



# Planning Ecological Networks to Enable Long-distance Connectivity

Thesis submitted in accordance with the requirements of the  
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For Robert Taylor,

who saw a failing A-level student and refused to give up on him

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# Abstract

Climate change is shifting the region of climatic suitability for many species, but the compounding impacts of anthropogenic land use make it increasingly difficult for species to track the change. Local management can build resilience to climate change, but incorporating regional and national connectivity into conservation planning will be vital if we are to safeguard species' ability to respond to changes in climate. We have recently seen a global shift towards promoting functionally connected networks, which will require reconsidering where to prioritise the restoration and protection of habitats. Past research has shown the importance of protected areas (PAs) to range expanding species and highlighted the disconnected nature of most PA networks. However, few have studied the protection of patches critical to long-distance connectivity. Similarly, little attention has been given to past large-scale conservation projects to ascertain if our current landscape planning methodology is capable of delivering the connected networks necessary to facilitate range shifts. In this thesis, I explore these two important avenues of research. Using England as an exemplar I quantify how South-North connectivity is currently protected in PAs across fragmented habitat networks. I show that past protection decisions have led to an under-representation of important connective patches in the PA estate and present evidence of how connectivity tools can be used to easily identify such patches for future protection. Next, I evaluate how recent large-scale conservation projects with a focus on connectivity have impacted the permeability of the landscapes they sit within. The results show that the projects studied increased connectivity at a level comparable to random, highlighting that, without the inclusion of a long-distance connectivity metric at the planning stage, projects are unlikely to increase connectivity at scales relevant for climate change adaptation. I go on to present an extension to the Condatis methodology capable of identifying specific places where habitat creation or restoration would be best situated to improve long distance connectivity. This new method is applicable over a broad range of habitat structures and economical in its data requirements. Finally, I explore the use of connectivity metrics in conservation. I find that while connectivity metrics are used, a substantial proportion of projects still rely on either simplistic analogues of connectivity, expert opinion, or do not measure connectivity at all, and that conservation reporting is insufficient in quantity and quality. I finish by discussing the scepticism of connectivity tools that pervades conservation and put forward three routes to ease it: Evaluation and validation, reduction in the proliferation of tools and the development of a decision tree. Ultimately, this thesis highlights how long-distance connectivity has been overlooked in conservation and puts forward ways we can correct this, allowing species to better adapt to their changing environment.

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# Chapter 1 General Introduction

*“Don't Panic. It's the first helpful or  
intelligible thing anybody's said to me all  
day.”*

- *Arthur Dent*

## *1.1 Preface*

This chapter is intended to provide an overview of the importance of connectivity and its current place in conservation, serving as an introduction to the topics that chapters 2, 3, 4 and 5 will discuss. Beginning with a brief description of the backdrop to modern conservation, namely human induced pressures and their effects on the natural world (1.2 Background), I go on to explain why habitat loss and fragmentation, and the subsequent reduction in connectivity of habitats is a cause for concern (1.3 Why does the spatial arrangement of habitat matter?), as well as defining connectivity (1.4 What do we mean by connectivity?). I then describe connectivity's place in conservation, beginning with the importance put upon ecological networks and how conservation related to them is planned, before summarising how connectivity measurement has evolved since its first inclusion in conservation (1.5 How is connectivity included in conservation?). Next, I go on to explain areas I believe warrant further study (1.6 What progress is still to be made?). Finally, I explain my rationale for the focus on England in this work (1.7 A word on anglocentricity), describe the connectivity model at the core of my work (1.8 Connectivity with Condatis), and lay out the themes of the chapters that follow (1.9 Research objectives).

## *1.2 Background*

The human population is increasing rapidly, doubling in the last 50 years (United Nations, 2019). As the populace increases, so too have the demands humankind puts upon natural resources and spaces (Steffen et al., 2015). The by-products of industrial resource exploitation on the scale required to support population growth of this magnitude are having an ongoing and extensive detrimental impact on the natural environment. These impacts manifest in the twin spectres of climate change and biodiversity loss, which herald the Anthropocene (Crutzen, 2002). The multifaceted benefits that biodiversity provides are well documented, and include pollination and pest control (Hooper et al., 2005), carbon storage and sequestration (Yang et al., 2019), cultural significance, and physical and mental well-being (Barton and Pretty, 2010). However, in humankind's efforts to sustain itself it has

built, farmed, fished, mined, and destroyed to such an extent that 70% of land and 59% of the oceans have been directly altered or impacted (Watson et al., 2016; IPCC, 2019). The destruction and fragmentation of habitat directly caused by these activities is recognised as the major driver of biodiversity declines (Haddad et al., 2015; Chase et al., 2020), now at levels comparable with the previous five mass extinction events (Barnosky et al., 2011). Simultaneously, nature also need now adapt to the profound changes at every level of global atmospheric and natural systems brought about by anthropogenic climate change (Scheffers et al., 2016).

### *1.3 Why does the spatial arrangement of habitat matter?*

While there is a general consensus of the detrimental effect of habitat loss on biodiversity (Chase et al., 2020), there still exists an active, and lively, debate regarding the extent to which fragmentation plays a role (Fahrig, 2003; Haddad et al., 2015; Fahrig, 2017; Fletcher et al., 2018; Fahrig et al., 2019). However, whatever their true individual effect sizes, both are fundamental to the amount of habitat, size of patches, and, as a function of patch size due to edge effects (Murcia, 1995), the quality of habitat available to a population. Consequently, habitat loss and fragmentation are essential traits of the landscape, controlling the maintenance of populations, whether viewed through the lens of island biogeography or metapopulation dynamics, and is of importance because population extinction is usually a precursor to species extinction (Ceballos et al., 2017).

