76 in Wales, and 48 in Scotland), and around 6600 SSSIs (4122 in England, 1078 in Wales, and 1423 in Scotland) (Natural England 2020; Natural Resources Wales 2020; Scottish Government 2020). There are also 46 AONBs in the UK (across England, Wales and Northern Ireland). European Natura 2000 sites added more recently, such as Special Areas of Conservation and Special Protection areas, usually also fall under national legislation through parallel SSSI designation (Starnes et al. 2021).

All UK designations vary in level of protection, have been designated for different reasons, and have been added over an extended period of time largely on the basis of individual site properties, not those of the aggregated network (Gaston et al., 2006). Focusing on NNR and SSSI which cover the vast majority of land designated and managed for biological diversity within the Britain, the rationale for designation was based upon habitat representation (Ratcliffe 1986), specifically in terms of climatic, physiographic, edaphic and anthropogenic habitat diversity (Ratcliffe 1977). Although site selection was systematic, network-level metrics were not explicitly considered in the designation process and selection was not standardised throughout the network between habitat and UK nation, and as such cannot strictly be considered a ‘systematically planned’ conservation network under contemporary definitions. In this thesis I use British terrestrial protected areas (within England, Scotland, and Wales) to explore questions in conservation planning.

Implementing Systematic Conservation Planning

Despite the third highest number of SCP publications originating in the UK, behind USA and Australia (Kukkala & Moilanen 2013), SCP has not been used to guide national policy implementation in the UK itself. However, there are many examples in other countries that have previously implemented SCP plans. Australia and South Africa have both utilised SCP extensively for development and implementation of conservation plans. Perhaps the most famous example is the rezoning of the Great Barrier Reef Marine Park, undertaken between 1999-2004 in Australia under the Representative Areas Program (RAP) using Marxan. SCP approaches have also been used in Australia to inform numerous large-scale forestry management agreements using C-Plan (McIntosh 2019). In South Africa, many regional conservation plans have been developed using SCP approaches (Knight et al. 2006). In contrast, the UK tends to be used more as a study area to research advances in SCP, rather than for SCP plans designed for implementation (Sinclair et al. 2018; but see Smith et al. 2021).

Conservation is an applied discipline, and so as well as planning considerations such as feature layers, prioritisation methods, and costs: how to manage the transition from planning to implementing conservation actions is also crucial (Pressey & Bottrill 2009). Learning from previous SCP implementations, key considerations for best practice include ensuring a straightforward and transparent planning process; employing an experienced spatial prioritisation team; collaborating with diverse stakeholders, such as landowners, NGOs, and government employees; and ensuring those stakeholders are engaged with the process though products (e.g., maps) (Knight et al. 2006). Every conservation plan is unique and so lessons learned from one implementation may not be valid for another, and it is difficult to make generalisable rules (Adams et al. 2018). However, for any SCP implementation it is crucial that any plans are subsequently evaluated using suitable monitoring data, and with adequate resources and preparation (McIntosh 2019).

For SCP to be implemented successfully in the UK, in addition to lessons from previous implementations, addressing the challenges identified within section 1.2 are also pertinent. As with the global conservation community, there are differing perspectives in the UK about how to value different aspects of nature. The majority of protected sites (SSSI and NNR) were established to protect specific habitat features (Ratcliffe 1977), but considering *how to incorporate different viewpoints* is important now given the calls for a broader approach to evaluating the benefits that area-based conservation delivers. The performance of these sites is typically assessed using site condition monitoring based on goals set at the time of designation (Starnes et al. 2021). However, this approach doesn't consider the dynamism of nature or climate change, and isn't compatible with typical systematic approaches which assess value at the network-scale. So *how to measure long-term performance* of these UK area-based conservation networks is an important question. The UK has heavily modified much of its land (Robinson & Sutherland 2002) and so, as well as conservation of existing high-quality features, the 'recovery' of landscapes is now commonly regarded as important to ensure the long-term conservation of biodiversity through resilient ecological networks (Crick et al. 2020; Duigan et al. 2020). This will be achieved through targeted habitat creation and enhancement, but *how to integrate landscape recovery with existing priorities* is an important question in UK landscape restoration. Addressing these challenges, alongside learning from previous implementations of SCP in different contexts and countries, can contribute towards improving outcomes of conservation planning in the future.

Global and UK policy opportunities

The global conservation movement is at a crossroads at the time of writing this thesis. Despite the missed Aichi biodiversity targets set in 2010 (UNEP-WCMC & IUCN 2016), the post-2020 global biodiversity framework will shortly be set in Kunming, Yunnan Province, China as part of the UN Biodiversity Conference (COP 15). The date has been repeatedly postponed, due to the ongoing COVID-19 pandemic, but the initial meetings will now take place 11 to 24 October 2021. Through the setting of goals and targets, this presents a huge opportunity for the conservation community to address issues with the current global area-based conservation network and to generate positive biodiversity outcomes (Bhola et al. 2021; CBD 2021). The first draft of the post-2020 global biodiversity framework has already been published, with a number of key targets especially relevant to this thesis (Table 1.2).

There are also unique national opportunities for conservation policy within the UK, driven by the UK leaving the European Union (EU) and the associated transition from EU to national legislation, and by the 25 Year Environment Plan within the Environment Bill 2019-21 (DEFRA 2018). The bill will include details on legislation to drive the recovery of nature and, although there is still uncertainty over the exact legislation that will be produced, the use of systematic planning methods could be used to inform associated conservation plans.

Table 1.2 2030 action targets from the first draft of the post-2020 global biodiversity framework. Targets 1, 2, and 3 are considered especially relevant to this thesis and listed below. See (CBD 2021) for full drafted targets.

Target 1	Ensure that all land and sea areas globally are under integrated biodiversity-inclusive spatial planning addressing land- and sea-use change, retaining existing intact and wilderness areas.
Target 2	Ensure that at least 20 per cent of degraded freshwater, marine and terrestrial ecosystems are under restoration, ensuring connectivity among them and focusing on priority ecosystems.
Target 3	Ensure that at least 30 per cent globally of land areas and of sea areas, especially areas of particular importance for biodiversity and its contributions to people, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes.

1.4 Objectives and rationale of thesis

The overall aim of the thesis is to apply SCP methodologies to the British terrestrial protected area network to inform how we might efficiently and effectively prioritise sites for conservation. This thesis will also identify where new conservation areas in Britain might deliver the best outcomes, with a view to this being used to inform policy and conservation practice within the UK, and globally. Here I focus on conservation at the British, rather than the UK scale, due to ease of species distribution modelling over a relatively contiguous landmass, but results will be qualitatively valid applied to the entire UK. Chapters two to five of the thesis investigate specific fundamental conservation planning questions, and these are outlined below.

Chapter 2 The effectiveness of the protected area network of Great Britain

Conservation networks are often assessed for effectiveness but, despite this being a long-term measure of network performance, these assessments rarely incorporate a temporal component. I investigate the effectiveness of the GB protected area network in terms of species representativeness and persistence over a 40-year period. I also test the impact the protected area network has had in reducing loss of species from landscapes over the period and whether certain landscape characteristics can predict long-term effectiveness. This long-term assessment will hopefully shed light on the performance of PA networks and inform improvements to make conservation networks more effective.

Chapter 3 Translating area-based conservation pledges into efficient biodiversity protection outcomes

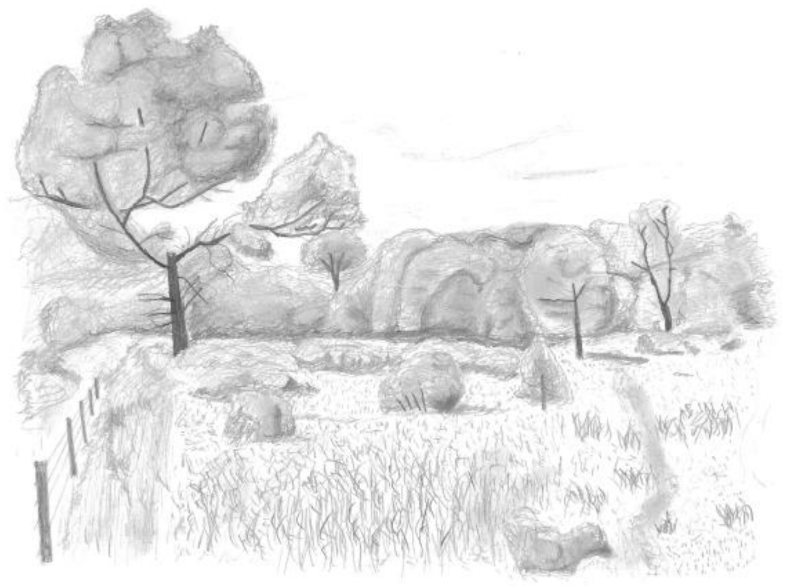
The UK has recently pledged to protect 30 percent of land for nature by 2030 (UK Government 2020). The pledged areas were not selected systematically, and some of the included areas are designated for landscape, aesthetic, and cultural value, and not the importance of ecological features. I assess how efficient this strategy has been and, using spatial prioritisation and systematic planning tools, whether an alternative strategy using SCP could perform significantly better in delivering conservation outcomes.

Chapter 4 Incorporating a diversity of viewpoints within conservation planning can deliver on different conservation objectives with minimal trade-offs

Different individuals within conservation hold differing values and perspectives on how to implement conservation. Although powerful decision-making tools exist, and can be carried out within designated stages of SCP, there are many social biases that can mean that consensus on conservation action may not be a fair compromise. Here I identify caricature conservation viewpoints from across the conservation community, and I develop and evaluate several methods to equitably integrate viewpoints in conservation into compromise approaches.

Chapter 5 Balancing existing conservation priorities with restoration potential in delivering landscape recovery

Currently, English conservation areas do not form a ‘coherent ecological network’ (Lawton et al. 2010), and hence degraded landscapes must be ‘recovered’ in order to restore effective ecological networks. Creating a coherent strategy that maximises potential for landscape recovery while also conserving existing diversity is difficult as there are many knowledge gaps (Adams et al. 2016; Verdone & Seidl 2017). In this chapter I quantify recovery potential using the species pool concept, and use this to test how existing conservation features and recovery of different habitats can be balanced within conservation plans.



The Middle Wood of Askham Bog, Site of Special Scientific Interest, situated to the southeast of York

CHAPTER 2

The effectiveness of the protected area network of Great Britain

2.1 Abstract

Protected Areas (PAs) are core components of conservation strategies, but the networks they form are rarely assessed for their effectiveness over time. We tested different aspects of effectiveness of the British PA network in achieving long-term biodiversity outcomes, including species representativeness of initial location choices and network resilience (in terms of species persistence). Using 10 × 10 km cells, 'landscapes', with contrasting cover of protected areas managed specifically for biodiversity conservation, we evaluated these aspects of effectiveness by analysing species distribution changes of over 2800 species of animals and plants from 1974 to 2014. Landscapes that contained PAs in 1974 had higher species representativeness than landscapes without PAs, but landscapes with low PA

coverage (<median) were more representative than those with high PA coverage (>median). Many species distributions have declined since 1974, and the distributional trends of declining and priority species were similar (on average) in landscapes containing PAs and in the wider countryside, implying PA-containing landscapes were not resilient to landscape-scale pressures. Nonetheless, PAs did have a small positive impact over time on landscape-scale representation trends of declining species, and priority species. Regardless of PA coverage, topographically heterogeneous landscapes were more likely to retain priority species between 1974 and 2014, and less likely to be colonised by expanding species. Despite landscapes with low PA coverage disproportionately contributing to overall PA network representativeness, they are less resilient than landscapes with high PA coverage, which jeopardises their value in the long-term and will require landscape-scale habitat conservation and restoration to address.

2.2 Introduction

Species declines continue globally (Pimm et al. 2014; Ceballos et al. 2015; Secretariat of the Convention on Biological Diversity 2020), and conservation efforts to prevent them have been largely unsuccessful (Hoffmann et al. 2010; Johnson et al. 2017). Protected areas (PAs) are one of the main area-based tools to combat species loss, by preventing or limiting changes to land use and other pressures that are causing declines outside PAs (Watson et al. 2014; Maxwell et al. 2020). Global terrestrial PA coverage currently stands at 15% (Stokstad 2020; UNEP-WCMC et al. 2020), and a coverage target of 17% by 2020 agreed under the Convention on Biological Diversity Aichi Target 11 (CBD 2010) has been missed. Although PA extent is increasing, and higher coverage targets are likely as part of the post-2020 global biodiversity framework (Bhola et al. 2021; CBD 2021), assessing the effectiveness of PA networks (the set of all PAs within an area) is essential in understanding the degree to which they contribute to the long-term conservation of nature. This requires a multi-faceted evaluation of all component PAs of the network: both of initial establishment locations, usually in terms of representativeness of species or habitats; and the extent to which long-term biodiversity outcomes are achieved through appropriate management and PA network design (Rodrigues & Cazalis 2020).

Previous evaluations of protected area network effectiveness have primarily focused on evaluating PA extent and locations, through identifying network representativeness, rather than biodiversity outcomes which require evaluation over time (Butchart et al. 2015; Maxwell et al. 2020). For a PA network to be effective initially, component PAs must be 'representative': located in areas that support the full variety of species and/or habitat diversity, in order to be able to conserve the full range of species in a region or country (Margules & Pressey 2000). Current representativeness may be used to identify missing or underrepresented 'features' (usually populations, species, ecosystems, but may include cultural and ecosystem service targets too) so as to recommend improvements (Oldfield et al. 2004; Shwartz et al. 2017; Fonseca & Venticinque 2018). Systematic Conservation Planning (SCP) is often used to improve network representativeness by prioritising areas that maximise 'complementarity' using spatially-explicit methods, whereby proposed additions (priority areas) to a PA network disproportionately add underrepresented biodiversity features (Wilson et al. 2009). SCP enables a rigorous and accountable way of allocating funds to protect a coherent network of PAs, through planning to optimise the ability to meet overarching conservation goals (Margules & Pressey 2000; Kukkala & Moilanen 2013), and may include informative planning layers in addition to biodiversity data (Magris et al. 2018). Evaluating representativeness (representation of the full variety of biodiversity within the PA network (Kukkala & Moilanen 2013)) is important, but it is only one facet of long-term nature conservation, and understanding biodiversity outcomes through time is ultimately just as important in evaluating network effectiveness (Nicholson et al. 2006; Rodrigues & Cazalis 2020).

As well as representing biodiversity, a PA network should retain initial conservation value through reducing habitat loss and maintaining species populations (Watson et al. 2014) but evidence for the ability of individual PAs to deliver these long-term biodiversity outcomes is limited (Rodrigues & Cazalis 2020). There is support for PAs conserving habitat, especially forest cover (Geldmann et al. 2013; Spracklen et al. 2015), even though pressure on

PAs has actually increased since the turn of the century (Geldmann et al. 2019). However evidence for maintaining species populations is more mixed: better outcomes for species richness and abundance have been reported (Coetzee et al. 2014; Cazalis et al. 2020), but other studies have found this benefit largely explained by land use and habitat type (Gray et al. 2016; Pellissier et al. 2020), or no benefit at all (Rada et al. 2019). Additionally, when evaluating an entire PA network it is important to evaluate overall biodiversity outcomes across the network, rather than individual site-specific ones: many PAs are established to protect a single species or community and may keep to these limited targets well, but the network as a whole may fail to be effective if biodiversity outcomes are poor overall across the covered area. A number of factors have been proposed to improve long-term PA network outcomes, including increasing area of protection (Isaac et al. 2018), improving connectivity (Saura et al. 2014), incorporating topographic heterogeneity (Oliver et al. 2010), and strengthening law enforcement (Hilborn et al. 2006). Furthermore, although SCP approaches facilitate improving initial representativeness, evidence that they also increase effectiveness in maintaining long term outcomes, through location and design factors improving the resilience of PA networks, is lacking (McIntosh et al. 2018; McIntosh 2019).

Quantifying long-term biodiversity outcomes across entire PA networks over time is inherently difficult. Evaluations can simulate future outcomes based, for example, upon species persistence (Nicholson et al. 2006), projected distributions (Stralberg et al. 2015) or modelled future abundance (Johnston et al. 2013). Although these evaluations raise important considerations in PA network planning, they do not consider how effective a PA network has been in achieving outcomes to date across a broad range of taxa (Bottrill & Pressey 2012) and they are a product, ultimately, of the predictive models used and not empirical observation. The gold standard of long term monitoring of PA outcomes is conservation ‘impact’ evaluation, which involves comparing outcomes in ‘identical’ paired sites through time, one with a conservation intervention and one without, to measure the positive effect of the PA (Pressey et al. 2015; McIntosh et al. 2017). Although this is possible for individual or small numbers of PAs, it is not practical when considering an entire PA network, and other retrospective methods are needed to evaluate outcomes (Sacre et al. 2020). Long-term outcome evaluation is still possible for PA networks through analysing variation in long-term species distribution datasets. A network's resilience in maintaining representation of populations over time, through increased meta-population persistence against wider landscape threats, can be assessed and hence another measurable aspect of network effectiveness (Gaston et al. 2006; Isaac et al. 2018). As well as overall PA network resilience, robust analysis of representation over time would also permit an evaluation of the impact of PAs on achieving these long-term biodiversity outcomes, and support policy-makers to make evidence-based conservation decisions (McIntosh et al. 2017).

The PA network of Great Britain (GB) is extensive, with >10,000 current statutory terrestrial PAs and many different protection categories (Gaston et al. 2006). National Nature Reserves (NNR) and Sites of Special Scientific Interest (SSSI) formed the initial designation structure of the network, as they focus on species and habitats (and in some cases geological or geomorphological features). Sites with more recent designations, such as those under the Natura 2000 network, are usually also SSSIs. NNRs and SSSIs were historically largely selected based upon habitat representation (Ratcliffe 1986). The process of selecting NNR and SSSI sites involved finding high quality areas of habitat that were typical of climatic, physiographic, edaphic and anthropogenic variation within those habitats. The quality of the site itself was based on a range of criteria including size, diversity, naturalness, typicalness, and fragility, and sites were then graded and assigned NNR or SSSI designations depending upon importance [see Ratcliffe (1977) for full description]. Although site selection was methodical and aimed at being representative, species-level complementarity was not considered explicitly: as such it cannot be considered a systematically planned network, as understood today.

The government's 25 Year Environment Plan (25YEP) (DEFRA 2018) creates a context of policy change for England that presents an important opportunity to evaluate the current network performance, and to use this to inform and improve the selection of new sites for conservation action. The

25YEP envisages moving to a landscape scale approach, with a Nature Recovery Network (NRN) at its core, but also the commitment to create 500,000 ha of new priority habitat and plant millions of trees in England (DEFRA 2018). Similar commitments are to be found in current and proposed legislation and biodiversity strategies in Wales and Scotland (Duigan et al. 2020). Investigating the effectiveness to date of the existing GB PA network, as well as evaluating improvements that could potentially be achieved by using SCP, would contribute useful insights to the forthcoming implementation of the 25YEP and similar conservation strategies.

Here, we evaluate how the changing distributions of species relate to the distributions of PAs managed for biodiversity conservation (SSSIs and NNRs) at a 10 × 10 km spatial resolution (which we refer to as ‘landscapes’) as designated in 1974, to reflect an historic baseline shortly after the bulk of the GB PA network had been created. We assess network effectiveness through both the initial representativeness, representation of species across the PA network at that time; and its resilience, by analysing subsequent changes to the distributions of species in PA-containing landscapes though to 2014. We further evaluate whether a PA network based on SCP would have initially performed better, in terms of higher species representativeness than the actual network. We predicted that PA locations would initially be well sited (i.e. have greater species representation than landscapes that lacked PAs), and that there would be higher levels of species representation in landscapes with greater PA coverage, but also that species representation could have been initially significantly improved through the use of SCP. We also expected that landscapes containing PAs, and particularly landscapes containing larger areas of PA land, would be most resilient in maintaining species distributions over time, compared to landscapes without PAs. Additionally, in order to investigate potential drivers of landscape resilience in GB in greater detail, we divided the UK into 100 × 100 km regions and tested the importance of different factors associated with resilience within them. These included level of protection in each landscape, to evaluate PA impact over time, and also overall regional connectivity and topographic roughness. Finally, we included regional similarity of the actual PA network to an optimised SCP network as a factor, to test if regional PA configurations matching SCP priorities were more resilient.

2.3 Methods

In order to investigate different facets of PA network effectiveness within Britain, we firstly calculate the initial representation of species within protected and non-protected landscapes at a baseline date (representativeness), and then how this representation has changed over time up to the present (resilience), based on recorded species distribution changes. An optimised national network was also created using systematic conservation planning software to investigate how its species representativeness compares to the actual network. Finally, to investigate potential drivers of resilience, we model current landscape representation on a regional scale using a number of different predictors, e.g. landscape PA coverage, as well as regional connectivity, topographic roughness and similarity to the counterfactual SCP optimised network. All analysis was carried out at 10 × 10 km (henceforth 'landscape') resolution. An overview of the methodological workflow for assessing effectiveness is given in Figure 2.1, and a glossary of terms in Supplementary Table 1.1.

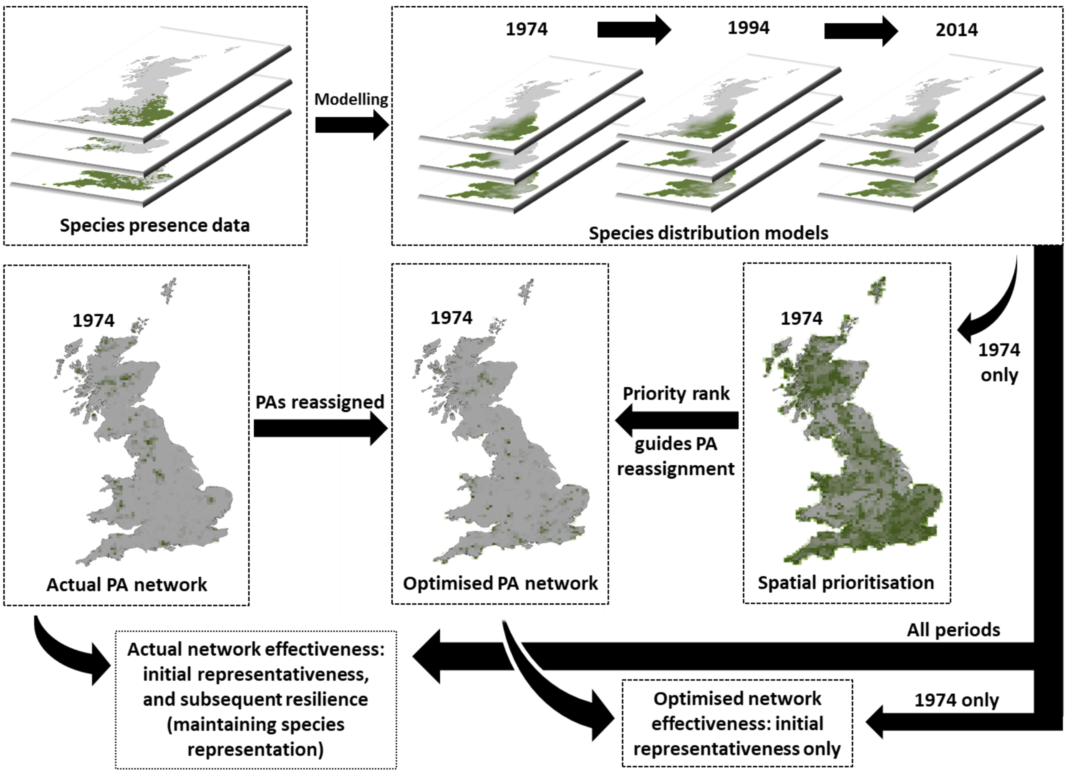


Figure 2.1 Study methodology workflow for national PA network effectiveness analysis. We spatially modelled species presence data, based on bioclimatic variables, and mapped

the PA network as it existed in 1974. Only sites managed specifically for biodiversity conservation (SSSIs and NNRs) were included in the PA network. Effectiveness was assessed firstly from initial national representativeness, calculated in 1974 from summed species distributions within different PA categories. We then compared this to species representation in subsequent periods in 1994 and 2014 to investigate long-term PA network resilience. An optimised network was created that would have been selected in 1974, using up-to-1974 species distribution data, had SCP conservation prioritisation software been used to determine selection. We then used this optimised counterfactual to compare initial representativeness with the actual PA network. Additionally, not shown in figure, mean landscape representation in 100 × 100 km ‘regions’ was modelled to investigate predictors of landscape resilience.

Protected areas

We defined our study area as Great Britain and associated islands greater than 20 km^2 in area. We considered the protected area network to consist of NNRs and biological SSSIs (5838 sites), as these constituted all PAs designated for the protection of biodiversity within Britain at our selected baseline date. SSSIs designated solely for geological reasons were excluded as they were not selected with biodiversity in mind, or likely to have been subsequently managed for nature conservation (912 sites). Data on the geographical boundaries and first date of notification for SSSIs were provided by Scottish National Heritage (SNH), Natural Resources Wales (NRW), and Natural England (NE) (Hinton, George; Personal Correspondence). Our study started with the PA network present in 1974, by which a large proportion of today's PA network area was already designated (Supplementary Figure 1.1; England: 61.1%, Scotland: 40.1%, Wales: 65.4%, total: 51.5% by area).

PAs in Britain are typically less than 10 km^2 in area (Supplementary Figure 1.2) and when aggregated into 10 × 10 km cells (landscapes), PA landscape coverage is heavily skewed to lower levels of protection (Supplementary Figure 1.3). Hence, landscapes were split into the following 3 protection categories and assessed separately in both the national and regional analyses; ‘PA absent’ where there were no protected areas in a given landscape, ‘low PA coverage’ cells had less than the median PA coverage by area (up to 1.39% landscape protected), and ‘high PA coverage’ cells had more than median coverage (1.39–90.91% landscape area protected).

We undertook a sensitivity analysis by repeating our analyses using 40% and 60% PA coverage quantiles (0.89% and 2.39% absolute landscape coverage respectively) as a cut-off instead of the median (1.39% coverage).

Additionally, as these were all objectively low levels of protection, we also repeated the analysis for the higher 80% quantile (8.20% coverage). Results were consistent with those in the main text (Supplementary Table 1.4 through to Supplementary Table 1.12) and only reported in the main text if they differ.

Species distributions

Historic distribution data were provided by a number of recording organisations including Biological Records Centre (BRC) and Butterfly Conservation (BC), and breeding bird distributions (Gillings et al. 2019) from British Trust for Ornithology (BTO). We were able to include a total of 4855 species distributions in the analysis as they were present in all three periods, from a total of 11 taxonomic groups (Supplementary Table 1.2). Species not present for every time period were not included (174, 404, and 572 species for periods 1, 2, and 3 respectively) to remove inconsistently monitored species, but this also resulted in species GB extinction and colonisation events being excluded. Species distributions were in the form of annual presence records.

Our study started in 1974 when recording activity in a number of taxonomic groups was well established (Period 1). We identified monitoring points at 20-year intervals in 1994 (Period 2) and 2014 (Period 3) when we measured changes in species representation over time. Due to differences in recorder effort between time periods we calculated sampling periods (Supplementary Table 1.3) for each taxonomic group, except birds and vascular plants [atlas data were only available for specific time periods in birds (1968–72, 1988–91, 2007–11), and vascular plants (1930–69, 1987–99, 2010-17)]. We took all records during the monitoring point year and then successively added data from previous years for each species separately, stopping when the number of new landscapes added to the cumulative species distribution was below 5%. The median species sampling period was used as the taxonomic group's sampling period.

For each species with over 10 presence records (3452 species) we interpolated their range using Integrated Nested Laplace Approximations (INLA) in the *inlabru* package (Bachl et al. 2019) for each period. A joint model of distribution intensity and recording effort was used, including four biologically relevant covariates: seasonality, growing degree days, water availability and winter cold [see Beale et al. (2014) for details]. Soil pH was additionally included as a covariate for butterfly, moth, and vascular plant models as it can have a strong influence on plant distribution (Barbour et al. 1987), and hence dependent lepidopteran species. We calculated the biologically relevant covariates using climate variables obtained from the Met Office (Met Office 2017), specifically mean temperature, sunshine and rainfall. We then extracted monthly means of the weather data for 10-year intervals preceding each period date. Soil pH used in the models was obtained from Countryside Survey datasets; dated 1978, 1998, and 2007 for each period respectively (UK Soil Observatory 2007). We also used soil moisture in the calculation of water availability (Batjes 1996).

To estimate recorder effort we needed broad habitat layers which we extracted from the Countryside Survey datasets: for 1974 (Period 1), we used the 1978 Countryside Survey dataset (Sheail & Bunce 2003); for 1994 (Period 2), Land Cover Map 1990 (CEH 1990); and for 2014 (Period 3), Land Cover Map 2015 (Rowland et al. 2017). The habitat layers were then used in a Frescalo analysis (Hill 2012) to estimate recorder effort by comparing species records within each landscape to its neighbours, weighting for spatial proximity and habitat similarity. Recording effort was calculated for each taxonomic group for each period separately. 2687 species models converged. Although undertaking model cross-validation was not possible due to the large number of models, models predictions were tested using the area under curve (AUC) of the receiver operating characteristic (ROC) approach (Araújo et al. 2005; Bahn & McGill 2013) and found to be a fair approximation of actual species distributions for the given time period within Britain (AUC: period 1 mean = 0.836, SD = 0.124; period 2 mean = 0.834, SD = 0.120; period 3 mean = 0.829, SD = 0.122). In order to include species with genuinely restricted distributions, rather than species with very low recorder effort, we included un-modelled presence records for the species without converged models when there was greater than 50% spatial overlap between chronological periods. This resulted in a final total of 2861 species being included in the effectiveness analysis (Supplementary Table 1.2).

Evaluating effectiveness

Factors contributing to overall PA network effectiveness were assessed differently. The initial effectiveness in the establishment of PA locations was assessed through representativeness soon after original designation (period 1). We used this initial species representation as a baseline for evaluating resilience (i.e., ability to maintain representation over time). Representation of each species in each time period was calculated as the summed modelled presence within each of the three PA categories (landscapes with zero, <median PA, or >median PA cover). As the number of landscapes differed between PA categories we normalised this to compute representation per landscape. We computed this measure of representation for each PA category in all 3 periods, and repeated the analysis for: (1) ‘all species’ (2861 species); (2) ‘declining species’, species with ranges that contracted over the study period (1362 species); (3) ‘expanding species’, species with ranges that expanded over the study period (1463 species); and (4) ‘priority species’, any species listed under Section 41 (S41) of the 2006 Natural Environment and Rural Communities (NERC) Act (179 species).

In order to test potential benefits of SCP, we carried out spatial prioritisation for GB landscapes as though it had been conducted in 1974 (with the 2861 ‘all species’ distributions from 1974) using Zonation (Moilanen 2007). This spatial prioritisation produced a complementarity-based ranking of conservation priority over GB which we used to create a counterfactual ‘optimised’ PA network (i.e., as if the same total PA area had been allocated using Zonation in 1974). We created this by reassigning PAs using the 1974 baseline spatial prioritisation rank (‘optimised’ sites) such that the largest protected area coverage was assigned to the highest priority hectad, the second largest to second highest priority etc. Hence both real and optimised PA networks had exactly the same distribution of landscape PA coverage (Supplementary Figure 1.4). Species representativeness could then be assessed for the initial period in the optimised and the actual PA network.

We carried out analyses at two spatial scales. The analyses described so far considered different aspects of effectiveness using all 10 × 10 km cells across GB. However in order to further investigate drivers of landscape resilience, and because species distribution trends and PA designation vary geographically, we carried out a second set of analyses in which 10 × 10 km cells were nested within 'regions'. Each region consisted of a 100 × 100 km sample, incrementing in 50 km latitudinal and longitudinal steps, with spatial non-independence accounted for in later modelling. Only regions with greater than 50% land coverage that had at least one landscape from each PA category were considered (106 overlapping regions). In each region representation was aggregated into a single metric for each PA category separately, and this was calculated as the mean species representation per landscape within the PA category (henceforth 'mean representation'). This analysis also allowed us to investigate the impact of protection by comparing resilience trends within protected and unprotected 10 × 10 km cells within and between regions. The analysis was repeated for the same categories of species (all, declining, expanding, and priority) used for the national analysis.

To identify factors driving landscape resilience, a Bayesian conditional autoregressive spatial regression analysis was undertaken using *INLA* (Lindgren & Rue 2015). We fitted a model with regional mean representation in the most recent period (Period 3 – 2014) as the dependent variable (*r*). We also included representation during the baseline period (Period 1 - 1974) (*base_rep*) as a predictor variable to control for initial representation, thus allowing *r* to function as a proxy for resilience. Other predictor variables included protection category (zero, <median PA, >median PA) as a categorical variable (*PA_cat*) to investigate PA impact, and the change in regional PA coverage from the baseline (1974) to current (2014) period (*PA_change*) to control for later additional protection (Supplementary Figure 1.1). Other regional covariates expected to influence resilience were also included with interaction terms with the protection category; PA connectivity, topographic heterogeneity, and similarity between actual network configuration and SCP optimised network (Eq. 1). We computed the PA connectivity (*PA_conn*) within a region as the inverse of the median nearest neighbour edge to edge distances between PAs (Calabrese & Fagan 2004), and we calculated similarity to optimised network (*PA_sim*) as the Spearman's rank correlation between actual and optimised PA distribution. We computed topographic roughness (*Topo*) as the standard deviation of elevation (SD across 30 m cells within each region). We obtained elevation data from Google Earth Engine, using the ALOS DSM: Global 30 m dataset (Takaku et al. 2016).

$$
\begin{aligned}
logit(r_i) = \; & b_o \\
& + b_1 PA\_cat_i \\
& \times \left(b_2 PA_{conn_i} + b_3 PA_{sim_i} + b_4 Topo_i \right) \\
& + b_5 base\_rep_i + b_6 PA\_change_i + SE_i
\end{aligned}
$$

Eq. 1

where $logit(r_i)$ is the mean representation in region *i* within a given PA category, PA_cat_i, included as a categorical variable. PA_conn_i is the connectivity between PAs in the region, PA_sim_i is the correlation between actual and optimised PA distribution within the region, $Topo_i$ is the regional topographic roughness, $base\_rep_i$ is the initial representation at period 1 for the PA category (PA_cat_i) and PA_change_i is the change in protection coverage area from baseline to current period within the region. SE_i is the structured and random spatial effect for region i, b_0 is the intercept, and $b_{1\text{-}6}$ are the estimated parameters for the corresponding covariates.

2.4 Results

National PA network effectiveness

These analyses consider initial PA network effectiveness in achieving long-term conservation outcomes though the network's starting representativeness, and subsequent resilience through the extent species representation was maintained. This was undertaken across the whole of GB, split into three landscape categories (10 × 10 km cells containing zero, <median PA and >median PA coverage by area), and repeated for four categories of species (all, declining, expanding, and conservation priorities).

Baseline PA locations were 'well chosen', as landscapes with protection typically had higher representation of priority species per landscape than 'PA absent' areas (Wilcoxon signed-ranks, two-tailed: Absent-Low: median = 0.327–0.477, $Z = -9.000$, $P < 0.001$; Absent-High: median = 0.327–0.385, $Z = -8.942$, $P < 0.001$; Figure 2.2). Unless otherwise stated results reported are from the 'priority species' category since these are the main targets for conservation, and hence most closely reflect conservation priorities. We found comparable results for every species category (Supplementary Table 1.4), with the exception that the landscapes with highest PA coverage (80% quantile 'high PA' areas) did not have higher priority species representation than 'PA absent' landscapes (Supplementary Table 1.10).

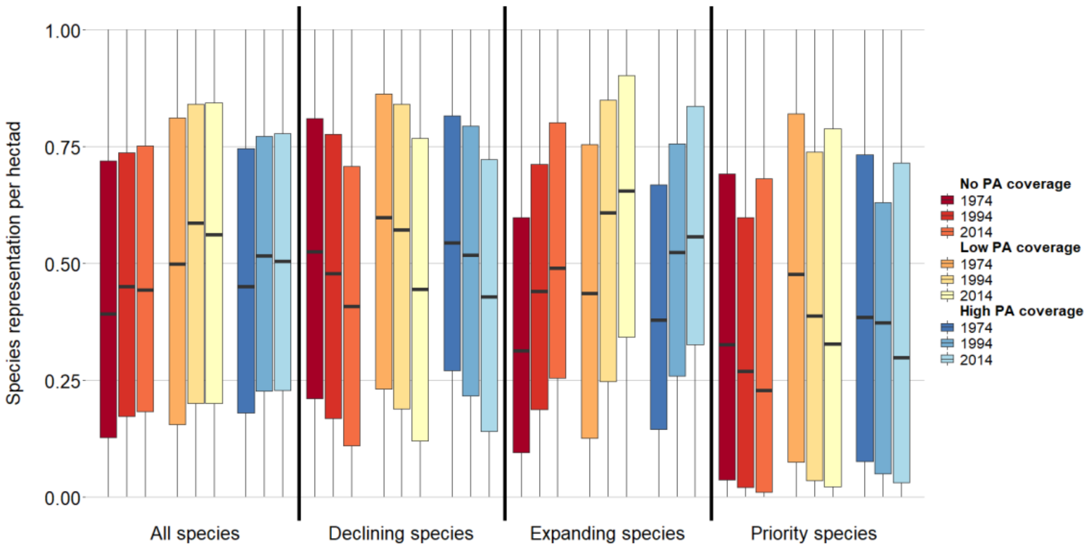


Figure 2.2 Representation per landscape within different GB PA categories of 4 different categories of species: all species (n = 2861), declining species (n = 1362), expanding species (n = 1463), and priority species (n = 179). Species were assessed within each PA category (colours - 'PA absent', 'low PA' and 'high PA') for each of the three periods (dark to light shading through time – 1974, 1994, 2014) to investigate initial representativeness, and resilience through changes in representation over time. The lower and upper borders of the box are lower and upper quartiles, respectively; the horizontal bar is the median; and whiskers represent the lowest and highest observations.

If SCP had been used at the baseline date, optimised through spatial prioritisation using Zonation, the initial network representativeness would have improved. Initial representation per landscape would have been increased slightly for 'high PA' category protected areas (Wilcoxon signed-ranks, two-tailed: High PA Actual-optimised: median = 0.385–0.451, $Z = -7.764$, $P < 0.001$ two-tailed; Figure 2.3). Due to the 'high PA' landscapes being assigned to optimal areas more efficiently, the optimised 'low PA' category in fact had lower representation (Wilcoxon signed-ranks, two-tailed: Low PA Actual-Optimised: median = 0.477–0.404, $Z = 8.383$, $P < 0.001$; Figure 2.3). These patterns were seen for all categories of species (Supplementary Table 1.5).

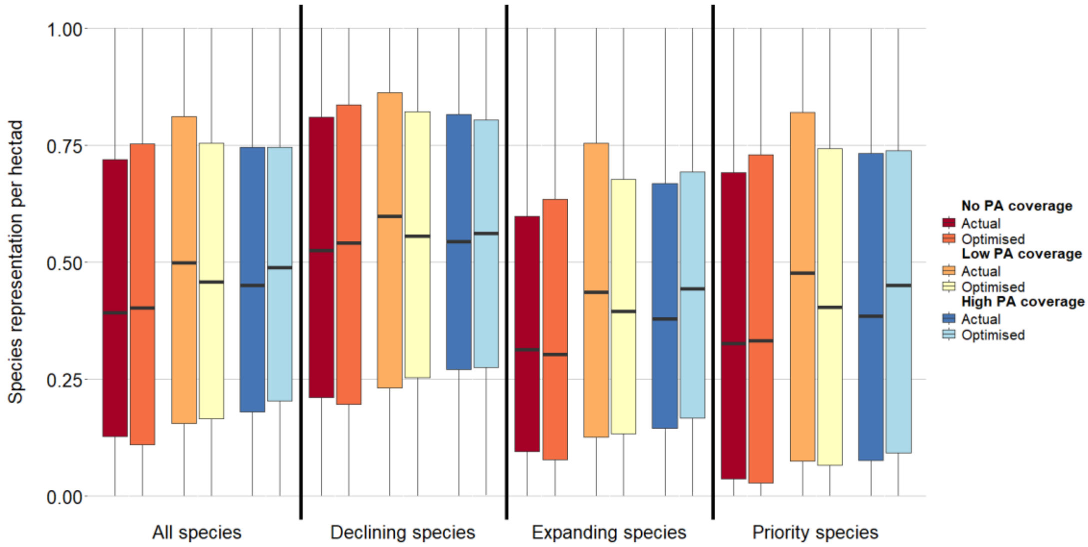


Figure 2.3 Initial representation per landscape of the actual PA network, and the optimised PA network, for period 1 (1974). Species were assessed within each protection category categories (colours - 'PA absent', 'low PA' and 'high PA') for both the actual (dark shading) and optimised network (light shading). The lower and upper borders of the box are lower and upper quartiles, respectively; the horizontal bar is the median; and whiskers represent the lowest and highest observations.

Surprisingly, 'low PA' landscapes had higher initial representation of species distributions than 'high PA' landscapes, and this pattern continued through time (Wilcoxon signed-ranks, two-tailed: 1974 Low-High: median = 0.477–0.385, $Z = 5.972$, $P < 0.001$; 1994 Low-High: median = 0.388–0.373, $Z = 5.367$, $P < 0.001$; 2014 Low-High: median = 0.328–0.298, $Z = 3.497$, $P = 0.001$; Figure 2.2). In fact every PA category showed similar temporal trends in representation (Figure 2.2). This meant initial differences between PA categories remained for subsequent periods (Supplementary Table 1.4) and, thus, PA-containing landscapes did not appear to be more resilient than unprotected ones at maintaining populations of declining and priority species at the national scale.

Priority species declined consistently over time, whereas 'all species' increased between the first two periods (Figure 2.2). This resulted in an overall net gain in representation per landscape of ‘all species’ for each PA category (including for zero PA landscapes) from the 1974 baseline to the present 2014 period (Wilcoxon signed-ranks, two-tailed: PA absent 1974–2014: median = 0.393–0.444, $Z = -7.336$, $P < 0.001$; Low PA coverage 1974–2014: median = 0.498–0.561, $Z = -4.854$, $P < 0.001$; High PA coverage 1974–2014: median = 0.451–0.504, $Z = -7.006$, $P < 0.001$; Figure 2.2).