Yet, a third important characteristic of the environment exists, intertwined with habitat loss and fragmentation, and also instrumental to species persistence and ecosystem function: connectivity. Habitat loss and fragmentation often reduce the size of patches and increase the distance between them, both tend to decrease connectivity because larger network gaps are costlier to traverse and small habitat patches are more difficult to locate (Kareiva, 1985). Through connection to a mainland source from which emigrants arrive as posed in island biogeography (MacArthur and Wilson, 1967), or through supplementation of local extinctions via recolonization, as in metapopulation dynamics (Levins, 1970; Fahrig and

Merriam, 1994; Hanski, 1998; Hanski and Ovaskainen, 2000), the isolation of a patch relative to the rest of the network is pivotal to the survival of the population as a whole, as well as that within any one focal patch. Isolated and disconnected areas have been noted to experience more severe population crashes following perturbation (Oliver et al., 2013; Oliver et al., 2015), the frequency of which may increase under climate change due to a higher likelihood of extreme weather events (Arnell et al., 2019). Connectivity can help to counteract the negative effects of disturbance on local populations (Altermatt et al., 2011), and in instances where population crashes occur, provide a ‘rescue effect’ via a steady inflow of immigrants (Brown and Kodric-Brown, 1977; Hanski, 1998; Doerr et al., 2011). Emigration and immigration are particularly relevant in small populations that are either unable to maintain themselves through self-recruitment, or where the absence of movement can lead to fixation or loss of random alleles through ‘genetic drift’ (Lande, 1995) and the accumulation of deleterious mutations (Lynch et al., 1995). These processes are both slow, but the fitness reduction of inbreeding depression that occurs in small populations is not, and can also be offset through the steady movement of individuals (Keller and Waller, 2002).

Beyond individual populations, connectivity is an important component in the maintenance of ecosystem function. Through ‘spatial insurance’ (Loreau et al., 2003) connected networks strengthen the synergy between biodiversity and ecosystem services (Ziter et al., 2013), and, following disturbance, help return ecosystem function to original levels (Symons and Arnott, 2013). For instance, through facilitating the movement of large-bodied animals throughout their large home ranges, habitat connectivity also connects ecosystems and the transference of energy between them (McCauley et al., 2012).

Additionally, connectivity plays an important role in life history stages of organisms, such as those that undergo regular migrations, including mammals, birds, amphibians, insects, reptiles, fish, and marine invertebrates (reviewed in Alerstam et al., 2003). Migratory routes often include geographic bottlenecks (Myers et al., 1987; Berger, 2004; Morrison and Bolger, 2014), such as stop-over sites for migratory birds (Newton, 2008; Downs and

Horner, 2008); these areas can act as linchpins for connectivity, the loss of which can be devastating to migratory communities (Holdo et al., 2011; Iwamura et al., 2013). Even in the absence of geographic bottlenecks, features such as railways can completely block migration routes (Ito et al., 2005). Interrupting migrations also limits the subsequent benefits migrating individuals provide to the ecosystems they temporarily inhabit, through processes such as population control of the species they consume along the way and nutrient redistribution (Knapp et al., 1999; Wilcove and Wikelski, 2008). Freshwater systems are particularly vulnerable. Indeed, 77% of rivers longer than 100 km no longer flow freely from source to sea (Grill et al., 2019). Dams have been shown to delay and reduce migration success (Acou et al., 2008; Marschall et al., 2011), which, while certainly severely detrimental to those species, also impacts the rest of the river ecosystem, and that of the surrounding area, through reduction in a major food and nutrient source (Gresh et al., 2000).

Now, with the advent of anthropogenic climate change, connectivity has another important role in helping species persistence. The global climate is warming at a rate of approximately 0.2°C per decade (Hansen et al., 2006; Hansen et al., 2010), in response species must adjust either through rapid evolutionary adaptation to alter behaviour or phenotype, or move to follow their climatic niche – a process called ‘range shifts’. Habitat that covers a larger area, either as a contiguous patch or a series of connected ones, is more likely to provide a broader range of resources and micro climates (Hodgson et al., 2011), and support the stable populations needed to fuel large scale movements such as range shifts. Evidence for past shifts in species ranges to follow suitable climates as a result of warming can be found in the fossil record from the post-glacial period (Huntley and Webb, 1989; Huntley, 1991). The first evidence of range shifts in response to contemporary atmospheric warming began to emerge in the 1980s and 90s (Kullman, 1986; Barry et al., 1995; Roemmich and McGowan, 1995). Parmesan (1996) was the first to provide evidence of a wholesale shift in species ranges, but it took a further 15 years before a direct link between warming and range shifts was demonstrated conclusively (Chen et al., 2011). Since then, moving to different

altitudes or latitudes has been evidenced in over 30,000 species encompassing bacteria, plants, fungi and animals both on land and at sea (Lenoir et al., 2020).

Thus, for all these reasons connectivity can be thought of as a core principle in population dynamics and therefore conservation (Taylor et al., 1993), affecting ecosystem function, emigration and recolonization, as well as a population's ability to access and utilise the necessary resources to survive across a range of spatial scales from local to supranational (Rayfield et al., 2016).

## *1.4 What do we mean by connectivity?*

Before going further, it would be prudent to define two words that will see extensive use in this text: 'landscape' and 'connectivity'.

### **1.4.1 Landscape**

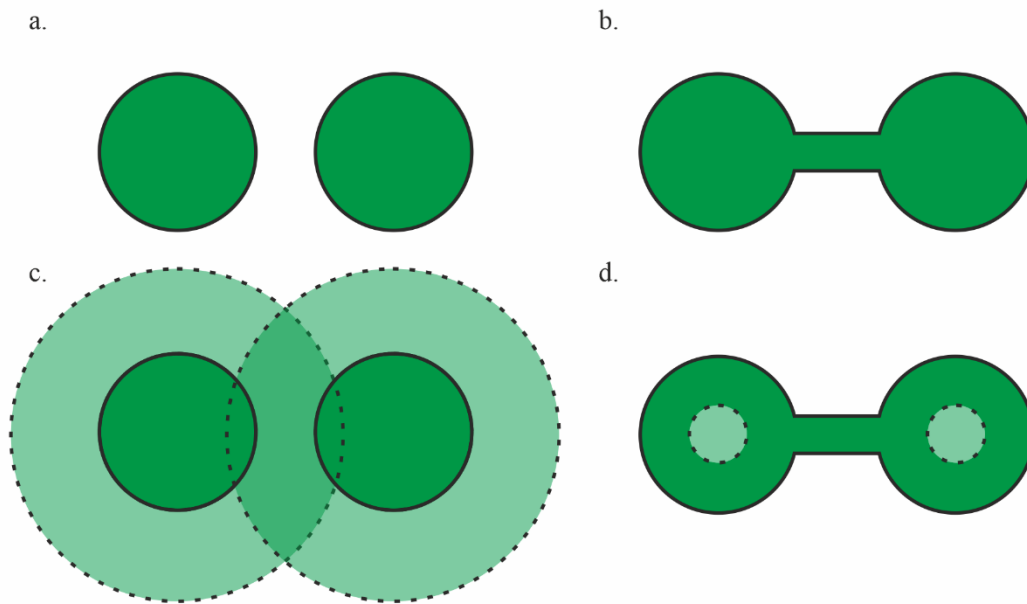
At its most fundamental, habitat can be thought of as simply a place where an animal lives (Morrison et al., 2006). In the past, this gave rise to the analogy of the landscape consisting of islands of habitat surrounded by a hostile matrix used in both the classical paradigms of island biogeography (MacArthur and Wilson, 1967) and meta-population dynamics (Hanski, 1998). Yet, over time this binary representation has given way to an understanding that the matrix between those islands consists of a mosaic of land cover types (Ricketts, 2001) that present on a spectrum from those that facilitate movement (complementary land cover types an individual might move through between areas of habitat), to those that do not (impassable land cover types). These are now commonly referred to as "matrix habitat" and "non-habitat matrix" respectively. Thus, the landscape can be subdivided into habitat, matrix habitat and non-habitat.