Representation trends varied between species within PA landscape categories in Britain, which when considered together produce the previously reported results. In some species, distribution contraction was less severe in landscapes in the ‘high PA’ category; for example European nightjar *Caprimulgus europaeus* distribution contracted 53.3% in PA absent landscapes, but only 37.9% in ‘high PA’ landscapes. However, representation of some species in fact declined more in landscapes with protected areas, such as brown hairstreak *Thecla betulae* which contracted 70.5% in PA absent landscapes, but 74.2% in ‘high PA’ landscapes. In this case, other factors with a regional basis are driving change which protection cannot offset. Further illustrative species and distribution maps are provided in Supplementary Figure 1.5.

Predictors of landscape resilience

The regional analyses again considered long-term effectiveness for GB 10 × 10 km ‘landscapes’, but we now investigated the drivers of resilience through modelling representation outcomes within 100 × 100 km ‘regions’. Landscapes-within-region are still split into the same three protection categories and we repeated the analysis for all, declining, expanding and priority species. Baseline representation had a large positive effect on current representation for every species category (All species: effect size = 0.863, Credible Interval (CI) = 0.821, 0.906; Declining: effect size = 0.746, CI = 0.677, 0.819; Expanding: effect size = 0.752, CI = 0.712, 0.792; Priority: effect size = 1.088, CI = 1.051, 1.125; Supplementary Table 1.12). Hence the results for the other variables indicate their effects on change in representation through time, i.e. impact on resilience, controlling for baseline variations in diversity and spatial effects.

For our analysis of factors driving resilience, in terms of PA impact we found strong support for correlations between 'high PA' landscapes and more positive trends of declining (effect size = 0.054, CI = 0.036, 0.072) and priority species (effect size = 0.028, CI = 0.016, 0.041), but a negative effect on expanding species (effect size = −0.034, CI = −0.055, −0.012, Figure 2.4). 'Low PA' landscapes also had positive, but weaker, association with priority species trends (Figure 2.4; effect size = 0.020, CI = 0.008, 0.032).

Regions that matched the optimised SCP network configuration more closely also had improved declining species trends (effect size = 0.069, CI = 0.022, 0.117, Figure 2.4). PA connectivity had a small positive effect on 'high PA' landscape declining species trends (effect size = 0.029, CI = 0.011, 0.047). Additionally, topographic roughness was strongly positively associated with priority species trends, and negatively with expanding species (Figure 2.4; effect size = 0.084, CI = 0.040, 0.128, and; effect size = −0.247, CI = −0.360, −0.135, respectively).

Despite the overall difference in landscape resilience between PA categories, spatial trends in representation change between regions were largely similar between PA categories (Supplementary Figure 1.6). Only the 'PA absent' category (Figure 2.4, inset map) is described here, as it is the intercept of the regression models. There were slight declines in south-west England for 'all species' representation but increases in the rest of Britain (Figure 2.4, inset map). The trends for declining and expanding species were opposite, with western Scotland and East Anglia having a particularly large decrease in declining species and large increase in expanding species representation. There was clear north-south spatial structuring for priority species representation change, with northwest Scotland increasing whereas representation decreased in the majority of England.

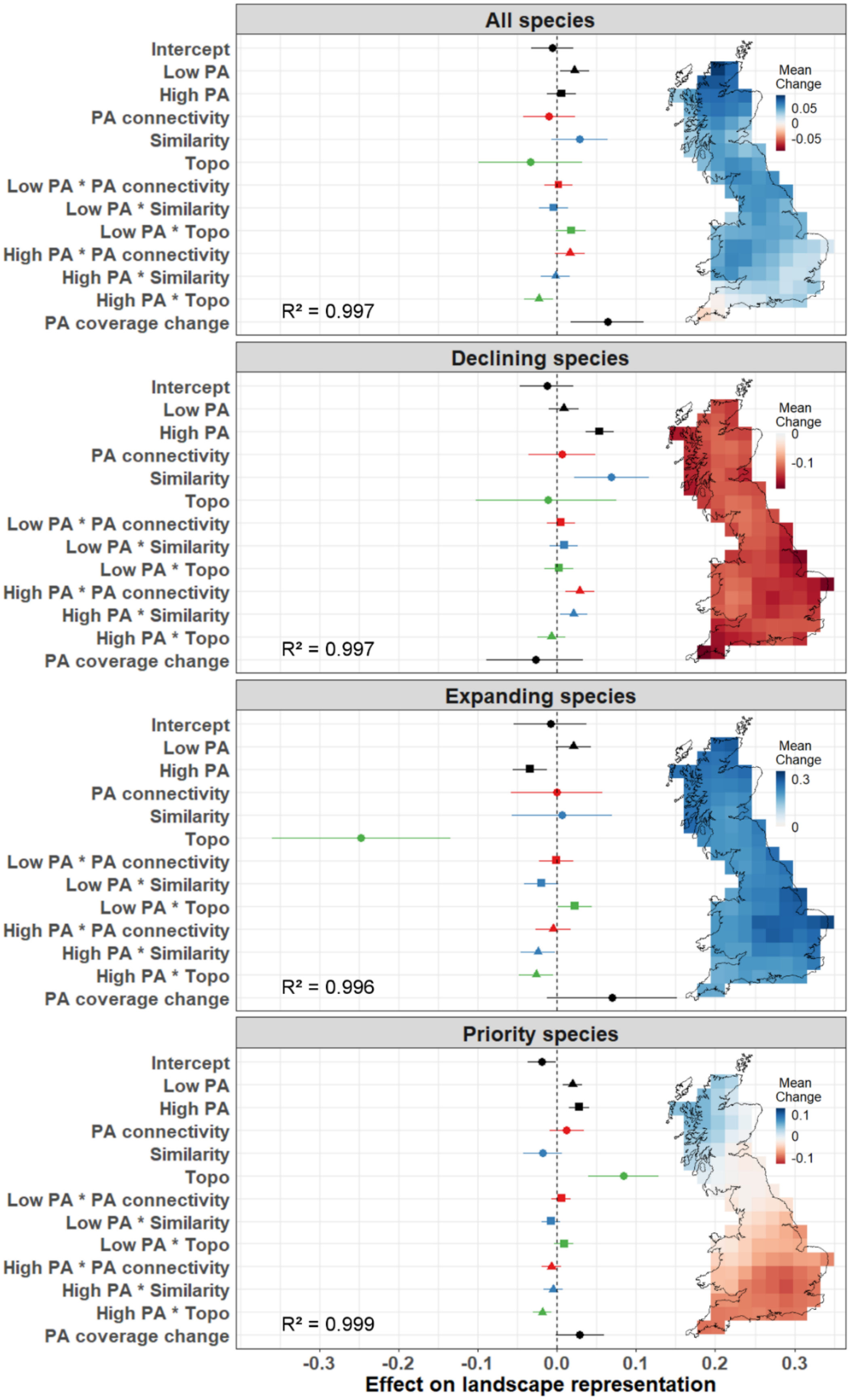


Figure 2.4 Factors affecting landscape (10 × 10 km) resilience at maintaining species representation in 100 × 100 km square regions across GB. We carried out spatial regression analysis on 4 different species categories (all, declining, increasing, and conservation

priorities), with mean PA category representation per landscape (10 × 10 km square) in period 3 (2014) within the region included as the dependent variable. Baseline representation in period 1 (1974) was controlled for by including it as a covariate in the model (not plotted), and this allowed the dependent variable to function as a proxy for landscape resilience. 'Low PA' and 'high PA' are factorial covariates in the models (triangle and square points respectively). All other covariates are continuous (colours: connectivity – red, similarity to optimised network – blue, topography – green, and change in PA coverage between periods 1 and 3 - black). Points indicate the mean effect size, and horizontal lines the credible interval. Spatial trends between regions are also shown (inset maps) with change in mean representation for individual regions (period 3 – period 1) plotted for each species category. Only the 'PA absent' protection category spatial trends are presented as it is the intercept factor for the model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.5 Discussion

We found that PAs managed for biodiversity conservation were initially well sited, in the sense that landscapes containing PAs had higher species representation than 'PA absent' landscapes in 1974, and these 'protected landscapes' still had relatively good species representation in 2014. However, we found that species declined (or increased) in generally similar ways, averaged across landscapes that either did or did not contain PAs. Nonetheless, when we controlled for regional differences (i.e. considering landscapes within and between regions), our analyses revealed weak tendency for 'high' (and to a lesser extent 'low') PA coverage to have a positive impact on landscape representation outcomes for declining and priority species through time – a conservation benefit.

Effectiveness: baseline representativeness

Our results agreed with previous studies that the initial PA locations in Britain were picked well overall (Rodrigues et al. 1999; Hopkinson et al. 2000), somewhat validating the original site selection strategy (Ratcliffe 1977) which, although not as efficient or representative as an SCP approach, had significantly higher species representation in 'protected' landscapes than in unprotected ones. However, landscapes with the very highest PA coverage (in the upper 80% quantile) did not have higher priority species representation than unprotected landscapes, primarily because 'high PA' landscapes are mainly located in relatively low diversity regions in north-western and upland Britain (Shwartz et al. 2017).

Landscapes with low protection had the highest initial species representation, highlighting the relatively important contribution of small PAs to conservation networks (Wintle et al. 2019). This likely reflects national patterns of species distributions and habitat fragmentation. Species with restricted distributions, and species richness as a whole, tend to be concentrated in southern and lowland Britain, reflecting climatic and soil factors, but there is a smaller amount of semi-natural habitat there, as a consequence of a greater intensity of agriculture amongst other factors (Oldfield et al. 2004). Hence lowland priority species often occupy small sites in fragmented ‘low PA’ landscapes (Supplementary Figure 1.1,Supplementary Figure 1.4).

If an SCP strategy had been used nationally in 1974 to designate PAs, with the distribution data available at the time, then this spatially optimised historic counterfactual network would have significantly higher initial representativeness than the actual PA network. For example, priority species median representation in ‘high PA’ landscapes would have increased by 6.6%. The largest differences between the actual and optimised network were decreases in ‘low PA’ and corresponding increases in ‘high PA’ representation; echoing that although PAs in the actual network are well distributed for species representation, ‘low PA’ landscapes contribute disproportionately to network representativeness. The prioritisation for this analysis was based on ‘all species’ distributions, however, there are many possible prioritisation considerations which can also be included, i.e. cost-efficiency, connectivity, species vulnerability, and climate change; and this would have changed the priority rank of different areas (Kullberg et al. 2015; Troupin & Carmel 2018). The relevance and importance including these considerations could be assessed as part of a full SCP implementation.

Effectiveness: resilience

Despite their higher initial species representation, landscapes with protection experienced similar temporal trends in representation decline to landscapes with less or no PA coverage. These landscape trends result from a combination of factors (Hayhow et al. 2019), such as agricultural intensification (Robinson & Sutherland 2002), climate change (Walther 2010), or development (Hansen et al. 2005; Veach et al. 2017b). These trends suggest PA outcomes have been largely due to where they were originally sited rather than because they have ameliorated declines, i.e. they are well placed but not resilient.

Whilst highlighting trends for declining and priority species, as this was the primary focus in assessing PA performance, we also note that the ‘all species’ analyses indicate that overall species representation for every PA category, hence species distributions, actually increased since 1974 despite a partial reversal since 1994. Other studies have found similar net positive biodiversity change globally (Dornelas et al. 2014; Daskalova et al. 2020), elsewhere in Northern Europe (Nielsen et al. 2019), and in Britain (Macgregor et al. 2019; Outhwaite et al. 2020). Spatially, these increases occurred largely in Scotland, Wales and northern England, and the spatial pattern was similar for priority species (Figure 2.4 inset map). This may be driven by recent climate change allowing southern species to expand at their northern margins (Gillings et al. 2015; Mason et al. 2015). This same expansion was not seen in southern England, possibly due to the physical barrier of the English Channel, or that species colonising GB post-1974 could not be included in the analysis. Equally, species losses were generally offset by turnover in assemblage composition; regions with large distribution declines in some species often saw the largest increases in other species. This corresponded with previously identified areas of high species turnover in birds (Harrison et al. 2016).

PA impact

The national analysis looked at aspects of PA network effectiveness through a combination of initial representativeness, and subsequent resilience though representation trends within landscapes with different levels of protection. Although the resilience observed in Britain was poor, PAs could still have had a positive impact such that species declines would have been even more severe in those landscapes without their designation. A comprehensive impact evaluation is not possible retrospectively, and impractical for a national network, but we were able to provide a level of evaluation through the regional modelling analysis, controlling for baseline and spatial trends.

Despite following general landscape trends, PA coverage was found to have had a small positive impact on landscape resilience within regions for declining and priority species. PA coverage was associated with less negative representation trends, albeit not enough to prevent overall declines within protected landscape categories, caused by a combination of agricultural intensification, urbanisation, pollution, climate change and other factors (Hayhow et al. 2019). PA coverage within landscapes within Britain is mostly below 20% coverage (Supplementary Figure 1.3), and much larger protected area coverage may convey greater impact in improving resilience to these factors, or other additional benefits, but such places do not occur in Britain in numbers where these effects would be detectable in this analysis.

This analysis did not find a link between expanding species and PAs that has previously been identified in some taxa (Thomas et al. 2012; Gillingham et al. 2015), in fact 'high PA' areas had a small negative association. Although PAs can act as 'landing pads' for range-shifting species (Hiley et al. 2013), this benefit may have been missed because species colonising the GB post-1974 were not included within the analysis.

PAs in 'low PA' landscapes were found to have less positive impact than in landscapes with 'high PA' coverage at retaining representation of priority and declining species at the regional scale. This highlights the current vulnerability of landscapes with 'low PA' coverage comprising of small sites in fragmented habitat, despite their disproportionate contribution to network species representativeness. Smaller sites may have poor resilience due to higher relative management costs limiting conservation actions (Armsworth et al. 2011), smaller populations with reduced connectivity to nearby sites (Isaac et al. 2018) or a range of other factors leading to extinction debt, such that these smaller isolated populations will tend to decline over time (Watts et al. 2020). This is important when considering the expected changes in climate to which populations will have to adapt (Oliver et al. 2015; Gaüzère et al. 2016), and is urgent to address in policy if current network representativeness is to be maintained.

There are a number of approaches which could address this differential PA impact. The PA network could be optimised such that larger PAs are created in landscapes that currently have ‘low PA’ coverage by expanding or joining up small fragments of semi-natural habitat. Implementing this may be difficult however because of the intensity and socio-economic value of surrounding land use for other purposes, such as agriculture, and habitat creation or restoration may be required to obtain the same long-term benefit seen from ‘high PA’ coverage in this analysis. Thus more investment could be directed to small PA management to be put towards landscape-scale approaches, such as the establishment of non-statutory large-scale conservation initiatives (LSCI) to buffer and link up small PAs (Shwartz et al. 2017). England is currently in the process of establishing a Nature Recovery Network (NRN), which is a key part of the 25-year Environment Plan (DEFRA 2018), included in the forthcoming Environment Bill, and this provides an unprecedented opportunity to implement landscape-scale LSCI approaches nationally.

Other factors predicting landscape resilience

Aside from baseline representation the landscape factor most strongly predicting landscape resilience was regional topographic roughness (standard deviation of elevation), positively for ‘priority species’ but negatively for ‘expanding species’. The increased resilience for ‘priority species’ can be explained by microclimatic refugia present in these areas created by microclimate heterogeneity (Oliver et al. 2010; Suggitt et al. 2018), allowing species to persist in the face of changing climatic conditions. This suggests topography should be considered in future prioritisation exercises to identify possible new sites for protection: topographically heterogeneous areas are more intrinsically resilient and so would make good candidate sites for resilient PAs, but these landscapes may not contribute as much to the representativeness of the PA network as more vulnerable flatter areas. The negative effect on ‘expanding species’ is more difficult to interpret, and several different processes may contribute to the observed pattern: topographically heterogeneous areas may possess more stable communities or more specialised niches, and might therefore be more resistant to new colonists; topographically diverse landscapes are, on average, at higher elevations, and hence only a small proportion of these landscapes may be suitable for expanding, heat-adapted species; and cold-adapted upland species may be unable to disperse between geographically-separated blocks of ‘upland’ habitats.

PA connectivity did have a small positive effect on declining species trends in ‘high PA’ landscapes and, interestingly, the outcomes for declining species were improved the most in regions where there was the closest match between the actual and optimised SCP distribution of PAs. Resilience of landscapes may have been improved through increased initial capacity of PAs to collectively conserve species in the long-term within these regions. Unfortunately levels of similarity within landscapes were low (range $R_s = -0.163, 0.606$) and so regions where SCP optimisation is followed more closely could not be investigated.

Conclusions

GB PA network representation of declining and priority species has declined over time, despite the network being reasonably well designed in terms of initial spatial configuration, albeit not in terms of PA sizes. Protected areas retain their relative importance within the landscape but undergo the same landscape effects as non-protected areas, meaning there have been similar landscape changes in species representation regardless of protection level. Although PAs have had some positive impact on priority and declining species, the network cannot be considered fully effective due to failing to be resilient in buffering wider negative landscape trends. ‘Low PA’ landscapes have had less positive impact than ‘high PA’ landscapes, despite contributing more to overall network representativeness, and will require conservation intervention to improve landscape resilience. The English Nature Recovery Network and similar initiatives in the other countries of GB provide opportunities to tackle this, through implementing landscape-scale restoration approaches in a systematic way.

For the last 40 years, only landscapes with high levels of protection or topographic variation have had a significant positive effect on achieving long-term conservation outcomes, and this should be considered within future conservation plans. Long-term monitoring for the entire network continues to be important in facilitating further investigation into network effectiveness and to learn from past network performance. SCP would have improved the GB network had it been used through improving initial PA network representativeness, and to a lesser extent resilience, and it thus would be a valuable tool in improving future conservation planning.

Wheat fields to the north of Bulmer in the
Howardian Hills Area of Outstanding Natural Beauty

CHAPTER 3

Translating area-based conservation pledges into efficient biodiversity protection outcomes

3.1 Abstract

Ambitious national and global pledges to protect increasing areas of land risk trading conservation effectiveness for convenience of designation. We show that UK conservation areas often lie outside the highest biodiversity priority landscapes, and that systematic conservation planning can improve site selection.

3.2 Main text

National commitments under the Convention on Biological Diversity (CBD) have repeatedly under-delivered: global biodiversity indicators continue to decline (Secretariat of the Convention on Biological Diversity 2020) and the Aichi target 11 to protect 17% of the global terrestrial area by 2020 has not quite been met, with coverage currently standing at around 16.64% (Stokstad 2020; UNEP-WCMC et al. 2020). As elsewhere, the UK's 2010 commitments to halt biodiversity loss by 2020 have not been realised (Hayhow et al. 2019). Globally, the response of conservationists and policymakers to these failed targets has been to propose ever more ambitious targets as we move towards the post-2020 global biodiversity framework (Bhola et al. 2021; CBD 2021). Thus, the CBD has drafted a proposal to ensure that, by 2030, at least 30% of global land and sea are conserved, "especially areas of particular importance for biodiversity and its contributions to people" (CBD 2021). However, there is a risk that states will then designate land to maximise 'apparent protection', and not necessarily outcomes for biodiversity (Barnes et al. 2018).

The UK 30by30 pledge

In this context, the British Prime Minister announced a new commitment on the 28th September 2020 to protect 30% of the UK's land by 2030 to support the recovery of nature (UK Government 2020). This extends to the terrestrial environment the existing '30by30' pledge to protect 30% of British seas by 2030 (UK Government 2019). The potential for such pledges to prevent biodiversity loss will depend on the extent to which targets are met, and whether they are met in a way that delivers effective conservation outcomes (Pouzols et al. 2014).

Newly designated protected areas or other effective area-based conservation measures (OECMs) should complement the existing network of conservation sites if they are to maximise the representation (and thereafter protection) of species (Maxwell et al. 2020). Currently, only 9.04% of Britain's land area has a legal status that specifically mandates biodiversity protection, equivalent to IUCN level IV (Crofts & Phillips 2013). The British Prime Minister's 30by30 pledge also includes an additional 17.67% of land that is currently designated as 'protected landscapes', such as National Parks and

Areas of Outstanding Natural Beauty, which are classed as lower-grade IUCN level V protection (Crofts & Phillips 2013). They are multi-purpose landscapes with a focus on planning and development constraints that do not confer additional legal protection for wildlife (above any national legislation that applies to all land, or additional biodiversity designations at specific locations within these protected landscapes). Thus, two-thirds of the land that has been identified as contributing to the 30% pledge has neither been selected to protect important biodiversity, nor offers specific protection to biodiversity. In order to reach the 30% goal, a further 3.29% of the land surface outside these sites still requires protection.

As is characteristic of ambitious conservation aspirations, delivering nature recovery in practice is far from straight-forward. In densely populated countries like the UK and elsewhere in Europe, priority species are often confined to small habitat fragments (Müller et al. 2020). This makes it hard to establish the landscape-scale protection and restoration of nature that is necessary if long-term species survival is to be ensured (Shwartz et al. 2017). Area-based conservation priorities should thus focus on locations where a combination of extending and managing existing sites, improving marginal habitats nearby, restoring additional habitats and improving landscape-scale connectivity are most likely to be effective (Isaac et al. 2018). The likelihood that individual threatened species will recover would be increased in these areas because they are already present, and thus available to colonise improved habitats that are delivered by upgraded protection and management in the surrounding landscape (Shwartz et al. 2017; Isaac et al. 2018). To inform this expansion, we explore alternative scenarios to identify the highest conservation priority locations in Great Britain. We identify priority areas that currently fall outside of national biodiversity designations (minimum IUCN level IV protection) and, separately, those that fall outside biodiversity designations and protected landscapes combined (minimum IUCN level V protection). We deduce how well these strategies deliver species conservation priorities in 30% of Britain’s land area (see Supplementary Figure 2.1 for analysis workflow).

Achieving 30% land coverage with systematic planning

The best outcomes for biodiversity are expected when priority sites are selected (and conservation measures implemented) on the basis of the species or habitats on all sites, unconstrained by historic conservation decisions. In practice, sites currently protected primarily for biodiversity are very unlikely to lose their protection in the UK, so our first scenario (scenario 1, Figure 3.1a) represents a systematic conservation prioritisation that includes all the sites currently protected for biodiversity. We identified the highest priority areas for network expansion that maximises coverage of 445 priority species distributions including birds, plants and a wide variety of invertebrates (Online Supplementary Data https://static-content.springer.com/esm/art%3A10.1038%2Fs42003-021-02590-4/MediaObjects/42003_2021_2590_MOESM4_ESM.csv). An important additional consideration is the existing land use of the cell (Naidoo et al. 2006; Brown et al. 2015), and so we also undertook a parallel analysis incorporating opportunity costs of protecting or restoring land using an agricultural/urban land classification (Supplementary Figure 2.2; Supplementary Table 2.4). Note that prioritisations are undertaken at the 10 × 10 km scale (henceforth ‘cells’) due to the resolution of spatial data for certain taxa. Attaining 30% national coverage by protecting *all* the land within selected 10 × 10 km cells is not practical as most British landscapes have fragmented semi-natural habitat. The priority cells recognised here represent foci for identifying and directing subsequent conservation actions and funding, accepting that different blends of conservation actions will be required in different landscapes. Given this constraint, an additional 50% coverage target is presented, within which a subset of higher-priority sites can be identified as foci for biodiversity and habitat ‘recovery’ in the wider countryside (Figure 3.1, Supplementary Table 2.2).

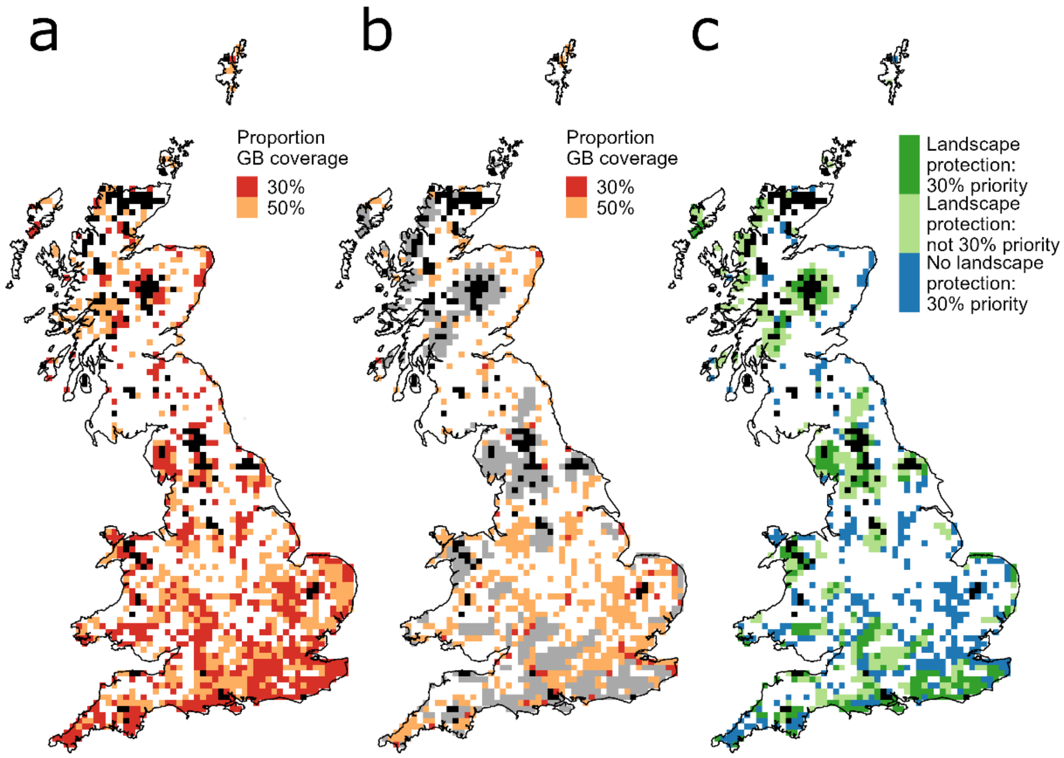


Figure 3.1 (a) Scenario 1: prioritisation constrained only by the inclusion of current biodiversity protected sites. (b) Scenario 2: constrained by maintaining both biodiversity and landscape protection sites, as suggested by the 30by30 announcement. (c) Overlap between top 30% priority cells for biodiversity from scenario 1 and current protected landscapes. Cells already protected for biodiversity are shaded black (which are included as part of the 'top 30% in both scenarios). For panels (a) and (b), top 30% priority cells are shaded red, top 50% orange, and landscape protection cells are grey. In panel (c), priority cells for biodiversity are dark green if in a landscape protection cell and dark blue if outside a landscape protection cell; light green shows those landscape protected cells that are not a priority for biodiversity conservation.

Under scenario 1, the most important areas to prioritise for attaining at least 30% network coverage, in a way that is likely to benefit the most species, are largely concentrated in southern and eastern England (Figure 3.1a), although priority cells were less concentrated in the south if land (opportunity) costs were included (Supplementary Figure 2.3a). Northern and upland areas of Britain have disproportionately larger areas protected for biodiversity (Shwartz et al. 2017), so the greatest gains in species representation can potentially be achieved by increased levels of protection and habitat restoration in southern and lowland areas.

Achieving 30% land coverage with pledged landscapes

In a second analysis, we identified spatial conservation priorities when constrained by including both biodiversity and landscape protection cells (scenario 2, Figure 3.1b, Supplementary Figure 2.3b). In line with the 30by30 pledge, this scenario additionally includes all current protected landscapes, and we identify further priorities to expand the network to achieve 30% coverage. Under this scenario, cells with the highest priority are again scattered primarily in southern England (Figure 3.1b), but are again more spread when opportunity costs are considered (Supplementary Figure 2.3b). Both scenarios would protect more of the ranges of threatened species than the cells currently protected for biodiversity (median 1.63% distribution protected): the less constrained first scenario would ensure an additional 59.54% could be protected within 30% of cells in scenario 1, compared to 37.69% under scenario 2 (Figure 3.2, Supplementary Table 2.2). The latter comprises 29.47% from existing biodiversity and landscape protection (in 27.80% of national cells), with the additional prioritised land contributing the extra 9.85% (in 2.20% of national cells). This is only slightly more effective than undertaking scenario 2 by replacing landscape protection cells with the same number of randomly sampled cells (mean 32.48%, min 30.04%, max 34.30%; based on 10,000 iterations).

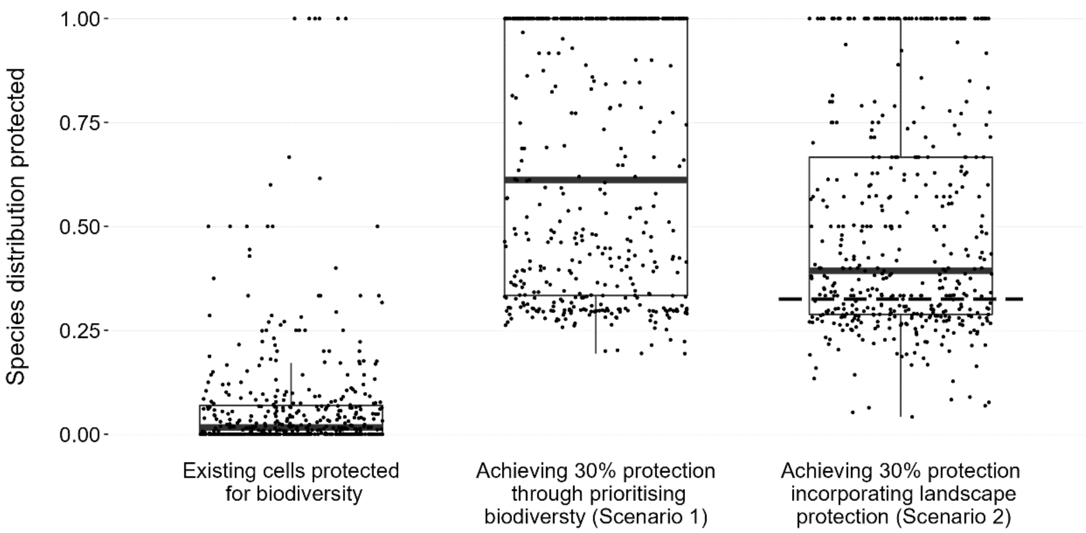


Figure 3.2 Cells were considered currently protected for biodiversity if >40% of the cell was designated IUCN level IV land or higher (6.41% of national cells). Scenario 1 involved attaining 30% GB cell coverage by maximising proportion of species distributions covered, constrained only by the inclusion of current cells protected for biodiversity. Scenario 2 was constrained by maintaining cells protected for biodiversity along with additional protected landscape cells (27.80% of national cells), as suggested by the 30by30 announcement. The lower and upper borders of the box are first and third quartiles, respectively; the horizontal bar is the median; and whiskers extend to 1.5 * inter-quartile range. Individual species are overlaid as points. The dashed line on scenario 2 shows the average of 10,000 sample medians where a randomly selected equivalent number of cells were incorporated instead of landscape protection, before prioritisation.

The higher representativeness of scenario 1 reflects the fact that 62.39% of priority 30% cells in scenario 1 fall outside currently protected landscape cells (Figure 3.1c blue, Supplementary Table 2.3), and just 4.77% of the land within these cells is already protected for biodiversity (mostly as small individual reserves). These are regions where new area-based biodiversity conservation would bring greatest rewards *outside* protected landscapes. In contrast, only 41.50% of protected landscape cells lie within scenario 1 priority 30% cells (Figure 3.1c dark green, Supplementary Table 2.3). These form the highest priority cells for upgrading biodiversity conservation *within* protected landscape cells: current protection for biodiversity (at higher level IUCN level IV designation) is only 10.27% of the total area within these protected landscape cells. This indicates that to meet the 30by30 target efficiently, biodiversity protection would need to be targeted in a subset of the protected landscapes as well as in additional areas outside protected landscapes. The planned Nature Recovery Network provides an opportunity to implement this, potentially including 25 catchment or landscape-scale Nature Recovery Areas in currently non-designated areas, as well as creating/restoring 500,000 ha of new priority habitat (DEFRA 2018).

Making conservation pledges deliver for nature

The 30by30 commitment is a positive step for UK conservation, but requires detailed planning and implementation if it is to deliver its intended goals. Careful targeting of new area-based conservation is required to maximise biodiversity representation, with protection and management needed to ensure that priority species (and other beneficial features of the landscapes) are not lost, and that populations can subsequently expand into the surrounding landscapes. These conservation goals will be met more efficiently if prioritisation occurs with the fewest possible constraints. However, if protected landscapes (National Parks, Areas of Outstanding Natural Beauty, Scottish National Scenic Areas) are included in the 30% coverage target, the impact on rare species will be limited unless habitats are improved within them, as well as carefully targeting the extension of the conservation network beyond currently designated landscapes (Figure 3.1). Further development of priority conservation networks should consider how climate change will likely affect the distribution of species, habitats, and land use pressure (Groves et al. 2012; Stralberg et al. 2020), but securing the existing distributions of currently threatened species remains a priority. As more ambitious area-based conservation targets are likely to be adopted by other states as part of the post-2020 global biodiversity framework, our analysis exemplifies how important it is that such areas are chosen for their ability to deliver efficiently and effectively for biodiversity, given that there are increasing demands on land for a wide range of other uses.

3.3 Methods

All analysis was undertaken in Great Britain and associated islands over 20 km^2. All prioritisations were undertaken at a 10 × 10 km landscape-scale on cells with greater than half land coverage. We considered designations ‘protected for biodiversity’ to be Sites of Special Scientific Interest (SSSI) and National Nature Reserves (NNR); and landscape protection designations to include National Parks (NP), Areas of Outstanding Natural Beauty (AONB), and Scottish National Scenic Areas (NSA). Different cell protection 'cutoffs' were tested at 30, 40, 50, 60, and 70% (Supplementary Table 2.1). Hence cells were considered to be 'protected for biodiversity' at the landscape-scale if SSSI/NNR coverage was above the percentage land cutoff, e.g. at least 40% IUCN IV protection (Figure 3.1: black cells). 'Protected landscapes' were 10 × 10 km cells with total coverage from all of the designations above the cutoff, e.g. at least 40% IUCN V (or greater) protection, but under 40% level IV protection (Figure 3.1b: grey cells). Results were qualitatively similar for all cutoffs (Supplementary Table 2.2 and Supplementary Table 2.3). The joint proportion of cells protected for biodiversity and protected landscapes were most similar to the actual coverage at the 40% 'cutoff' (27.80% of 10 × 10 km cells 'protected' compared to 26.71% actual area coverage), and this is presented in the main text. All designation data used is publicly available from the respective national spatial data repositories for England (Natural England 2020) (SSSI/NNR/NP/AONB), Scotland (Scottish Government 2020) (SSSI/NNR/NP/NSA), and Wales (Natural Resources Wales 2020) (SSSI/NNR/NP/AONB).

We used the recorded distributions of 445 priority species listed under the Section 41 (Natural Environment and Rural Communities Act, 2006), provided by Butterfly Conservation (BC), Biological Records Centre (BRC); and breeding bird atlas data from British Trust for Ornithology (BTO) (Gillings et al. 2019). BTO bird atlas data are only available at the 10 × 10 km scale, which limited the spatial resolution of the analysis. We used all priority species that we were able to acquire from the above recording bodies between 2000 and 2014 (Online Supplementary Data https://static-content.springer.com/esm/art%3A10.1038%2Fs42003-021-02590-4/MediaObjects/42003_2021_2590_MOESM4_ESM.csv). We used the raw distribution records for 156 species that were very localised (10 or fewer presence records) and for a further 77 species which could not be modelled (most of which were also very rare, and for which models did not converge). For the remaining 212 species with over 10 presence records, we interpolated their range using Integrated Nested Laplace Approximations (INLA) in the *inlabru* R package (Bachl et al. 2019). We used a joint model predicting distribution while accounting for recording effort, including biologically relevant covariates: seasonality, growing degree days, water availability, winter cold (Beale et al. 2014), and soil pH from the Countryside Survey 2007 dataset (UK Soil Observatory 2007). These covariates were calculated from monthly means of weather data (mean temperature, sunshine and rainfall) for the decade to 2014 provided by the Met Office (Met Office 2017). We also included soil moisture in the calculation of water availability (Batjes 1996). We used raw data records from all 445 species, along with broad habitat layers extracted from the Land Cover Map 2015 (Rowland et al. 2017), in a Frescalo analysis (Hill 2012) to estimate recorder effort. See Supplementary Methods (Appendix 1) for further details of modelling.

We carried out a spatial prioritisation using Core Area Zonation (Moilanen 2007), whereby cells are removed iteratively, first removing those that contribute the smallest cell value: the maximum proportion of species distributions within the remaining cells. In this way cells remaining longer within the solution complement species representation of other cells to a greater extent, and hence contribute most to underrepresented species' distributions. However, priorities were constrained by masking or 'locking in' different relevant areas to each scenario such that all other cells must be removed first; reducing overall solution optimality but ensuring complementarity to masked areas. Scenario 1 only masked cells protected for biodiversity and didn't consider other designations beyond that. Scenario 2 also masked cells protected for biodiversity but, corresponding to the 30by30 pledge, additionally masked protected landscapes.

We undertook a parallel analysis additionally incorporating opportunity costs calculated from agricultural land classification and urban areas (Natural Resources Wales 2019; The James Hutton Institute 2019; England 2021) (Supplementary Figure 2.2, Supplementary Table 2.4). Although urban areas are often excluded from SCP analyses, it is important to consider species complementarity of all landscapes (the government 30% target applies to the entire land surface). Since some urban/near-urban areas contain nationally rare species, we include urban areas, albeit imposing the maximum opportunity cost in these cells. In this analysis, cell value was calculated as the maximum proportion of species distributions within the remaining cells divided by the mean opportunity cost of the cell (Supplementary Figure 2.3, Supplementary Table 2.2 and Supplementary Table 2.3).

Boardwalk through wet woodland in Malham Tarn National Nature Reserve in the Yorkshire Dales National Park

CHAPTER 4

Incorporating a diversity of viewpoints within conservation planning can deliver on different conservation objectives with minimal trade-offs

4.1 Abstract

Reconciling differing values and perspectives in policy development and implementation is a perennial challenge. Conservation encompasses numerous alternative viewpoints on what to value (features such as biodiversity, ecosystem services or well-being benefits) and how to convert these values into conservation policies that deliver for biodiversity and people. Here I spatially quantify four such possible viewpoints, caricatured by ‘traditional’ conservation, ‘new’ conservation, ‘international market ecocentrism’, and ‘local social instrumentalism’. Each viewpoint prioritises different locations, dependent on the extent to which they deliver a variety of different biodiversity, well-being and economic goals. I find that a pluralist

approach to spatially reconciling these caricature viewpoints, which accounts for the similarities between as well as the distinctiveness of each viewpoint, is able to deliver effectively for multiple conservation features. This pluralist approach provides a coherent spatial conservation strategy with the capacity to satisfy advocates of quite divergent approaches to conservation.

4.2 Introduction

In conservation, individuals differ in the values they attribute to different conservation priorities (Sandbrook et al. 2019; Bhola et al. 2021). As in other applied disciplines, different perspectives often seem contradictory and even irreconcilable in planning decisions (Matulis & Moyer 2017). Two different types of approach are commonly used to unify opposing viewpoints within conservation. Inclusive approaches seek to accommodate all perspectives, by building consensus and finding compromise between people holding different views, thus creating a single voice for conservation that carries more weight (Tallis & Lubchenco 2014). In contrast, proponents of pluralist approaches contend that inclusive approaches reinforce current dominant perspectives and suppress marginal views (Matulis & Moyer 2017) asserting that we need to find better ways to accept and engage with diverse perspectives on biodiversity and give voice to marginalised values (Pascual et al. 2021). The risk is that a pluralist approach results in a divided, and thereby potentially unconvincing, voice for conservation. How to combine these different perspectives, in a way that ensures all viewpoints are represented but that nonetheless garners widespread support, is a pressing question for conservation and more widely in society.

Viewpoints within the conservation community are often considered in terms of ‘traditional’ or ‘new’ conservation (Matulis & Moyer 2017). ‘Traditional’ conservation follows an ecocentric viewpoint, conserving species diversity and natural habitats for their intrinsic value (Soulé 1985; Taylor et al. 2020). It is often regarded as the antithesis of ‘new’ conservation, which follows a more anthropocentric viewpoint motivated by achieving conservation action through attaining economic and social benefit (Marvier 2014b). However, this is a simplification of the diverse range of views on approaches to conservation.

Hence, the Future of Conservation survey (http://futureconservation.org) sought to establish a framework to further categorise different viewpoints within conservation (https://www.futureconservation.org/about-the-debate). In addition to 'traditional' and 'new' conservation, two other positions were included: 'critical social science' and 'market ecocentrism' (Holmes et al. 2017). 'Critical social science' favours conservation that benefits human well-being, but is opposed to 'intrinsic value of nature' arguments and to links with capitalism and corporations. Conversely, 'market ecocentrism' utilises capitalist economic arguments to enable delivery of ecocentric conservation through protecting a large amount of land (Wilson 2016; Kopnina et al. 2018), but tends to ignore social impacts (Schleicher et al. 2019). In reality, the views of conservation researchers and practitioners are spread over a continuum between and beyond these four viewpoint groupings, with no clear 'camps' (Sandbrook et al. 2019), making it difficult to evaluate potential approaches against each other (Hunter Jr et al. 2014).

Every individual viewpoint in conservation encompasses its own set of values and aims, and hence there are trade-offs when seeking to reconcile different viewpoints during policy implementation (McShane et al. 2011). It is not this work's aim to revisit debate about the relative merit of any conservation viewpoint. Rather, it accepts that there exist a breadth of perspectives that need to be reconciled during conservation policy development, whilst recognising that conservation is likely to be more successful if focused on common ground within the conservation community (Hunter Jr et al. 2014). There has been little work to try to quantify different approaches to spatially integrating different perspectives on how to implement area-based conservation, but this is vital in implementing a coherent and representative conservation framework (Bhola et al. 2021).

Spatial prioritisation methods provide the main tool to evaluate potential spatial synergies and trade-offs between different conservation goals. Spatial prioritisation is often an important stage of systematic conservation planning (SCP), which utilises network-scale and spatially explicit methods to inform important conservation planning decisions (Watson et al. 2011). SCP provides a way to incorporate these techniques in a robust and auditable process, incorporating the principle of complementarity to design an optimal network for a given planning objective (Margules & Pressey 2000; Wilson et al. 2009). Although typically focused on improving representativeness of species distributions within area-based conservation measures, spatial prioritisation can also be used to investigate the effect of including different socio-economic and ecosystem service (ES) information on spatial priorities to inform conservation policy (Naidoo et al. 2008). In this way, trade-offs between protecting biodiversity and different societal or policy objectives can be assessed; such as carbon storage (Thomas et al. 2013; Soto-Navarro et al. 2020), or other ecosystem services and land use simultaneously (Anderson et al. 2009; Moilanen et al. 2011; Fastré et al. 2020). Hence, although not previously used for this purpose, spatial prioritisation provides a powerful tool to support spatially integrating different viewpoints in conservation.

As part of a full SCP implementation there is opportunity to build consensus between differing stakeholders' perspectives within the initial planning stages, but this is carried out primarily when conservation goals are being set rather than the spatial prioritisation stage. Decision support tools can be used to facilitate decision-making between stakeholders, preferably using structured methods such as multi-criteria decision analysis (MCDA), which assesses performance of alternative solutions across criteria, explores trade-offs, and generates a decision (Davies et al. 2013; Esmail & Geneletti 2018); or the Delphi technique, which iteratively and anonymously surveys a panel of experts or stakeholders (Mukherjee et al. 2015, 2018). Although these tools provide powerful methods to generate decisions through reconciling different perspectives, there are many social biases such as group think and the dominance effect that cannot be overcome completely (Mukherjee et al. 2018), and hence consensus on conservation action attained may risk not providing an equitably integrated solution. Here I implement spatial prioritisation combined with numeric aggregation methods, which avoids potential social biases, in order to fairly test different approaches to viewpoint integration that combine caricature viewpoints into single solutions.

Using the biological, environmental, social, and economic landscape conditions of Great Britain, I implement four caricature conservation viewpoint prioritisations ('traditional', 'new', 'local social instrumentalism', and 'international market ecocentrism') at a national scale to illustrate the diverse range of viewpoints within the conservation community. I assign weights to species distributions and other resources corresponding with the values of each viewpoint, and then carry out spatial prioritisation at a 10x10 km ('landscape') resolution for Britain. I expect prioritisations for each viewpoint to perform well at covering resource types (conservation features) that are highly valued within that viewpoint, but they may overlook other features. For example, 'non-traditional' methods may perform relatively poorly in covering species distributions. Finally, I develop both 'inclusive' and 'pluralist' approaches to evaluate the extent to which it is possible to reconcile and integrate the four viewpoints into a collaborative and coherent conservation plan.

4.3 Methods

Feature layers

I searched for and collated social, economic and ecological spatial data that: (i) was publicly available for the entirety of Great Britain (GB), (ii) had a resolution of 10x10km scale or finer, and (iii) could be used to create informative ecosystem service (ES) or socio-environmental value layers. After the data search, a total of seven non-biological layers were found to be suitable and are detailed below. I defined the study area as GB, excluding islands smaller than $20km^2$.

Five ES layers were adapted from published, publicly available resources: (i) carbon storage (Bradley et al. 2005; Henrys et al. 2016), (ii) agricultural/land value (urban areas were assigned the highest 'agricultural value', indicating locations unsuitable for terrestrial conservation) (Natural Resources Wales 2019; The James Hutton Institute 2019; England 2021), (iii) recreational services (Schägner et al. 2016), (iv) flood regulation (Stürck et al. 2014), and (v) pollination services (Schulp et al. 2014).

In addition, two socio-environmental value layers were included: (vi) wilderness (Kuiters et al. 2013) and (vii) landscape aesthetic value (Van Zanten et al. 2016). Full details of calculation, and data sources, of ES and socio-environmental value layers are provided in Supplementary Methods (Appendix 3). All feature layers were rescaled to allow for direct comparison, and aggregated to 10x10 km (henceforth 'landscape') resolution for the analysis (Figure 4.1). Only landscapes with majority land cover were considered.

To incorporate biodiversity value, I included the interpolated distributions of 445 priority species with distribution data available listed under Section 41 (Natural Environment and Rural Communities Act, 2006). Although which species constitute 'priorities' may change depending upon viewpoint, here I use the same species to allow for direct comparisons of different viewpoint prioritisation performance. Distribution data were provided by Butterfly Conservation (BC), Biological Records Centre (BRC) and breeding bird distributions by British Trust for Ornithology (BTO). Data were in the form of annual records between 2000 and 2014, except for two taxa where atlas data were only available for specific time periods (birds [2007-11] (Gillings et al. 2019), and vascular plants [2010-2017]). I used the raw distribution records for 156 species that were very localised (≤10 presence records) and for a further 77 species which could not be modelled (most of which were also very rare, and for which models did not converge). For the remaining 212 species with over 10 presence records, I interpolated their range using Integrated Nested Laplace Approximations (INLA) in the *inlabru* package (Bachl et al. 2019). I used a joint model predicting distribution while accounting for recording effort (see Appendix 3 Supplementary Methods for full details).

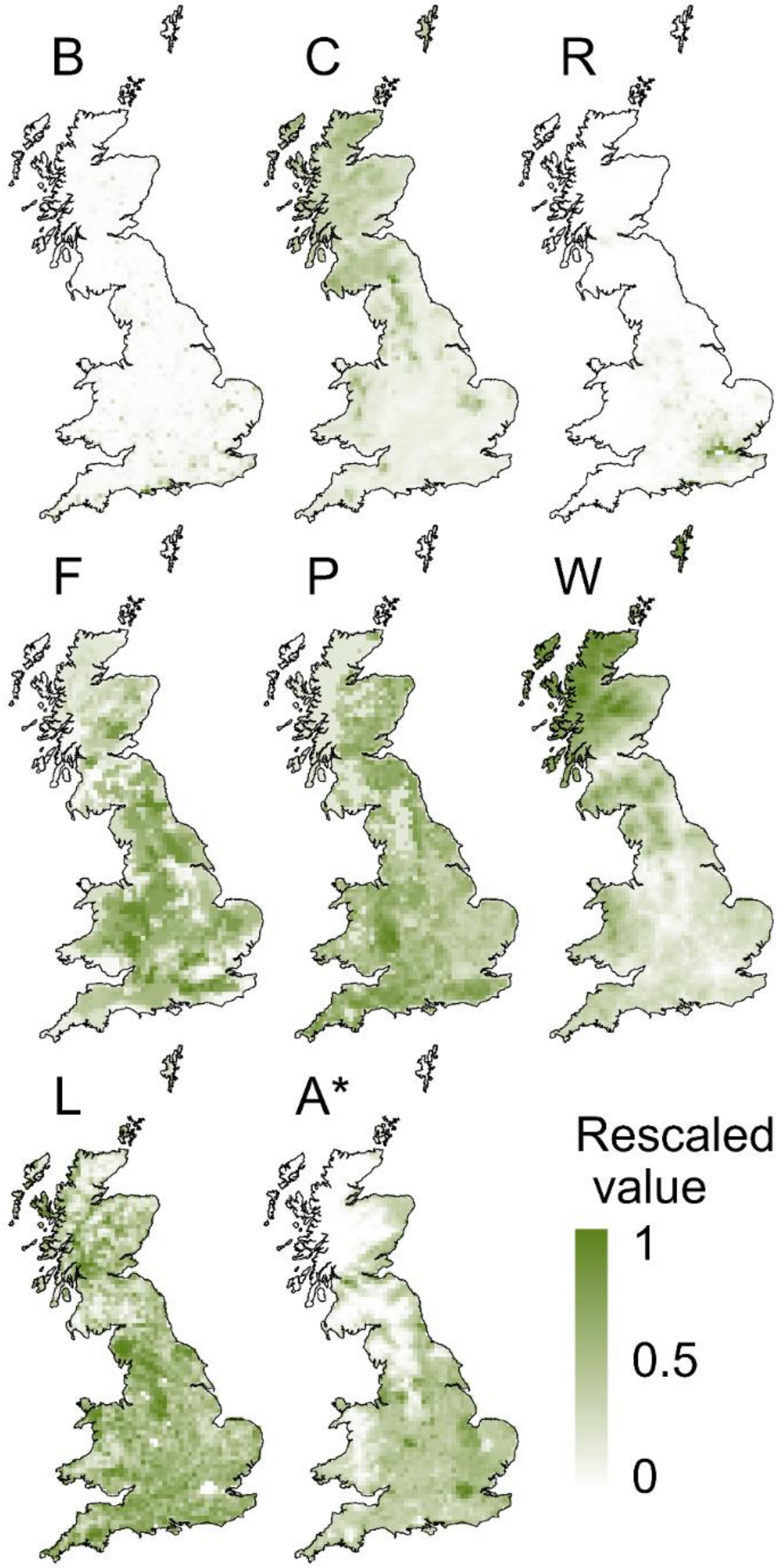


Figure 4.1 Rescaled ecosystem service, biodiversity and socio-environmental value feature layers included within the analysis including; mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*).

Viewpoint prioritisation

Four conservation viewpoint caricatures were created that included ‘traditional’ conservation (TRAD), ‘new’ conservation (NEW), ‘international market ecocentrism’ (ECON), and ‘local social instrumentalism’ (SOC) (see Table 4.1 for definitions). Weightings were not based upon wider consultation, and it must be emphasised that they are not designed to be accurate representations of the viewpoints of any group of conservationists. Instead, they capture an illustrative range of perspectives from across the conservation community. Definitions of caricature viewpoints and integration approaches are provided in Table 4.1.

In order to identify the highest priority areas for each viewpoint, I carried out a spatial prioritisation using the software Zonation (Moilanen 2007) which produces a complementarity-based ranking of conservation priority over the study area. As it is important in joint species and ES prioritisations to ensure localised species are not overlooked (Thomas et al. 2013), I used ‘core area zonation’ (landscape value based upon the single highest value feature) to ensure complementarity was incorporated. Although I present ‘core area zonation’ prioritisations in the main text, I also tested viewpoint prioritisations and integration approaches using the alternative ‘additive benefit function’ prioritisation algorithm (landscape value summed across all weighted features) within Zonation. The results from these analyses were qualitatively similar, and I do not consider them further in the main text, reporting these analyses in Supplementary Methods, Figures and Discussion in Appendix 3.

I incorporated ES, biodiversity and socio-environmental values into the viewpoint prioritisations through weightings commensurate with each viewpoint (Table 4.2). Weights for feature layers were generally positive, representing a desirable resource to include, with the exception of agricultural value (negative weights), which represented an alternative land use to conservation. Species distributions were collectively considered a single biodiversity feature layer for weightings, so that each species received a weighting corresponding to (biodiversity weighting)/(number of species), but were included as separate feature layers within the prioritisation.

Table 4.1 Definitions of caricature viewpoints and viewpoint integration approaches.

Conservation viewpoint	A personal perspective that determines how nature is valued, and how to best conserve it. This analysis uses four arbitrary caricature conservation viewpoints to analyse approaches to viewpoint integration.
'Traditional' (TRAD)	Ecocentric viewpoint, aiming to conserve species diversity and natural habitats for their intrinsic value and for their ability to regulate ecosystem services. Intrinsic value is ascribed to biotic diversity and ecological complexity, with a preference for 'natural' systems. Adapted from Soulé (1985). Weightings used: species distributions and wilderness.
'New' (NEW)	Anthropocentric viewpoint, motivated by achieving conservation action through attaining economic and social benefit. Seeks to conserve biodiversity in human-modified as well as 'natural' landscapes, whilst also maximising human well-being and economic objectives. Adapted from Marvier (2014b). Weightings: widest scope of the four viewpoints, including species and all economic and social value data, apart from wilderness.
International market ecocentrism (ECON)	Utilises capitalist economic arguments to deliver ecocentric conservation, but ignores human well-being and local benefits. Aims to protect intrinsic ecological value over a large area, typically 30-50% of land. This is achieved by employing a free market approach to resource extraction on the remaining land, with the view that this would maximise profit to resource consumption efficiency, and hence protect the 'spared' land. Adapted from Wilson (2016). Weightings: agricultural value (avoid) and related pollination service flow, as well as carbon storage and species distributions.
Local social instrumentalism (SOC)	Favours prioritising conservation benefitting human well-being at the local scale, but opposed to intrinsic value of nature arguments, economic objectives, and links with capitalism and corporations. Adapted from 'social instrumentalism' in Matulis and Moyer (2017). Weightings: ecosystem services that benefit the local population, i.e. flood prevention and recreation, as well as landscapes that are important to people, and a lower weighting for species distributions.
Viewpoint integration approach	Numeric aggregation methods to spatially reconcile differences between individual viewpoints into a single, coherent conservation plan.
Inclusive	Seek to embrace and bring together all perspectives, by building consensus and reducing disputes between people holding different views, and creating a single voice for conservation that is more unified, and hence carries more weight (Tallis & Lubchenco 2014). Here I implement this using an additive vote counting formula.
Pluralist	Accept and engage with diverse perspectives on biodiversity conservation, and give voice to marginalised values and views (Pascual et al. 2021). This is implemented by accounting for similarity between viewpoints and upweighting more distinct viewpoints.

I considered each prioritisation individually and tested feature coverage for the top 5%, 10%, 17% [corresponding to the Aichi 2020 target (CBD 2010)] and 30% priority areas [corresponding to the first draft of the post-2020 global biodiversity framework (CBD 2021)]. Coverage of biodiversity was calculated as the mean species distribution proportion coverage. The distribution of each ES feature is likely to have a large effect on prioritisation ranks for each viewpoint, as the more concentrated a feature is, the larger its effect on the prioritisation. Here I rescaled each feature but did not normalise the distribution, doing so would ensure each feature had an equal effect on prioritisations, but may mean return on coverage would be artificially inflated.

I also investigated the similarity of the existing protected area network in Britain to the different viewpoints, expecting the existing network to match the 'traditional' viewpoint prioritisation most closely since the designation rationale for protected areas is typically to prioritise species and ecosystems representatively. I considered all Sites of Special Scientific Interest (SSSI) and National Nature Reserves (NNR) (https://naturalengland-defra.opendata.arcgis.com) as 'protected areas' (Supplementary Figure 3.1, Appendix 3 Supplementary Discussion).

Table 4.2 Weightings for feature layers included within each of the four conservation viewpoints.

Feature	**Traditional conservation (TRAD)**	**'New' conservation (NEW)**	**International market ecocentrism (ECON)**	**Local social instrumentalism (SOC)**
Biodiversity (B)	1	1	1	0.5
Carbon (C)	0	1	1	0
Number of visits to recreation space (R)	0	1	0	1
Flood regulation (F)	0	1	0	1
Pollinator services (P)	0	0.5	0.5	0
Wilderness (W)	0.25	0	0	0
Landscape aesthetic value (L)	0	1	0	1
Agricultural land classification (A)*	0	-0.5	-1	0

Viewpoint integration

Given that decision support tools risk being influenced by social biases of participants, I developed novel numerical aggregation approaches to reconcile the individual viewpoints into single spatial conservation plans. Firstly, an inclusive approach was used. This produced an aggregate priority map by taking the individual viewpoint prioritisations (Figure 4.2), and summing the landscape priority ranks of each viewpoint (Eq. 2). This represents an integrated conservation solution generated through a vote counting method with equal weight given to each viewpoint.

$$I_j = \sum_v r_{vj}$$

Eq. 2

where I_j is the inclusive value I for landscape j, r_{vj} is the priority rank for viewpoint v and landscape j.

However, as there are correlations between viewpoints in their weighting of individual feature layers, inclusive vote counting methods may result in combined priority areas that are simply shared by more similar viewpoints, and therefore under-represent the level of importance of other features valued by more distinctive viewpoints. Hence, I also implemented a pluralist approach to integration accounting for correlation between feature layer choice (Table 4.2), weighting by the distinctiveness of each viewpoint, to ensure more marginal viewpoints were more equitably represented.

For the pluralist approach I initially undertook a principle component analysis (PCA) to partition the variance from viewpoint weightings of feature layers, creating a number of principal components (PC) which are linear combinations (eigenvectors) of the viewpoints (Supplementary Table 3.1). The first PC is fitted in the direction that accounts for the maximum variance of the data and further PCs, orthogonal to the previous PCs, maximise the remaining variance. Thus PCs are the combinations of viewpoints that explain the variance in weightings in the most efficient way. For each PC, I then multiplied the four viewpoint prioritisation landscape rankings by the corresponding PC eigenvectors and took the sum (dot product). I iteratively added viewpoint rank/PC dot product absolute values until the 'main' PC of each viewpoint was included (Eq. 3), to ensure the distinctiveness of each viewpoint was represented.

$$P_j = \sum_{c=1}^{n_c} \left| r_{j_{1\times v}} \cdot W_{c_{v\times 1}} \right|$$

Eq. 3

where P_j is the pluralist value P for landscape j, r_j is a 1 x v matrix of viewpoint priority ranks for landscape j, and W_c is the corresponding v x 1 eigenvector matrix from principal component c of a viewpoint feature layer weightings PCA (Supplementary Table 3.1). n_c is the smallest number of principal components where the highest PC loading for each viewpoint can be included (i.e. for all viewpoints I found the PC with the highest loading for that viewpoint, and included all PCs up to and including that viewpoint).

I evaluated viewpoint and viewpoint integration approach performance as the efficiency with which feature layers were included into each prioritisation. Efficiency was calculated as the proportion of each feature covered by prioritisations at each coverage threshold, compared to the maximum amount of feature coverage possible. Mean efficiency between feature layers was used as a measure of overall approach optimality, and minimum efficiency was used as a measure of how equitably features were included.

In addition to the inclusive and pluralist approaches listed in the main text, I also tested two other integration approaches to integrating viewpoints. Both performed less well under 'core area zonation' for most thresholds, and so are not discussed further here. See Supplementary Methods, Figures and Discussion in Appendix 3 for further details on these other approaches (and 'additive benefit function' prioritisations).

4.4 Results

The viewpoint prioritisations selected different landscape priorities based upon their valued features (Figure 4.2). The ‘traditional’ conservation viewpoint priorities had the highest average proportion coverage of species distributions, primarily concentrated in NW Scotland and scattered landscapes in the south of England. Conversely ‘local social instrumentalism’ spatial priorities were focused in landscapes in England close to large conurbations, especially London, maximising recreational value but resulting in lower exclusion of agricultural land; as well as landscapes in N England, which delivered landscape aesthetic value and flood protection services. ‘International market ecocentrism’ priorities almost exclusively occurred in Scotland, and upland areas in Wales and northern England, driven by positive selection for carbon storage and avoiding the opportunity costs of more southerly productive farmland. The ‘new’ conservation spatial prioritisation selected landscapes appearing in both the ‘international market ecocentrism’ and ‘local social instrumentalism’ viewpoints, due the more balanced weightings across feature layers. These landscapes were primarily located in Scotland, upland areas in N England, and SE England close to London.

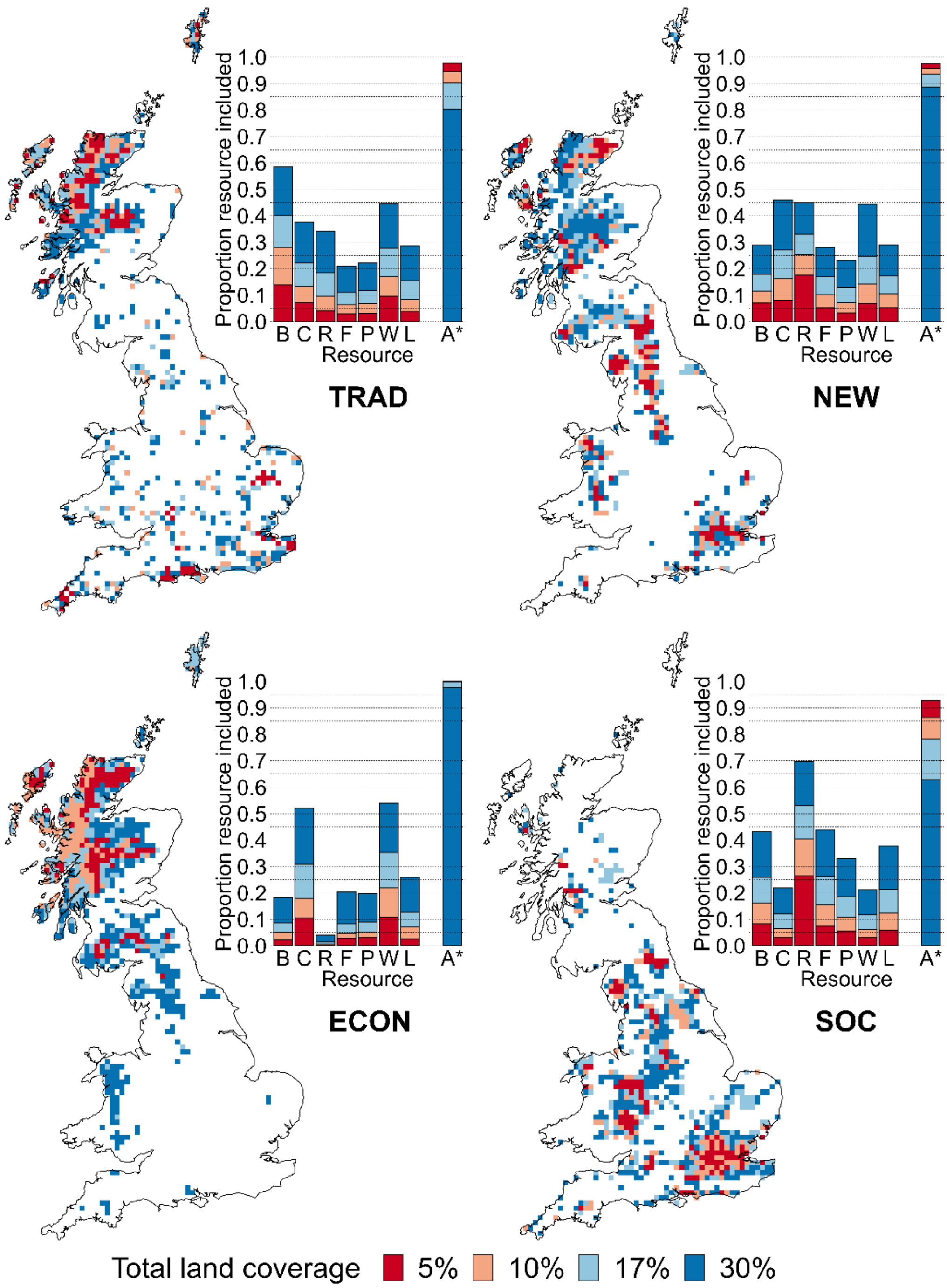


Figure 4.2 Feature coverage using spatial prioritisation for each of the four viewpoints; TRAD – 'traditional', NEW – 'new' conservation, ECON – 'international market ecocentrism', SOC – 'local social instrumentalism'. Maps indicate the priority areas for different coverage thresholds, and corresponding bar plots present proportion of feature included for each, including mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*). A* indicates the only negative weighting where proportion excluded, not included, is shown and so higher land coverage results in lower proportion excluded.

I integrated the four viewpoints into single conservation strategies using two approaches (Figure 4.3). The inclusive approach selected landscapes in Scotland, upland Wales, N England, and SE England. The pluralist approach contained similar priority areas, but higher priority landscapes were more concentrated in SE England. The pluralist approach had lower coverage of carbon and exclusion of agricultural value, but recreational value coverage was much higher than the inclusive approach (feature coverage, Figure 4.3; efficiency, Supplementary Figure 3.7). Species distributions received the best coverage through the 'traditional' viewpoint. The inclusive and pluralist integration approaches had higher species representation than the other viewpoints, although coverage was lower than the 'traditional' viewpoint (mean species distribution proportion coverage at 17% coverage threshold: TRAD 40.3%, NEW 17.9%, ECON 8.6%, SOC 25.9%, Inclusive 27.2%, Pluralist 28.8%).

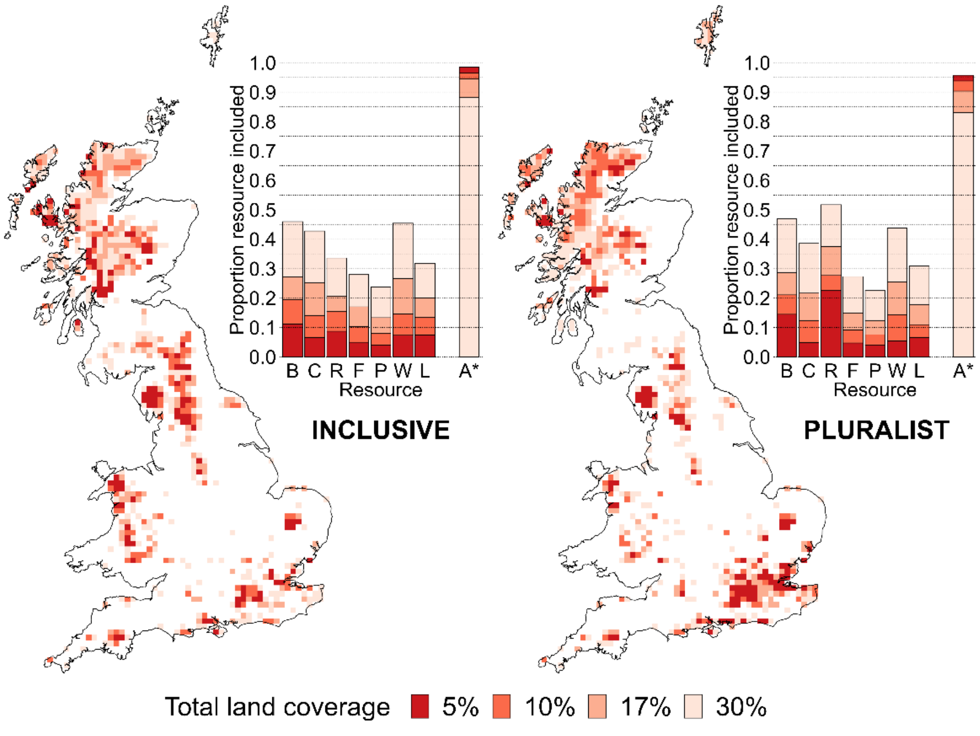


Figure 4.3 Spatially aggregating the four conservation viewpoint priorities (TRAD – 'traditional', NEW – 'new' conservation, ECON – 'international market ecocentrism', SOC – 'local social instrumentalism') using inclusive (vote counting) and pluralist (accounting for distinctiveness) integration methods. Maps indicate the priority areas for different coverage thresholds, and corresponding bar plots present proportion of feature included for each, including mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*). A* indicates the only negative weighting where proportion excluded, not included, is shown and so higher land coverage results in lower proportion excluded.

I found that both integration approaches had similar mean feature coverage efficiency (17% coverage threshold: inclusive 60.0%, pluralist 59.0%; Figure 4.4) indicating similar overall optimality. However, the pluralist approach had higher minimum coverage efficiency for all thresholds, meaning features were included more equitably (17% coverage threshold: inclusive 27.6%, pluralist 42.3%; Figure 4.4).

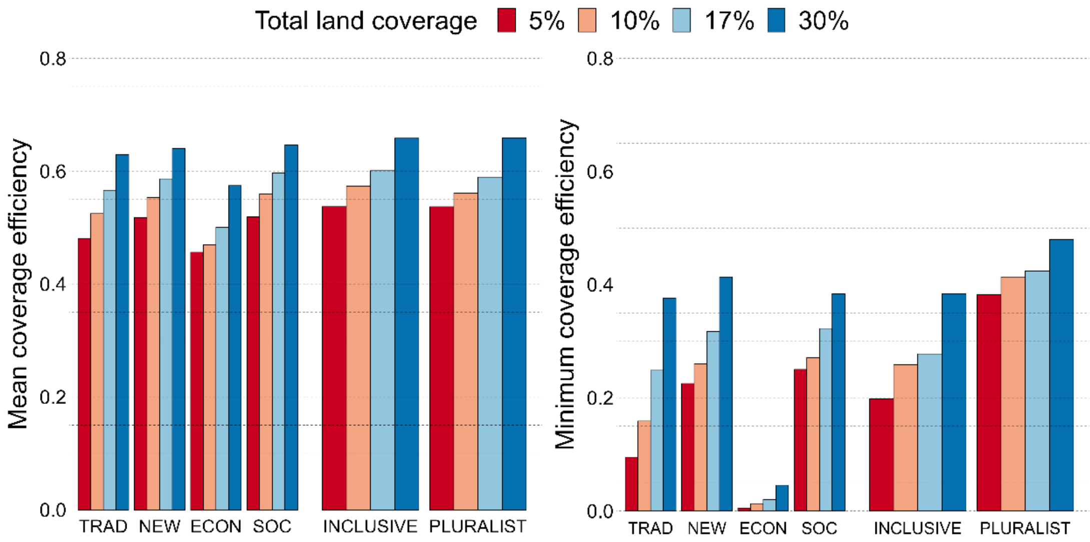


Figure 4.4 Mean and minimum feature coverage efficiency of viewpoint prioritisation performance (TRAD – 'traditional', NEW – 'new' conservation, ECON – 'international market ecocentrism', SOC – 'local social instrumentalism') and integration approach (inclusive and pluralist conservation). Efficiency is calculated as the proportion of a feature covered by a prioritisation for each land coverage threshold (5%, 10%, 17%, and 30%), compared to the maximum possible if only that feature was prioritised. Features included are mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*). The left-hand panel shows the mean performance across all resource types (conservation features), whereas the right-hand panel shows the efficiency of the feature that is least well covered by a particular approach. Inclusive and pluralist approaches perform similarly, but pluralism has a higher minimum feature coverage threshold.

4.5 Discussion

Each conservation viewpoint has passionate proponents and opponents (Kareiva & Marvier 2012; Noss et al. 2013; Soulé 2013; Doak et al. 2014) with seemingly irreconcilable differences. As expected I found that each caricature viewpoint spatially prioritised different landscapes depending on the values held, and resulted in different levels of feature coverage. However, I then aggregated viewpoint priorities together for the first time by implementing inclusive and pluralist integration approaches. Although inclusiveness is typically associated with consensus building, our results demonstrate that through applying pluralism to systematic conservation planning methods, a conservation plan can be produced that is just as coherent.

By accounting for conceptual similarity between viewpoints within a pluralist approach, similar viewpoints were prevented from ‘crowding out’ more marginal viewpoints. Here this included ‘local social instrumentalism’ and, to a lesser extent, ‘traditional’ conservation. The main difference between approaches was that the pluralist approach efficiently incorporated higher recreational value, concentrated around large conurbations, with minimal loss of other features. Although the pluralist approach performed less well for some features than the inclusive approach, overall it included features more equitably while maintaining similar mean coverage efficiency. This shows, at least spatially, that a coherent conservation plan can be created while also representing potentially marginalised viewpoints.

These viewpoint integration approaches are generalisable beyond conservation planning to any situation where perspectives need spatial reconciliation and could incorporate a larger number of viewpoints, for example through stakeholder questionnaires or discussion fora. The objective viewpoint integration approaches developed here can be incorporated into decision-making tools to assist balancing different perspectives, for example either through iteratively presenting integrated prioritisations to participants within the Delphi technique (Mukherjee et al. 2015), or exploring trade-offs as part of a broader MCDA approach (Esmail & Geneletti 2018). Although here I use a small number of caricature viewpoint weightings from within the conservation community, a pluralist approach could also be used to incorporate many more viewpoints from the wider public, sampled through workshops and surveys (Rust et al. 2021), or choice experiments (Badura et al. 2020). Local stakeholder engagement, for example through local partnerships and public participation, can be especially overlooked within conservation planning, but is important to ensure a protected area network that delivers for all (Blicharska et al. 2016; Sterling et al. 2017).

This work focuses on reconciling spatial prioritisation of existing conservation features, not establishment opportunity. Using carbon storage as an example, given its importance as a likely future driver for land use and management policy (Committee on Climate Change 2020), these two distinct approaches are important: protecting and restoring existing high carbon habitats, particularly peatlands; and increasing carbon sequestration through the creation of new habitats, particularly woodlands (Gregg et al. 2021). Our approach has only taken account of the first of these, but a conservation strategy using a combination of protecting existing high-value landscapes, and implementing habitat enhancement or creation in others is needed for both biodiversity and other ecosystem commitments (Soto-Navarro et al. 2020).

Within each landscape, different types of action will be required depending on what is important and the local land use context, considering that the distributions of ecosystem carbon, biodiversity value and other ecosystem services may be positively correlated in some landscapes but negatively so in others (Anderson et al. 2009). For example, if a low intensity agricultural landscape is prioritised for carbon storage, flood prevention or biodiversity, then enhanced protection and additional habitat management to further deliver on these ecosystem features may be implemented. However, strictly protected areas for biodiversity are unlikely to be the method to best incorporate all features, especially those valued by critical social science. Thus, other non-statutory area-based conservation measures may be needed to deliver for aspects such as human well-being. Similarly, other national schemes, such as tree planting, can also have hugely varying outcomes depending upon the spatial distribution of implementation (UNEP-WCMC 2014), and these could also be considered within a pluralist framework.

As well as balancing differing viewpoints on existing resource protection, it is important to consider future expected changes in landscape feature values due to climate change within any implemented conservation plan (Bateman et al. 2013). Similarly, in addition to conservation feature values changing over time; conservation perspectives, the needs of society, and value systems themselves change and develop (Mace 2014), and so joint conservation plans have to be re-evaluated periodically. However, whilst the weight attached to different conservation objectives will inevitably change, including a broad range of benefits in conservation planning will remain important. In developing the post-2020 global biodiversity framework (CBD 2021), it is vital to acknowledge and carefully consider how to spatially integrate different viewpoints on how to implement area-based conservation.

Sheep pasture in Farndale within the North York Moors National Park

CHAPTER 5

Balancing existing conservation priorities with restoration potential in delivering landscape recovery

5.1 Abstract

Habitat restoration is increasingly being recognised as necessary to deliver effective long-term conservation of biodiversity through landscape recovery. Incorporating restoration potential into conservation planning is difficult as future return on conservation investment has to be estimated and balanced against protecting existing biodiversity. Here I use the species pool concept to estimate potential restoration value for seven different land cover types within the UK; arable, bog, broadleaf woodland, coniferous woodland, grassland, heathland and wetland. Potential species distributions were calculated using abiotic environmental convex hulls around presence locations recorded since 1950 for each species. I find that restoration priorities often differ from existing priority landscapes, and so for some land cover types the

highest priorities for enhancement and creation may not be adjacent to existing high-value habitats, in terms of potential contribution to overall species representativeness. I also test the relative benefit of habitat creation and enhancement for different land cover types, and find that bog and heathland benefit most from creating new habitat, whereas grassland and arable would benefit more from enhancing existing habitat. Species pools offer a method to adapt systematic conservation planning to design and manage recovery networks, by allowing planners to view habitat creation and enhancement in the context of potential contribution to the existing conservation network.

5.2 Introduction

Biological communities are undergoing unprecedented change across the globe (Butchart et al. 2010; Pimm et al. 2014). Whether biodiversity change is viewed as a sixth mass extinction (Ceballos et al. 2015) or inevitable environmental change (Thomas 2020), there is a need for effective conservation to mitigate the worst negative changes and safeguard biodiversity and ecosystem function into the future. Protection of land is a favoured conservation strategy to reduce negative changes to natural systems, working by preventing degradation of the most valuable areas for biodiversity or natural capital (Watson et al. 2014). However, many countries already have highly modified landscapes with limited semi-natural habitat. Even though a large proportion of semi-natural habitat falls within protected areas (PA) (Müller et al. 2020), there is uncertainty over whether or not protection of this fragment of biodiversity alone is adequate to conserve vulnerable species (Gaston et al. 2008).

The focus within the UK conservation community has recently shifted away from focusing on highly protected nature ‘reserves’, to enabling landscape-scale conservation outside of protected areas to support PAs (Donaldson et al. 2017; Crick et al. 2020). This is also a global perspective shift: the first draft of the post-2020 global biodiversity framework includes a target to “ensure that at least 20 per cent of degraded freshwater, marine and terrestrial ecosystems are under restoration, ensuring connectivity among them and focusing on priority ecosystems” (CBD 2021). This involves incorporating the Lawtonian principles of ‘‘more, bigger, better and joined’’ (Lawton et al. 2010) into conservation strategy to create ecological networks. In heavily modified landscapes, typical of Britain and many other parts of the world, ‘‘more, bigger, better and joined’’ requires increases in environmental quality within and between existing PAs. Through allowing population dispersal through the landscape, effective population size is increased, and so are the chances of species persisting locally and preventing isolated PA ‘islands’ (Isaac et al. 2018). However, most of the non-statutory land outside PAs within Europe is of low ecological value, and unable to support ‘core’ areas through improving connectivity or functioning as buffer areas (Ockendon et al. 2018). Hence delivering effective ecological networks within currently degraded landscapes is inevitably a complex task, involving many different species, habitat and stakeholder considerations (Adams et al. 2016; Verdone & Seidl 2017).

Landscape recovery involves habitat *restoration*: improving site conditions for a particular set of species (Miller & Hobbs 2007). This can broadly be divided into either habitat *enhancement* of existing ‘low’ quality habitat (e.g., removing nutrients and re-seeding species-poor grassland with a traditional grassland mix); or habitat *creation*, the establishment of novel habitat by replacing another, less-valued habitat (e.g. tree planting in species-poor grassland or flooding arable land to create wetland) (Box 1996). Both habitat enhancement and creation provide alternative landscape conservation strategies, sometimes used together. Here I refer to *restoration* interventions to refer to both (Table 5.1), although restoration can sometimes refer to just habitat enhancement. Creating a coherent strategy that maximises potential for landscape restoration while also conserving existing diversity is difficult as there are many knowledge gaps, with an important one being how you prioritise where to establish ‘recovery areas’ in the first place (Ockendon et al. 2018).

Table 5.1 Glossary of terms.

Term	Definition
(Landscape) Recovery	Broad concept encompassing improving resilience of large-scale ecological networks, and delivering other ecosystem services for people
(Habitat) Restoration	Action to improve conditions at a site to benefit a particular set of species, undertaken here on a specific land cover type.
(Habitat) Enhancement	Habitat restoration that involves improvement to an existing land cover type
(Habitat) Creation	Habitat restoration that involves establishing a new habitat to replace existing land cover type

Spatial prioritisation is a tool often used by policymakers as part of Systematic Conservation Planning (SCP) to prioritise conservation action through a transparent and auditable approach (Margules & Pressey 2000; Watson et al. 2011). It utilises the principle of complementarity to assess network representativeness, meaning sites can be valued on what they contribute to the conservation network in terms of underrepresented species or ecological features (Wilson et al. 2009). However, although spatial prioritisation is commonly carried out for existing biodiversity (conservation prioritisation), it is rarely undertaken incorporating restoration potential (Wilson et al. 2011). Quantifying the value of 'recovering' landscapes is inherently difficult, as assessing potential future ecological return requires quantification of the relative benefit of taking restoration action for particular habitats in different areas. Species each have different habitat preferences: restoring wetland habitat will not benefit species strongly associated with woodland, for example. As not all potential future restoration actions can be undertaken at the same site, restoration of different habitats should be spatially prioritised separately, as it involves different potential future benefits to local diversity. Despite this, spatial prioritisation can provide powerful systematic guidance on the establishment of recovery areas if undertaken carefully (Arponen 2019; Gilby et al. 2021).

In order for a landscape to be a priority recovery area, its restoration potential must be of relatively high importance to the conservation network, but this can be quantified in different ways. Previous work has estimated restoration potential using a variety of metrics including existing environmental conditions and species distributions (Crossman & Bryan 2006), habitat suitability (Thomson et al. 2009), modelled return on restoration investment (Wilson et al. 2011), historic species distributions (Yoshioka et al. 2014), and reduction in projected extinctions (Strassburg et al. 2019). The restoration potential of a landscape can also be considered in terms of the species pool: all species, both those currently present and those that could potentially inhabit a focal habitat within an area (Cornell & Harrison 2014). The absent species that belong to a species pool but are not present locally are sometimes referred to as 'dark diversity' (Pärtel et al. 2011). I have not found any work where species pools have been incorporated directly in SCP before, but this would allow potential increases in biodiversity to be estimated, conditional on suitable restoration actions being taken (Lewis et al. 2017). Use of species pools to assess restoration value of landscapes has advantages over other potential metrics, as it allows (i) complementarity with existing conservation areas to be assessed; and (ii) does not require historic distribution information to calculate, which does not exist for many species.

Policy makers also need to consider *existing* biodiversity in planning recovery areas, as landscape-scale conservation has the potential to greatly increase representation of existing species and ecosystems (Shwartz et al. 2017). As well as increasing protection of existing features, factoring in high value existing areas may also benefit landscape restoration. Species can colonise restoration areas from nearby high ecological value sites, so the area is likely to 'recover' more quickly (Isaac et al. 2018). Although both existing biodiversity value and restoration potential are important to an effective recovery network, areas with high existing value and those with restoration value may not spatially coincide; landscapes with high restoration value to the network may have low existing value, and vice versa. Existing diversity and restoration potential priorities have to be balanced in order that conservation efforts enable opportunities for landscapes to recover, while improving the existing representativeness of the network. However, any restoration complementarity is conditional upon future conservation action, and so is complex to include within a spatial prioritisation (Thomson et al. 2009; Yoshioka et al. 2014).

Currently, the suite of PAs in England do not form a ‘coherent ecological network’, in that protected sites are generally not of adequate size, lack sufficient ecological connectivity, and do not have appropriate long-term management in place (Lawton et al. 2010). To improve, as well as ensuring any currently unprotected habitat that is important for biodiversity receives adequate long-term protection, we need to identify non-protected areas which can fill connectivity gaps in the PA network and buffer small vulnerable sites through landscape recovery (Crick et al. 2020). England is currently in the process of establishing the Nature Recovery Network (NRN), which is a key part of the 25-year environment plan described in the Environment Bill 2019-21 (DEFRA 2018). Although the legislation still has to be finalised, currently an important component will be the development of Local Nature Recovery Strategies (LNRS) guiding local action based on national guidance; and will be focused on Nature Recovery Areas (NRA), a subsection of the NRN that will form the core of the network. There is uncertainty over how NRAs will be selected, and this provides an ideal opportunity to use an SCP approach to inform prioritisation of recovery areas by investigating balancing existing and restoration priorities.