In connectivity modelling, what we define as habitat and how we utilise these different landscape categories within those models fundamentally alters the inferences we can make. In this body of work, I am concerned with connectivity to facilitate range shifts. Due to the timescales and distances over which these occur (Huntley et al., 2008; Chen et al.,

2011) species will need to persist and found new populations to continue following their climatic niche (Hannah et al., 2007; Hodgson et al., 2009). Therefore, the spatial arrangement of breeding habitat is most important. As such, in this thesis “habitat” will refer to breeding habitat specifically, and “matrix” will refer to both matrix habitat and non-habitat matrix.

## **1.4.2 Connectivity**

Defining connectivity is a less straight forward process. Taylor et al., (1993) described ‘landscape connectivity’ as “*The degree to which the landscape facilitates or impedes movement among resource patches*”. Although often adopted, many more diffuse definitions and measurements have been proposed in the intervening years (Kindlmann and Burel, 2008). In general, however, descriptions of connectivity fall into one of two camps: structural connectivity and functional connectivity (Fig. 1.1). Structural connectivity is solely concerned with landscape structure (Tischendorf and Fahrig, 2000; Taylor et al., 2006). Functional connectivity describes the connectedness of a landscape as a function of the landscape *and* the organism, taking into account the physical layout of habitat patches as well as the behavioural and morphological traits of the organism being studied (Taylor et al., 1993). Landscape connectivity can be thought of as a summation of elements of functional and structural connectivity. In essence, whether measured structurally or functionally the concept of connectivity from an ecological perspective revolves around the exchange of individuals between two areas. Measures of connectivity attempt to discern the probability of that exchange. As will be set out in Section 1.5, the first of those measures were largely structural in nature (Goodwin, 2003), but over time functional connectivity has become the norm due to the prevailing understanding that landscape connectivity is not fixed, and changes depending on the mover in question (Kindlmann and Burel, 2008). Functional measures usually combine data about the landscape and species’ ecology, but can also be gleaned indirectly through measures such as population synchrony (Powney et al., 2011) or genetic dissimilarity (McRae and Beier, 2007).



**Figure 1.1: Functional vs structural connectivity.** Through the lens of structural connectivity habitat patches are either spatially separated (a) or joined (b). Alternatively, functional connectivity considers the life history of the organism being modelled, and therefore two structurally disconnected habitat patches (a) may, to a well dispersing species, be functionally connected (c). Similarly, to a species that eschews habitat edges, two structurally connected areas of habitat (b), may be functionally disconnected (d). Here dark green represents the spatial extent of the habitat, the light green represents the focal species' functional habitat. Adapted from SCALES-project, 2010.



## *1.5 How is connectivity included in conservation?*

The growth of our understanding of the role the spatial configuration of habitat has on mediating biodiversity and fostering adaptation has been reflected in our conservation strategies, legislation and targets. Principal among these is the championing of large-scale ecological networks.

### **1.5.1 Ecological networks**

The first two decades of the 21<sup>st</sup> century has seen a step-change in how governmental bodies and NGOs consider our natural environment, shifting from a predominantly protected area (PA)-led approach that has prevailed since the advent of nature conservation (Watson et al., 2014), to one that strives to produce ‘ecological networks’. The promotion of this landscape-scale approach to conservation has arisen from evidence that areas of habitat are markedly more effective at conserving biodiversity when they are part of a network (Hilty et al., 2019). While the exact structure of each ecological network varies, they consist of a number of key components: core areas, corridors, restoration areas, buffer zones, and the matrix (Fig. 1.2; Bennet and Mulongoy, 2006; Lawton et al., 2010; Samways and Pryke, 2016; Isaac et al., 2018; Hilty et al., 2020).

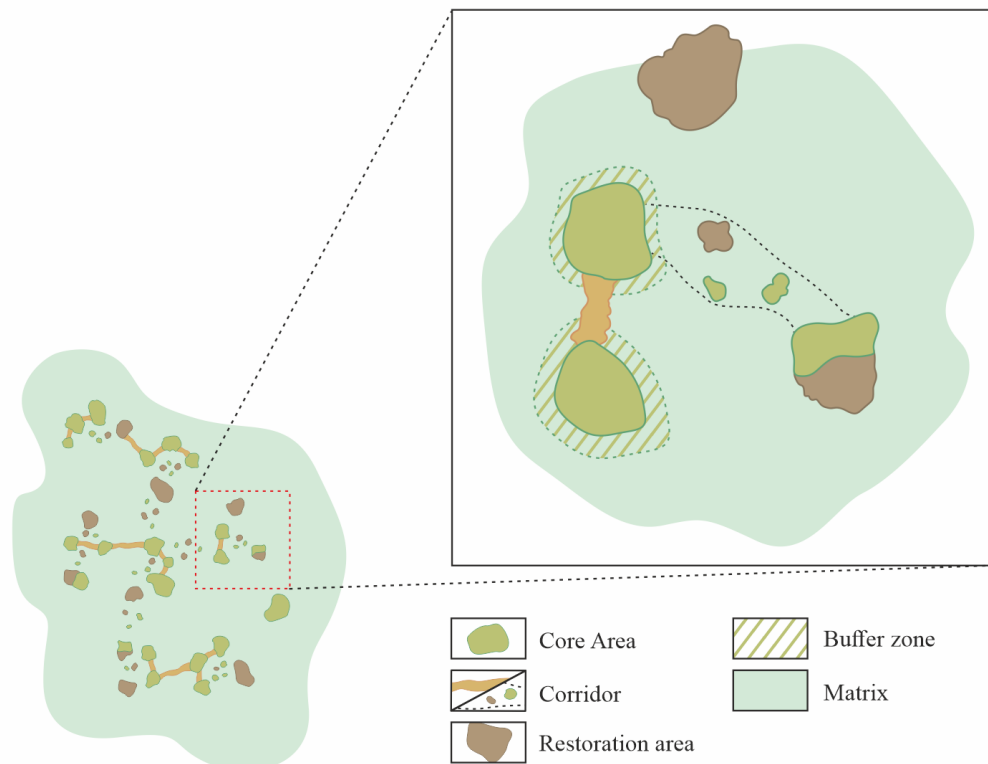
- **Core areas** represent extensive spaces of high-quality habitat with high ecological value, capable of supporting viable populations. These can be represented in PAs, which naturally form the core of many ecological networks due to their long-standing established place as the cornerstone of conservation (Watson et al., 2014). However, recently other effective area-based conservation measures (OECMs) have emerged to complement them (Dudley et al., 2018), such as large-scale independent conservation initiatives;
- **Corridors** are specifically established to improve functional connectivity between core areas, facilitating the necessary movement across spatial scales (Rayfield et al., 2016) to feed, disperse, migrate, reproduce and react to climate change. These can

comprise linear features, stepping-stones, or interlinked landscape types that facilitate movement;

- **Restoration areas** comprise spaces where efforts can be targeted to restore or create new high value habitat which may subsequently become core areas, or fill gaps in the network;
- **Buffer zones** act as transitional regions between network features and the matrix, protecting the network components from detrimental ‘edge-effects’ (Bennet and Mulongoy, 2006). In these zones land-use is restricted to only those activities that would not negatively impact the core of the network; and
- **The Matrix** which can be ‘softened’ through activities such as agri-environment schemes, making it less hostile to wildlife, reducing the detrimental effect it can have on local biodiversity (Driscoll et al., 2013), while also facilitating movement.

This ecological network approach was pioneered in European countries in the 70s and 80s (Jongman, 1995; Bennett and Wit, 2001; Lawton et al., 2010), and saw wide adoption through the 90s and early 2000s across the globe (Bennett and Wit, 2001; Bennet and Mulongoy, 2006; Bonnin et al., 2007). However, in the UK, while conservation was taking an ecosystem approach (Defra, 2007), it was not until the influential Lawton report (Lawton et al., 2010) with the mantra of “*More, Bigger, Better and Joined*” that the idea of large-scale ecological networks was adopted in the conservation strategies of the four devolved nations. Today, ecological networks is the dominant paradigm at the heart of conservation legislation of many countries (i.e. DEFRA, 2018; Bai et al., 2018; European Union, 2020; DeFazio, 2021; Environment Act 2021). This approach is set to continue, with global targets such as those set out in the post-2020 global biodiversity framework (CBD, 2020; CBD, 2021), likely to include connectivity and resilience, a term regarding the amount of disturbance that an ecosystem can withstand and how readily it recovers from disturbance (Morecroft et al., 2012). Both connectivity and resilience are core concepts of ecological networks. Similarly, conservation initiatives such as the ‘Thirty by thirty’ (30x30) that aims to protect 30% of

land and sea by 2030, have been endorsed by the IUCN at its World Conservation Congress (IUCN, 2021) and sit within the new strategy of the OSPAR network of marine protected areas (OSPAR, 2020). 30x30 is also likely to be included within the post-2020 global biodiversity framework (CBD, 2021), and recommendations have been made that in its implementation a network approach should be considered (Bailey et al., 2022).



**Figure 1.2: A hypothetical terrestrial ecological network.** An example ecological network consisting of core areas of habitat, connected by corridors, sitting within a matrix, protected by buffer zones and reinforced with targeted restoration actions. Adapted from Lawton et al., 2010 and Isaac et al., 2018.

## **1.5.2 Planning ecological networks**

The approaches used to establish ecological networks depend on the existing condition of the natural environment. Locke et al. (2019) and Belote et al., (2020) both describe the landscape and primary conservation measures in three categories:

- **Heavily modified landscapes** inexorably changed by centuries of human influence, such as western Europe. Here preservation of the remaining natural elements and the maintenance or restoration of connectivity are key conservation objectives;
- **Shared landscapes** where many natural elements remain, such as parts of the USA. In these landscapes focus is on protecting, restoring and connecting the large core areas of habitat. This approach can be seen in large-scale conservation initiatives such as the Yellowstone to Yukon program (Chester, 2015); and
- **Wild areas** where large swaths of natural habitat still exist, such as the Amazon. Here, conservation efforts involve protection and maintaining low human-influence.

The first two categories are where the ecological network approach is most applicable.

Due to the disparity between the desire for action and the resources available to act (Butchart et al., 2010), careful planning will be required to establish the landscape-scale ecological networks demanded by the legislature, science, and the global state of nature. Expert opinion can struggle to evaluate problems of the complexity and scale required for ecological networks (Cowling et al., 2003; Martin et al., 2012). Therefore, a myriad of planning tools have been developed to aid conservation planners in designing such networks. Systematic conservation planning (SCP; Margules and Pressey, 2000), is one such tool that uses the principles of representation and persistence (Kukkala and Moilanen, 2013; McIntosh et al., 2018) to prioritise areas to protect for conservation. Representation ensures nature is thoroughly protected at different spatial, compositional and hierarchical levels, while persistence means nature can be supported in the long term. SCP is widely used throughout the world (Watson et al., 2011; Kukkala and Moilanen, 2013; McIntosh et al.,

2018) through programs such as MARXAN (Ball et al., 2009) and ZONATION (Moilanen, 2007). However, SCP has been criticised for the ambiguity with which its principles are often defined, leading to variation in their application which begets uncertainty and misunderstanding (Carey and Burgman, 2008; but see Kukkala and Moilanen, 2013). Furthermore, while Systematic Conservation Plans are widely implemented, the outcomes of those plans are rarely reported (Knight et al., 2008; McIntosh et al., 2018), and as such we do not fully understand the scope of their successes and failures. Finally, SCP is largely concerned with PA placement; these areas are important to climate change adaptation (Thomas et al., 2012) and will continue to be important into the future (Thomas and Gillingham, 2015), but as demonstrated above do not constitute an ecological network on their own.