I investigate how conservation and restoration priorities can be balanced within a systematic conservation planning approach to selecting recovery areas. Firstly I find existing conservation priorities, using current species distributions; and restoration priorities, using potential species distributions, for different land cover classes at 10x10 km resolution (‘landscapes’) in Britain. I expect current protected species distributions within Britain are more likely to be driven by historic land use than environmental suitability, given the intensity and extent of land use change (Robinson & Sutherland 2002), meaning differing patterns of current and potential species richness for different habitats. Given this, I also expect existing and restoration priority landscapes to differ as well and hence this would mean that restoration prioritisations may not necessarily perform well at representing existing species distributions. I also compare restoration priorities of different habitats and expect low levels of overlap between them, as rare species are more likely to be habitat specialists and hence their potential species distributions occupy different climatic envelopes. Finally, I test specific prioritisations for habitat enhancement and creation, and expect creation to have greater benefit when there is greater discrepancy between the potential species distributions and current species distribution richness patterns.

5.3 Methods

Species pools

I carried out separate prioritisations for different habitats, so that habitat-specific restoration action could be assessed independently. This required habitats to be sorted into discrete land cover types; created using the CEH Land Cover map 2015 (Rowland et al. 2017), and Joint Nature Conservation Committee priority habitat classes. These included seven land cover types; arable, bog, broadleaf woodland, coniferous woodland, grassland, heathland and wetland which were standardised between the various datasets (Figure 5.1, Supplementary Table 4.1).

Distribution data on priority species listed under Section 41 (Natural Environment and Rural Communities Act, 2006) were provided by Butterfly Conservation (BC), Biological Records Centre (BRC) and breeding bird distributions by British Trust for Ornithology (BTO). I included priority species in the analysis with habitat association information available from the Natural England NERR024 report (Natural England 2010). Data were in the form of annual records between 1950 and 2014 for all species available, except for two taxa where atlas data were only available for specific time periods [birds (1968–72, 1988–91, 2007–11 (Gillings et al. 2019), and vascular plants (1930–69, 1987–99, 2010-2017)]. 290 species had at least one presence record within the study area, and were associated with at least one of the land cover types used in the analysis. Note that some species were identified as associated with multiple land cover types, and were included in the analysis for each. I then used these priority species records to calculate (i) approximate potential distributions and (ii) modelled existing species distributions, to incorporate restoration potential and existing value into spatial prioritisations respectively. All spatial analyses were carried out at the 10km x 10km scale ('landscape').

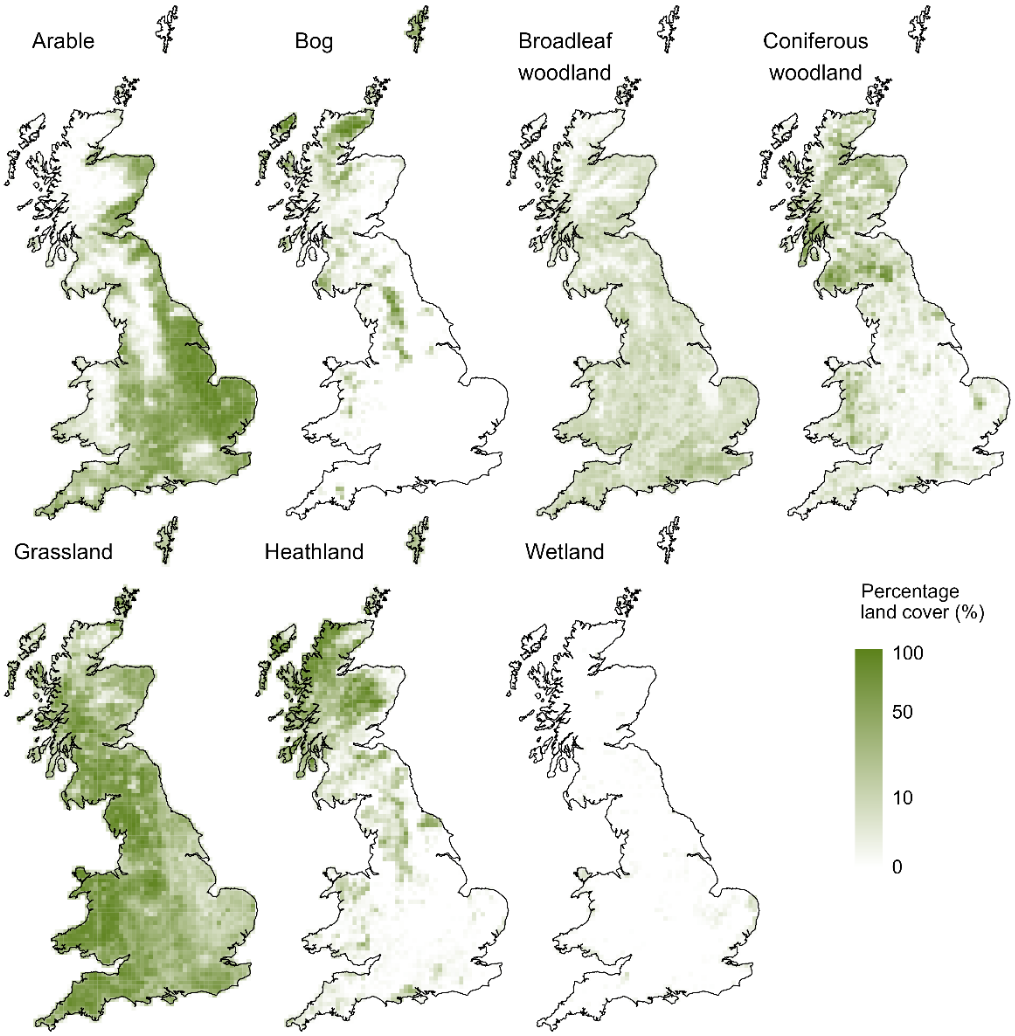


Figure 5.1 Percentage landscape (10x10km cell) coverage of the seven different land cover types used to investigate existing and restoration spatial priorities. Wetland coverage never increased above 10% landscape coverage.

I calculated potential species distributions from observed records by applying the convex hull volume method (Cornwell et al. 2006), using five environmental covariates; seasonality, growing degree days, minimum winter temperature, soil moisture, and soil PH. For each species, environmental convex hulls were created using values from every species record location between 1950 and 2014. All landscapes falling within the created 5-D environmental convex hull were considered within the potential species distribution, and this was used as a conservative approximation for the area within which the species can be considered part of the species pool. Here I only considered the abiotic environmental factors, other biotic factors can also have a large effect on potential species distributions but are too complex to individually model for hundreds of species. A total of 259 environmental convex hulls were created for species (Supplementary Table 4.2), requiring minimum 6 presence records, and species for which pools could not be created were not involved in the analysis further.

In order to assess existing conservation priorities, I also modelled current species distributions from species records after 2000 using a Bayesian Gaussian spatial modelling approach. Distributions were interpolated using a joint model of distribution intensity and recording effort, using the same environmental covariates used to calculate the environmental envelopes (see Appendix 2 Supplementary Methods for details). This involved using Integrated Nested Laplace Approximations (INLA) from the *inlabru* package (Bachl et al. 2019). Wherever the modelled current distribution was >0 outside the environmental convex hull, the modelled current distribution was taken to be the potential distribution value.

Spatial prioritisation

I carried out spatial prioritisation using the conservation planning tool *Zonation* (Moilanen 2007) on each of the seven land cover types separately, as each requires different and potentially conflicting conservation action to restore. Priority ranks are assigned through removing landscapes iteratively that have the lowest cell value, which is calculated as the maximum proportion of feature layer within remaining landscapes, usually species distributions. I used potential species distributions as feature layers for restoration potential prioritisations, and modelled current species distributions as feature layers for existing conservation value. For each land cover type I then compared prioritisations through the proportion of overlap in top 30% priorities, and pairwise correlation of all landscape priorities. This was used to compare restoration and existing conservation value priorities, and also between land cover types for restoration value priorities.

I additionally created two conceptual cost layers to evaluate the main approaches to habitat restoration separately. These illustrate aiming to restore landscapes through either habitat *enhancement* or habitat *creation* in landscapes with varying coverage of the land cover of interest. The enhancement cost layer was calculated according to the proportion of the landscape covered by the land cover type of interest (Eq. 4). At very low coverage levels, cost is high as there is limited habitat within which to fulfil conservation objectives for different species (cost is infinite when habitat coverage equals zero as it is impossible to restore). As habitat extent increases, costs reduce as it becomes easier to meet restoration priorities within the larger (and also more likely to contain connected, higher quality and more varied) habitat coverage.

$$E_i = 1 - \ln h_i$$

Eq. 4

where E_i is the estimated enhancement cost for land cover type *i*, and h_i is the proportion of the landscape covered by land cover type *i. ln* denotes a natural logarithm function applied to h_i, which causes costs to fall rapidly with small increases of land cover type at low levels, but costs level off as proportion coverage increases further.

I also created an illustrative habitat creation cost layer, calculated through multiplying the proportion of each non-interest land cover type within the landscape by an approximate relative effort required for conversion to the focal land cover type (weightings in Supplementary Table 4.3). These were then summed to find the approximate landscape habitat creation cost (Eq. 5). This reflects the fact that it is likely to be less costly to create habitat to deliver on conservation objectives within landscapes that already have some of the focal land cover type present, due to improved connectivity and colonisation opportunities, especially if the other land use present is easier to convert to the focal land cover. The cost of creation was zero for all areas that already were the focal land cover type, and conversion of urban land received a maximum weight of 10.

$$C_i = \sum_j h_j w_{ji}$$

Eq. 5

where C_i is the estimated habitat creation cost for land cover type i, h_j is the proportion of landscape occupied by non-focal land cover type j, and w_{ji} is the weighting of approximate relative effort required to convert land cover type j into focal type i (weightings listed in Supplementary Table 4.3).

I then used these two cost layers within subsequent restoration prioritisations using potential species distributions. In these enhancement and creation prioritisations, priority rank was based upon landscape value as before but then additionally divided by the landscape cost value. The two cost layers are not directly comparable, they are illustrative of the relative costs involved in the two types of restoration action, but the prioritisations themselves can be compared. I tested each cost layer at 5%, 10%, 17% and 30% GB coverage thresholds, by evaluating how they performed in overall priority species representativeness through comparing mean proportion of potential distribution coverage at those thresholds. See

Figure 5.2 for an example of the six primary comparison maps used within the analysis.

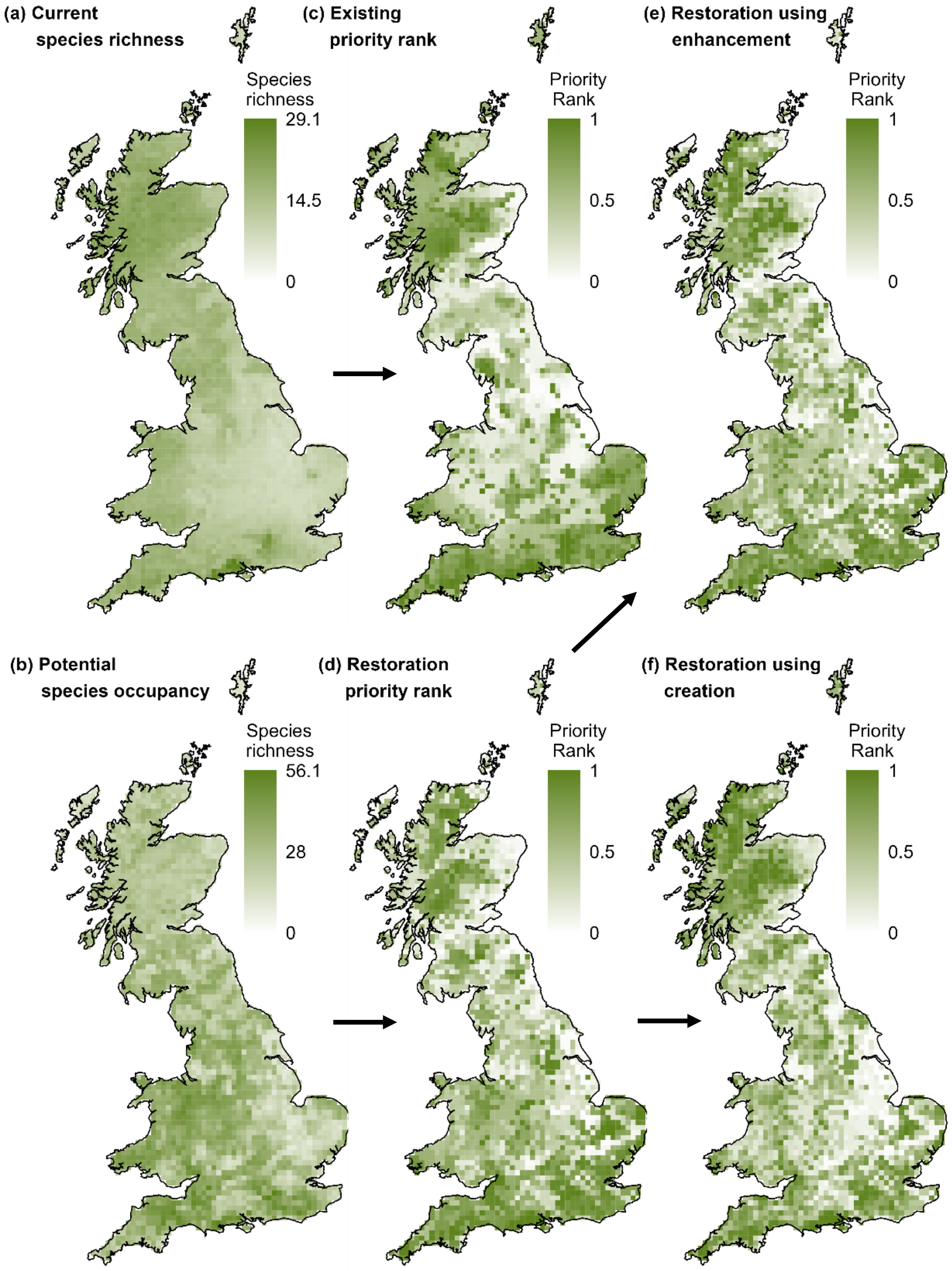


Figure 5.2 Different prioritisations undertaken within the analysis, using heathland as an example. Richness patterns for each land cover type were identified for (a) current distributions and (b) potential species distributions. Next, these distributions were used to calculate (c) existing and (d) restoration landscape priorities respectively, based upon maximising species representation. Finally, the restoration prioritisation was repeated with two cost layers simulating utilising an (e) habitat enhancement approach, and (f) habitat creation approach to restoration. Maps for all land cover types are presented within Appendix 4. (a) and (b), and (c) and (d) are compared in Table 5.2.

5.4 Results

Overlap between landscapes with the (30%) highest current and potential species distribution richness ranged widely between land cover types, from 69.8% for broadleaf woodland to 26.1% for heathland. Correlation between current and potential species distribution richness also varied considerably from arable (ρ=0.816) to wetland (ρ=0.016) (Table 5.2, Supplementary Figure 4.1 and Supplementary Figure 4.2).

Existing and restoration priority ranks had more consistent levels of overlap between the top (30%) priorities (Table 5.2, Supplementary Figure 4.3 and Supplementary Figure 4.4). Most land cover types had between 50% to 60% overlap of landscape priorities, apart from bog (39.2%) and coniferous woodland (24.7%). Overall correlation between existing and restoration priority ranks ranged from broadleaf woodland (ρ=0.518) to coniferous woodland (ρ=0.213) (Supplementary Figure 4.3 and Supplementary Figure 4.4).

Table 5.2 Overlap and correlation between (i) existing priority species richness and potential priority species distribution richness, and (ii) existing priorities (current priority species distributions) and restoration priorities (potential priority species distributions). Percentage overlap of the top 30% richness or priority rank landscapes presented in bold, and spearman correlation of all landscape values in parentheses.

	Overlap and correlation between existing and potential species richness	**Overlap and correlation between existing restoration priorities**
Arable	**60** (0.816)	**59.3** (0.491)
Bog	**55.1** (0.518)	**39.2** (0.446)
Broadleaf woodland	**69.8** (0.84)	**58.2** (0.518)
Coniferous woodland	**57.1** (0.155)	**24.7** (0.213)
Grassland	**42.7** (0.315)	**52.8** (0.47)
Heathland	**26.1** (0.24)	**57.3** (0.477)
Wetland	**26.7** (0.016)	**50.5** (0.338)

Spatial similarity of restoration priority ranks between land cover type also varied between habitat, ranging from arable/broadleaf woodland (66.1%), to arable/coniferous woodland (28.1%) (Table 5.3). Considering all land cover types together, priority landscapes were broadly similar between existing and restoration priorities (Supplementary Figure 4.3, Supplementary Figure 4.4). However, when considered together, there were differences such as large areas of Scotland having much larger number of existing priorities for land cover types, and conversely the West Midlands having a higher number of restoration priorities (Figure 5.3). Habitats that were a top priority for conserving existing high-quality sites within a landscape were not necessarily top priorities for landscape restoration.

Table 5.3 Overlap and correlation between different land cover type restoration priority ranks (Supplementary Figure 4.4) based on species pools. Percentage overlap of the top 30% priority landscapes presented in bold, and spearman correlation of all landscape values in parentheses.

	Arable	*Bog*	*Broadleaf woodland*	*Coniferous woodland*	*Grassland*	*Heathland*
Bog	**39.2** (0.017)					
Broadleaf woodland	**66.1** (0.656)	**46.3** (0.271)				
Coniferous woodland	**28.1** (0.235)	**55.3** (0.625)	**35.1** (0.328)			
Grassland	**55.7** (0.458)	**47.9** (0.233)	**55.1** (0.46)	**34.9** (0.213)		
Heathland	**55.1** (0.386)	**46.2** (0.349)	**53.4** (0.463)	**26.4** (0.244)	**65.1** (0.68)	
Wetland	**48.6** (0.389)	**62** (0.575)	**46.9** (0.444)	**39.8** (0.456)	**58.3** (0.513)	**57.1** (0.524)

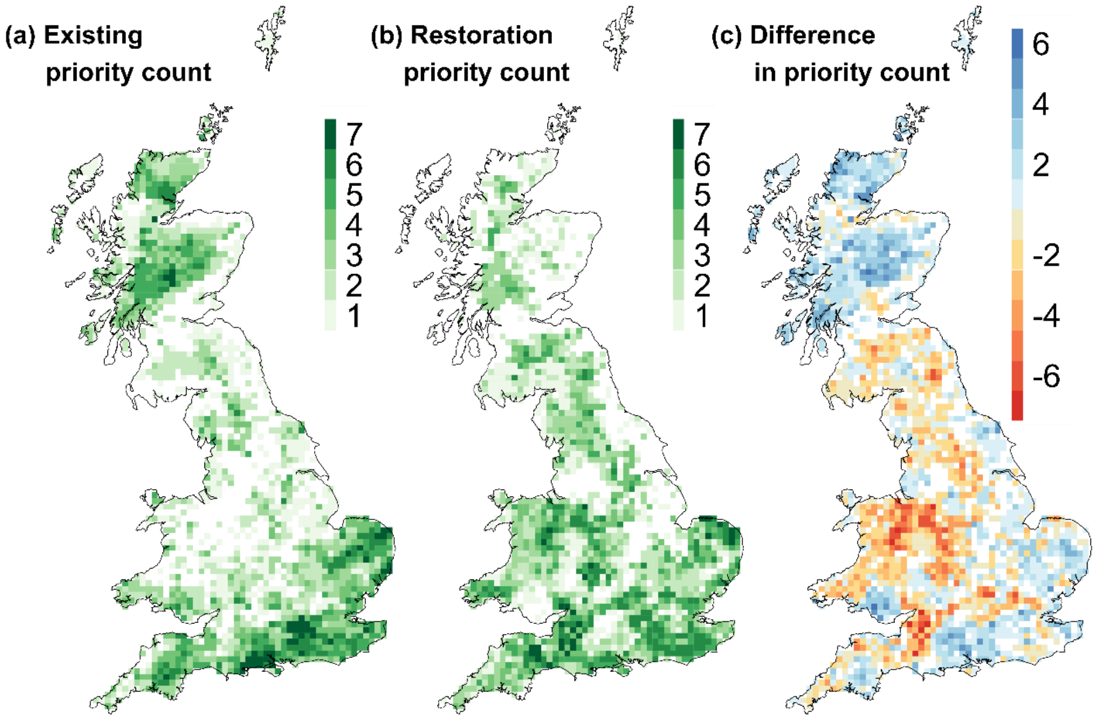


Figure 5.3 Existing and restoration landscape priorities. Number of land cover types within the top 30% priority rank threshold for (a) existing and (b) restoration prioritisations, and (c) the difference between them. Positive values in (c) indicate the landscape has a greater number of existing priority than restoration priority land cover types.

Restoration strategies involving habitat creation could potentially offer higher national returns on representation of species in bog, heathland, and wetland habitats (Figure 5.4, Supplementary Figure 4.5, Supplementary Figure 4.6). Conversely, arable, broadleaf woodland and grassland benefit more from habitat enhancement (Figure 5.4). Lower similarity between existing species and species pool richness (Table 5.2) did not predict greater returns on habitat creation compared to enhancement (Figure 5.4) for any threshold (30% coverage threshold: $\beta_1 \pm$ s.e.: -0.026 ± 0.036; $p = 0.484$).

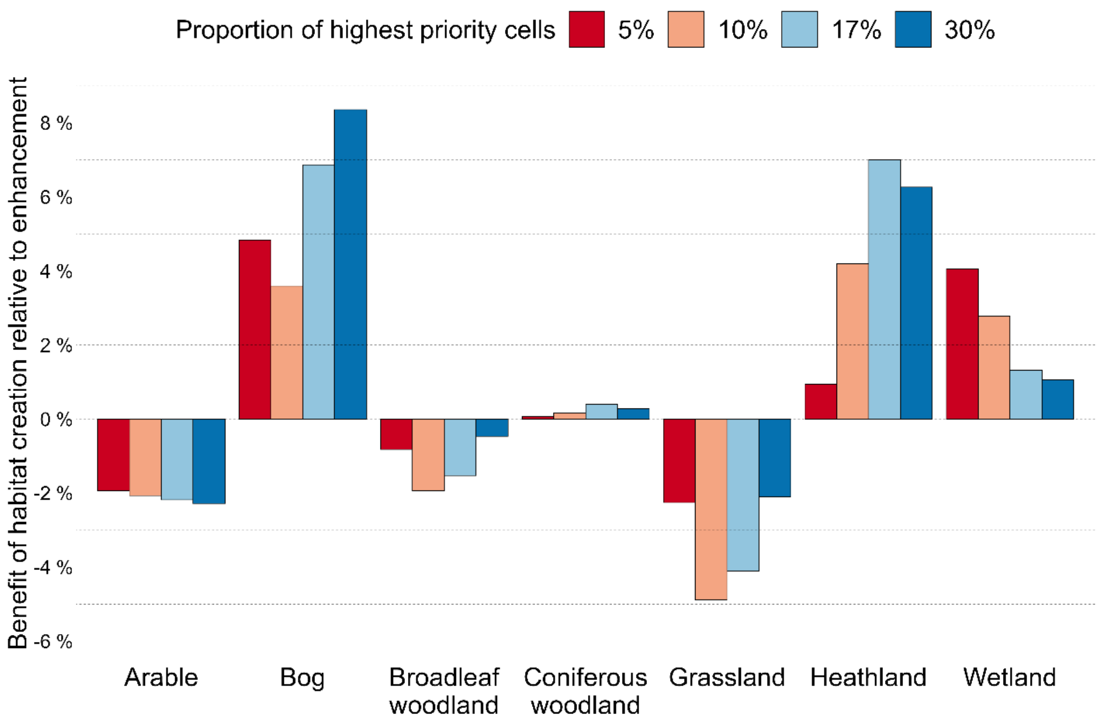


Figure 5.4 Difference between habitat enhancement and creation strategies (Supplementary Figure 4.5 and Supplementary Figure 4.6) for restoration of different habitats within Britain. Benefit was assessed as the absolute difference in mean proportion coverage of potential species distributions within different landscape coverage thresholds.

5.5 Discussion

I use the species pool concept for the first time to identify habitat restoration priorities within Britain, and compare this against existing priorities to inform future conservation planning of recovery areas. I found that restoration priorities often broadly overlap with existing priorities, but there are large differences in some landscapes. Similarly, different land cover types varied in the amount that restoration priorities between them overlap, highlighting that trade-offs may be more common for certain habitats. I also found differences in the relative benefits of using habitat enhancement or creation strategies for each of the seven land cover types I tested, but this was not predicted by differences between existing and species pool richness patterns.

Differences in existing and restoration priorities

Restoration priority locations sometimes differed from existing priorities, especially for coniferous woodland and bog habitats (Table 5.2); and so optimal areas to restore, in terms of maximising total representativeness of a recovery network, may not necessarily be adjacent to the highest existing priority areas. This may be due to certain landscapes losing species distributions due to historic changes in land use: those landscapes are no longer existing priorities, but they may still be restoration priorities as the lost species are still contained within the species pool of the area. Selecting and managing recovery areas solely based on existing high priority habitat is therefore not an efficient strategy.

Landscape restoration potential is only translated into tangible conservation benefit if appropriate actions are implemented. Recovery planning can be carried out at multiple spatial scales; an initial national or regional broad-scale prioritisation where overall effort can be allocated, such as this analysis, followed by local-scale planning that identifies sites and actions that will best deliver outcomes for the broad-scale identified priorities (Gilby et al. 2021). Restoration priorities of individual land cover types did not greatly overlap with others, although there were several exceptions (Table 5.3). This suggests that trade-offs in selecting which habitat to restore are concentrated in specific regions (Figure 5.3) and balancing priorities between habitats will be most important in these landscapes. Although land cover types provide a convenient framework to carry out conservation planning over at a broad-scale, each species will have its own preferred conditions and these that should be considered as part of local-scale conservation action (Miller & Hobbs 2007).

Recovery areas must be chosen carefully in terms of future contributions to the network (Rappaport et al. 2015); sometimes habitats other than what a site is currently a priority for will contribute more to total representation, and sometimes areas away from existing high priority habitats will deliver higher conservation return. Nature Recovery Areas (NRA) could be crucial to recovering landscapes that are not adjacent to existing high value landscapes, but can nevertheless potentially contribute underrepresented features to the network of conservation sites in the future. However, connectivity between existing high priority areas and restoration sites must always be considered such that colonisation is facilitated as much as possible (Shwartz et al. 2017).

Habitat enhancement and creation considerations

I also found the land cover types for which utilising habitat creation was more beneficial nationally compared to enhancement approaches to restoration, and vice versa. Conditional on the appropriate habitat management taking place, habitat creation led to the greatest increase in species representation in bog habitats, whereas for habitat restoration this would be achieved from grassland. Importantly, this was considered within the artificial scenario where only one type of conservation intervention is used. In practice, creation and enhancement will both contribute to the existing network in certain locations and contexts, and a mixture will be required to deliver conservation targets efficiently. Nevertheless, these findings do suggest that more bog, heathland and wetland would need to be created than the other land cover types, in the most appropriate locations, in order to maximise overall contributions of restoration to species representation.

Here I consider conservation return on landscape restoration in terms of biodiversity, specifically in terms of priority species representativeness, but ecosystem services (ES) can also be considered in SCP (Comín et al. 2018). For example, heathland restoration priorities in Northern Scotland (Figure 5.3) may not be desirable due to potential impact on the existing peat bogs present, and the large carbon storage services they represent (Bradfer-Lawrence et al. 2021). Much like existing distributions versus restoration potential for species, including ES in conservation plans must differentiate between protecting *existing* ES, i.e. current carbon storage in peat bogs, and *potential gain* in ES, i.e. carbon sequestration by woodland habitat creation (Gregg et al. 2021). Delivering increased ES provision is often considered through nature-based solutions (NbS), including tree planting and peatland restoration (Stafford et al. 2021). However, potential carbon sequestration gains from these are likely modest and should not overshadow protecting existing high-quality features and also maximising conservation outcomes for biodiversity (Bradfer-

Lawrence et al. 2021). Ideally potential gain in both ES and biodiversity, as well as how this contributes to the existing representation of those features in the conservation network, should be considered when systematically planning recovery actions.

Within the analysis, relative costs of enhancement and creation approaches were approximated using landscape coverage of land cover types. Although appropriate for a preliminary study, costs would have to be robustly calculated for an SCP implementation incorporating restoration. This would require economic data similar to that required for conservation planning such as approximate land acquisition costs within different areas, as well as maintenance and management costs for different habitats (Naidoo et al. 2006). However it would also additionally have to include site preparation costs for restoration (Kimball et al. 2015), and these will differ between enhancement and creation. As well as costs, including benefits of restoration action on ES can also change priorities (De Groot et al. 2013).

Enhancement and creation are not overnight management tools, and require a period of decades, or longer for some habitats, to achieve restoration objectives (Thomson et al. 2009; Watts et al. 2020). Over this time, spatial habitat priorities will change due to drivers including shifts in species ranges, changes in relative rarity of species, and also climate change driving shifts in community composition within different habitats (Stralberg et al. 2015) meaning that conservation plans will have to be periodically revisited. Ultimately it is conservation outcomes, not the number of landscapes restored, that are important and any recovery plan should be evaluated and outcomes assessed (Kimball et al. 2015)

Summary

Overall, these results suggest that incorporating restoration potential explicitly into comprehensive nature recovery plans can help to make them more efficient. Using habitat species pools based on environmental convex hulls offers a pragmatic approach to balancing restoration and conservation action within systematic conservation planning.

Pond within the enclosed beaver trial site near Cropton in the North York Moors National Park

CHAPTER 6

General Discussion

6.1 Summary of thesis findings

This thesis set out to investigate identified knowledge gaps within systematic conservation planning (SCP), using Britain as the study area. This included evaluating the long-term effectiveness of conservation networks, testing how different perspectives in conservation can be equitably included in conservation plans, and developing methods to balance restoration with existing conservation priorities. I also evaluated the efficiency of the UK's 30by30 pledge using a systematic approach.

In this final chapter I summarise the findings of each data chapter individually, then discuss these findings together in the context of wider conservation work and research. I also suggest avenues for future research based upon the thesis findings, and provide concluding remarks.

Chapter 2 The effectiveness of the protected area network of Great Britain

Here we evaluated the effectiveness of the British protected area network, testing initial representativeness as well as whether sites were adequate to deliver long term conservation outcomes in maintaining representation of species. We found that although the network was initially generally designated in representative locations (even if the largest PAs were not), sites track wider regional species declines. Hence, they cannot be considered fully effective, although we found that PAs did have some conservation impact in buffering species decline, especially in landscapes with high PA coverage. We also found that systematic planning, increased topographic roughness and greater connectivity were associated with more effective conservation.

Chapter 3 Translating area-based conservation pledges into efficient biodiversity protection outcomes

We evaluated the efficiency of including protected landscapes within conservation pledges that use land coverage as a target to deliver for nature, specifically testing the UK 30by30 pledge made in September 2020. We found that a mixture of protected landscapes and land outside these designations deliver the best conservation returns for priority species, and arbitrarily including all protected landscapes is an inefficient strategy. We also noted that if protected landscapes are considered as counting toward coverage commitments on delivering for nature, any biodiversity benefit will be limited unless habitat restoration is carefully targeted within these protected landscapes. Finally, this work highlighted the importance of carefully and systematically considering additions to the conservation network based upon what they contribute in terms of representation of conservation features.

Chapter 4 Incorporating a diversity of viewpoints within conservation planning can deliver on different conservation objectives with minimal trade-offs

In this chapter, I sought to spatially reconcile different viewpoints on how to prioritise conservation areas. Depending upon your perspective on what constitutes conservation 'value', you will select different locations to conserve. I implemented an inclusive and pluralist approach to reconciling four different conservation caricature viewpoints, using numeric aggregation methods to equitably include all voices. I found both inclusive and pluralist approaches offered coherent integrated plans, but the pluralist approach incorporated features more equitably.

Chapter 5 Balancing existing conservation priorities with restoration potential in delivering landscape recovery

I developed methods to incorporate landscape restoration potential into systematic conservation planning, such that it can be balanced with existing conservation value. I found restoration priorities are sometimes present in areas that are not existing priorities, and so building a recovery strategy based purely upon existing priorities is inefficient. I also tested the relative benefit of the two main methods of implementing restoration; habitat enhancement and creation. I identified the land cover types that would benefit most from creation, bog and heathland; and most from enhancement, grassland and arable land.

6.2 Implications for systematic conservation planning

This thesis contributes valuable research on undertaking spatial prioritisation as part of a wider SCP approach, not just for the UK but with relevant implications for implementing conservation plans in the rest of Europe, and the world. Chapter two and three highlight the importance of systematically planning conservation networks for delivering long-term conservation outcomes and conservation pledges, respectively. This is especially pertinent as the post-2020 global biodiversity framework still has to be finalised, setting the next round of targets for global conservation. It is crucial that areal coverage targets concerning protecting land and seas also take in to account what is being protected, in terms of representation of features. Without this, the conservation impact of meeting areal coverage targets will be limited.

In addition to highlighting the value of systematic planning, this thesis also identified the importance of considering restoration and other landscape factors in delivering conservation outcomes. In chapter three I identified that protected landscapes in the UK do not contribute efficiently to protecting existing conservation priorities for the 30by30 pledge. As it seems likely that these areas will count for the 30by30 target, this means that carefully targeted habitat restoration will be required if they, and other inefficient pledges, are to deliver for nature. Chapter two highlighted the importance of incorporating connectivity, and especially topographic heterogeneity, into conservation networks. Within Britain specifically, the region that is currently underrepresented with the PA network in terms of priority species distribution coverage is southern England, and addressing this should be a focus of future UK conservation plans. This also reflects global trends of areas with more intensive land use being under-represented within the global PA network (Joppa & Pfaff 2009).

I used spatial prioritisation within these chapters to investigate conservation planning approaches, but this should be differentiated from a full SCP implementation which also involves a number of other planning stages involving development, implementation and monitoring of the plan (Pressey & Bottrill 2009). Although SCP is a tool with potential to improve efficiency and effectiveness of conservation strategy, there is a discrepancy between the amount of research into SCP, and the extent that this knowledge is applied within conservation policy. This is due to a variety of factors including research being disconnected from conservation policy makers and practitioners through lack of applicability to specific, real, conservation problems; and not fitting into the broader conservation planning context (Knight et al. 2008; Adams et al. 2018). However the theory-practice gap can, and is beginning to, be bridged by collaboration between academics and practitioners (Sinclair et al. 2018). Within the thesis, I have sought to minimise potential research-implementation barriers as much as possible. For example, chapter three evaluated a UK government conservation pledge, and the rationale behind chapter five was generated during a placement with Natural England where the specific need to balance restoration value against existing value was identified.

The prioritisations within this thesis are all at the multi-national level (GB), but these should be viewed as an initial overview which can be used to guide further finer-scale planning. SCP can, and should, be applied on smaller (eco-) regional scales (Cowling et al. 2003; Rosauer et al. 2018), and can be used to inform local conservation implementation strategies in much more detail, building on broad-scale prioritisations (Smith et al. 2021). However, implementing SCP at a regional scale provides a number of additional challenges and there are often unique conditions which will have to be incorporated (Morrison et al. 2009).

Regional conservation planning often suffers from data paucity of species records at a useful local resolution, but despite incomplete datasets it is usually preferable to utilise incomplete feature distributions rather than delay conservation planning (Grantham et al. 2009). As well as biodiversity it is also important that natural capital is incorporated into local systematic conservation prioritisations (Verhagen et al. 2017). For example, within the UK an important area for both biodiversity and carbon storage is The Fens in East Anglia (Moilanen et al. 2011; Thomas et al. 2013). Although national systematic conservation planning can identify the importance of The Fens, a local plan would be needed to implement conservation action to address carbon and biodiversity priorities most efficiently, and incorporating the local environmental and socio-economic context. Local plans could also utilise the approaches to

SCP I have tested in this thesis, including equitably incorporating different stakeholder perspectives and restoration potential.

6.3 Increasing importance of restoration

One of the key future challenges for conservation planning is incorporating landscape recovery and habitat restoration. It is important that recovery planning is not solely based off existing features, as this leads to inefficiency in conservation network design (Rappaport et al. 2015). I show in chapter five that generating potential species distributions is a useful potential tool to improve overall conservation efficiency by identifying where habitat creation or enhancement can contribute the most to existing species representation. Delivering effective habitat restoration alongside existing protected areas will require a variety of integrated legislative and policy tools that need to be carefully considered, including other effective area-based conservation measures (OECM) in addition to more traditional area-based approaches.

Landscape recovery is increasingly being considered within UK policy, such as through the Nature Recovery Network in the 25 Year Environment Plan (DEFRA 2018); and globally, for example the CBD post-2020 global biodiversity framework draft includes a target for restoration (Table 1.2). Carefully targeted restoration is perhaps most important though for countries that have had more intensive historic land use, such as in Western Europe. In addition to balancing these priorities within spatial prioritisation, implementing ecological restoration in Europe faces a number of additional challenges such as insufficient funding and political priority, and conflicting interests amongst stakeholders (Cortina-Segarra et al. 2021). These are all difficult challenges for restoration, but reconciling differing stakeholder perspectives could be partially resolved through SCP implementation as demonstrated within chapter four.

Another related concept associated with restoration is ‘rewilding’ which concerns returning, or increasing, *non-human autonomy* to the environment to ensure self-sustaining populations and ecological processes (Prior & Ward

2016). Rewilding is sometimes criticised for having a ‘fuzzy’ definition, so much so that some argue rewilding is unhelpful as an additional ecological management concept to restoration (Hayward et al. 2019). However, it differs from restoration as a concept in that it places explicit value on lower intensity management, whereas restoration of a landscape may require ongoing management and places no greater value on reduced management, beyond practical considerations such as cost. Confusion between the concepts is further hampered as many rewilding projects often do involve habitat management during the initial phase to achieve the desired ‘starting’ habitat. As rewilding is a relatively new concept, there is a lack of research and data on project outcomes (Pettorelli et al. 2018), possibly hampered by the fact that no rewilding project has yet progressed so far as to reach a state of substantially reduced intervention.

Regardless of whether rewilding is a helpful or unconstructive concept, and similarly whether or not non-human autonomy should be intrinsically valued; rewilding is likely to attract funding given that it is currently a popular concept with the public (Pettorelli et al. 2018). If this could be harnessed by using SCP approaches to direct this funding to where conservation intervention could deliver maximum benefit, i.e. in Britain this would involve expanding conservation areas in southern lowland landscapes, then it could prove a powerful force for conservation. However, this would also have to be balanced against existing land uses to minimise opportunity costs, and this would likely mean selecting less agriculturally productive locations.

6.4 Conservation in the Anthropocene

The concept of rewilding in some ways may fit into an Anthropocene or ‘new’ conservation viewpoint more neatly than habitat restoration and landscape recovery. Habitat restoration is concerned with actions that improve site conditions for a particular set of species (Miller & Hobbs 2007). The terms *restoration* and *recovery* also linguistically imply seeking to implement conservation action that will return to an historic baseline, although this may not be the intention of the user. Conversely, rewilding involves returning ‘autonomy’ to natural processes without relation to previous conditions, although in reality advocates often do reference historic ecological states due to the pervading conservation paradigm (Pettorelli et al. 2018). Hence, faced with an existing high priority habitat which would require ongoing management to maintain or improve the existing features in the face of invasive species and climate change, a rewilding approach focusing on non-human autonomy is less likely to implement the management which would maintain the current habitat. Thus, rewilding and traditional restoration approaches will sometimes pursue different conservation action at sites. This highlights that different viewpoints to implementing conservation action will have differing outcomes at different locations. In chapter four the interventions at each priority location were not included in the analysis, although these can be determined from identifying which feature layers were most important within a specific location, and basing appropriate conservation action accordingly. Alternatively, balancing different conflicting conservation actions, i.e. those promoted by rewilding vs restoration approaches, could be reconciled using a method similar to that used in chapter five.

With expected changes to habitat and species distributions from climate change (Pearce-Higgins et al. 2017), considering which actions to take and which habitats to prioritise at specific locations will be key to maximising positive conservation outcomes (Duffield et al. 2021). This could be achieved through using a formalised spatial framework to guide conservation action within SCP applications. Carefully evaluating where conservation action to maintain or restore current habitat, or not to intervene to allow species turnover and habitat succession to occur, would result in more beneficial outcomes to biodiversity overall. An non-spatial example of this is the resist-accept-direct structure (Lynch et al. 2021) for managing changes in ecosystems.

In order for conservation networks to be effective, they need to deliver conservation outcomes in the long-term. However, given climate change there are many complex, interacting effects on nature expected this century (Oliver & Morecroft 2014). In order for SCP approaches to continue to provide current, effective planning solutions in the 21st century, conservation planning stages must be revisited frequently and the conservation network priorities regularly updated.

6.5 Recommendations for future research

Throughout this thesis, I have used SCP approaches to test existing network performance or incorporate new considerations into conservation planning. Although this has demonstrated the versatility and capability of SCP for the task of building a coherent plan for the UK, incorporating the different elements touched on within this thesis, this still has to be comprehensively undertaken as a full SCP implementation. Incorporating the findings of this thesis within an SCP application would bridge the theory-practice gap and lead to more effective conservation plans. For example, factors leading to greater landscape effectiveness that were found in chapter three should be considered; topographic heterogeneity, PA size, and connectivity.

Such a project would engage with a wide range of stakeholders at multiple spatial and implementation scales to collect perspectives to include, possibly through the approaches developed in chapter four. Given the likely importance of restoration with future UK conservation policy, it would also have to balance restoration against existing priorities, incorporating perspectives on the relative importance of restoration and rewilding. Another crucial consideration to incorporate within SCP is projected future species distributions due to climate change. This was not investigated as part of this thesis due to previous, and recently published, work (Critchlow et al. 2022), but it is nevertheless also important to balance expected future changes against existing distributions.