### **1.5.3 Measures of connectivity**

Understanding connectivity, identifying where habitat networks facilitate movement, and where conservation action may be necessary, requires suitable methods of its measurement. This has been, and continues to be, a fertile area of research (Correa Ayram et al., 2016; Dickson et al., 2019; Keeley et al., 2021).

#### **1.5.3.1 Initial measurements**

Initial connectivity measures favoured structural connectivity, because traditionally, landscape connectivity was treated as an independent variable, rather than one dependent on structure and species (Goodwin, 2003). These early measures focused on structural features such as corridors and stepping-stones, or the amount of habitat in the landscape. For instance, connectivity could be equated to the presence of corridors (Hunter, 2002; Goodwin, 2003), structural properties of those corridors (Andreassen et al., 1996; Haddad, 2000), or the area of habitat within a buffer around each habitat patch (Wiegand et al., 1999). Slightly more nuance was achieved by distance-based measures, which did away with the generalisation of organisms not venturing into non-habitat and used Euclidean distance to describe connectivity (Fig. 1.3b). These ranged from simplistic measures of distance, to

those that consider the distance between a patch and all others within a dispersal range, such as the incidence function model (Moilanen and Hanski, 2001; Moilanen and Nieminen, 2002). Such measures may have developed in reaction to the scientific and conservation community's shift from site-level to landscape-level conservation caused by the metapopulation studies of the late 20<sup>th</sup> and early 21<sup>st</sup> centuries (Santini et al., 2016).

### *1.5.3.2 Graph theory*

The introduction of graph theory to the ecological discipline (Bunn et al., 2000; Urban and Keitt, 2001) resulted in another leap towards measurement of functional connectivity (Fig. 1.3c). The representation of landscapes as graphs consisting of nodes (habitat patches) connected by edges (given a value representing some ecological connection), facilitated the use of more than just dispersal ability to calculate connectivity (Urban and Keitt, 2001; Laita et al., 2011). Furthermore, graph theory enabled the importance of constituent patches to landscape connectivity to be evaluated through minimum spanning trees – a subset of the graph where all nodes are connected by single edges whose sum is as small as possible – this had the secondary benefit of increasing the computational efficiency of connectivity analysis (Urban and Keitt, 2001), allowing analyses to be conducted at global scales (Santini et al., 2016; Saura et al., 2017; Ward et al., 2020). The appeal of the benefits offered by graph theory is clear in the diversity with which it has been applied to conservation studies, including the design of wildlife corridors (Hofman et al., 2018), landscape planning (Santini et al., 2016) and invasive species management (Drake et al., 2017). Yet, the graph theoretic perception of the landscape has numerous limitations (Moilanen, 2011), such as needing clear delineations between habitat and non-habitat, and being unable to account for multiple paths between two habitat patches.

### *1.5.3.3 Least cost analysis*

Least cost analysis, often called least cost paths or least cost distance, was the first method that facilitated the inclusion of the matrix into measurements of connectivity. Originating from transport geography (Etherington, 2016), it was later co-opted by

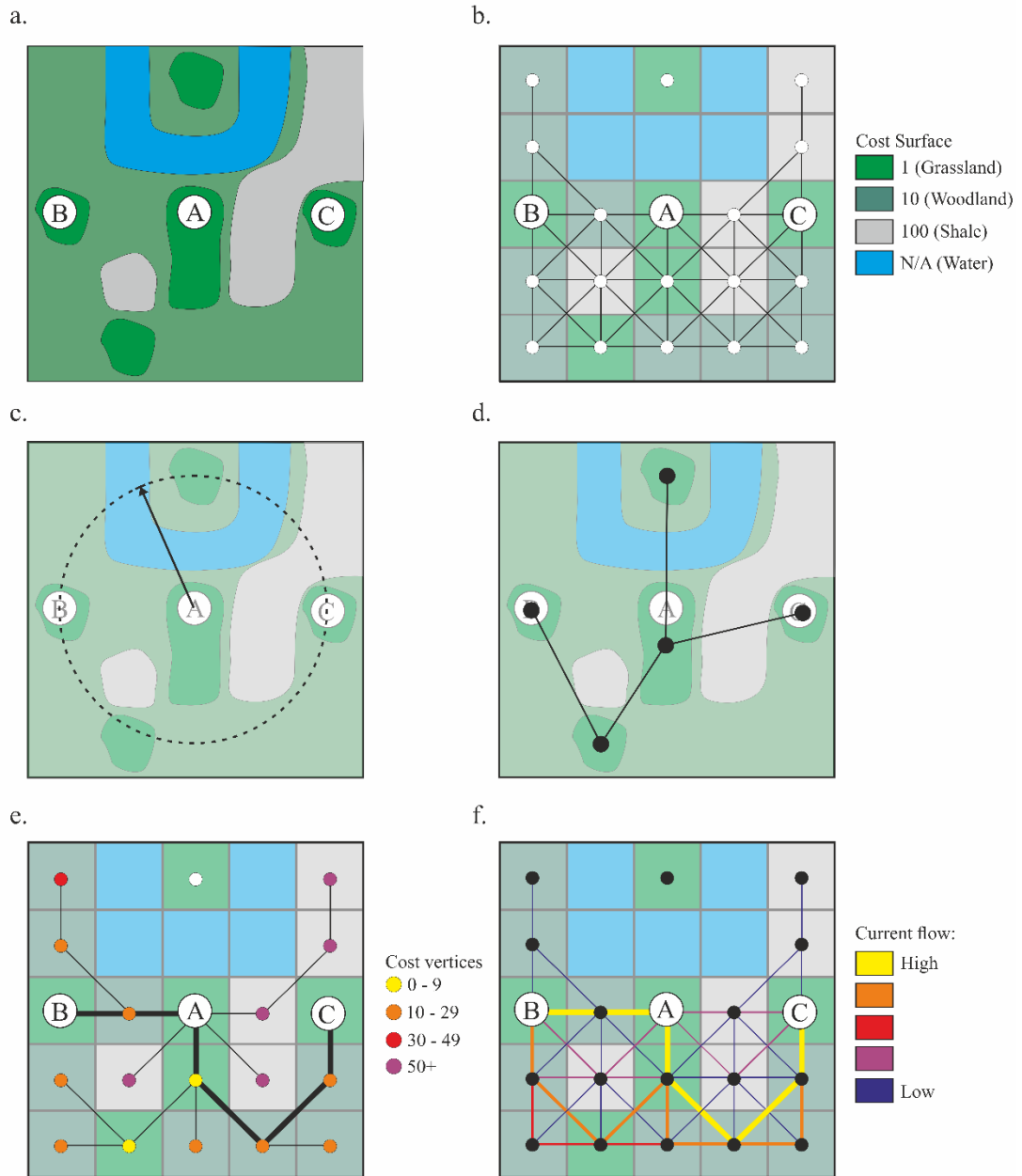
ecologists (Knaapen et al., 1992) who found it outperformed simpler Euclidean distance-based measures for explaining patch occupancy as a function of connectivity (Chardon et al., 2003). The key development least cost methods brought to connectivity analysis was the ‘cost surface’, which allowed the non-habitat of the matrix to be assigned values based upon the difficulty, or ease, an individual could move through them (Fig 1.3d). This in turn could be used to assign values to the edges between nodes in a graphical representation of the whole landscape, not just habitat patches. Least cost analysis quickly became the new paradigm and has remained popular since (Correa Ayram et al., 2016). However, the identification of the easiest route between two points implies that individual movers have absolute knowledge of their surroundings (Fig. 1.3e; McClure et al., 2016), which is unlikely during processes such as natal dispersal or range shifts. To circumvent this, some have utilised a process called factorial least cost analysis which applies a smoothing function to multiple additional suboptimal routes (e.g. Cushman et al., 2013). Yet, this only constitutes a slight easing of the assumption of a single optimal path, as these sub-routes are still in the optimal path’s vicinity.

#### *1.5.3.4 Circuit theory*

If least cost analysis assumes total knowledge of the landscape, circuit theory is its diametric opposite. This technique measures connectivity through all possible routes (Fig. 1.3f), thereby implying no knowledge of the surrounds. In a series of three papers (McRae, 2006; McRae and Beier, 2007; McRae et al., 2008) the late Brad McRae and colleagues demonstrated that electrical circuit theory could be applied in an ecological context. McRae et al., (2008) proposed that movement through an ecological network should abide by the same rules as current through an electrical circuit, where current flows from source to ground through all possible routes, and the amount of current moving through each node (habitat patch) represents the importance of that node to connectivity. In doing so, the findings that resistance distances are proportionate to the movements of random walkers on graphs (Doyle and Snell, 1984) and can be related to the commute times of those random

walkers (Chandra et al., 1996) were combined into a measurement termed ‘Isolation by Resistance’ (McRae, 2006) – a play on the traditional ‘Isolation by Distance’ in genetics (Wright, 1943). Due to all possible routes between habitat patches contributing to the calculation of connectivity, circuit theory allows the effect that adding, or removing, a single patch might have on the whole network to be determined, even if that patch is away from the least cost path (McRae et al., 2008). Furthermore, because of this ability to consider multiple pathways, circuit theory is able to identify redundancy and pinch points in habitat networks – crucial for restoration planning. However, while suitable for movements such as dispersal, its omission of the role of information (van Moorter et al., 2021) is less applicable to movements like migrations (McClure et al., 2016). Recently, methods have been developed that introduce the capacity to vary the assumption of the mover’s knowledge of its surrounds when modelling connectivity (van Moorter et al., 2022), bridging the gap between least cost and circuit theory methods.





**Figure 1.3: Representation of different measures of connectivity.** (a) A theoretic landscape in which the connectivity between habitat patches A, B, and C needs to be measured. (b) The raster cost surface of the theoretic landscape with lattice graph showing connection routes between cells. (c) Without the cost surface Euclidean distance might show A is equally connected to both B and C. (d) A minimum spanning tree might show that A and C are directly connected, but B is connected to A via a secondary habitat patch. (e) Least cost path modelling will identify the single best path between the two pairs via, for example, a Dijkstra tree, which identifies the cheapest path from a start point to every other node by cumulatively summing the costs of moving from node to node – as defined by the cost surface. (f) Circuit theory will define the connection between pairs of habitat patches as the total current flow between them through all possible routes. Note that the northern patch is considered connected to the rest of the network in (c) and (d), but when a cost surface is included it is not (b), (e) and (f). Adapted from Etherington, 2016.

### *1.5.3.5 Cost surfaces*

Most connectivity metrics in use today can likely be split into two groups. Those based upon cost surfaces and those not. The cost surface incorporates the capacity of the matrix to facilitate movement into connectivity calculations, allowing them to be species-specific, mirroring the species-specific nature of dispersal. Therefore, cost surface-based models certainly make for better approximations of ecological distance than those relying wholly on distance-based measures (Sutherland et al., 2015). Thus, you could be forgiven for asking “Why do measures without cost surfaces continue to see use?”. The answer comes from issues with defining a cost surface. For instance, it assumes that individuals base movement decisions on the same preferences as when selecting habitat (Zeller et al., 2012); but given that habitat specialist species have been known to move considerable distances through a hostile matrix while dispersing (Keeley et al., 2017) this is clearly not always accurate. Additionally, the generation of a cost surface relies on biotic data that are often not readily available (Keeley et al., 2021). In instances where data is lacking, there are two options. The first is expert opinion, which remains popular (Zeller et al., 2012) despite improvements in inferences of species-specific cost surfaces (Zeller et al., 2016). However, this process is highly subjective (Beier et al., 2008) and variation in the cost surface can have drastic effects on the results of connectivity analysis (Sawyer et al., 2011). Alternatively, a representative focal species for which data are available can be used (Beier et al., 2008). Yet, as landscape use can differ within a species (Conde et al., 2010) let alone between species, it is not certain that a connective feature designed using a proxy species would be suitable, as has been evidenced in corridor design (Hilty et al., 2019). Finally, the use of cost surfaces increases the computational burden of the analysis, which can become prohibitive over large landscapes unless the resolution of the underlying landscape is reduced (e.g. Critchlow et al., 2022). Coarser resolution reduces the ability of those analyses to identify individual important features. For these reasons the current thought is that functional metrics based upon cost surfaces are best at assessing connectivity at local and regional scales, while those without cost surfaces are better at larger-scales (Keeley et al., 2021). Indeed, many global