The spatial scale at which SCP is undertaken has a large impact on conservation priorities and how these can be used to inform conservation planning (Hartley & Kunin 2003; Arponen 2012). When SCP is applied at global (Kullberg et al. 2015), continental (Verhagen et al. 2018), or national (Dyer et al. 2017) scales it typically uses coarse feature resolution for broad spatial priorities and policy objectives. Within this thesis, national prioritisations were undertaken, but weighting for global priorities would have changed the conservation rankings of sites. Although I used national priority species within chapter four when looking at integrating conservation viewpoints, in order to more easily compare integration approach performance, the effect of the spatial scale of priorities should also be considered. Future work could identify the effect of spatial scale on feature priorities on conservation plans: different stakeholders will be working on different spatial scales, with different associated priority species, and this should also be considered when building consensus conservation plans.

SCP can also be undertaken at multiple scales: initially at a broad-scale to identify conservation goals, with subsequent prioritisation at narrower scales to select sites (Gilby et al. 2021). In a UK context, for the broad approach this could be undertaken in a similar way as this thesis, which would then inform narrower scale prioritisations, perhaps similar to the nature recovery network conservation plans in Smith et al. (2021). A multi-scale SCP approach may resolve some of the issues around scale affecting priorities, and investigating and developing this approach further may lead to improved conservation outcomes.

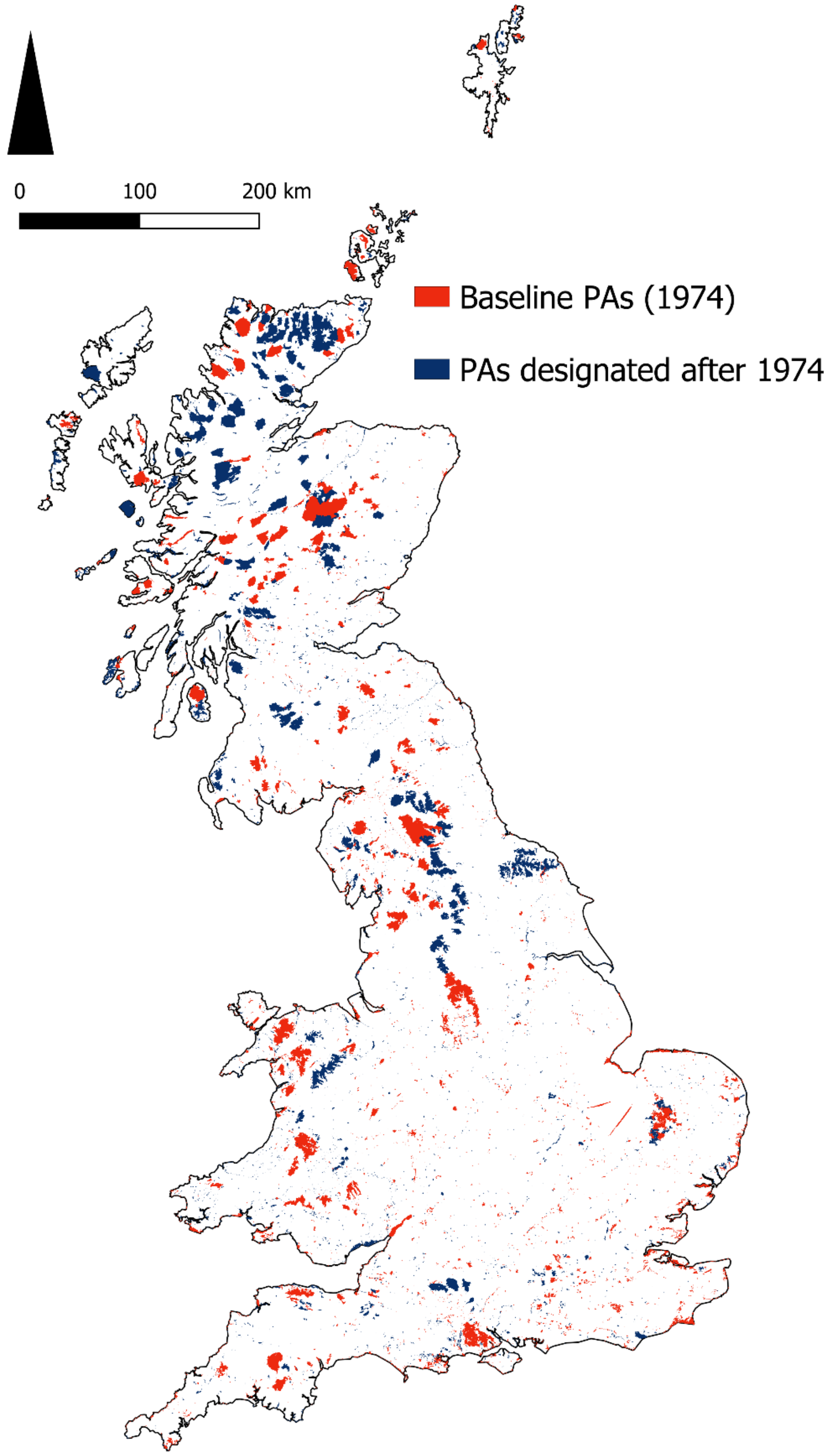
6.6 Concluding remarks

Within the UK, and globally, we need a coherent nature recovery plan to deliver for nature which the current conservation network is failing to do. Expanding the conservation network without considering what those sites add to the network is a highly inefficient strategy, but systematic conservation planning approaches can help deliver effective plans if they are adopted into policy. Systematic approaches are robust and versatile: in this thesis they have been shown to be capable of assessing long-term effectiveness, reconciling different perspectives, and balancing restoration and existing value. All of which will be important considerations in delivering an effective spatial conservation plan for the UK.

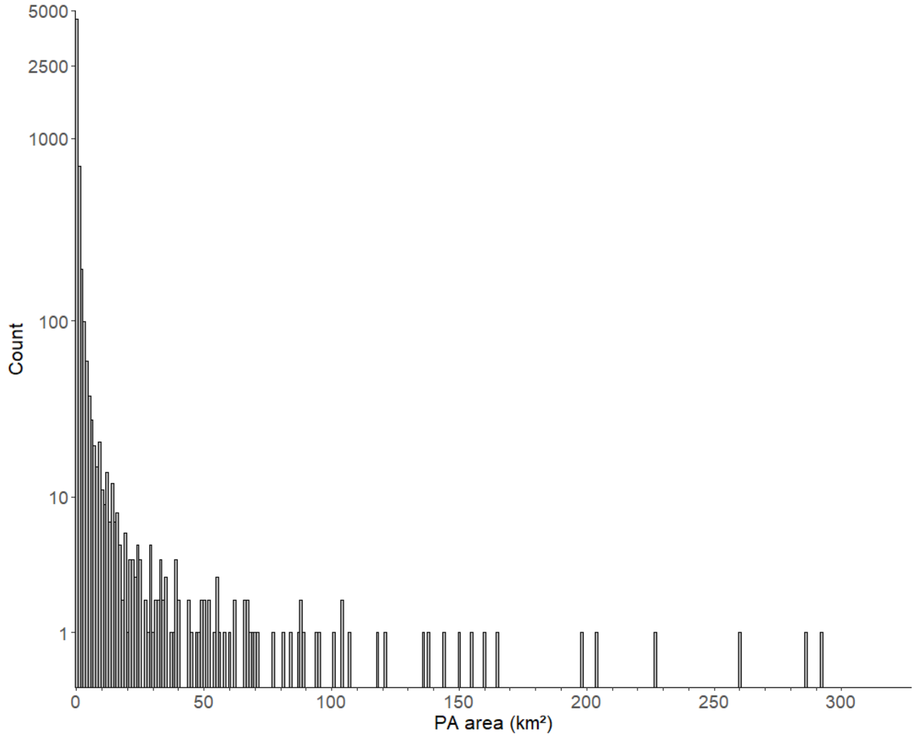
Appendices

List of Appendices

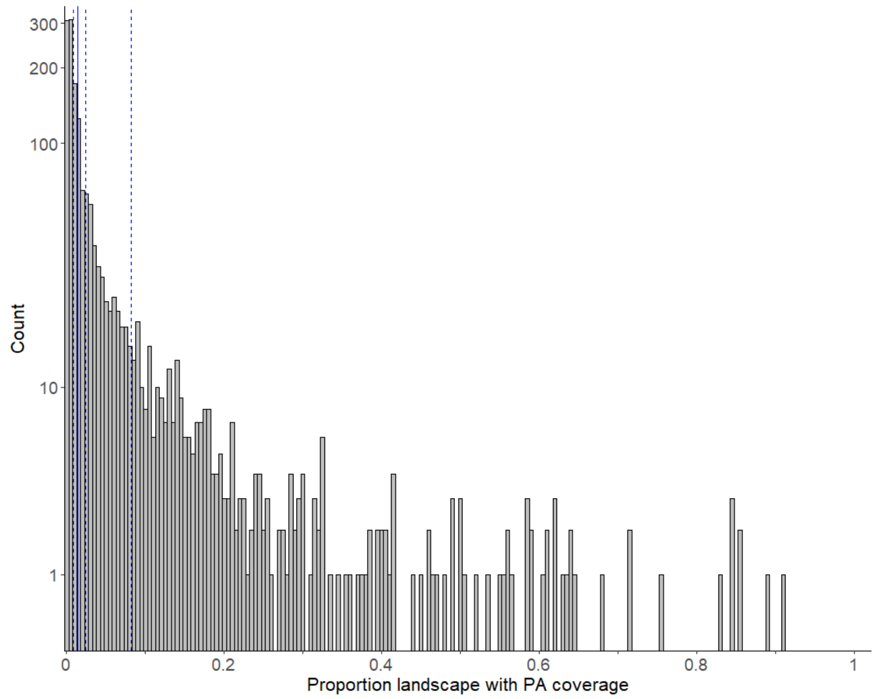
Appendix 1 - Supporting information for Chapter 2



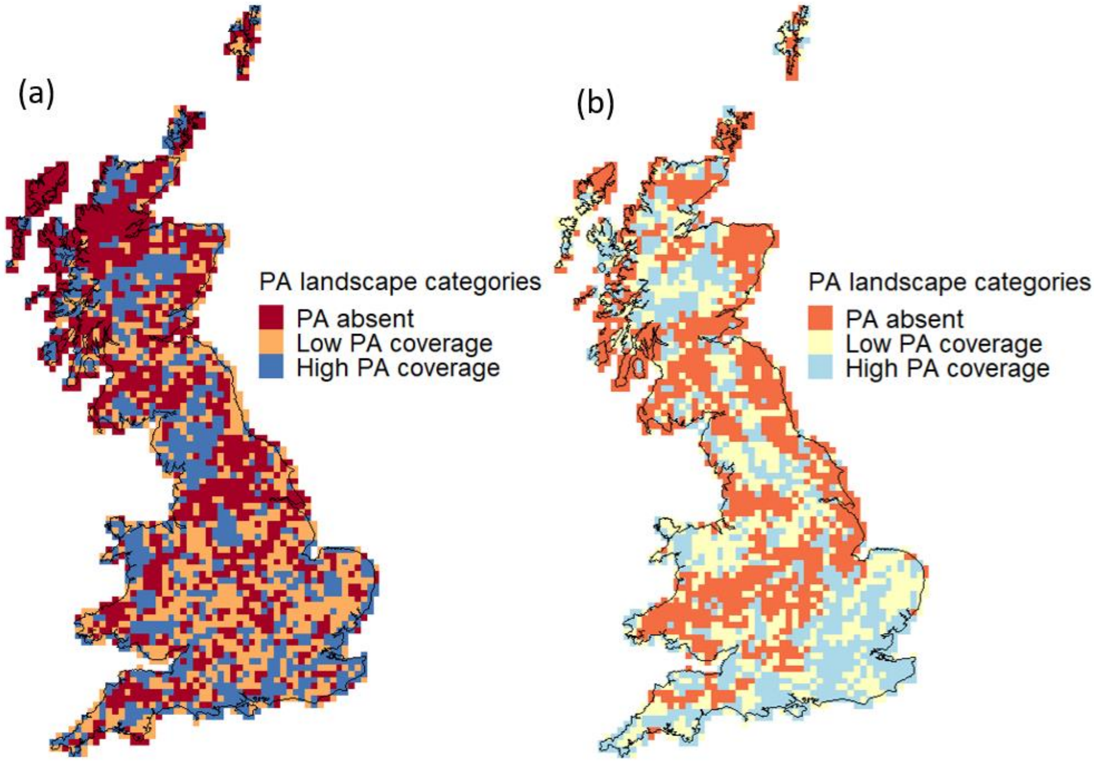
Supplementary Figure 1.1 Baseline PA network of NNRs and biological SSSIs (the 'PA network') comprising 5838 sites designated by 1974, and the subsequent 7556 NNR and biological SSSI sites designated until 2014.



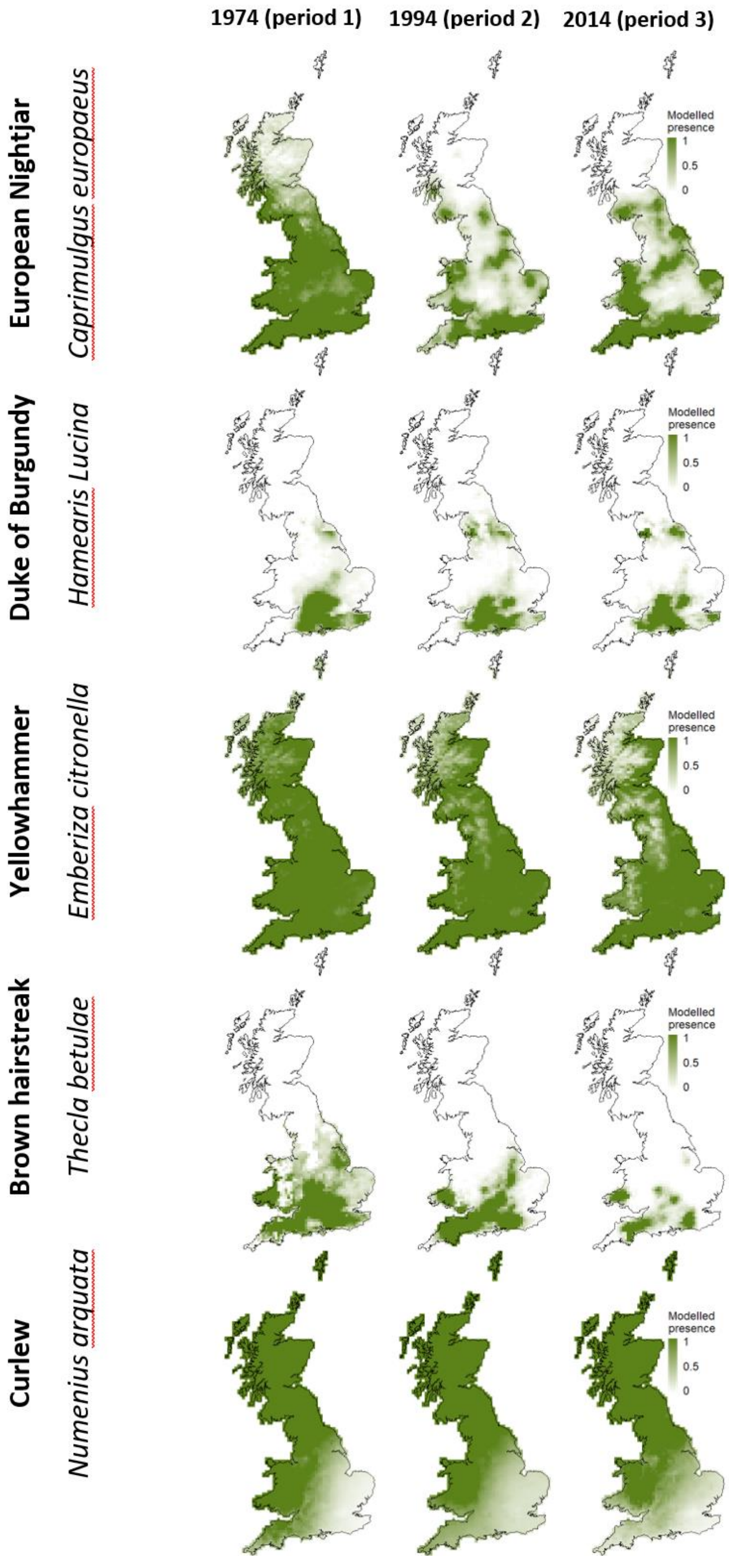
Supplementary Figure 1.2 Area of individual PAs (5838 NNR and biological SSSI) included in analysis as the baseline PA network.



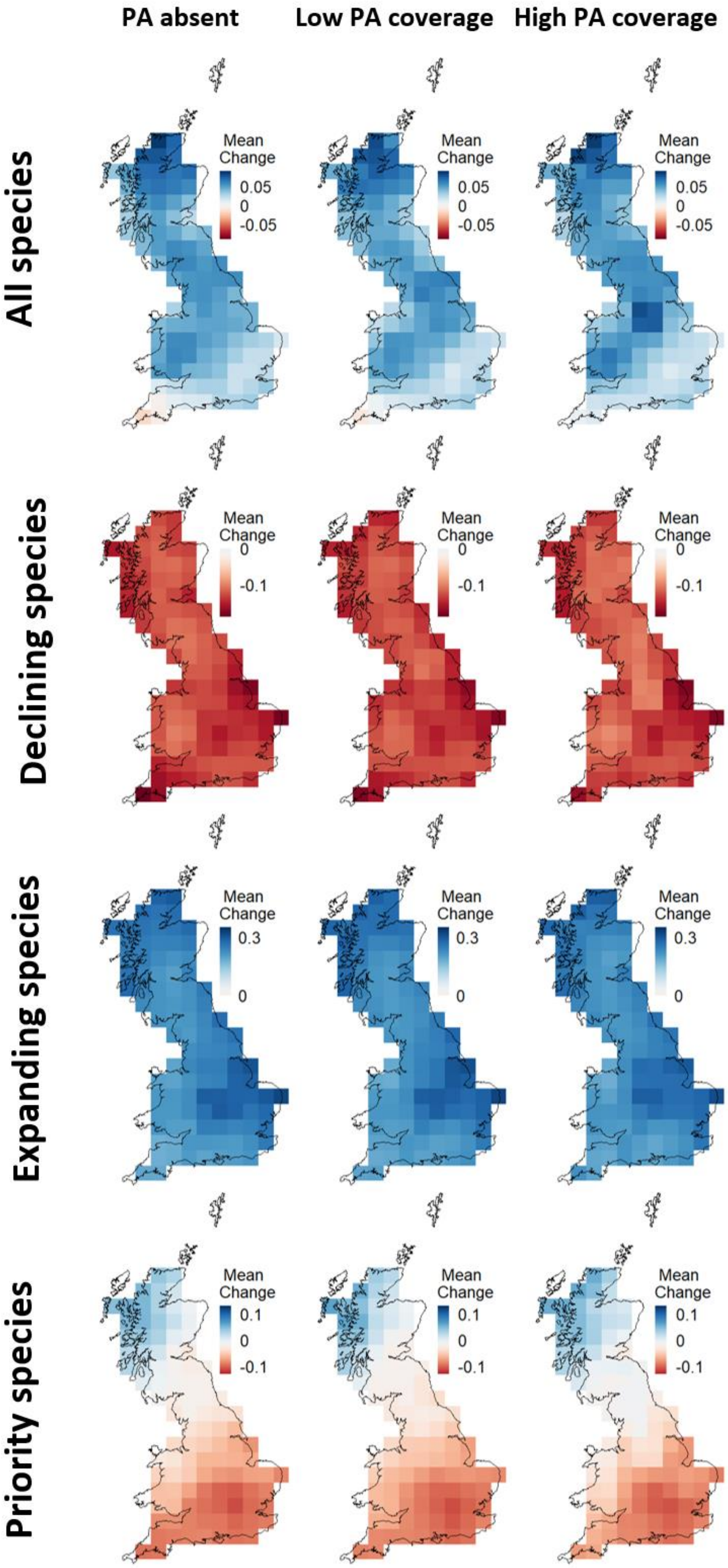
Supplementary Figure 1.3 Proportion PA coverage in 10x10 km landscapes with PA present (1676 of total 2773 landscapes). Median denoted with solid blue line, and 40%, 60% an 80% quantile with dashed blue lines. Numbers of landscapes within ‘low PA’ and ‘high PA’ category for each analysis as follows: median - 838 low, 838 high; 40% - 671 low, 1676 high; 60% - 1007 low, 669 high; 80% - 1341 low, 335 high.



Supplementary Figure 1.4 Spatial distribution of PA categories at period 1 (1974) for the (a) actual protected area network, and (b) counterfactual optimised PA network. The three PA categories were assigned to 10x10 km ‘landscapes’ containing zero, <median PA and >median PA coverage by area for the actual PA network. For the optimised network, PAs were reassigned to landscapes based upon a spatial prioritisation carried out with the distribution records of 2861 species available in 1974. They were then split into the three PA categories as before.


1974 (period 1)
1994 (period 2)
2014 (period 3)
European Nightjar
Caprimulgus europaeus
Duke of Burgundy
Hamearis Lucina
Yellowhammer
Emberiza citronella
Brown hairstreak
Thecla betulae
Curlew
Numenius arquata
Modelled presence
1
0.5
0

Supplementary Figure 1.5 Priority bird and butterfly species distributions to illustrate different representation trends within PA landscape categories in Britain, which when considered together with all 2861 species distributions produce the main reported results. Representation of each species in each time period was calculated as summed modelled presence within each of the three PA categories (Fig A4). In some species, distribution contraction was less severe in landscapes in the ‘high PA’ category; for example European nightjar *Caprimulgus europaeus* (proportion distribution decline within landscape category between first and last period - PA absent: -53.3%, Low PA: -45.8%, High PA: -37.9%), and Duke of Burgundy *Hamearis Lucina* (PA absent: -9.9%, Low PA: -16.7%, High PA: -4.5%). In others, declines were lowest within the ‘low PA’ landscape category, for example yellowhammer *Emberiza citronella* (PA absent: -23.6%, Low PA: -9.0%, High PA: -21.4%). However, representation of some species actually declined more in landscapes with protected areas; such as brown hairstreak *Thecla betulae* (PA absent: -70.5%, Low PA: -75.8%, High PA: -74.2%), and curlew *Numenius arquata* (PA absent: -3.2%, Low PA: -4.8%, High PA: -6.2%).


PA absent
Low PA coverage
High PA coverage
All species
Declining species
Expanding species
Priority species
Mean Change
0.05
0
-0.05
-0.1
0.3
0.1

Supplementary Figure 1.6 Change in mean representation per landscape for individual 'regions'. Change was calculated as the difference in representativeness between the most recent period (Period 3 – 2014) and the baseline period (Period 1 – 1974). The four species categories are mapped separately, as are the PA categories - within each region representation change is calculated from landscapes falling into each PA category separately.

Supplementary Table 1.1 Glossary of important terms.

Effectiveness	"Effectiveness is ... a multifaceted gradient measuring the extent to which PAs contribute to conservation outcomes", resulting from a combination of initial location and subsequent management decisions (Rodrigues and Cazalis 2020)**.** We evaluate PA network effectiveness in terms of both initial species representativeness of establishment locations, and the ability of the network to achieve long-term biodiversity outcomes through maintaining representation (resilience).
Representation	"The extent of occurrence of a particular species or other biodiversity feature within a specific area" (Cabeza and Moilanen 2001). Here we calculate representation of each species as the summed modelled presence within each of the PA categories.
Representativeness	"The extent to which a PA network represents the full variety of biodiversity at all levels of organisation" (Margules and Pressey 2000), here considering representation of all species across the PA network.
Resilience	A resilient network is one "in which species can persist even in the face of natural perturbations and human activities (including climate change)" (Isaac, et al. 2018). Here we investigate it through the long-term representation trends of the PA network.
Impact	"...the difference that protected areas make to one or more intended (or unintended) outcomes, relative to the counterfactual of no intervention or a different intervention" (Pressey, Visconti and Ferraro 2015). In relation to effectiveness, it is the difference between the long-term biodiversity outcomes seen in a protected area, and what would be seen if it had not been established.

Supplementary Table 1.2 Numbers of species within each taxonomic group included within different stages of processing for inclusion in the analysis.

	Period 1 total	Period 2 total	Period 3 total	Present all periods	Present all periods and >10 landscapes (modelled)	Model converged species	Model converged species, and filtered unconverged species
Arachnids	603	628	641	551	335	187	193
Birds	223	261	273	210	190	159	164
Bryophytes	967	948	1021	910	630	528	553
Butterflies	58	58	58	58	57	46	48
Carabids	307	336	335	303	165	88	94
Coccinellidae	36	40	48	36	19	13	13
Hoverflies	237	274	278	235	143	82	83
Hymenoptera	424	516	529	410	50	12	15
Moths	786	805	847	761	641	556	562
Odonata	39	43	50	39	30	21	21
Vascular plants	1349	1350	1347	1342	1192	995	1115
Total	5029	5259	5427	4855	3452	2687	2861

Supplementary Table 1.3 Sampling periods generated for each taxonomic group included in analysis (* indicates taxonomic groups where data were available only for specific time periods).

	Sampling period 1	**Sampling period 2**	**Sampling period 3**
Arachnids	1967 - 1974	1986 - 1994	2001 - 2014
Birds*	1968 - 1972	1988 - 1991	2007 - 2011
Bryophytes	1964 - 1974	1986 - 1994	2005 - 2014
Butterflies	1967 - 1974	1989 - 1994	2011 - 2014
Carabids	1968 - 1974	1984 - 1994	2004 - 2014
Coccinellidae	1970 - 1974	1987 - 1994	2005 - 2014
Hoverflies	1968 - 1974	1984 - 1994	2006 - 2014
Hymenoptera	1971 - 1974	1989 - 1994	2008 - 2014
Moths	1966 - 1974	1987 - 1994	2007 - 2014
Odonata	1967 - 1974	1987 - 1994	2006 - 2014
Vascular plants*	1930 - 1969	1987 -1999	2010

Supplementary Table 1.4 Differences in national representation per landscape between PA categories. For each period column, the 'median' column relates to the species category/PA category row. Other cells report the result of a Wilcoxon signed-rank test between the PA category listed as the row name, and column name. Tests were carried out for each species category, and each time period. Bold indicates a statistically significant result, shading represents a negative relationship, i.e. that the column name PA category representation is significantly lower than the row name PA category.

		Period 1 (1974)			Period 2 (1994)			Period 3 (2014)		
		Median	PA absent	Low PA coverage	Median	PA absent	Low PA coverage	Median	PA absent	Low PA coverage
All species	PA absent	0.393	**-**	**-**	0.450	**-**	**-**	0.444	**-**	**-**
	Low PA coverage	0.498	**$Z = -24.209$ $p < 0.001$**	**-**	0.587	**$Z = -26.086$ $p < 0.001$**	**-**	0.561	**$Z = -21.731$ $p < 0.001$**	**-**
	High PA coverage	0.451	**$Z = -28.003$ $p < 0.001$**	**$Z = 15.189$ $p < 0.001$**	0.516	**$Z = -30.114$ $p < 0.001$**	**$Z = 17.939$ $p < 0.001$**	0.504	**$Z = -26.263$ $p < 0.001$**	**$Z = 13.034$ $p < 0.001$**
Declining species	PA absent	0.525	**-**	**-**	0.478	**-**	**-**	0.409	**-**	**-**
	Low PA coverage	0.599	**$Z = -10.048$ $p < 0.001$**	**-**	0.572	**$Z = -11.361$ $p < 0.001$**	**-**	0.445	**$Z = -7.713$ $p < 0.001$**	**-**
	High PA coverage	0.544	**$Z = -12.136$ $p < 0.001$**	**$Z = 5.941$ $p < 0.001$**	0.519	**$Z = -15.706$ $p = 0.001$**	**$Z = 5.477$ $p < 0.001$**	0.428	**$Z = -12.741$ $p < 0.001$**	$Z = 1.465$ $p = 0.143$
Expanding species	PA absent	0.313	**-**	**-**	0.440	**-**	**-**	0.490	**-**	-
	Low PA coverage	0.436	**$Z = -23.661$ $p < 0.001$**	**-**	0.609	**$Z = -24.481$ $p < 0.001$**	**-**	0.656	**$Z = -21.901$ $p < 0.001$**	-
	High PA coverage	0.379	**$Z = -26.148$ $p < 0.001$**	**$Z = 15.788$ $p < 0.001$**	0.524	**$Z = -25.845$ $p < 0.001$**	**$Z = 19.412$ $p < 0.001$**	0.557	**$Z = -23.282$ $p < 0.001$**	**$Z = 16.500$ $p < 0.001$**
Priority species	PA absent	0.327	**-**	**-**	0.270	**-**	**-**	0.229	**-**	**-**
	Low PA coverage	0.477	**$Z = -9.000$ $p < 0.001$**	**-**	0.388	**$Z = -8.408$ $p < 0.001$**	**-**	0.328	**$Z = -6.674$ $p < 0.001$**	**-**
	High PA coverage	0.385	**$Z = -8.942$ $p < 0.001$**	**$Z = 5.972$ $p < 0.001$**	0.373	**$Z = -8.361$ $p < 0.001$**	**$Z = 5.367$ $p < 0.001$**	0.298	**$Z = -6.208$ $p < 0.001$**	**$Z = 3.497$ $p < 0.001$**

Supplementary Table 1.5 Differences in national representation per landscape between the actual PA network and the optimised counterfactual created using SCP techniques, for period 1 (1974). Median species representation per landscape is reported for both actual and counterfactual networks. The final column reports the result of a Wilcoxon signed-rank test between actual and counterfactual representation in the first period. Tests were carried out for each species category, and each PA category. Bold indicates a statistically significant result, shading denotes a negative relationship, i.e. that the actual PA network had lower representation per landscape than the counterfactual.

		Actual PA network median	Counterfactual optimised median	**Pairwise species comparison**
All species	PA absent	0.393	0.403	**Z = -9.282 $p < 0.001$**
	Low PA coverage	0.498	0.458	**Z = 20.611 $p < 0.001$**
	High PA coverage	0.451	0.488	**Z = -17.460 $p < 0.001$**
Declining species	PA absent	0.525	0.541	**Z = -8.785 $p < 0.001$**
	Low PA coverage	0.599	0.555	**Z = 8.543 $p < 0.001$**
	High PA coverage	0.544	0.561	**Z = -4.043 $p < 0.001$**
Expanding species	PA absent	0.313	0.303	**Z = -4.729 $p < 0.001$**
	Low PA coverage	0.436	0.395	**Z = 20.473 $p < 0.001$**
	High PA coverage	0.379	0.443	**Z = -20.161 $p < 0.001$**
Priority species	PA absent	0.327	0.332	**Z = -4.434 $p < 0.001$**
	Low PA coverage	0.477	0.404	**Z = 8.383 $p < 0.001$**
	High PA coverage	0.385	0.451	**Z = -7.764 $p < 0.001$**

Supplementary Table 1.6 *Sensitivity analysis 40% quantile results* for differences in national representation per landscape between PA categories. The cutoff between ‘low PA’ and ‘high PA’ was taken to be the 40% quantile of landscape PA coverage, rather than the median coverage in the main results. For each period column, the ‘median’ column relates to the species category/PA category row. Other cells report the result of a Wilcoxon signed-rank test between the PA category listed as the row name, and column name. Tests were carried out for each species category, and each time period. Bold indicates a statistically significant result, shading represents a negative relationship, i.e. that the column name PA category representation is significantly lower than the row name PA category.

		Period 1 (1974)			Period 2 (1994)			Period 3 (2014)		
		Median	PA absent	Low PA coverage	Median	PA absent	Low PA coverage	Median	PA absent	Low PA coverage
All species	PA absent	0.393	-	-	0.450	-	-	0.444	-	-
	Low PA coverage	0.494	**Z = -24.025 p < 0.001**	-	0.584	**Z = -26.193 p < 0.001**	-	0.559	**Z = -21.742 p < 0.001**	-
	High PA coverage	0.461	**Z = -27.651 p < 0.001**	**Z = 13.067 p < 0.001**	0.528	**Z = -29.420 p < 0.001**	**Z = 17.048 p < 0.001**	0.515	**Z = -25.539 p < 0.001**	**Z = 11.837 p < 0.001**
Declining species	PA absent	0.525	-	-	0.478	-	-	0.409	-	-
	Low PA coverage	0.598	**Z = -9.932 p < 0.001**	-	0.573	**Z = -11.467 p < 0.001**	-	0.441	**Z = -7.689 p < 0.001**	-
	High PA coverage	0.556	**Z = -11.969 p < 0.001**	**Z = 5.308 p < 0.001**	0.524	**Z = -14.736 p = 0.001**	**Z = 5.184 p < 0.001**	0.427	**Z = -11.692 p < 0.001**	Z = 0.775 p = 0.438
Expanding species	PA absent	0.313	-	-	0.440	-	-	0.490	-	-
	Low PA coverage	0.429	**Z = -23.527 p < 0.001**	-	0.608	**Z = -24.519 p < 0.001**	-	0.652	**Z = -21.926 p < 0.001**	-
	High PA coverage	0.397	**Z = -25.958 p < 0.001**	**Z = 13.445 p < 0.001**	0.543	**Z = -25.800 p < 0.001**	**Z = 18.508 p < 0.001**	0.574	**Z = -23.244 p < 0.001**	**Z = 15.533 p < 0.001**
Priority species	PA absent	0.327	-	-	0.270	-	-	0.229	-	-
	Low PA coverage	0.472	**Z = -8.889 p < 0.001**	-	0.376	**Z = -8.313 p < 0.001**	-	0.322	**Z = -6.513 p < 0.001**	-
	High PA coverage	0.412	**Z = -9.094 p < 0.001**	**Z = 5.409 p < 0.001**	0.390	**Z = -8.485 p < 0.001**	**Z = 4.857 p < 0.001**	0.310	**Z = -6.710 p < 0.001**	**Z = 2.869 p = 0.004**

Supplementary Table 1.7 *Sensitivity analysis 40% quantile results* for differences in national representation per landscape between the actual PA network and the optimised counterfactual created using SCP techniques, for period 1 (1974). The cutoff between 'low PA' and 'high PA' was taken to be the 40% quantile of landscape PA coverage, rather than the median coverage in the main results. Median species representation per landscape is reported for both actual and counterfactual networks. The final column reports the result of a Wilcoxon signed-rank test between actual and counterfactual representation in the first period. Tests were carried out for each species category, and each PA category. Bold indicates a statistically significant result, shading denotes a negative relationship, i.e. that the actual PA network had lower representation per landscape than the counterfactual.

		Actual PA network median	Counterfactual optimised median	**Pairwise species comparison**
All species	PA absent	0.393	0.403	**Z = -9.282 p < 0.001**
	Low PA coverage	0.494	0.457	**Z = 20.991 p < 0.001**
	High PA coverage	0.461	0.485	**Z = -13.850 p < 0.001**
Declining species	PA absent	0.525	0.541	**Z = -8.785 p < 0.001**
	Low PA coverage	0.598	0.556	**Z = 8.560 p < 0.001**
	High PA coverage	0.556	0.555	Z = -1.230 p = 0.219
Expanding species	PA absent	0.313	0.303	**Z = -4.729 p < 0.001**
	Low PA coverage	0.429	0.392	**Z = 20.874 p < 0.001**
	High PA coverage	0.397	0.439	**Z = -17.752 p < 0.001**
Priority species	PA absent	0.327	0.332	**Z = -4.434 p < 0.001**
	Low PA coverage	0.472	0.402	**Z = 8.337 p < 0.001**
	High PA coverage	0.412	0.449	**Z = -5.302 p < 0.001**

Supplementary Table 1.8 *Sensitivity analysis 60% quantile results* for differences in national representation per landscape between PA categories. The cutoff between 'low PA' and 'high PA' was taken to be the 60% quantile of landscape PA coverage, rather than the median coverage in the main results. For each period column, the 'median' column relates to the species category/PA category row. Other cells report the result of a Wilcoxon signed-rank test between the PA category listed as the row name, and column name. Tests were carried out for each species category, and each time period. Bold indicates a statistically significant result, shading represents a negative relationship, i.e. that the column name PA category representation is significantly lower than the row name PA category.

		Period 1 (1974)			Period 2 (1994)			Period 3 (2014)		
		Median	PA absent	Low PA coverage	Median	PA absent	Low PA coverage	Median	PA absent	Low PA coverage
All species	PA absent	0.393	-	-	0.450	-	-	0.444	-	-
	Low PA coverage	0.497	**Z = -24.355 p < 0.001**	-	0.584	**Z = -26.128 p < 0.001**	-	0.560	**Z = -21.878 p < 0.001**	-
	High PA coverage	0.436	**Z = -27.915 p < 0.001**	**Z = 15.431 p < 0.001**	0.506	**Z = -30.367 p < 0.001**	**Z = 17.655 p < 0.001**	0.491	**Z = -26.585 p < 0.001**	**Z = 13.114 p < 0.001**
Declining species	PA absent	0.525	-	-	0.478	-	-	0.409	-	-
	Low PA coverage	0.598	**Z = -10.090 p < 0.001**	-	0.569	**Z = -11.411 p < 0.001**	-	0.442	**Z = -7.877 p < 0.001**	-
	High PA coverage	0.542	**Z = -12.110 p < 0.001**	**Z = 5.797 p < 0.001**	0.513	**Z = -16.605 p = 0.001**	**Z = 5.135 p < 0.001**	0.427	**Z = -13.684 p < 0.001**	Z = 1.636 p = 0.102
Expanding species	PA absent	0.313	-	-	0.440	-	-	0.490	-	-
	Low PA coverage	0.436	**Z = -23.773 p < 0.001**	-	0.606	**Z = -24.484 p < 0.001**	-	0.650	**Z = -21.945 p < 0.001**	-
	High PA coverage	0.366	**Z = -25.988 p < 0.001**	**Z = 16.286 p < 0.001**	0.509	**Z = -25.403 p < 0.001**	**Z = 19.355 p < 0.001**	0.551	**Z = -22.935 p < 0.001**	**Z = 16.502 p < 0.001**
Priority species	PA absent	0.327	-	-	0.270	-	-	0.229	-	-
	Low PA coverage	0.473	**Z = -9.081 p < 0.001**	-	0.390	**Z = -8.430 p < 0.001**	-	0.330	**Z = -6.801 p < 0.001**	-
	High PA coverage	0.367	**Z = -8.433 p < 0.001**	**Z = 6.100 p < 0.001**	0.350	**Z = -7.620 p < 0.001**	**Z = 5.515 p < 0.001**	0.304	**Z = -5.575 p < 0.001**	**Z = 3.901 p < 0.001**

Supplementary Table 1.9 *Sensitivity analysis 60% quantile results* for differences in national representation per landscape between the actual PA network and the optimised counterfactual created using SCP techniques, for period 1 (1974). The cutoff between 'low PA' and 'high PA' was taken to be the 60% quantile of landscape PA coverage, rather than the median coverage in the main results. Median species representation per landscape is reported for both actual and counterfactual networks. The final column reports the result of a Wilcoxon signed-rank test between actual and counterfactual representation in the first period. Tests were carried out for each species category, and each PA category. Bold indicates a statistically significant result, shading denotes a negative relationship, i.e. that the actual PA network had lower representation per landscape than the counterfactual.

		Actual PA network median	Counterfactual optimised median	**Pairwise species comparison**
All species	PA absent	0.393	0.403	**Z = -9.282 p < 0.001**
	Low PA coverage	0.497	0.465	**Z = 20.790 p < 0.001**
	High PA coverage	0.436	0.488	**Z = -18.078 p < 0.001**
Declining species	PA absent	0.525	0.541	**Z = -8.785 p < 0.001**
	Low PA coverage	0.598	0.557	**Z = 9.122 p < 0.001**
	High PA coverage	0.542	0.555	**Z = -4.866 p < 0.001**
Expanding species	PA absent	0.313	0.303	**Z = -4.729 p < 0.001**
	Low PA coverage	0.436	0.407	**Z = 20.163 p < 0.001**
	High PA coverage	0.366	0.437	**Z = -20.257 p < 0.001**
Priority species	PA absent	0.327	0.332	**Z = -4.434 p = 0.002**
	Low PA coverage	0.473	0.417	**Z = 8.433 p < 0.001**
	High PA coverage	0.367	0.449	**Z = -8.242 p < 0.001**

Supplementary Table 1.10 *Sensitivity analysis 80% quantile results* for differences in national representation per landscape between PA categories. The cutoff between 'low PA' and 'high PA' was taken to be the 80% quantile of landscape PA coverage, rather than the median coverage in the main results. For each period column, the 'median' column relates to the species category/PA category row. Other cells report the result of a Wilcoxon signed-rank test between the PA category listed as the row name, and column name. Tests were carried out for each species category, and each time period. Bold indicates a statistically significant result, shading represents a negative relationship, i.e. that the column name PA category representation is significantly lower than the row name PA category.