analyses of connectivity continue to use distance-based graph theoretical representations of the landscape (e.g. Santini et al., 2016; Saura et al., 2017; Ward et al., 2020).

### 1.5.3.6 Connectivity measures and climate change

Recently, connectivity improvement has emerged as a prominent recommendation to mitigate the negative effects of climate change on biodiversity. However, due to the distances and timescales over which range shifts occur (Huntley et al., 2008; Chen et al., 2011) the conservation considerations differ to that of increasing local or regional connectivity. Key to this is range expansion's dependence on a stable or increasing population and available habitat to expand into (Mair et al., 2014). As such, uncertainty exists regarding the benefits associated with increasing connectivity compared to increasing habitat area or quality (Hodgson et al., 2009), and has led to the argument that connectivity should be a secondary conservation objective when increasing the amount and quality of habitat is also an option (Hodgson et al., 2011). However, even as a lesser priority, we should be concerned that while great strides have been made in incorporating connectivity into the discipline of landscape planning, effort is still required to properly consider climate change (Mazaris et al., 2013; Keeley et al., 2018), such as adequately including dispersal related specifically to climate change when identifying spatial and temporal priorities (Reside et al., 2018). A trait shared by many of the methods discussed above is the basis of modelling individualistic movements within existing populations. This may not be suitable for climate change adaptation, in which connectivity over a series of scales needs to be measured (Rayfield et al., 2016), because range shifts may occur over distances greater than any one individual could traverse in their lifetime or even a few generations (Huntley et al., 2008; Chen et al., 2011). Furthermore, the spatial considerations for conservationists to improve climate change-relevant connectivity differ compared to connectivity related to meta-populations (Robillard et al., 2015). These climate-related spatial considerations include regions along climate trajectories that species will follow, including latitude and altitude (Chen et al., 2011; Pinsky et al., 2013; Senior et al., 2019; Lenoir et al., 2020), areas

that will act as climate refugia (Ashcroft, 2010; Keppel et al., 2012; Morelli et al., 2020), and future climate analogues (Littlefield et al., 2017).

There have been a number of advancements in recent years to develop methods to specifically account for climate change within connectivity measurement. Condatis (Hodgson et al., 2012; Hodgson et al., 2016) is an adaptation of circuit theory that incorporates aspects of metapopulation dynamics, and will be explained in more detail in Section 1.8. Tools such as Omniscap (McGuire et al., 2016; Littlefield et al., 2017) combine circuit theory and moving window algorithms to increase the computational efficiency of those techniques, allowing them to be applied at spatial scales relevant to modelling range shifts. Finally, individual-based models specifically designed for scales over which climate change acts, such as RangeShifter (Bocedi et al., 2014; Bocedi et al., 2021) are another example that allow for greater realism in how dispersal is modelled and the incorporation of population dynamics. Complex tools like Rangeshifter, capable of incorporating more than just connectivity, are likely to be the route by which all Lawton et al.'s (2010) recommendations of “*More, Bigger, Better and Joined*” can be integrated in ecological network design. However, the extensiveness of the data necessary to parameterise such models are, for the time being, largely prohibitive.

## *1.6 What progress is still to be made?*

Despite the gargantuan improvements in knowledge base, tool availability and implementation over the past half century, yet more progress remains to be made in how we protect and restore our ecological networks.

### **1.6.1 Protected areas**

Overall coverage of the PA estate is increasing (UNEP-WCMC, 2022), and with the substantial uptake of the 30x30 target we can be hopeful that this will continue. Expanding the PA network is a desirable aim, but the scientific community is calling for designation of effective PAs (di Minin and Toivonen, 2015; Geldmann et al., 2015; Gill et al., 2017).

Indeed, ~1.1million km<sup>2</sup> were removed from the PA estate annually between 2008 and 2016 due to no longer complying with IUCN definitions (Lewis et al., 2017), and PA gains made in relation to Aichi Target 11, which aimed to protected 17% of land by 2020 and was missed (CBD, 2020a), did not properly consider qualitative elements, focusing on quantity instead (Maxwell et al., 2020). In relation to connectivity specifically, global assessments have found our terrestrial PA networks are increasing but are not connected (Saura et al., 2017; Saura et al., 2018; Saura et al., 2019) and recommend targeted designation to improve connectivity as the most important step for many nations (Saura et al., 2019) . No such study has been conducted in fresh water or marine realms (Maxwell et al., 2020), but if we were to extrapolate from regional studies one might make similar conclusions (Endo et al., 2019). Ensuring that species can move between PAs is important because studies show they facilitate movement (Thomas et al., 2012), yet species respond to the connectedness of habitat rather than connection of PAs *per se*. Additionally, areas of high connectivity can improve reserve performance when protected (Olds et al., 2012). Therefore, a useful question, that to my knowledge is yet to be answered, is how do PA networks conserve habitat connectivity? Rather than just how connected the PA network is.

## **1.6.2 Restoration/creation of habitat**

Protection is not the only way connectivity is being implemented in ecological networks; restoration is vital because it is the only option capable of filling gaps in the network (see Fig. 1.2). As global ecosystems continue to degrade (WWF, 2020), restoration and creation will become increasingly important, and is reflected in the numerous and considerable pledges to create and restore habitat made by many governments and large conservation projects (e.g. DEFRA, 2018).