		Period 1 (1974)			Period 2 (1994)			Period 3 (2014)		
		Median	PA absent	Low PA coverage	Median	PA absent	Low PA coverage	Median	PA absent	Low PA coverage
All species	PA absent	0.393	**-**	**-**	0.450	**-**	**-**	0.444	**-**	**-**
	Low PA coverage	0.493	**Z = -25.192 p < 0.001**	**-**	0.574	**Z = -26.918 p < 0.001**	**-**	0.553	**Z = -22.720 p < 0.001**	**-**
	High PA coverage	0.391	**Z = -10.846 p < 0.001**	**Z = 19.007 p < 0.001**	0.447	**Z = -12.750 p < 0.001**	**Z = 20.376 p < 0.001**	0.451	**Z = -12.302 p < 0.001**	**Z = 15.980 p < 0.001**
Declining species	PA absent	0.525	**-**	**-**	0.478	**-**	**-**	0.409	**-**	**-**
	Low PA coverage	0.594	**Z = -10.657 p < 0.001**	**-**	0.561	**Z = -12.228 p < 0.001**	**-**	0.443	**Z = -8.711 p < 0.001**	**-**
	High PA coverage	0.508	**Z = -4.157 p < 0.001**	**Z = 7.809 p < 0.001**	0.478	**Z = -9.019 p = 0.001**	**Z = 7.598 p < 0.001**	0.407	**Z = -8.598 p < 0.001**	**Z = 4.186 p < 0.001**
Expanding species	PA absent	0.313	**-**	**-**	0.440	**-**	**-**	0.490	**-**	-
	Low PA coverage	0.434	**Z = -24.292 p < 0.001**	**-**	0.599	**Z = -24.778 p < 0.001**	**-**	0.642	**Z = -22.255 p < 0.001**	-
	High PA coverage	0.315	**Z = -11.074 p < 0.001**	**Z = 19.188 p < 0.001**	0.439	**Z = -8.822 p < 0.001**	**Z = 20.721 p < 0.001**	0.498	**Z = -8.654 p < 0.001**	**Z = 17.890 p < 0.001**
Priority species	PA absent	0.327	**-**	**-**	0.270	**-**	**-**	0.229	**-**	**-**
	Low PA coverage	0.453	**Z = -9.266 p < 0.001**	**-**	0.381	**Z = -8.572 p < 0.001**	**-**	0.321	**Z = -7.019 p < 0.001**	**-**
	High PA coverage	0.298	Z = -1.735 p = 0.083	**Z = 7.188 p < 0.001**	0.272	Z = -1.232 p = 0.218	**Z = 6.504 p < 0.001**	0.233	**Z = -2.008 p = 0.045**	**Z = 4.880 p < 0.001**

Supplementary Table 1.11 *Sensitivity analysis 80% quantile results* for differences in national representation per landscape between the actual PA network and the optimised counterfactual created using SCP techniques, for period 1 (1974). The cutoff between 'low PA' and 'high PA' was taken to be the 80% quantile of landscape PA coverage, rather than the median coverage in the main results. Median species representation per landscape is reported for both actual and counterfactual networks. The final column reports the result of a Wilcoxon signed-rank test between actual and counterfactual representation in the first period. Tests were carried out for each species category, and each PA category. Bold indicates a statistically significant result, shading denotes a negative relationship, i.e. that the actual PA network had lower representation per landscape than the counterfactual.

		Actual PA network median	Counterfactual optimised median	**Pairwise species comparison**
All species	PA absent	0.393	0.403	**Z = -9.282 p < 0.001**
	Low PA coverage	0.493	0.468	**Z = 21.734 p < 0.001**
	High PA coverage	0.391	0.498	**Z = -21.398 p < 0.001**
Declining species	PA absent	0.525	0.541	**Z = -8.785 p < 0.001**
	Low PA coverage	0.594	0.556	**Z = 10.716 p < 0.001**
	High PA coverage	0.508	0.560	**Z = -8.064 p < 0.001**
Expanding species	PA absent	0.313	0.303	**Z = -4.729 p < 0.001**
	Low PA coverage	0.434	0.416	**Z = 19.933 p < 0.001**
	High PA coverage	0.315	0.448	**Z = -21.839 p < 0.001**
Priority species	PA absent	0.327	0.332	**Z = -4.434 p = 0.002**
	Low PA coverage	0.453	0.420	**Z = 8.355 p < 0.001**
	High PA coverage	0.298	0.457	**Z = -8.703 p < 0.001**

Supplementary Table 1.12 Bayesian conditional autoregressive spatial regression analysis investigating drivers of landscape resilience (See section 2.3 for details). Results are presented for main analysis using median coverage as the cut off between ‘low PA’ and ‘high PA’ landscape categories, and well as the sensitivity analysis using the 40%, 60% and 80% quantiles. Effect sizes in bold denote that the credible interval was either entirely positive or negative, and for covariates in bold this was recorded in analyses for all quantile runs in the sensitivity analysis.

		Median coverage			**40% coverage quantile**			**60% coverage quantile**			**80% coverage quantile**		
		$Q_{2.5\%}$	**Mean**	**$Q_{97.5\%}$**	**$Q_{2.5\%}$**	**Mean**	**$Q_{97.5\%}$**	**$Q_{2.5\%}$**	**Mean**	**$Q_{97.5\%}$**	**$Q_{2.5\%}$**	**Mean**	**$Q_{97.5\%}$**
All species	Intercept	-0.032	-0.005	0.021	-0.031	-0.004	0.023	-0.027	-0.001	0.025	-0.025	0.000	0.025
	Low PA	**0.004**	**0.023**	**0.041**	-0.003	0.016	0.035	0.000	0.020	0.040	-0.014	0.009	0.032
	High PA	-0.012	0.006	0.024	-0.011	0.007	0.026	-0.019	0.001	0.020	-0.001	0.023	0.047
	Similarity	-0.007	0.028	0.064	-0.011	0.025	0.061	-0.020	0.015	0.049	-0.027	0.006	0.039
	Topo	-0.099	-0.033	0.032	-0.085	-0.018	0.049	-0.071	-0.010	0.051	-0.054	-0.001	0.052
	PA connectivity	-0.042	-0.010	0.023	-0.042	-0.009	0.024	-0.038	-0.006	0.025	-0.042	-0.011	0.020
	PA coverage change	**0.018**	**0.064**	**0.109**	**0.020**	**0.066**	**0.112**	**0.020**	**0.065**	**0.111**	-0.002	0.043	0.087
	Baseline representation	**0.821**	**0.863**	**0.906**	**0.837**	**0.884**	**0.930**	**0.846**	**0.887**	**0.928**	**0.903**	**0.941**	**0.979**
	Low PA * Similarity	-0.022	-0.004	0.014	-0.020	-0.001	0.018	-0.026	-0.006	0.013	-0.022	0.001	0.023
	High PA * Similarity	-0.020	-0.002	0.016	-0.021	-0.003	0.016	-0.015	0.005	0.024	-0.042	-0.019	0.004
	Low PA * Topo	-0.001	0.018	0.036	-0.015	0.004	0.023	-0.006	0.014	0.034	-0.026	-0.004	0.019
	High PA * Topo	**-0.041**	**-0.023**	**-0.004**	-0.032	-0.013	0.006	**-0.043**	**-0.023**	**-0.003**	-0.032	-0.009	0.014
	Low PA * PA connectivity	-0.016	0.002	0.020	-0.016	0.003	0.022	-0.022	-0.002	0.018	-0.020	0.003	0.026
	High PA * PA connectivity	-0.002	0.017	0.035	-0.002	0.017	0.036	**0.004**	**0.024**	**0.044**	**0.008**	**0.031**	**0.054**
Declining species	Intercept	-0.047	-0.013	0.021	-0.040	-0.008	0.024	-0.038	-0.006	0.026	-0.043	-0.014	0.016
	Low PA	-0.010	0.009	0.027	-0.019	0.000	0.019	-0.007	0.012	0.031	-0.011	0.013	0.036
	High PA	**0.036**	**0.054**	**0.072**	**0.031**	**0.048**	**0.066**	**0.036**	**0.054**	**0.072**	**0.073**	**0.097**	**0.122**
	Similarity	**0.022**	**0.069**	**0.117**	**0.014**	**0.058**	**0.104**	**0.023**	**0.067**	**0.113**	**0.007**	**0.047**	**0.087**
	Topo	-0.102	-0.011	0.075	-0.069	0.021	0.105	-0.084	-0.002	0.078	-0.061	0.007	0.073
	PA connectivity	-0.036	0.007	0.049	-0.033	0.007	0.046	-0.026	0.014	0.055	-0.007	0.030	0.068
	PA coverage change	-0.089	-0.027	0.034	-0.075	-0.016	0.041	-0.073	-0.012	0.047	**0.002**	**0.057**	**0.111**
	Baseline representation	**0.677**	**0.746**	**0.819**	**0.719**	**0.802**	**0.887**	**0.703**	**0.764**	**0.828**	**0.734**	**0.794**	**0.855**
	Low PA * Similarity	-0.008	0.009	0.027	-0.007	0.011	0.029	-0.012	0.006	0.024	-0.008	0.015	0.038
	High PA * Similarity	**0.004**	**0.021**	**0.039**	**0.001**	**0.019**	**0.037**	**0.012**	**0.030**	**0.047**	-0.026	-0.002	0.021
	Low PA * Topo	-0.016	0.003	0.021	-0.028	-0.008	0.011	-0.015	0.003	0.022	-0.024	-0.001	0.022
	High PA * Topo	-0.025	-0.007	0.011	-0.018	0.000	0.019	-0.024	-0.005	0.013	-0.031	-0.007	0.018

	Low PA * PA connectivity	-0.012	0.005	0.023	-0.012	0.006	0.024	-0.017	0.001	0.019	-0.019	0.004	0.027
	High PA * PA connectivity	**0.011**	**0.029**	**0.047**	**0.010**	**0.029**	**0.048**	**0.017**	**0.035**	**0.054**	**0.020**	**0.044**	**0.067**
Expanding species	Intercept	-0.054	-0.008	0.038	-0.056	-0.009	0.038	-0.046	-0.002	0.041	-0.038	0.001	0.039
	Low PA	-0.001	0.021	0.043	-0.004	0.017	0.039	-0.008	0.015	0.039	-0.027	-0.001	0.025
	High PA	**-0.055**	**-0.034**	**-0.012**	**-0.051**	**-0.030**	**-0.009**	**-0.066**	**-0.042**	**-0.018**	**-0.062**	**-0.034**	**-0.007**
	Similarity	-0.056	0.007	0.069	-0.060	0.004	0.068	-0.074	-0.014	0.045	-0.056	-0.004	0.049
	Topo	**-0.360**	**-0.247**	**-0.135**	**-0.356**	**-0.242**	**-0.127**	**-0.315**	**-0.212**	**-0.109**	**-0.284**	**-0.200**	**-0.116**
	PA connectivity	-0.058	0.000	0.058	-0.059	0.000	0.059	-0.055	-0.001	0.054	-0.069	-0.020	0.029
	PA coverage change	-0.013	0.069	0.152	-0.014	0.069	0.153	-0.024	0.055	0.135	-0.106	-0.032	0.042
	Baseline representation	**0.712**	**0.752**	**0.792**	**0.721**	**0.763**	**0.806**	**0.731**	**0.771**	**0.810**	**0.800**	**0.836**	**0.871**
	Low PA * Similarity	-0.041	-0.020	0.002	-0.039	-0.018	0.003	-0.044	-0.020	0.003	-0.041	-0.015	0.011
	High PA * Similarity	**-0.045**	**-0.024**	**-0.003**	**-0.045**	**-0.024**	**-0.004**	-0.043	-0.020	0.004	**-0.062**	**-0.036**	**-0.010**
	Low PA * Topo	**0.001**	**0.023**	**0.045**	-0.014	0.008	0.030	-0.006	0.018	0.042	-0.031	-0.005	0.022
	High PA * Topo	**-0.048**	**-0.026**	**-0.004**	-0.037	-0.016	0.005	**-0.051**	**-0.027**	**-0.003**	-0.028	-0.002	0.025
	Low PA * PA connectivity	-0.022	-0.001	0.021	-0.021	0.000	0.021	-0.028	-0.004	0.020	-0.025	0.001	0.027
	High PA * PA connectivity	-0.027	-0.005	0.018	-0.025	-0.003	0.019	-0.024	0.000	0.025	-0.023	0.003	0.030
Priority species	Intercept	**-0.037**	**-0.019**	**-0.002**	-0.036	-0.018	0.000	**-0.040**	**-0.022**	**-0.005**	**-0.045**	**-0.027**	**-0.010**
	Low PA	**0.008**	**0.020**	**0.032**	**0.006**	**0.018**	**0.030**	**0.009**	**0.022**	**0.035**	**0.007**	**0.023**	**0.039**
	High PA	**0.016**	**0.028**	**0.041**	**0.013**	**0.026**	**0.038**	**0.018**	**0.032**	**0.045**	**0.028**	**0.046**	**0.064**
	Similarity	-0.042	-0.018	0.006	-0.042	-0.018	0.006	-0.045	-0.021	0.003	**-0.054**	**-0.032**	**-0.009**
	Topo	**0.040**	**0.084**	**0.128**	**0.039**	**0.084**	**0.130**	**0.043**	**0.085**	**0.127**	**0.049**	**0.086**	**0.123**
	PA connectivity	-0.009	0.013	0.034	-0.010	0.012	0.034	-0.009	0.012	0.034	-0.011	0.010	0.031
	PA coverage change	-0.002	0.029	0.060	-0.004	0.027	0.058	**0.001**	**0.031**	**0.062**	-0.023	0.007	0.036
	Baseline representation	**1.051**	**1.088**	**1.125**	**1.048**	**1.088**	**1.127**	**1.054**	**1.092**	**1.129**	**1.065**	**1.103**	**1.142**
	Low PA * Similarity	-0.019	-0.008	0.004	-0.016	-0.004	0.008	-0.019	-0.006	0.007	-0.018	-0.002	0.014
	High PA * Similarity	-0.017	-0.005	0.007	-0.019	-0.006	0.006	-0.014	-0.001	0.012	-0.027	-0.011	0.005
	Low PA * Topo	-0.003	0.009	0.021	-0.008	0.005	0.017	-0.005	0.008	0.021	-0.016	0.000	0.016
	High PA * Topo	**-0.031**	**-0.018**	**-0.006**	-0.024	-0.011	0.001	**-0.039**	**-0.025**	**-0.012**	**-0.047**	**-0.030**	**-0.014**
	Low PA * PA connectivity	-0.006	0.006	0.018	-0.009	0.004	0.016	-0.009	0.005	0.018	-0.015	0.002	0.018
	High PA * PA connectivity	-0.019	-0.007	0.005	-0.015	-0.003	0.010	-0.020	-0.007	0.006	-0.026	-0.010	0.007

Appendix 2 - Supporting information for Chapter 3

Chapter 3 Supplementary methods

Species Distribution Models

For our models, we used the recorded distributions of 445 priority species listed under Section 41 (Natural Environment and Rural Communities Act, 2006), provided by Butterfly Conservation (BC), Biological Records Centre (BRC); and breeding bird atlas data from British Trust for Ornithology (BTO) (Gillings et al. 2019). Species distributions were in the form of annual presence records that were aggregated together for modelling between 2000 and 2014, apart from birds and vascular plants which were only available for specific time periods (2007-11, and 2010-17 respectively). Input data used was in the form of presence/ pseudo-absence at 10x10km scale, and we only used species with spatial records present in <50% land coverage cells.

Of the 445 total priority species, 156 species were very localised (10 or fewer presence records), and deemed unsuitable for modelling over the whole of Britain, hence we used the raw distribution records for prioritisations.

For the other species which had over 10 presence records, we carried out modelling individually for each species to interpolate their range using Integrated Nested Laplace Approximations (INLA) in the inlabru R package (Bachl et al. 2019). A joint model predicting distribution while accounting for recording effort was used (Eq. 6), including biologically relevant covariates: seasonality (cvTemp), the coefficient of temperature variation; growing degree days (GDD5), the number of days 5^{o}C or warmer as a measure of the plant growth season; water availability (water), calculated using rainfall and evapotranspiration as well as soil moisture; and winter cold (MTCO), the mean temperature of the coldest month. See Beale et al. (2014) for calculation methods of these covariates. These covariates were calculated using monthly means of weather data for 2004-2014, specifically mean temperature, sunshine and rainfall from the Met Office (Met Office 2017). We also included soil moisture to calculate water availability (Batjes 1996). Additionally we included soil PH, which was aggregated from 1x1 km resolution soil pH from the Countryside Survey 2007 dataset (UK Soil Observatory 2007) to 10x10km cells using the mean.

To estimate recorder effort, we used the raw species distribution data records from all 445 species. These were used, along with broad habitat layers extracted from the Land Cover Map 2015 (Rowland et al. 2017), in a Frescalo analysis. Frescalo works through a number of stages to estimate recorder effort, but see Hill (2012) for further details on use of Frescalo software. Simply, for each cell a matrix of weights is created for neighbouring cells, with higher weights for spatial proximity and habitat similarity. Species presences are then multiplied by these weights, and recorder effort is estimated based upon the difference between the focal cell value and the neighbourhood mean cell value. A hazard rate detection function was then used (Eq. 7) to estimate the effect of recorder effort on recorded species presence for each species. The models of 77 species for which modelling was attempted did not converge (most of which were very rare), and so the raw distributions were used in these instances.

$$\begin{aligned}\log(\lambda_i) = \ & b_0 + \ b_1 cvTemp_i + b_2 cvTemp_i{}^2 + b_3 GDD5_i \\ & + b_4 GDD5_i{}^2 + b_5 water_i + b_6 water_i{}^2 + b_7 MTCO_i \\ & + b_8 MTCO_i{}^2 + b_9 PH_i + b_{10} PH_i{}^2 + \log(p_i) + SE_i\end{aligned}$$

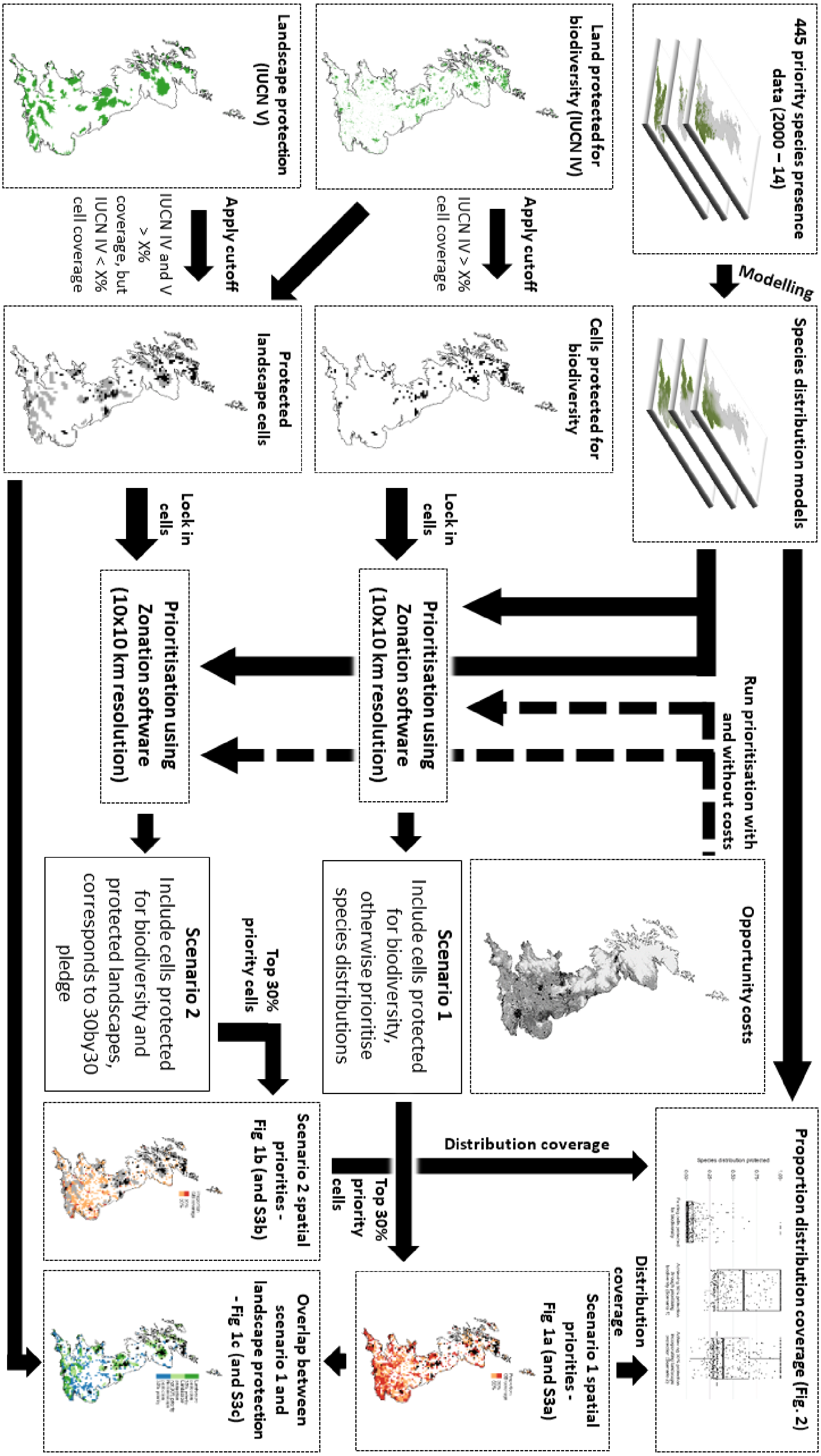
Eq. 6

where λ_i is the spatial intensity (density) of species presence at cell *i*, b_0 is the intercept, *cvTemp* is seasonality, *GDD5* is growing degree days, *water* is water availability, *MTCO* is winter cold, *PH* is the soil PH, p_i is the detection probability function, SE_i is the structured and random spatial effect for cell *i*, and $b_{1\text{-}10}$ are the estimated parameters for the corresponding covariates.

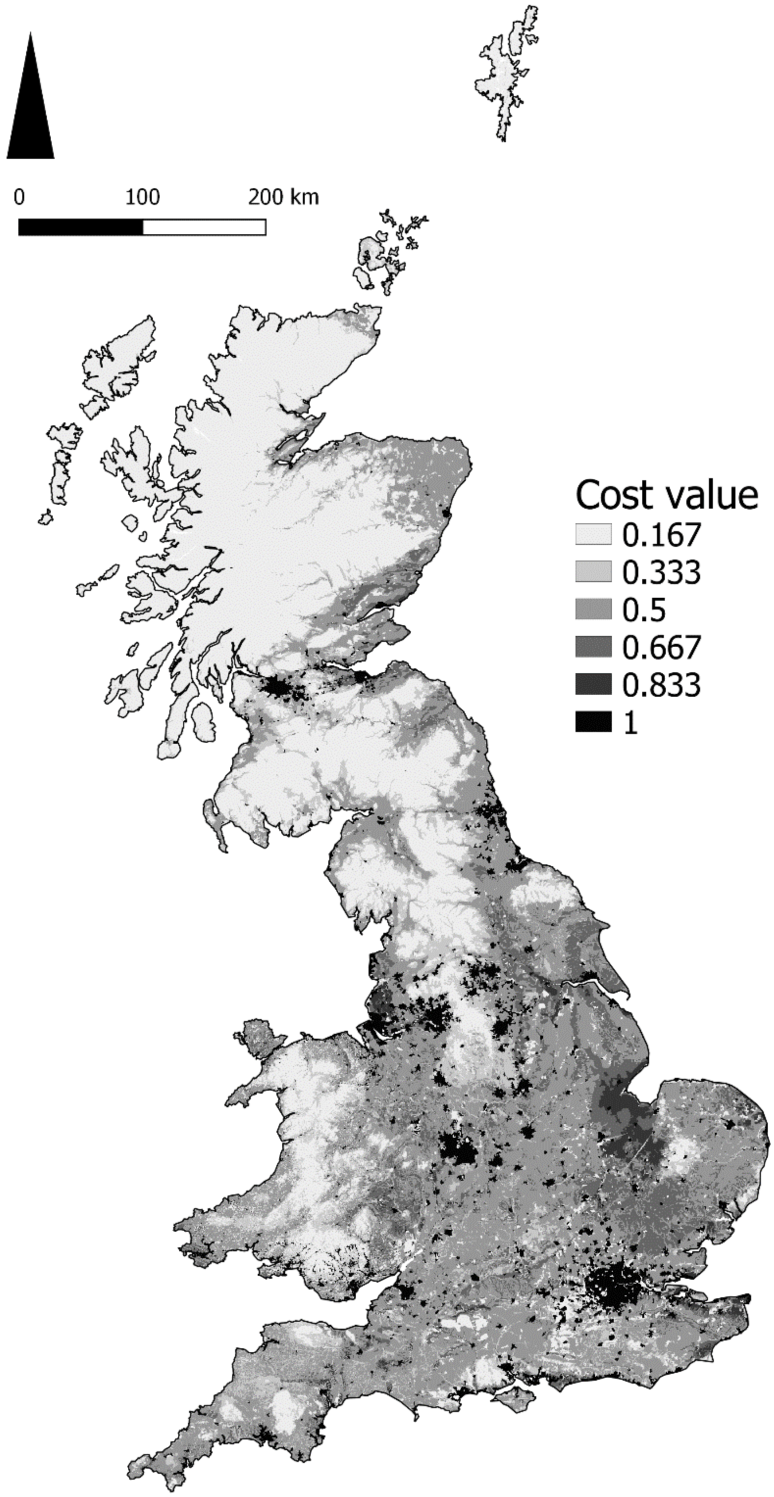
$$p_i = 1 - e^{-(\frac{d_i}{e^{\hat{\sigma}}})^{-1}}$$

Eq. 7

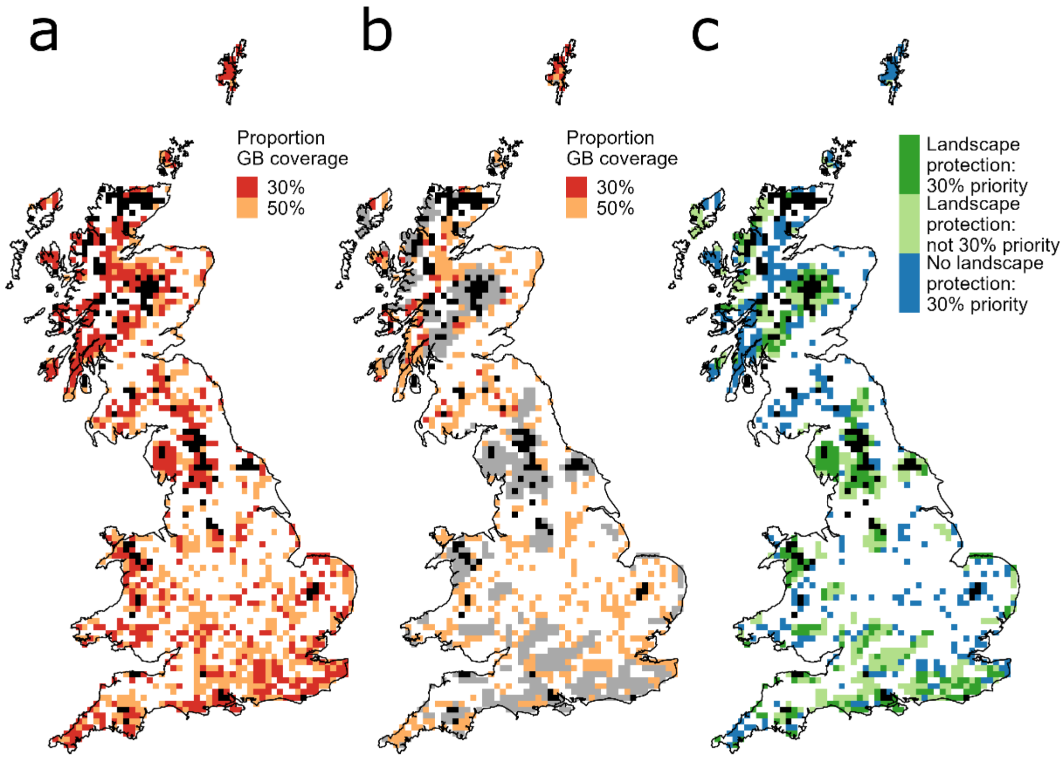
where d_i is the inverse of estimated recorder effort at cell *i,* and $\hat{\sigma}$ is the linear predictor of the sigma parameter.


445 priority species presence data (2000 – 14)
Modelling
Species distribution models
Proportion distribution coverage (Fig. 2)
Land protected for biodiversity (IUCN IV)
Apply cutoff
IUCN IV > X% cell coverage
Cells protected for biodiversity
Lock in cells
Run prioritisation with and without costs
Opportunity costs
Distribution coverage
Distribution coverage
Landscape protection (IUCN V)
Apply cutoff
IUCN IV and V > X% coverage, but IUCN IV < X% cell coverage
Protected landscape cells
Lock in cells
Prioritisation using Zonation software (10x10 km resolution)
Prioritisation using Zonation software (10x10 km resolution)
Scenario 1
Include cells protected for biodiversity, otherwise prioritise species distributions
Top 30% priority cells
Scenario 1 spatial priorities - Fig 1a (and S3a)
Scenario 2
Include cells protected for biodiversity and protected landscapes, corresponds to 30by30 pledge
Top 30% priority cells
Scenario 2 spatial priorities - Fig 1b (and S3b)
Overlap between scenario 1 and landscape protection - Fig 1c (and S3c)

Supplementary Figure 2.1 Approach workflow for evaluating different conservation scenarios in terms of coverage of species distributions. We firstly categorised conservation designations into two types; 'protection for biodiversity' (IUCN IV or higher protection), and 'landscape protection' (lower level IUCN V protection). SSSIs and NNRs are 'protected for biodiversity', and NPs, AONBs, and Scottish NSAs offer landscape protection. We then used these to classify 10x10km cells using several cutoffs (Supplementary Table 2.1). If cells had greater 'land protected for biodiversity' coverage than the cutoff, they were classified as 'protected for biodiversity' cells. Otherwise if cells met the cutoff with a combination of land 'protected for biodiversity' and landscape protection, but were not 'protected for biodiversity' cells, then they were classified as 'protected landscape' cells. We also used the recorded distributions of 445 priority species between 2000 and 2014. These distributions were modelled using INLA (See Chapter 2 Supplementary Methods) to interpolate distributions of less recorded species. The species distributions and protected cells were then used for two spatial prioritisations exploring different conservation scenarios. Scenario 1 required inclusion of 'protected for biodiversity' cells but didn't consider other designations beyond that. Scenario 2 also included cells 'protected for biodiversity' but, corresponding to the 30by30 pledge, additionally required all protected landscapes to be included in the solution. All prioritisations were undertaken at a 10x10 km landscape-scale on cells with greater than half land coverage. The spatial prioritisations were carried out using Core Area Zonation, whereby cells are removed iteratively, and cells remaining longer within the solution complement species representation of other cells to a greater extent. Cells with the lowest value are removed first, corresponding to the lowest maximum proportion of species distributions within the remaining cells. Priorities were constrained by masking or 'locking in' different areas relevant to each scenario such that all other cells must be removed first. In order to compare the scenarios, we calculated the proportion of each species distribution covered by the top 30% priority cells of each scenario (Figure 3.2, Supplementary Table 2.2). Finally, we compared the spatial overlap of protected landscape cells and scenario 1 30% priorities (Figure 3.1c, Supplementary Table 2.3). We also undertook a parallel analysis additionally incorporating opportunity costs calculated from agricultural land classification and urban areas (Supplementary Figure 2.2, Supplementary Table 2.4). In this analysis, cell value was divided by the mean opportunity cost of the cell (Supplementary Figure 2.3, Supplementary Table 2.2 and Supplementary Table 2.3).



Supplementary Figure 2.2 Agricultural land classifications used as a proxy for opportunity cost in spatial prioritisations. Opportunity costs were assigned based upon agricultural land classifications for England, Scotland, and Wales. Agricultural land classification was standardised between countries, then rescaled and subtracted from 1 as presented in Supplementary Table 2.4. Urban land was then given the largest possible cost value of 1. Costs were aggregated by mean cell cost for prioritisations undertaken at 10x10 km resolution.



Supplementary Figure 2.3 Spatial priorities for additional protection to meet 30by30 protection targets within Britain incorporating opportunity costs into the spatial prioritisation. (a) Scenario 1: prioritisation constrained only by the inclusion of current biodiversity protected sites. (b) Scenario 2: constrained by maintaining both biodiversity and landscape protection sites, as suggested by the 30by30 announcement. (c) Overlap between top 30% priority cells for biodiversity from scenario 1 and current protected landscapes. Cells already protected for biodiversity are shaded black (which are included as part of the 'top 30% in both scenarios). For panels (a) and (b), top 30% priority cells are shaded red, top 50% orange, and landscape protection cells are grey. In panel (c), priority cells for biodiversity are dark green if in a landscape protection cell and dark blue if outside a landscape protection cell; light green shows those landscape protected cells that are not a priority for biodiversity conservation.

Supplementary Table 2.1 Number of cells within each protection category for different protection level cutoffs, with percentages of total 2309 GB cells in parentheses. We considered land protected for biodiversity to include Sites of Special Scientific Interest (SSSI) and National Nature Reserves (NNR) (9.04% actual proportion GB coverage); and landscape protection to include National Parks (NP), Areas of Outstanding Natural Beauty (AONB), and Scottish National Scenic Areas (NSA) (22.22% actual proportion GB coverage) [intersection between categories 4.55%, union 26.71%]. 10x10 km cells listed below were considered to be 'protected for biodiversity' if SSSI/NNR coverage was greater than the cutoff proportion of the land area, i.e. at least X% IUCN minimum IV protection. 'Protected landscapes' contained total coverage from all of the designations > X%, i.e. at least X% minimum IUCN V protection, but the cell was not already 'protected for biodiversity'. *At the 30% protection cutoff more than 30% of GB cells are protected for biodiversity and protected landscapes at 10x10 km resolution.

	Minimum proportion of each cell currently protected				
	30%*	**40%**	**50%**	**60%**	**70%**
Protected for biodiversity	211 (9.14%)	148 (6.41%)	99 (4.29%)	61 (2.64%)	27 (1.17%)
Protected landscapes	531 (23.00%)	494 (21.39%)	459 (19.88%)	404 (17.50%)	362 (15.68%)
Total	742 (32.14%)	642 (27.80%)	558 (24.17%)	465 (20.14%)	389 (16.85%)

Supplementary Table 2.2 Median proportion of priority species distributions protected under different scenarios. For each current protection cutoff, and with/without inclusion of opportunity costs, the median species protected is presented for: *Scenario 1,* existing land protected for biodiversity and including additional cells on the basis of the distributions of priority species, unconstrained by current landscape protection, and; *Scenario 2*, includes existing cells protected for biodiversity *and* those with current landscape protection, before including additional cells on the basis of the distributions of priority species. For scenario 2, the median proportion covered by cells already protected for biodiversity and protected landscapes is included in parentheses. Scenario 1 consistently had median protection at least 10% higher than scenario 2 protecting 30% of land. *At the 30% protection cutoff more than 30% of GB cells are protected for biodiversity and protected landscapes at 10x10 km resolution.

		Median proportion priority species distribution protected (%)			
		Not including costs		**Including costs**	
Minimum proportion of each cell currently protected	**Cells**	**30% GB coverage**	**50% GB coverage**	**30% GB coverage**	**50% GB coverage**
30%*	Current land protected for biodiversity	3.96			
	Scenario 1 (includes cells already protected for biodiversity)	58.74	94.44	45.45	79.18
	Scenario 2 (includes cells already protected for biodiversity and protected landscapes)	- (34.75)	83.33 (34.75)	- (34.75)	76.02 (34.75)
40%	Current land protected for biodiversity	1.63			
	Scenario 1	61.18	96.23	48.39	81.28
	Scenario 2	39.32 (29.47)	90.31 (29.47)	31.30 (29.47)	76.47 (29.47)
50%	Current land protected for biodiversity	0.66			
	Scenario 1	65.04	97.71	50.00	81.28
	Scenario 2	48.52 (24.87)	92.23 (24.87)	33.33 (24.87)	75.33 (24.87)
60%	Current land protected for biodiversity	0.41			
	Scenario 1	68.19	98.12	50.00	81.77
	Scenario 2	55.14 (19.72)	93.79 (19.72)	37.44 (19.72)	77.40 (19.72)
70%	Current land protected for biodiversity	0.00			
	Scenario 1	66.13	98.48	50.00	82.26
	Scenario 2	55.56 (15.38)	93.87 (15.38)	40.00 (15.38)	79.18 (15.38)

Supplementary Table 2.3 Cell overlap between top 30% priority cells from scenario 1 (prioritising cells to add to existing cells protected for biodiversity unconstrained by current landscape protection), and protected landscape cells. Number of cells in three categories are presented; cells with landscape protection that are a 30% priority, cells with landscape protection that are not a 30% priority, and cells without landscape protection (or protection for biodiversity) that are a 30% priority. Of cells not protected for biodiversity, the majority of scenario 1 30% priority cells were outside protected landscapes, and a large proportion of protected landscape cells were not a 30% priority. Additionally, the mean proportion of land currently protected for biodiversity within each category is presented. 30% priority cells outside protected landscapes consistently had the lowest amount of land protected for biodiversity. Results presented for all protection cutoffs tested, both with costs (Figure 3.1c) and without (Supplementary Figure 2.3c).

Minimum proportion of each cell currently protected	**Cells**	**Not including costs**		**Including costs**	
		No. of cells	**% protected**	**No. of cells**	**% protected**
30%	Landscape protection: 30% priority	196	7.77	197	9.12
	Landscape protection: 30% non-priority	335	8.17	334	7.38
	No landscape protection: 30% priority	286	4.33	285	4.58
40%	Landscape protection: 30% priority	205	10.27	204	12.10
	Landscape protection: 30% non-priority	289	10.36	290	9.07
	No landscape protection: 30% priority	340	4.77	341	5.55
50%	Landscape protection: 30% priority	203	12.68	207	15.00
	Landscape protection: 30% non-priority	256	13.38	252	11.49
	No landscape protection: 30% priority	391	5.10	387	6.50
60%	Landscape protection: 30% priority	187	14.8	197	17.67
	Landscape protection: 30% non-priority	217	16.81	207	14.18
	No landscape protection: 30% priority	445	5.70	435	7.63
70%	Landscape protection: 30% priority	175	17.71	187	19.79
	Landscape protection: 30% non-priority	187	19.04	175	16.91
	No landscape protection: 30% priority	491	6.83	479	8.55

Supplementary Table 2.4 Agricultural land classifications within England, Scotland, and Wales. Classifications were standardised between nations into a single interoperable agricultural land value code. We rescaled these values and subtracted from 1 to calculate opportunity cost. Urban land was given the largest possible opportunity cost value (1).

England Code	Wales Code	England/Wales Description	England/ Wales Detail	Scotland Code	Scotland Description	Interoperable Code	Opportunity cost used in prioritisation
Grade 1	1	Excellent quality	No or very minor limitations on agricultural use. Wide range of agricultural and horticultural crops can be grown. High yielding and consistent.	1	Land capable of producing a very wide range of crops	1	0.833
Grade 2	2	Very good	Minor Limitations on crop yield, cultivations or harvesting. Wide range of crops but limitations on demanding crops (e.g. winter harvested veg). Yield high but lower than Grade 1.	2	Land capable of producing a wide range of crops	2	0.666
Grade 3	3a	Good	Moderate to high yields of narrow range of arable crops (e.g. cereals), or moderate yields of grass, oilseed rape, potatoes, sugar beet and less demanding horticultural crops	3.1	Land capable of producing consistently high yields of a narrow range of crops and/ or moderate yields of a wider range. Short grass leys are common	3	0.500
Grade 3	3b	Moderate	Moderate yields of cereals, grass and lower yields other crops. High yields of grass for grazing/ harvesting.	3.2	Land capable of average production though high yields of barley, oats and grass can be obtained. Grass leys are common		
Grade 4	4	Poor	Severe limitations which restrict range and/or level of yields. Mostly grass and occasional arable (cereals and forage), but highly variable yields. Very	4.1	Land capable of producing a narrow range of crops, primarily grassland with short arable breaks of forage crops and cereal	4	0.333

			droughty arable land included.	4.2	Land capable of producing a narrow range of crops, primarily on grassland with short arable breaks of forage crops		
Grade 5	5	Very poor	Severe limitations which restrict use to permanent pasture or rough grazing except for pioneering forage crops.	5.1	Land capable of use as improved grassland. Few problems with pasture establishment and maintenance and potential high yields	5	0.167
				5.2	Land capable of use as improved grassland. Few problems with pasture establishment but may be difficult to maintain		
				5.3	Land capable of use as improved grassland. Pasture deteriorates quickly		
				6.1	Land capable of use as rough grazings with a high proportion of palatable plants		
				6.2	Land capable of use as rough grazings with moderate quality plants		
				6.3	Land capable of use as rough grazings with low quality plants		
				7	Land of very limited agricultural value		
Non Agricultural	NA	Non-agricultural		999	Inland Water		
Exclusion	NA	Non-agricultural		9500	Unencoded Islands		
Urban	U	Urban		888	Built Up Areas	0	1.000

Appendix 3 - Supporting information for Chapter 4

Chapter 4 Supplementary methods

Feature layers

The complete list of seven ecosystem service and socio-environmental value layers were collated as follows:

Five ES layers were included; carbon storage (existing), agricultural value, recreational services, flood regulation, and pollination services. Carbon storage value was calculated as the sum of interpolated below-ground carbon from the CEH Soil Carbon Map to a depth of 100 cm (Bradley et al. 2005), and estimated above-ground carbon using the 2007 Land Cover Map (Henrys et al. 2016). Agricultural value was assigned based upon agricultural land classifications for England (Natural Resources Wales 2019; The James Hutton Institute 2019; England 2021). Classifications were standardised between countries into an interoperable code, and the mean landscape value was then rescaled and subtracted from 1 to calculate the final agricultural value used for the spatial prioritisations (see Appendix 1 Supplementary Methods for details). Urban areas were then given the highest value, indicating unsuitable land use for terrestrial conservation. Recreation value was estimated from the predicted annual visits/ha for a potential new National Park, see Schägner et al. (2016).

The value of protecting land for flood prevention depends on (a) supply: the degree to which upstream land reduces peak discharge volume (i.e. flooding risk); and (b) demand: the damage a flood could cause accounting for location within the catchment (i.e. aggregated damage within *and* downstream of each catchment). These factors interact such that if there is no valuable infrastructure downstream flood prevention action gains nothing, but equally if a location currently does little to reduce peak discharge then flood prevention value is again low. Hence, flood regulation value was estimated using a supply index (predicted total effect of upstream land on river discharge after precipitation events), and a catchment level demand index (downstream flood damage accounting for upstream area); see Stürck et al. (2014) for details of supply and demand indexes used in this analysis. These indices do not provide an absolute measure of service flow; however, the relative distributions can be compared. Flood regulation flow was estimated by ranking the supply and demand indices separately, and then taking the minimum rank of the two. In this way, areas that had both relatively high supply and demand received higher value. Pollination service flow was similarly calculated with a supply index (estimated visitation probability by pollinators), and demand index (area of pollinator crops weighted by dependency level), see Schulp et al. (2014).

Additionally two socio-environmental value layers were added; wilderness and landscape aesthetic value. Wilderness was included from the ‘wilderness register and indicator for Europe’ map, created from a combination of naturalness, remoteness from settlements and access, and terrain ruggedness (Kuiters et al. 2013). Landscape aesthetic value was quantified based on numbers of geolocated unique user uploads to three social media platforms, see Van Zanten et al. (2016). The mean landscape rank of the number of uploads to each platform was then taken as the ‘landscape aesthetic value’.

Other viewpoint integration approaches

In addition to the inclusive and pluralist approaches described within the main text, two additional MCDA spatial approaches to integrating viewpoints together were tested. The first approach involved calculating the mean feature weightings between viewpoints (mean of the four weightings for each feature in Table 4.2) prior to any spatial prioritisation. These mean weightings were then used within a single spatial prioritisation using Zonation (MEAN), and hence this approach approximates deciding on conservation priorities prior to any spatial prioritisation. The other integration approach involved using the output landscape rankings from the four viewpoint prioritisations (TRAD, NEW, ECON, SOC) to seek an overall compromise (RANK). A further Zonation prioritisation was carried out on these ranks (each individual viewpoint was treated as an input feature layer). Neither of these two alternative methods outperformed the inclusive and pluralist methods described in the main text in terms of mean or minimum feature coverage efficiency using CAZ (with the exception of higher RANK minimum efficiency at the highest [30%] area coverage threshold). MEAN consistently underperformed the other approaches using CAZ.

All four methods were tested using both the *core area zonation* (CAZ) and *additive benefit functio*n (ABF) prioritisation method. Both methods iteratively remove landscapes contributing the smallest value to the remaining landscapes. Through this removal, landscapes remaining within the solution longer complement other landscapes to a greater extent, in terms of contributing the most to underrepresented features. Using CAZ, landscape value is calculated as the *maximum* weighted proportion of any positive feature within the remaining landscapes (minus any negative alternative land use value within the landscape). Using ABF, this is *averaged across all positive features*, not just the maximum value. Inclusive and pluralist integration approaches using CAZ are presented in the main text, and all others are presented in Supplementary Figure 3.2 to Supplementary Figure 3.8. The following discussion considers similarities and differences between ABF and CAZ results.

Chapter 4 Supplementary discussion

Additive benefit prioritisation

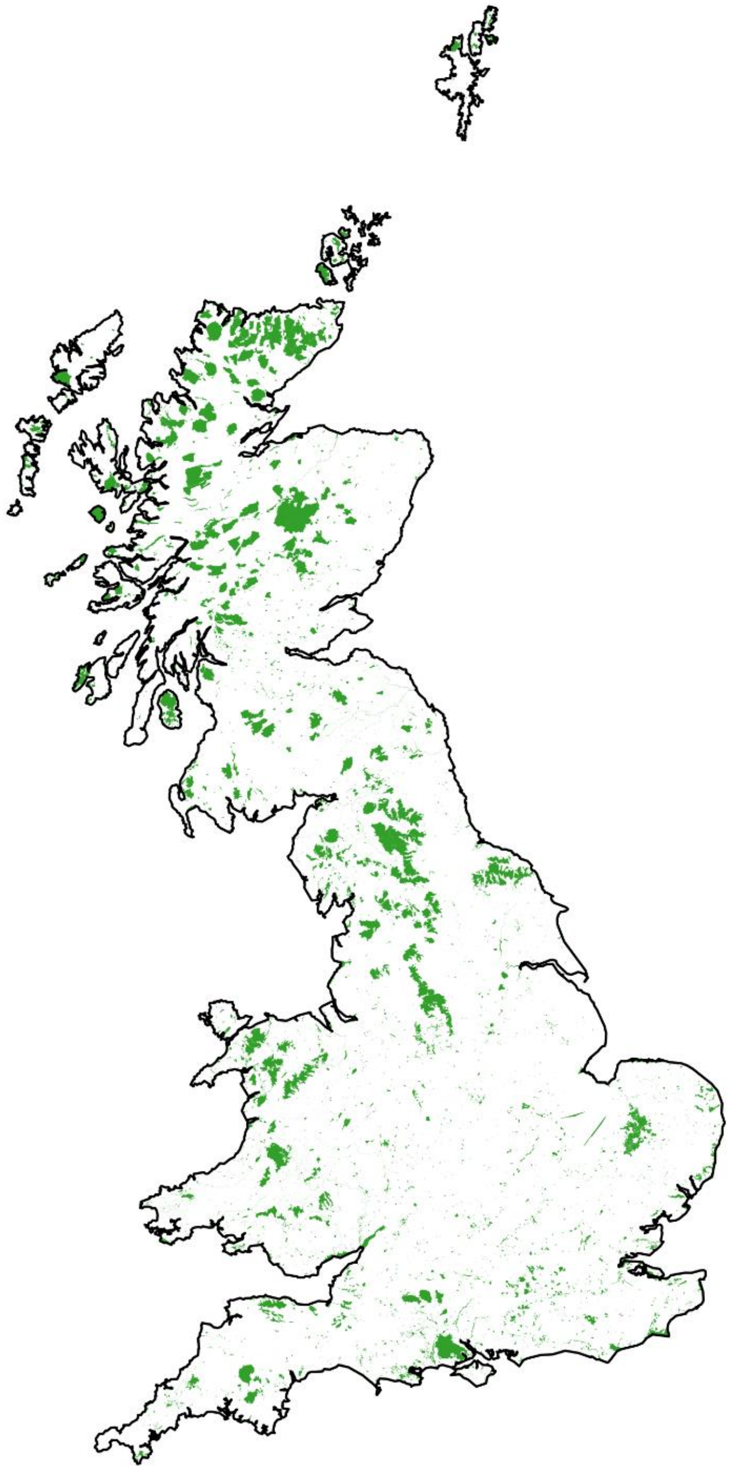
Since ABF averages across all features, it resulted in higher overall feature coverage but lower levels of complementarity between landscapes. Hence there was greater spatial similarity between the ABF viewpoint prioritisations than the CAZ prioritisations, with NEW and ECON prioritisations especially spatially correlated (Supplementary Figure 3.2). The greater convergence between viewpoints was due to ABF considering all landscape features, rather than the single highest weight*(positive proportion) in CAZ. Due to these increased similarities, ABF viewpoint integration approaches were also more spatially similar compared to CAZ (Supplementary Figure 3.3 and Supplementary Figure 3.4), with a particular concentration within the south of England suggesting that this is an area with potentially large gains in feature coverage, even if the most important landscapes for some features are not included.

Feature coverage was more consistent between the ABF integration approaches, and they provided a slightly higher mean feature coverage efficiency than CAZ (ABF 17% coverage efficiency range: 0.625-0.636; CAZ: 0.560-0.600; Supplementary Figure 3.5 to Supplementary Figure 3.8). For lower thresholds, minimum coverage efficiency was generally higher using ABF too (ABF 5% coverage efficiency range: 0.222-0.269; CAZ: 0.142-0.383). However, as the threshold rose CAZ minimum efficiency generally increased at a faster rate than ABF, and CAZ ultimately exceeded ABF for the pluralist and RANK approaches (ABF 30% coverage efficiency range: 0.424-0.458; CAZ: 0.376-0.545). This is illustrated by Supplementary Figure 3.5 and Supplementary Figure 3.6 (right hand panels), where ABF mainly outperforms CAZ at 5% area coverage (red columns) but not at 30% (dark blue columns), and some features may largely be 'missed' with the CAZ approach at 5% coverage if a single viewpoint is adopted. This reflects the fact that achieving multiple goals (satisfying multiple viewpoints and including many different features) is increasingly difficult at low coverage thresholds: CAZ priorities (aiming to include the very best examples of each feature included by a particular viewpoint) may be more difficult to reconcile than ABF (incorporating the places with the best mixture of features) when only a small percentage of the land is allocated to conservation. Nonetheless, the CAZ pluralist approach had relatively high minimum feature coverage efficiency for all area thresholds, ensuring that desired features (by any viewpoint) were not missed, even at low thresholds.

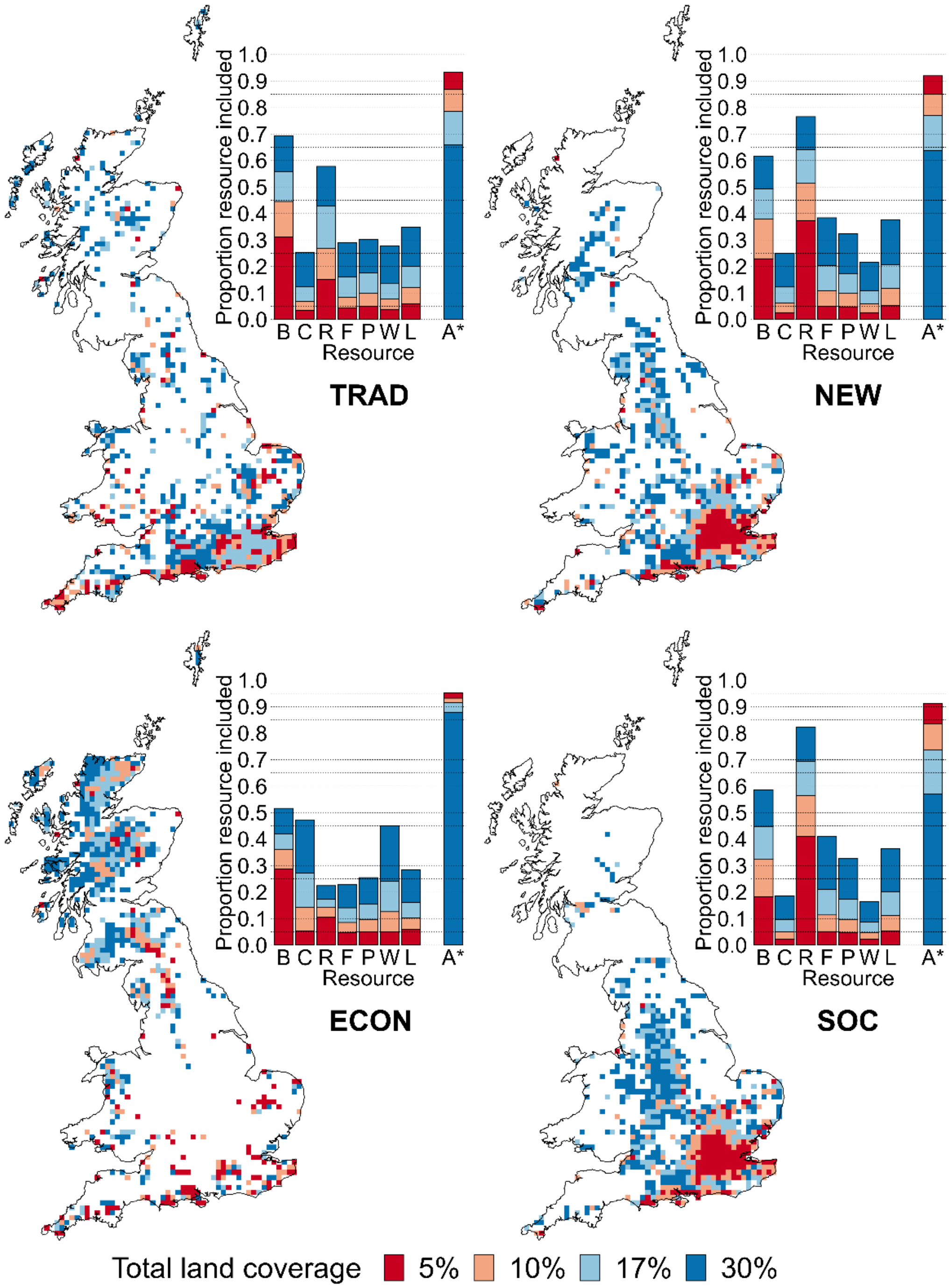
All ABF integration approaches resulted in high mean feature coverage efficiency and moderately high minimum efficiency. Hence, ABF could be considered a more inherently 'inclusive' prioritisation method in that the best combined-feature areas will be selected (most are well satisfied by any of the ABF integration approaches), but areas that are critically important for a single conservation feature may be disregarded (some individuals may be disappointed). Similarly CAZ could be considered a more 'pluralist' prioritisation method, in that the most important locations for each feature and viewpoint are maintained, even if the solution is slightly less efficient overall. Both ABF and CAZ prioritisation methods could offer coherent conservation plans by integrating viewpoints, and the prioritisation method used should depend upon conservation objectives and spatial context. However, I focused on CAZ prioritisation in the main text, here, because CAZ combined with a pluralist approach generally resulted in the highest minimum coverage.

Existing protected area network

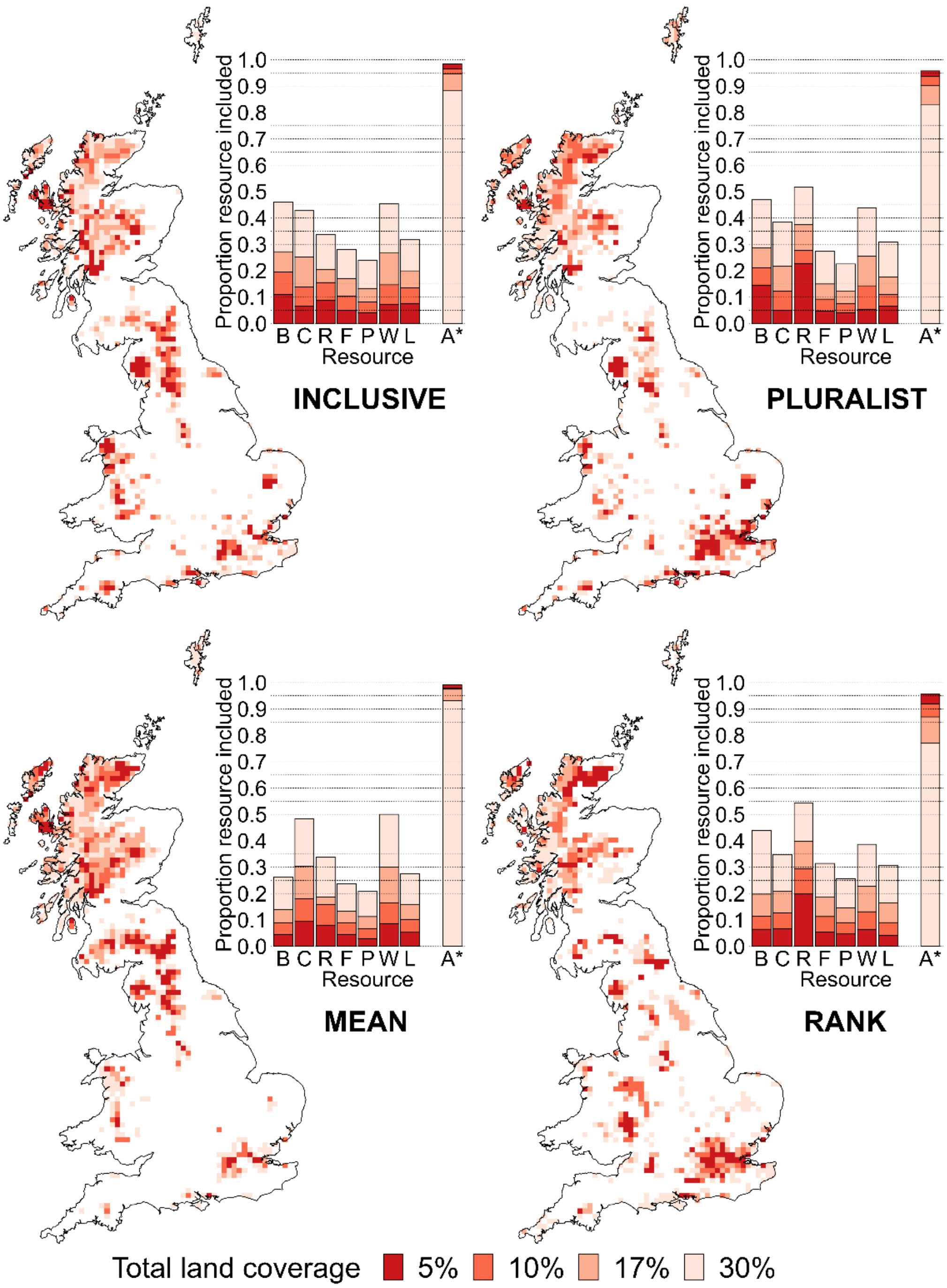
The existing protected area network (Supplementary Figure 3.1) matched ‘new’ and ‘market ecocentrism’ viewpoints more closely than ‘traditional’ (TRAD ρ = 0.379, NEW ρ = 0.423, ECON ρ = 0.413, SOC ρ = 0.068), which was contrary to our expectation given that the rationale and goals for identifying potential SSSIs and NNRs closely align with a traditional approach. The British protected area network was designed primarily to protect species and habitats in a representative way, and I expected more spatial overlap with a prioritisation based on the values of conserving species diversity. The suite of notified sites might be inefficient from the ‘traditional’ viewpoint for several reasons. Although the rationale behind the initial network designation and subsequent expansion may have been ‘traditional’, it may be that sites were not identified optimally through the notification process in terms of species representation. Additionally, notification will have depended not only on the quality of feature, but also on other conservation planning considerations such as land ownership and local socio-economic context. For example large SSSIs are primarily in upland areas, because less intensive land management occurred here in the past, allowing more semi-natural habitat to persist; in contrast to the lowlands where much smaller fragments of habitat remained to be protected.



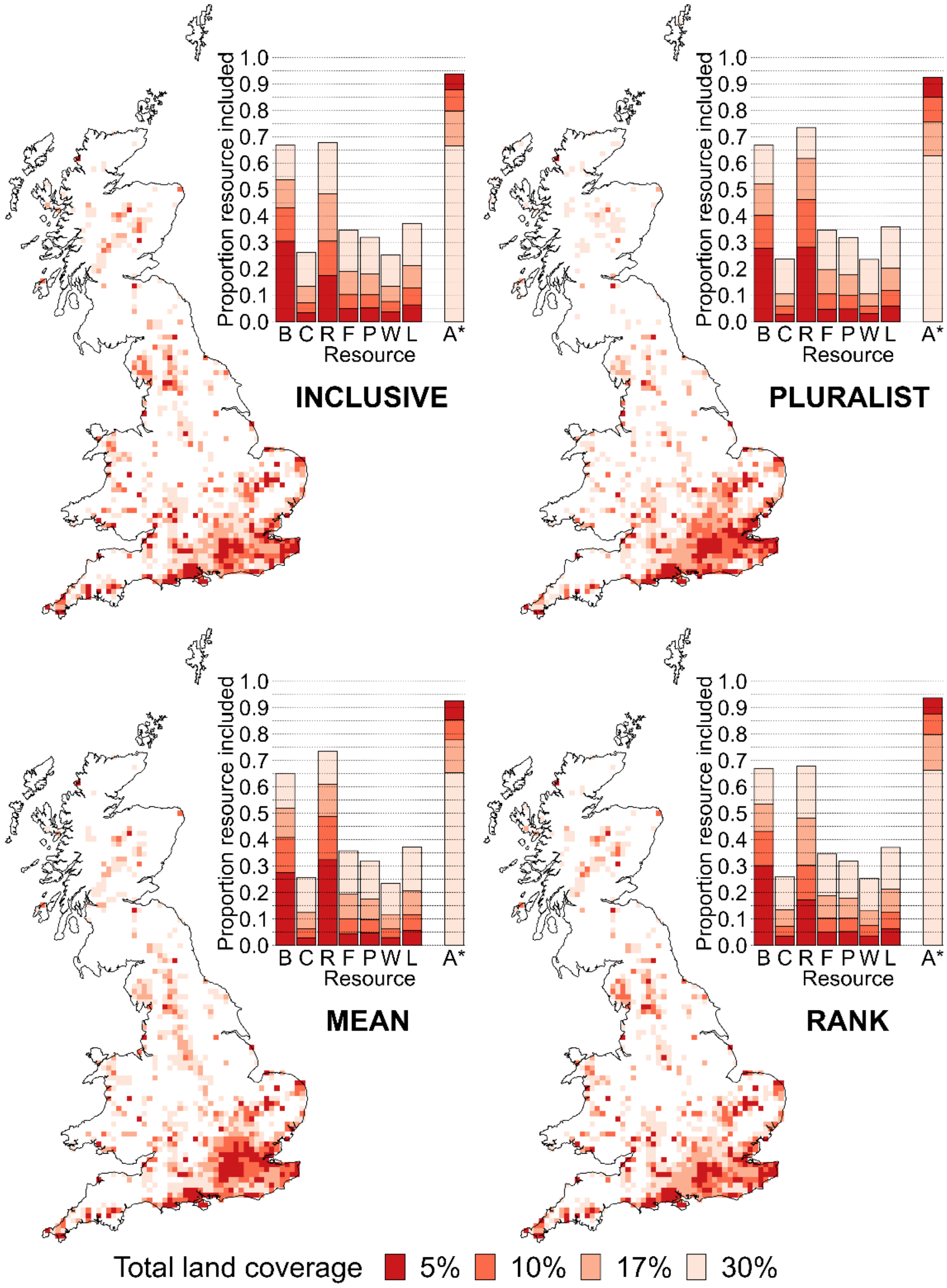
Supplementary Figure 3.1 Protected areas included within the analysis: Sites of Special Scientific Interest (SSSI) and National Nature Reserves (NNR) designated at the time of the study.



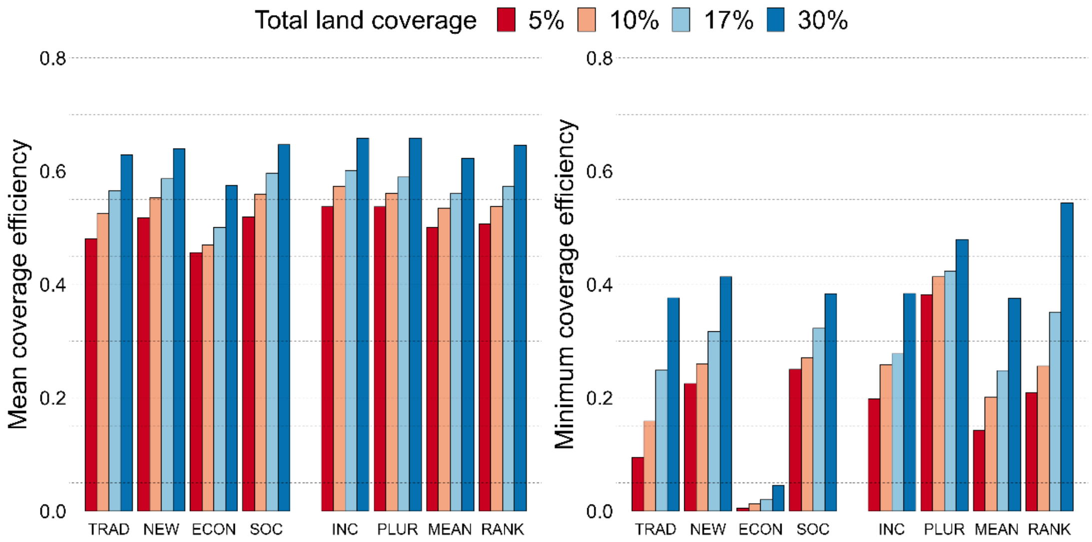
Supplementary Figure 3.2 Feature coverage using spatial prioritisation for each of the four viewpoints using the *additive benefit function* prioritisation method; TRAD – 'traditional', NEW – 'new conservation', ECON – 'international market ecocentrism', SOC – 'local social instrumentalism'. Maps indicate the priority areas for different coverage thresholds, and corresponding bar plots present proportion of feature included for each, including mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*). A* indicates the only negative weighting where proportion excluded, not included, is shown and so higher land coverage results in lower proportion excluded.



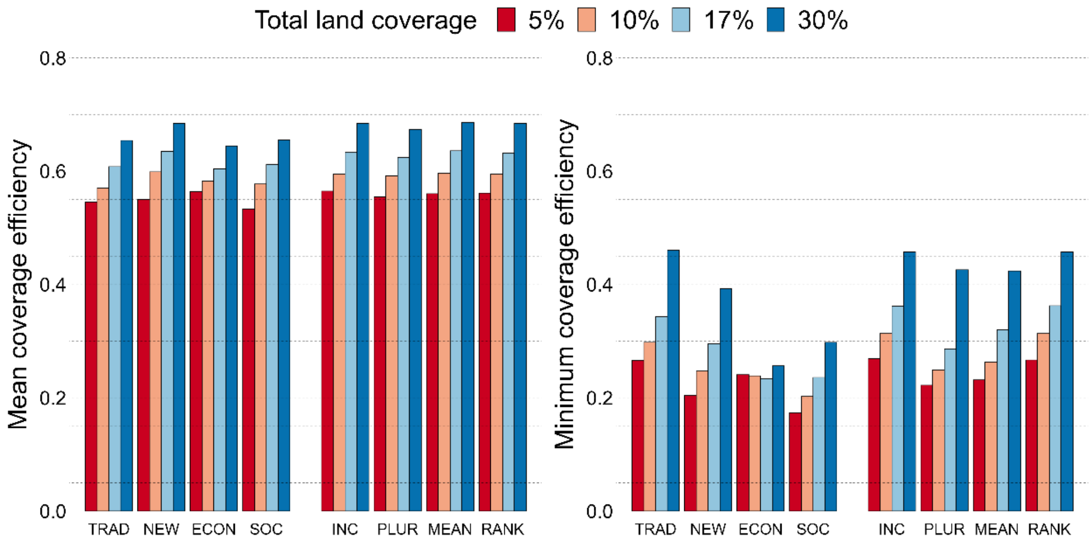
Supplementary Figure 3.3 Spatially aggregating the four conservation viewpoint priorities (TRAD – 'traditional', NEW – 'new conservation', ECON – 'international market ecocentrism', SOC – 'local social instrumentalism') using the *core area zonation* prioritisation method. I used inclusive (vote counting) and pluralist (accounting for distinctiveness) methods; as well as two additional integration approaches MEAN (averaging feature weightings before prioritisation), and RANK (undertaking additional prioritisation of viewpoint landscape ranks). Maps indicate the priority areas for different coverage thresholds, and corresponding bar plots present proportion of feature included for each, including mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*). A* indicates the only negative weighting where proportion excluded, not included, is shown and so higher land coverage results in lower proportion excluded.



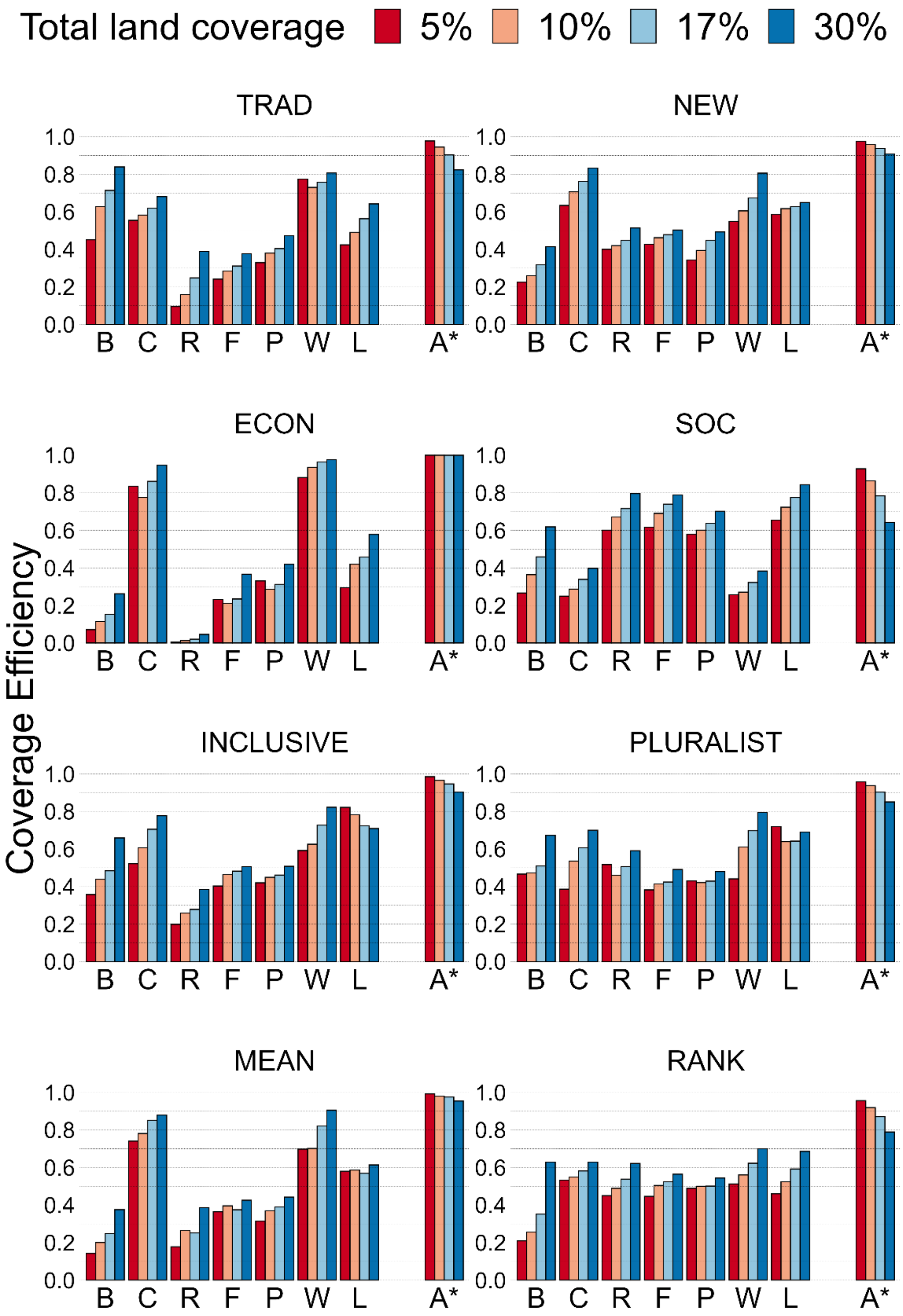
Supplementary Figure 3.4 Spatially aggregating the four conservation viewpoint priorities (TRAD – 'traditional', NEW – 'new conservation', ECON – 'international market ecocentrism', SOC – 'local social instrumentalism') using the *additive benefit function* prioritisation method. I used inclusive (vote counting) and pluralist (accounting for distinctiveness) methods; as well as two additional integration approaches MEAN (averaging feature weightings before prioritisation), and RANK (undertaking additional prioritisation of viewpoint landscape ranks). Maps indicate the priority areas for different coverage thresholds, and corresponding bar plots present proportion of feature included for each, including mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*). A* indicates the only negative weighting where proportion excluded, not included, is shown and so higher land coverage results in lower proportion excluded.



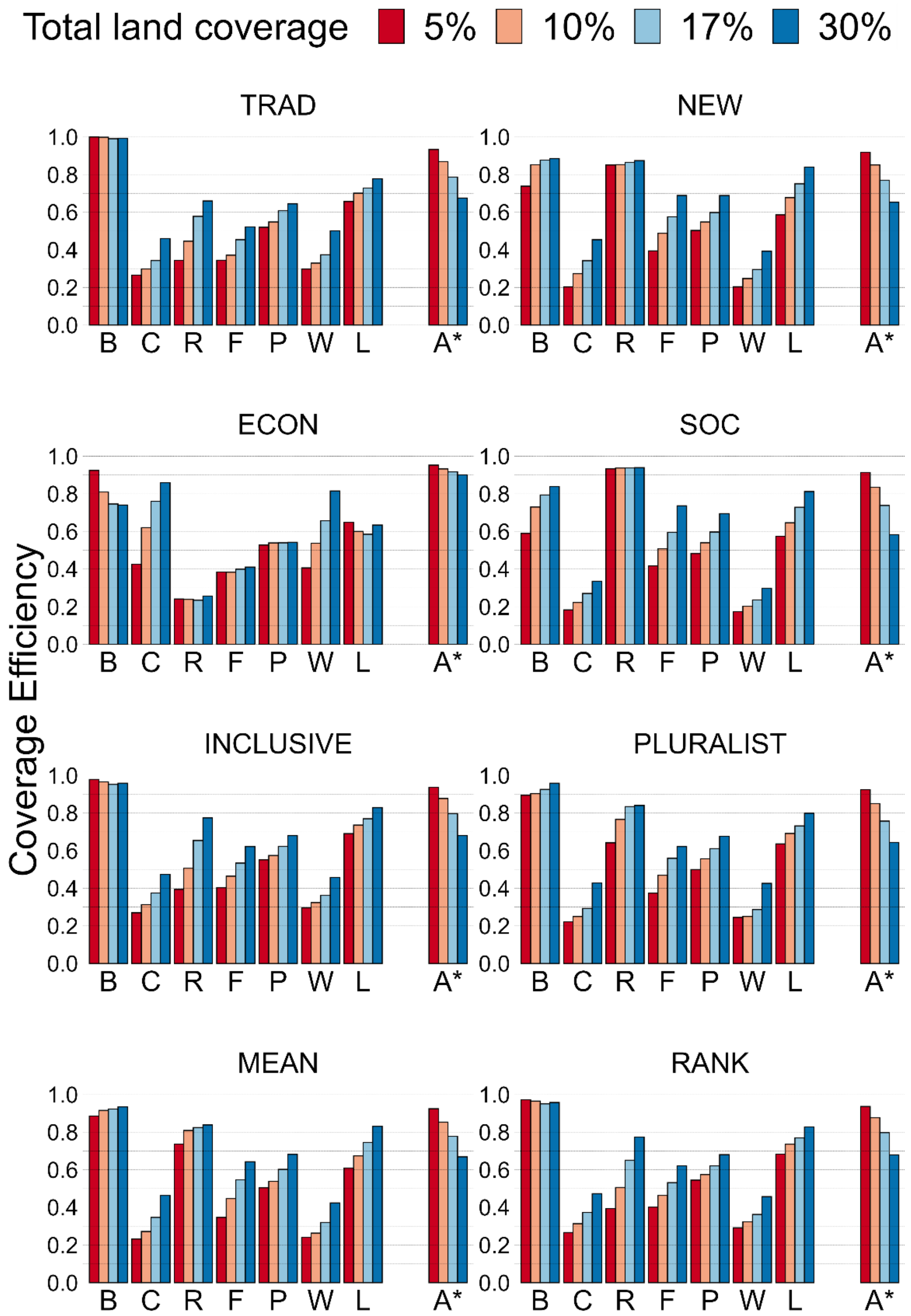
Supplementary Figure 3.5 Mean and minimum feature coverage efficiency of core area zonation prioritisation performance (TRAD – 'traditional', NEW – 'new conservation', ECON – 'international market ecocentrism', SOC – 'local social instrumentalism') and integration approach (Inclusive and Pluralist conservation, as well as two additional integration approaches MEAN and RANK). Efficiency is calculated as the proportion of features covered by a prioritisation for each land coverage threshold (5%, 10%, 17%, and 30%), compared to the maximum possible if only that feature was prioritised. Features included are mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*). The left-hand panel shows the mean performance across all resource types (conservation features), whereas the right-hand panel shows the coverage of the feature that is least well covered by a particular approach.



Supplementary Figure 3.6 Mean and minimum feature coverage efficiency of *additive benefit function* prioritisation performance (TRAD – 'traditional', NEW – 'new conservation', ECON – 'international market ecocentrism', SOC – 'local social instrumentalism') and integration approach (Inclusive, and Pluralist conservation as well as two additional integration approaches MEAN and RANK). Efficiency is calculated as the proportion of features covered by a prioritisation for each land coverage threshold (5%, 10%, 17%, and 30%), compared to the maximum possible if only that feature was prioritised. Features included are mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*). The left-hand panel shows the mean performance across all resource types (conservation features), whereas the right-hand panel shows the coverage of the feature that is *least well covered* by a particular approach.



Supplementary Figure 3.7 Efficiency of *core area zonation* prioritisation performance (TRAD – 'traditional', NEW – 'new conservation', ECON – 'international market ecocentrism', SOC – 'local social instrumentalism') and integration approach (inclusive, and pluralist conservation as well as two additional integration approaches MEAN and RANK). Efficiency was calculated as the proportion of each feature covered compared to the maximum possible for each land coverage threshold (5%, 10%, 17%, and 30%). Features included are mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*).

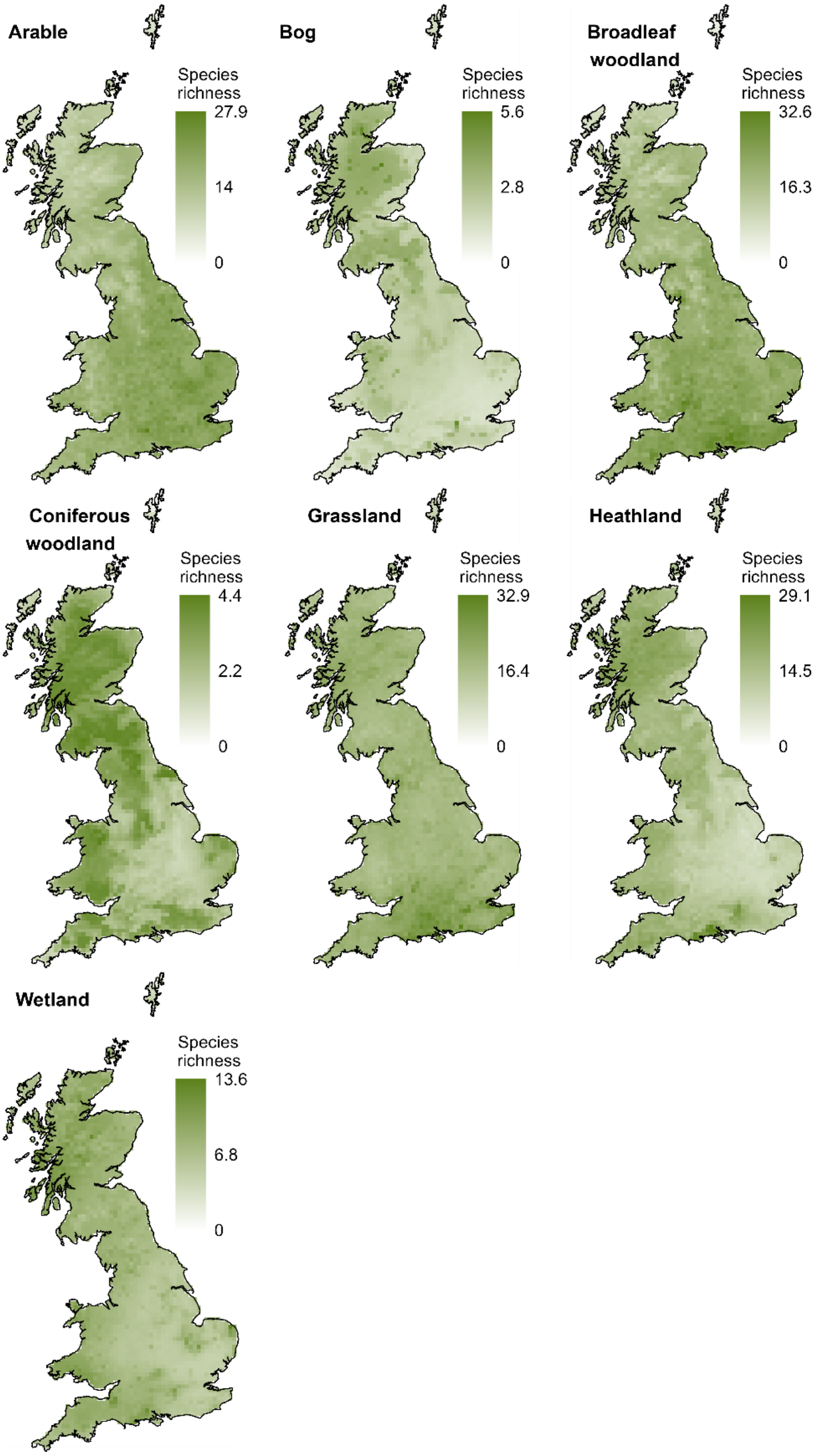


Supplementary Figure 3.8 Efficiency of *additive benefit function* prioritisation performance (TRAD – 'traditional', NEW – 'new conservation', ECON – 'international market ecocentrism', SOC – 'local social instrumentalism') and integration approach (Inclusive, and Pluralist conservation as well as two additional integration approaches MEAN and RANK). Efficiency was calculated as the proportion of each feature covered compared to the maximum possible for each land coverage threshold (5%, 10%, 17%, and 30%). Features included are mean priority species distribution proportion coverage (B), carbon storage (C), recreation (R), flood regulation (F), pollination (P), wilderness (W), landscape aesthetic value (L) and agricultural/land value (A*).

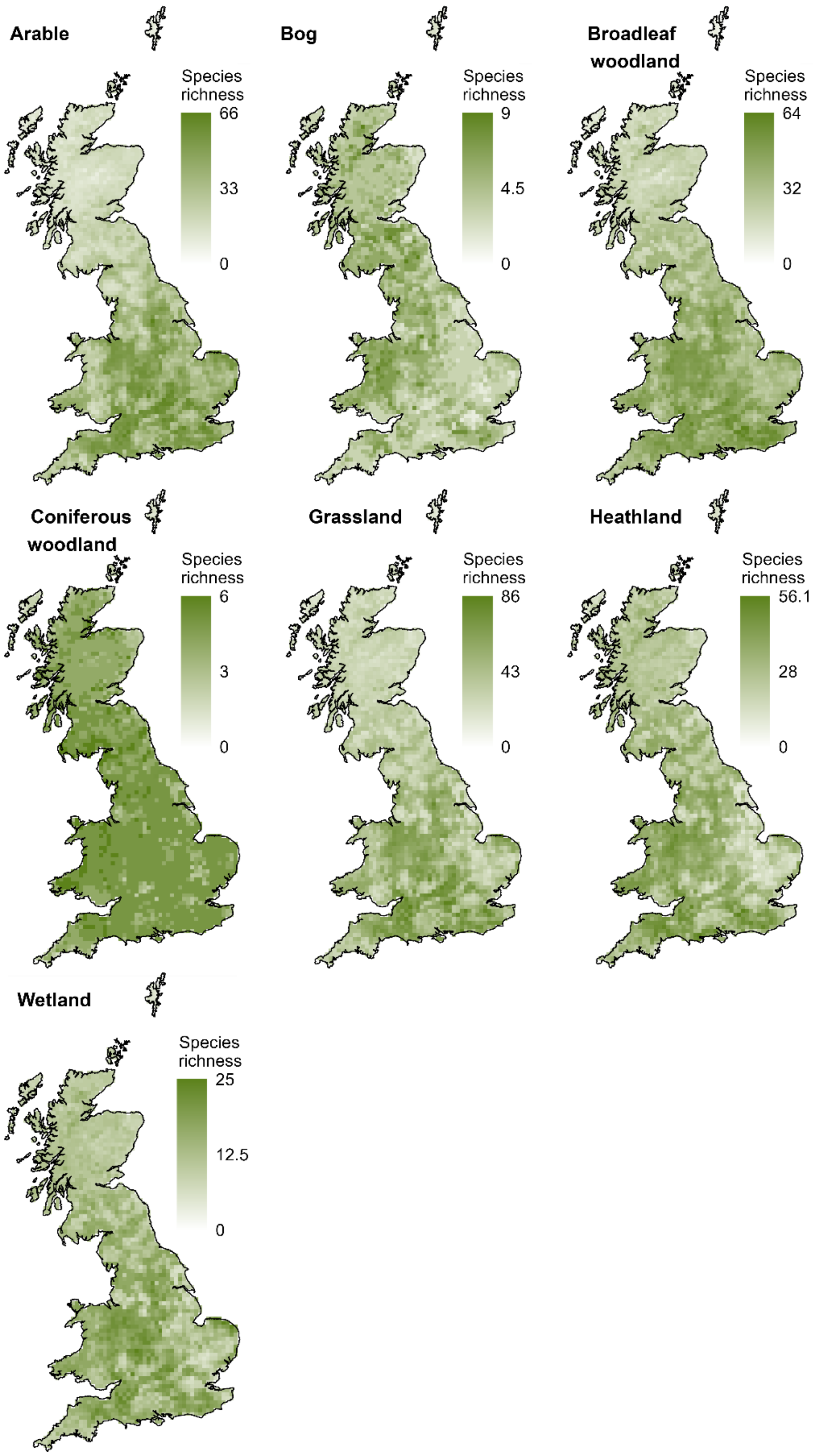
Supplementary Table 3.1 Output from the PCA analysis used to create the pluralist approach rankings. I partitioned variance from viewpoint weightings of feature layers, creating principal components (PC; columns). Cumulative proportion of variance explained by PCs included in brackets. I used each PC to multiply viewpoint prioritisation landscape rankings by corresponding PC eigenvectors, and took the absolute value of the sum (dot product). PCs were added iteratively until maximum viewpoint eigenvalue across PCs (bold) was included (PC3).

	PC1 (0.601)	**PC2 (0.911)**	**PC3 (0.999)**	**PC4 (1.000)**
TRAD	-0.168	0.234	**-0.927**	0.240
NEW	**-0.658**	-0.325	0.205	0.647
ECON	**-0.693**	0.515	0.129	-0.487
SOC	-0.241	**-0.758**	-0.286	-0.535

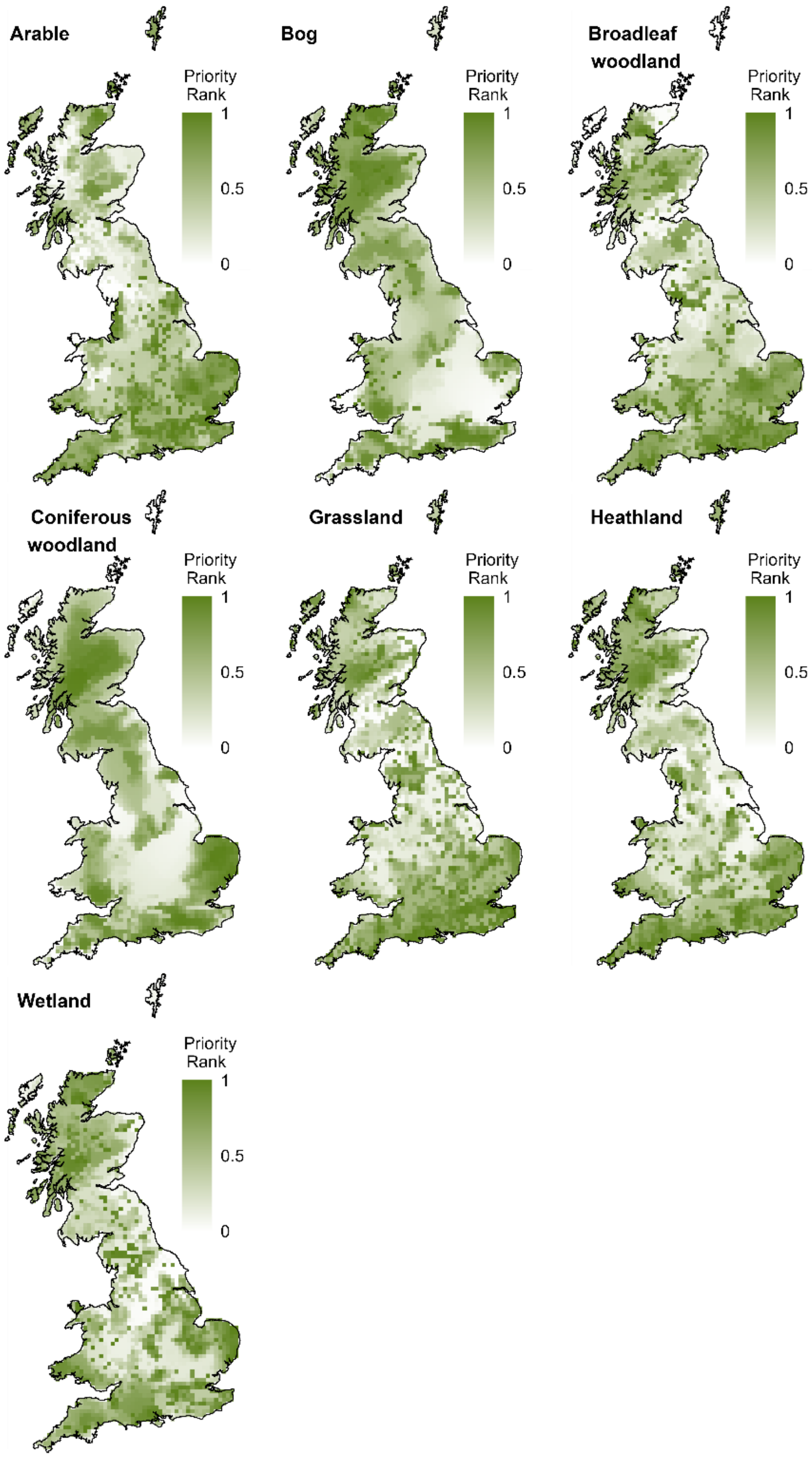
Appendix 4 - Supporting information for Chapter 5



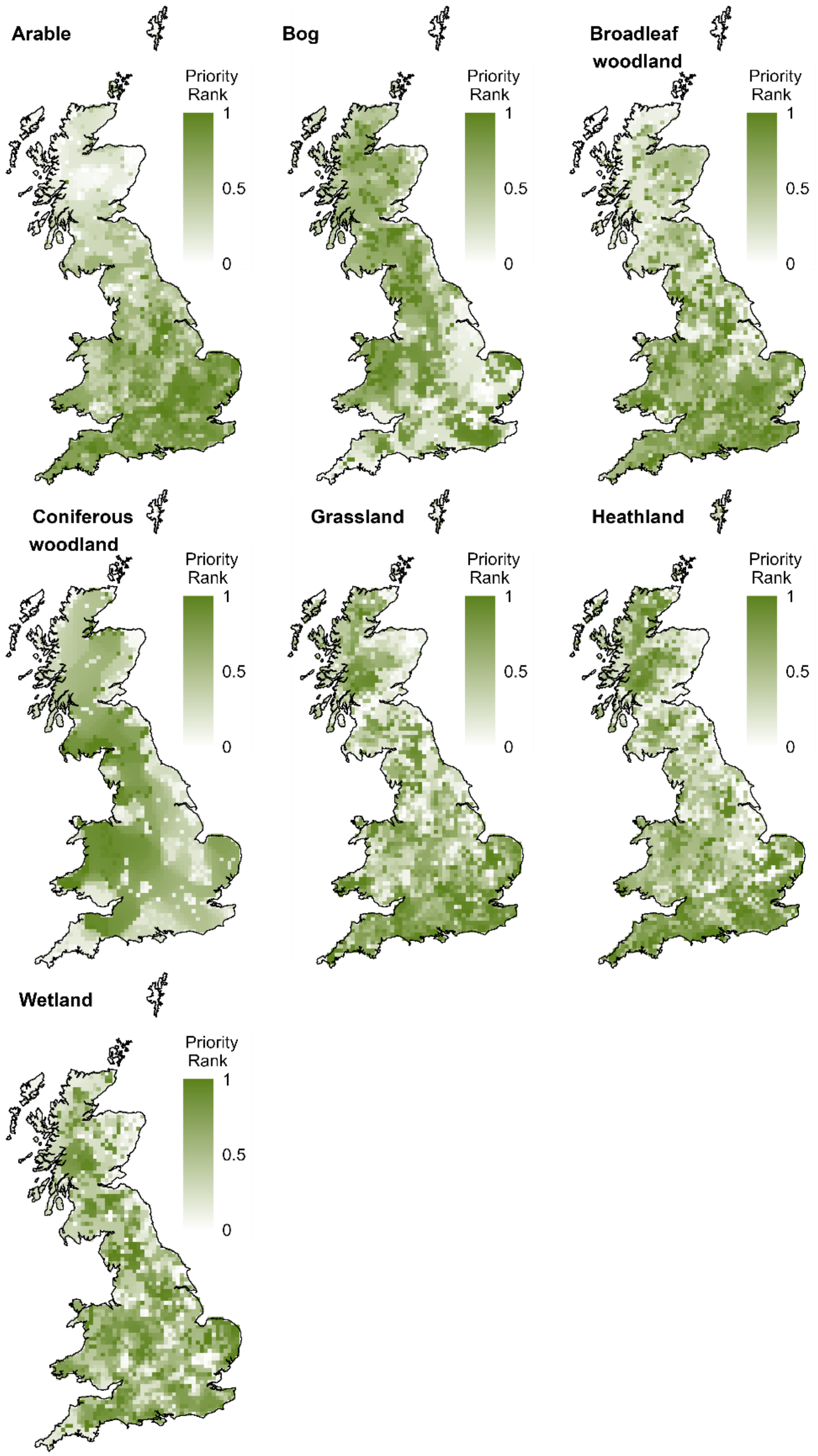
Supplementary Figure 4.1 Richness of current modelled species distributions associated with each of the 7 land cover types.



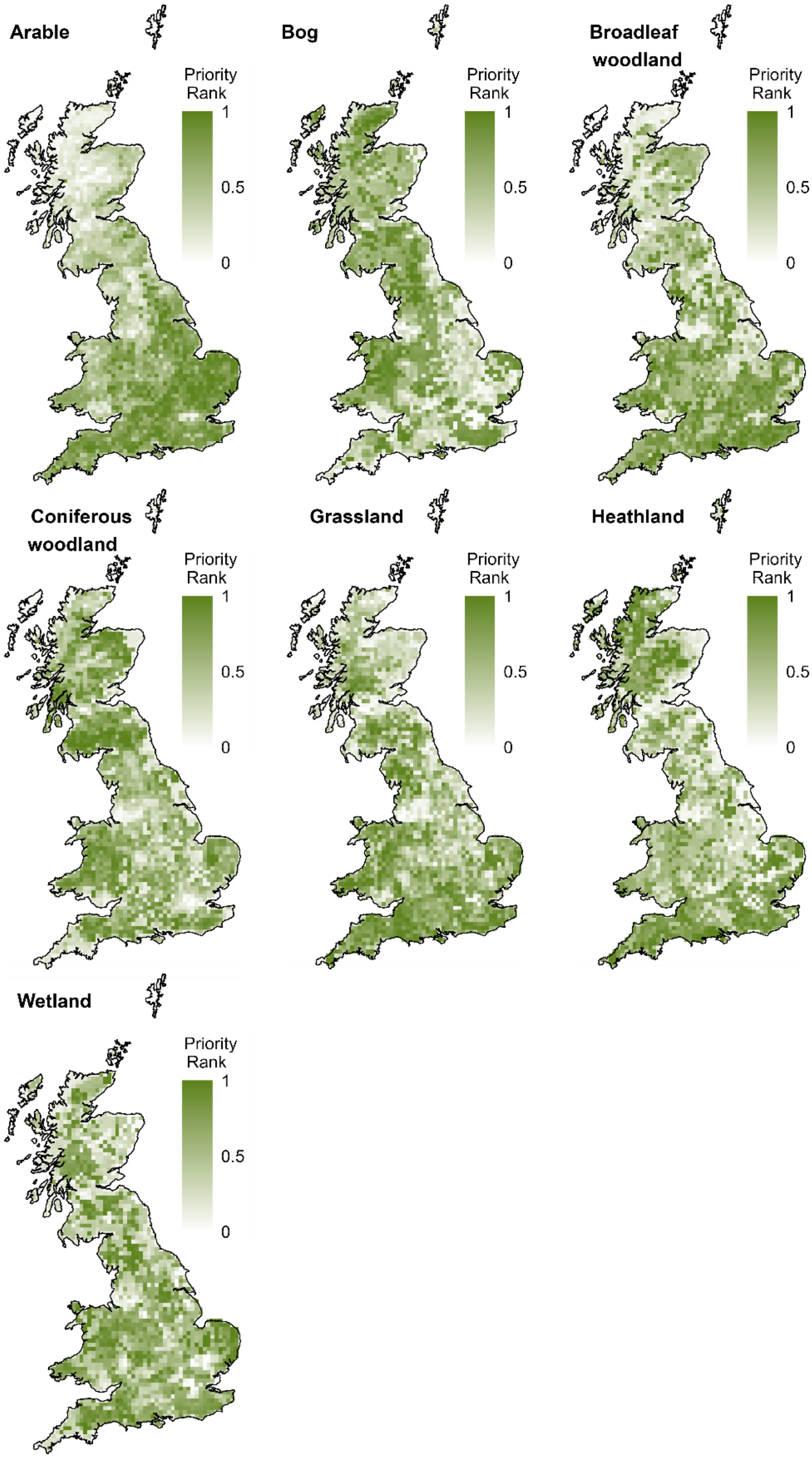
Supplementary Figure 4.2 Richness of potential species distributions, calculated using an environmental convex hull, for species associated with each of the 7 land cover types.



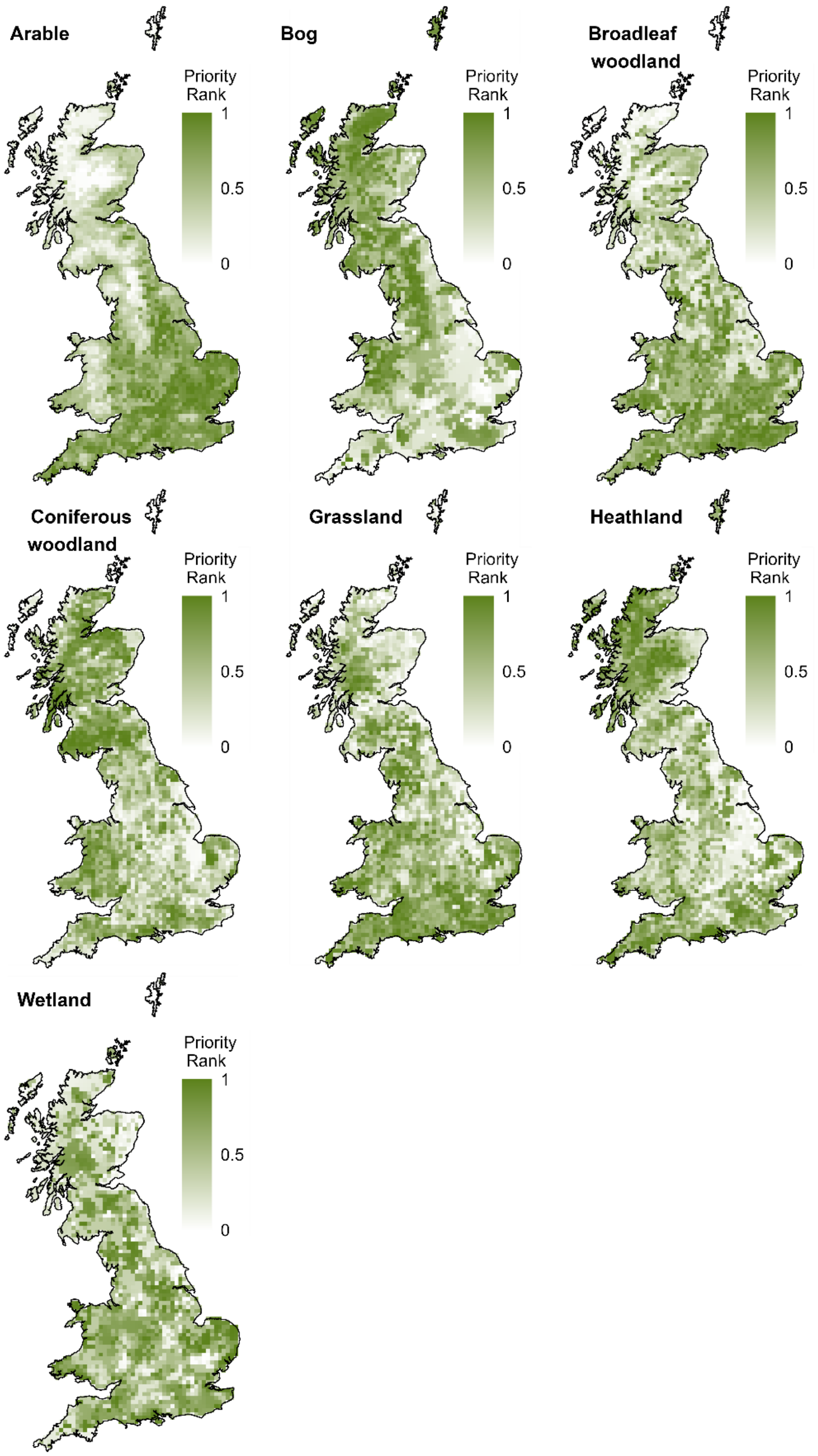
Supplementary Figure 4.3 Existing landscape priorities maximising representation of modelled current species distributions.



Supplementary Figure 4.4 Landscape restoration priorities, maximising representation species of potential species distributions.



Supplementary Figure 4.5 Restoration priority rank using an additional cost layer assuming only using habitat enhancement actions.



Supplementary Figure 4.6 Restoration priority rank using an additional cost layer assuming only using habitat creation actions.

Supplementary Table 4.1 Land cover types used in analysis compared with (i) all BAP priority habitats, (ii) BAP priority habitats from the NERR024 Natural England report, from with species habitat associations were extracted, and (iii) Land Cover Map 2015 classes, which were used to extract habitat coverage for each landscape. The priority habitats are similar to the BAP habitats, but some are grouped, such as grasslands. Freshwater and saltwater priority habitats that do not interface with terrestrial habitats were not included in this table. Inland Rock was not used in the analysis as there were not enough species that listed it as an associated habitat in the NERR024 report to carry out a robust spatial prioritisation.

All BAP Priority Habitats	Priority habitat from Natural England report	LCM2015 target class	Land cover type
Traditional Orchards	Traditional orchards	Broadleaved woodland	**Broadleaf woodland**
Wood-Pasture and Parkland	Wood-pasture & parkland (veteran trees)		
Upland Oakwood	Woodland (deciduous)		
Lowland Beech and Yew Woodland	Lowland beech and yew woodland		
Upland Mixed Ashwoods	Woodland (deciduous)		
Wet Woodland	Wet woodland		
Lowland Mixed Deciduous Woodland	Woodland (deciduous)		
Upland Birchwoods	Woodland (deciduous)		
Native Pine Woodlands	Conifer woodland	Coniferous Woodland	**Coniferous woodland**
Arable Field Margins	Arable field margins	Arable and Horticulture	**Arable**
Hedgerows	Hedgerows		
Coastal and Floodplain Grazing Marsh	Coastal and floodplain grazing marsh	Improved Grassland	**Grassland**
Lowland Meadows	Grasslands	Neutral Grassland	
Upland Hay Meadows	Upland hay meadows	Neutral Grassland	
Lowland Calcareous Grassland	Grasslands	Calcareous Grassland	
Upland Calcareous Grassland	Upland calcareous grassland	Calcareous Grassland	
Lowland Dry Acid Grassland	Grasslands	Acid Grassland	
Upland Flushes, Fens and Swamps	Upland flushes, fens and swamps	Fen, Marsh and Swamp	**Wetland**
Purple Moor Grass and Rush Pastures			
Lowland Fens	Lowland fens		
Reedbeds	Reedbeds		
Lowland Heathland	Lowland heathland	Heather	**Heathland**
Upland Heathland	Upland heathland		
Mountain Heaths and Willow Scrub	Mountain heaths and willow scrub		
Lowland Heathland	Lowland heathland	Heather grassland	
Upland Heathland	Upland heathland		
Mountain Heaths and Willow Scrub	Mountain heaths and willow scrub		
Lowland Raised Bog	Lowland Raised Bog	Bog	**Bog**

Blanket Bog	Blanket bog	
Inland Rock Outcrop and Scree Habitats	Inland rock outcrop and scree habitats	Inland Rock
Calaminarian Grasslands		
Open Mosaic Habitats on Previously Developed Land	Open mosaic habitats on previously developed land	
Limestone Pavements	Limestone pavements	
Maritime Cliff and Slopes	Maritime cliff and slopes	Supra-littoral Rock
Coastal Vegetated Shingle	Coastal vegetated shingle	Supra-littoral Sediment
Machair		
Coastal Sand Dunes	Coastal sand dunes	
Intertidal Chalk	Intertidal chalk	Littoral Rock
Intertidal Underboulder Communities	Intertidal boulder communities	
***Sabellaria alveolata* reefs**	*Sabellaria alveolata* reefs	
Coastal Saltmarsh	Coastal saltmarsh	Littoral sediment
Intertidal Mudflats	Intertidal mudflats	
Seagrass Beds	Seagrass beds	
Sheltered Muddy Gravels	Sheltered muddy gravels	
Peat and Clay Exposures with Piddocks		
Coastal Saltmarsh	Coastal saltmarsh	Saltmarsh
Intertidal Mudflats	Intertidal mudflats	
Seagrass Beds	Seagrass beds	
Sheltered Muddy Gravels	Sheltered muddy gravels	
Peat and Clay Exposures with Piddocks		
		Urban
		Suburban

Supplementary Table 4.2 List of species and associated land cover type included within the analysis.

Habitat	***Species***
Arable	Adonis annua
Arable	Ajuga chamaepitys
Arable	Alauda arvensis
Arable	Aleucis distinctata
Arable	Anthus trivialis
Arable	Arnoseris minima
Arable	Bombus humilis
Arable	Bombus muscorum
Arable	Bombus ruderarius
Arable	Bombus ruderatus
Arable	Bombus sylvarum
Arable	Bupleurum rotundifolium
Arable	Callicera spinolae
Arable	Carabus monilis
Arable	Carduelis cabaret
Arable	Carduelis cannabina
Arable	Centaurea calcitrapa
Arable	Centaurea cyanus
Arable	Chenopodium urbicum
Arable	Chenopodium vulvaria
Arable	Circus cyaneus
Arable	Clinopodium acinos
Arable	Cosmia diffinis
Arable	Cossus cossus
Arable	Cuculus canorus
Arable	Dendrocopos minor
Arable	Dicycla oo
Arable	Didymodon tomaculosus
Arable	Emberiza cirlus
Arable	Emberiza citrinella
Arable	Emberiza schoeniclus
Arable	Fallopia dumetorum
Arable	Filago lutescens
Arable	Filago pyramidata
Arable	Fumaria purpurea
Arable	Galeopsis anguolia
Arable	Galium tricornutum
Arable	Iberis amara
Arable	Lithostege griseata
Arable	Lolium temulentum
Arable	Lythrum hyssopifolia
Arable	Melampyrum cristatum
Arable	Melittis melissophyllum
Arable	Miliaria calandra

Arable	Minuartia hybrida
Arable	Muscari neglectum
Arable	Muscicapa striata
Arable	Ophonus laticollis
Arable	Orgyia recens
Arable	Oria musculosa
Arable	Orthotrichum pallens
Arable	Pareulype berberata
Arable	Parus montanus
Arable	Parus palustris
Arable	Passer domesticus
Arable	Passer montanus
Arable	Perdix perdix
Arable	Polia bombycina
Arable	Prunella modularis
Arable	Pyrrhula pyrrhula
Arable	Ranunculus arvensis
Arable	Satyrium w album
Arable	Scandix pecten veneris
Arable	Scleranthus annuus
Arable	Scleranthus perennis
Arable	Silene gallica
Arable	Sphaerocarpos texanus
Arable	Streptopelia turtur
Arable	Sturnus vulgaris
Arable	Thecla betulae
Arable	Torilis arvensis
Arable	Turdus philomelos
Arable	Valerianella rimosa
Arable	Veronica triphyllos
Arable	Weissia squarrosa
Bog	Caprimulgus europaeus
Bog	Coenonympha tullia
Bog	Cuculus canorus
Bog	Erigone welchi
Bog	Jamesoniella undulifolia
Bog	Notioscopus sarcinatus
Bog	Numenius arquata
Bog	Pallavicinia lyellii
Bog	Saaristoa firma
Bog	Semljicola caliginosus
Bog	Sitticus caricis
Bog	Sphagnum balticum
Bog	Splachnum vasculosum
Bog	Tetrao tetrix
Broadleaf woodland	Anomodon longifolius
Broadleaf woodland	Anthus trivialis

Broadleaf woodland	Argynnis adippe
Broadleaf woodland	Aricia artaxerxes
Broadleaf woodland	Artemisia campestris
Broadleaf woodland	Atrichum angustatum
Broadleaf woodland	Boloria euphrosyne
Broadleaf woodland	Boloria selene
Broadleaf woodland	Callicera spinolae
Broadleaf woodland	Calosoma inquisitor
Broadleaf woodland	Campanula patula
Broadleaf woodland	Caprimulgus europaeus
Broadleaf woodland	Carabus intricatus
Broadleaf woodland	Carduelis cabaret
Broadleaf woodland	Carduelis cannabina
Broadleaf woodland	Catocala promissa
Broadleaf woodland	Catocala sponsa
Broadleaf woodland	Centromerus serratus
Broadleaf woodland	Cephalanthera damasonium
Broadleaf woodland	Cephalanthera longifolia
Broadleaf woodland	Cephalanthera rubra
Broadleaf woodland	Coccothraustes coccothraustes
Broadleaf woodland	Cosmia diffinis
Broadleaf woodland	Cossus cossus
Broadleaf woodland	Cuculus canorus
Broadleaf woodland	Cyclophora porata
Broadleaf woodland	Cynoglossum germanicum
Broadleaf woodland	Cypripedium calceolus
Broadleaf woodland	Dendrocopos minor
Broadleaf woodland	Dicycla oo
Broadleaf woodland	Doros profuges
Broadleaf woodland	Emberiza citrinella
Broadleaf woodland	Emberiza schoeniclus
Broadleaf woodland	Epione vespertaria
Broadleaf woodland	Erynnis tages
Broadleaf woodland	Eustroma reticulatum
Broadleaf woodland	Fallopia dumetorum
Broadleaf woodland	Formicoxenus nitidulus
Broadleaf woodland	Habrodon perpusillus
Broadleaf woodland	Hamearis lucina
Broadleaf woodland	Hipparchia semele
Broadleaf woodland	Homomallium incurvatum
Broadleaf woodland	Jodia croceago
Broadleaf woodland	Lejeunea mandonii
Broadleaf woodland	Leptidea sinapis
Broadleaf woodland	Limenitis camilla
Broadleaf woodland	Locustella naevia
Broadleaf woodland	Melampyrum cristatum
Broadleaf woodland	Melitaea athalia

Broadleaf woodland	Melittis melissophyllum
Broadleaf woodland	Minoa murinata
Broadleaf woodland	Monocephalus castaneipes
Broadleaf woodland	Motacilla flava
Broadleaf woodland	Muscicapa striata
Broadleaf woodland	Noctua orbona
Broadleaf woodland	Notioscopus sarcinatus
Broadleaf woodland	Ophrys inseera
Broadleaf woodland	Orgyia recens
Broadleaf woodland	Orthotrichum obtusifolium
Broadleaf woodland	Orthotrichum pallens
Broadleaf woodland	Orthotrichum pumilum
Broadleaf woodland	Pallavicinia lyellii
Broadleaf woodland	Paracolax tristalis
Broadleaf woodland	Pareulype berberata
Broadleaf woodland	Parus montanus
Broadleaf woodland	Parus palustris
Broadleaf woodland	Passer domesticus
Broadleaf woodland	Passer montanus
Broadleaf woodland	Pechipogo strigilata
Broadleaf woodland	Perdix perdix
Broadleaf woodland	Philodromus margaritatus
Broadleaf woodland	Philorhizus quadrisignatus
Broadleaf woodland	Phylloscopus sibilatrix
Broadleaf woodland	Phyteuma spicatum
Broadleaf woodland	Platanthera bifolia
Broadleaf woodland	Prunella modularis
Broadleaf woodland	Pyrgus malvae
Broadleaf woodland	Pyrrhula pyrrhula
Broadleaf woodland	Rheumaptera hastata
Broadleaf woodland	Rhytidiadelphus subpinnatus
Broadleaf woodland	Saaristoa firma
Broadleaf woodland	Satyrium w album
Broadleaf woodland	Streptopelia turtur
Broadleaf woodland	Sturnus vulgaris
Broadleaf woodland	Tetrao tetrix
Broadleaf woodland	Thecla betulae
Broadleaf woodland	Trichopteryx polycommata
Broadleaf woodland	Trisateles emortualis
Broadleaf woodland	Turdus philomelos
Broadleaf woodland	Zygodon forsteri
Coniferous woodland	Anthus trivialis
Coniferous woodland	Caprimulgus europaeus
Coniferous woodland	Carduelis cabaret
Coniferous woodland	Emberiza schoeniclus
Coniferous woodland	Noctua orbona
Coniferous woodland	Tetrao tetrix

Grassland	Acosmetia caliginosa
Grassland	Acrocephalus palustris
Grassland	Adonis annua
Grassland	Aeshna isosceles
Grassland	Ajuga chamaepitys
Grassland	Ajuga pyramidalis
Grassland	Alauda arvensis
Grassland	Andrena tarsata
Grassland	Aricia artaxerxes
Grassland	Armeria maritima
Grassland	Artemisia campestris
Grassland	Aspitates gilvaria
Grassland	Astragalus danicus
Grassland	Athetis pallustris
Grassland	Blysmus compressus
Grassland	Boloria euphrosyne
Grassland	Boloria selene
Grassland	Bombus humilis
Grassland	Bombus muscorum
Grassland	Bombus ruderarius
Grassland	Bombus ruderatus
Grassland	Bombus sylvarum
Grassland	Bupleurum tenuissimum
Grassland	Campanula rapunculus
Grassland	Carduelis cannabina
Grassland	Carduelis flavirostris
Grassland	Carex divisa
Grassland	Centaurea calcitrapa
Grassland	Cephaloziella calyculata
Grassland	Ceratodon conicus
Grassland	Cerceris quinquefasciata
Grassland	Chamaemelum nobile
Grassland	Circus cyaneus
Grassland	Clinopodium acinos
Grassland	Coenagrion mercuriale
Grassland	Coenonympha pamphilus
Grassland	Crepis mollis
Grassland	Crex crex
Grassland	Cuculus canorus
Grassland	Cupido minimus
Grassland	Cyclophora pendularia
Grassland	Cyperus fuscus
Grassland	Cypripedium calceolus
Grassland	Damasonium alisma
Grassland	Dianthus armeria
Grassland	Dictyna pusilla
Grassland	Doros profuges

Grassland	Emberiza cirlus
Grassland	Emberiza citrinella
Grassland	Emberiza schoeniclus
Grassland	Erebia epiphron
Grassland	Eryngium campestre
Grassland	Erynnis tages
Grassland	Eucera longicornis
Grassland	Euphydryas aurinia
Grassland	Filago pyramidata
Grassland	Fossombronia foveolata
Grassland	Gentianella anglica
Grassland	Gentianella campestris
Grassland	Hadena albimacula
Grassland	Hamearis lucina
Grassland	Harpalus froelichii
Grassland	Helianthemum oelandicum
Grassland	Heliophobus reticulata
Grassland	Hemaris tityus
Grassland	Herminium monorchis
Grassland	Hipparchia semele
Grassland	Hordeum marinum
Grassland	Iberis amara
Grassland	Idaea dilutaria
Grassland	Juniperus communis
Grassland	Lasiommata megera
Grassland	Leersia oryzoides
Grassland	Leptidea sinapis
Grassland	Leptodontium gemmascens
Grassland	Lobelia urens
Grassland	Locustella naevia
Grassland	Lophozia capitata
Grassland	Meioneta mollis
Grassland	Melitaea athalia
Grassland	Melitaea cinxia
Grassland	Mentha pulegium
Grassland	Motacilla flava
Grassland	Muscari neglectum
Grassland	Noctua orbona
Grassland	Numenius arquata
Grassland	Odynerus melanocephalus
Grassland	Oenanthe fistulosa
Grassland	Ophonus laticollis
Grassland	Ophonus melletii
Grassland	Ophrys inseera
Grassland	Orchis anthropophora
Grassland	Osmia parietina
Grassland	Ozyptila nigrita

Grassland	Passer montanus
Grassland	Perdix perdix
Grassland	Phyteuma spicatum
Grassland	Platanthera bifolia
Grassland	Plebejus argus
Grassland	Poa glauca
Grassland	Polia bombycina
Grassland	Potamogeton acolius
Grassland	Potamogeton compressus
Grassland	Pseudorchis albida
Grassland	Pulicaria vulgaris
Grassland	Pulsatilla vulgaris
Grassland	Pyrgus malvae
Grassland	Rheumaptera hastata
Grassland	Salix lapponum
Grassland	Scleranthus annuus
Grassland	Scotopteryx bipunctaria
Grassland	Shargacucullia lychnitis
Grassland	Silene otites
Grassland	Sturnus vulgaris
Grassland	Tephroseris integrifolia
Grassland	Tetrao tetrix
Grassland	Thymelicus acteon
Grassland	Trichopteryx polycommata
Grassland	Turdus philomelos
Grassland	Turdus torquatus
Grassland	Vanellus vanellus
Grassland	Veronica triphyllos
Grassland	Weissia condensa
Grassland	Weissia multicapsularis
Grassland	Weissia sterilis
Heathland	Acosmetia caliginosa
Heathland	Agroeca cuprea
Heathland	Ajuga pyramidalis
Heathland	Alauda arvensis
Heathland	Aleucis distinctata
Heathland	Amara famelica
Heathland	Andrena tarsata
Heathland	Anisodactylus nemorivagus
Heathland	Anthus trivialis
Heathland	Argynnis adippe
Heathland	Boloria euphrosyne
Heathland	Boloria selene
Heathland	Bombus muscorum
Heathland	Bombus ruderarius
Heathland	Caprimulgus europaeus
Heathland	Carabus monilis

Heathland	Carduelis cannabina
Heathland	Carduelis flavirostris
Heathland	Cephaloziella baumgartneri
Heathland	Cephaloziella calyculata
Heathland	Cephaloziella integerrima
Heathland	Cerceris quinquefasciata
Heathland	Chamaemelum nobile
Heathland	Chrysotoxum octomaculatum
Heathland	Cicendia filiformis
Heathland	Cicindela sylvatica
Heathland	Circus cyaneus
Heathland	Coenagrion mercuriale
Heathland	Coenonympha pamphilus
Heathland	Coscinia cribraria
Heathland	Cossus cossus
Heathland	Cuculus canorus
Heathland	Cyclophora pendularia
Heathland	Cyclophora porata
Heathland	Dicranum spurium
Heathland	Dipoena inornata
Heathland	Emberiza citrinella
Heathland	Entephria caesiata
Heathland	Epione vespertaria
Heathland	Erebia epiphron
Heathland	Eristalis cryptarum
Heathland	Erynnis tages
Heathland	Eucera longicornis
Heathland	Euphydryas aurinia
Heathland	Filago lutescens
Heathland	Formicoxenus nitidulus
Heathland	Fossombronia foveolata
Heathland	Gentianella campestris
Heathland	Haplodrassus dalmatensis
Heathland	Harpalus froelichii
Heathland	Heliothis maritima
Heathland	Hemaris tityus
Heathland	Hipparchia semele
Heathland	Illecebrum verticillatum
Heathland	Juniperus communis
Heathland	Lagopus lagopus
Heathland	Leptodontium gemmascens
Heathland	Lobelia urens
Heathland	Locustella naevia
Heathland	Lophozia capitata
Heathland	Lycopodiella inundata
Heathland	Mecopisthes peusi
Heathland	Melitaea athalia

Heathland	Mentha pulegium
Heathland	Monocephalus castaneipes
Heathland	Noctua orbona
Heathland	Numenius arquata
Heathland	Odynerus melanocephalus
Heathland	Ophonus laticollis
Heathland	Orgyia recens
Heathland	Platanthera bifolia
Heathland	Plebejus argus
Heathland	Poecilus kugelanni
Heathland	Pseudorchis albida
Heathland	Rheumaptera hastata
Heathland	Saaristoa firma
Heathland	Salix lapponum
Heathland	Scleranthus annuus
Heathland	Scleranthus perennis
Heathland	Silene otites
Heathland	Sitticus caricis
Heathland	Tapinocyba mitis
Heathland	Temnothorax interruptus
Heathland	Tetrao tetrix
Heathland	Turdus torquatus
Heathland	Veronica triphyllos
Heathland	Viola lactea
Heathland	Xestia agathina
Heathland	Xestia alpicola
Heathland	Xestia castanea
Wetland	Aeshna isosceles
Wetland	Agonum scitulum
Wetland	Archanara neurica
Wetland	Athetis pallustris
Wetland	Bembidion quadripustulatum
Wetland	Blysmus compressus
Wetland	Boloria selene
Wetland	Botaurus stellaris
Wetland	Calamagrostis stricta
Wetland	Circus cyaneus
Wetland	Coenagrion mercuriale
Wetland	Coenonympha tullia
Wetland	Cossus cossus
Wetland	Cuculus canorus
Wetland	Dactylorhiza incarnata
Wetland	Dryopteris cristata
Wetland	Emberiza schoeniclus
Wetland	Erebia epiphron
Wetland	Erigone welchi
Wetland	Eristalis cryptarum

Wetland	Euphydryas aurinia
Wetland	Hemaris tityus
Wetland	Jamesoniella undulifolia
Wetland	Liparis loeselii
Wetland	Locustella naevia
Wetland	Notioscopus sarcinatus
Wetland	Numenius arquata
Wetland	Oenanthe fistulosa
Wetland	Orgyia recens
Wetland	Pallavicinia lyellii
Wetland	Platanthera bifolia
Wetland	Saaristoa firma
Wetland	Saxifraga hirculus
Wetland	Semljicola caliginosus
Wetland	Senecio paludosus
Wetland	Sitticus caricis
Wetland	Sium lolium
Wetland	Splachnum vasculosum
Wetland	Stellaria palustris
Wetland	Sturnus vulgaris
Wetland	Teucrium scordium
Wetland	Viola persicifolia

Supplementary Table 4.3 Approximate conversion effort from one land cover type (column) to another land cover of interest (row) used in the calculation of the habitat creation cost layer (Eq. 5). Effort is approximated based upon similarity between typical climatic and environmental conditions of each land cover type, and the envisaged amount of time and physical change needed for conversion. Note that conversion effort need not be symmetrical. For example, converting woodland to arable land receives a lower effort value than converting arable to woodland as, although it requires greater initial physical change to the habitat, the timeframe is far shorter.

	Arable	*Bog*	*Broadleaf woodland*	*Coniferous woodland*	*Grassland*	*Heathland*	*Wetland*
Arable	**1**	**4**	**2**	**2**	**2**	**3**	**4**
Bog	**5**	**1**	**6**	**6**	**5**	**6**	**3**
Broadleaf woodland	**4**	**6**	**1**	**2**	**4**	**4**	**6**
Coniferous woodland	**4**	**6**	**2**	**1**	**4**	**4**	**6**
Grassland	**2**	**6**	**3**	**3**	**1**	**3**	**5**
Heathland	**4**	**6**	**4**	**4**	**4**	**1**	**5**
Wetland	**5**	**3**	**6**	**6**	**5**	**6**	**1**

Abbreviations

Abbreviation	Meaning
ABF	additive benefit function
ALOS DSM	advanced land observing satellite digital surface model
AONB	area of outstanding natural beauty
AUC	area under curve
BC	Butterfly Conservation
BQP	boundary-quality penalty
BRC	Biological Records Centre
BTO	British Trust for Ornithology
CAZ	core area zonation
CBD	Convention on Biological Diversity
CEH	Centre for Ecology & Hydrology
DEFRA	Department for Environment, Food & Rural Affairs
ES	ecosystem services
EU	European Union
GB	Great Britain
IUCN	International Union for Conservation of Nature
LNRS	local nature recovery strategy
LSCI	large-scale conservation initiative
MCDA	multi-criteria decision analysis
NbS	nature-based solutions
NE	Natural England
NNR	national nature reserve
NRA	nature recovery area
NRN	nature recovery network
NRW	Natural Resources Wales
NP	national park
NSA	national scenic area
OECM	other area-based conservation measure
PA	protected area
PC	principal component
PCA	principal component analysis
ROC	receiver operating characteristic
SAC	special area of conservation
SCP	systematic conservation planning
SNH	Scottish Natural Heritage (now NatureScot)
SPA	special protection area
SSSI	site of special scientific interest
UK	United Kingdom
UNEP-WCMC	UN environment programme world conservation monitoring centre

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