Making these efforts count will require evidence-based actions, but whether this is the norm is doubtful. Our conservation strategies have been described as being based on belief systems (Pressey et al., 2017), and likened to the medical practices of old where decisions were influenced more by anecdote than evidence (Sutherland et al., 2004). Indeed, numerous

studies have found peer-reviewed science often takes a backseat in the decision-making process (Sutherland and Wordley, 2017; Kadykalo et al., 2021), such that there is an evidence-implementation gap (Knight et al., 2008) and calls for implementation strategies to be included within assessments (Adams et al., 2019). Perhaps the crux of the issue is that we do not fully understand how successful our conservation efforts are because results of systematic conservation plans rarely enter the literature (Pullin et al., 2004; Sinclair et al., 2018). Recently, reviews have been conducted on the implementation of conservation plans, and noted that they do often lead to conservation outcomes (e.g. Keeley et al., 2019); but these reviews did not determine how connectivity was assessed. If we are to halt the trend of missed biodiversity targets (CBD, 2010; Hawkins et al., 2019; SCBD, 2020a; European Union, 2020), we must be able to assess the methods that are likely to be used when striving to achieve future targets.

The tools we use in conservation planning also need adjustment. While, as noted above, much progress has been made in their development, still more needs to be made in their accounting for anthropogenic climate change (Reside et al., 2018). Furthermore, many of the connectivity assessment tools in use are not capable of highlighting where to create/restore habitat to best improve connectivity, instead focusing on describing the current state of connectivity. Some are able to identify pinch points (McRae et al., 2008), but although these are good indicators of where restoration may be beneficial, they do not quantify the improvements that could be made or recommend specific areas, both of which would be helpful in the planning process. A few methods have been developed (McRae et al., 2012; Torrubia et al., 2014; Hodgson et al., 2016) but, while offering important advancements, either do not consider where it is possible to act given available information such as soil type and land ownership, or do not add habitat iteratively, and therefore cannot account for changes in connectivity that would occur over time as restoration is undertaken at different points. Naturally, these suggestions may not always be implemented as plans are tailored to local circumstance (Pressey et al., 2013), but the production of a suite of

restoration options can be useful for prioritisation, and, if implemented effectively, can allow small scale action to have far reaching impact (Baldwin et al., 2012).

## *1.7 A word on anglocentricity*

I suggest that the topics I discuss in the following chapters are applicable to conservation wherever it takes place. However, much as behavioural ecologists need a study organism, I required a study region. I chose England as the focus and what follows explains my rationale in doing so.

### **1.7.1 England's natural environment**

Following centuries of human modification, England's landscape is highly degraded and fragmented, such that the nation is largely dominated by semi-natural habitats (Lawton et al., 2010; Hayhow et al., 2019; WWF, 2020), and the UK as a whole is one of the most biodiversity-depleted countries in the world (Hayhow et al., 2019). Considering the habitat landscape categories put forward by Locke et al., (2019) and Belote et al., (2020) we can place England in the category of heavily modified landscapes. Furthermore, while there has been a long history of conservation in England, with what can be considered its first protected areas emerging in the early 20<sup>th</sup> century (Sheail, 1998), growth of the protected area network has largely been piecemeal, occurring on a site by site basis (Ratcliffe, 1986), with little consideration to the wider context (Gaston et al., 2006). As a result, much like the habitats it serves to protect, the protected area network of England consists of sites that are generally small (Lawton et al., 2010), in unfavourable condition (Starnes et al., 2021), and disconnected (Santini et al., 2016; Saura et al., 2017; Saura et al., 2018). This is a natural environment with characteristics the topics I discuss are most pertinent to.

### **1.7.2 England's burgeoning environmental policy**

Recent decades have seen a step-change in how conservation is considered in England and the UK as a whole. The Lawton review set this ball rolling by describing a need for "*More, Bigger, Better and Joined*" wildlife sites (Lawton et al., 2010) and the Glover review

continued this by proposing that national landscapes should form the backbone of a Nature Recovery Network (Glover, 2019). This is reflected in significant policy changes in recent years. The 25-year environment plan (DEFRA, 2018) committed to the creation of 500,000 ha of new habitat, increasing woodland coverage, improving the condition of protected areas, and developing metrics to evaluate progress towards those goals. Subsequently, we have seen the passing of the Environment Act into law (Environment Act 2021), which makes considerable changes to the legislation such as the introduction of biodiversity net gain requirements, conservation covenants, and local nature recovery strategies. Finally, the UK government has committed to a number of targets like that to protect 30% of land and sea by 2030 (UK Government, 2019; UK Government, 2021b) and to halt and reverse biodiversity decline by the same date (UK Government, 2021a). There are considerable amounts of conservation on the horizon in England, much of which will focus on producing resilient ecological networks and are applicable to the topics I discuss.

## *1.8 Connectivity with Condati*

In this work, I measure and analyse connectivity through the Condati conservation decision support tool. Condati adapts circuit theory (McRae et al., 2008) to calculate the speed at which a population can expand its range through a habitat network (Hodgson et al., 2012; Hodgson et al., 2016).

While using similar principles, Condati differs from McRae style circuit theoretic models (McRae et al., 2008) in key respects (Table 1.1) largely due to modelling multi-generational rather than within-generational movements. In the Condati analogy, the landscape is represented as a grid of cells and each cell containing breeding habitat becomes a node in the circuit network. In place of a resistance surface based on landcover between habitat patches, a colonisation kernel is used to define the resistance between habitat cells, whether they are adjacent or far from one other, and no matter what lies between them. In other words, the matrix outside breeding habitat is assumed to be homogeneous, through which the population can move, but cannot breed, meaning that matrix cells are not a



consideration in Condatis calculations. This simplified dispersal process is a considerable assumption, and means physical barriers to dispersal cannot be modelled as in other programs that utilise cost surfaces. However, by not directly considering the matrix Condatis is able to analyse more extensive networks before computation limits are reached, facilitating the efficient representation of range expansion whose success depends on both reproduction within, as well as dispersal between, habitat cells (Hodgson et al., 2012).

### **1.8.1 Overview of parameters and outputs**

In order to evaluate connectivity Condatis requires a number of parameters to be defined:

- **Source and Target:** a raster representing areas of the population's current range (source) and where the population will end up once range shifts are complete (target);
- **Habitat:** a raster defining breeding (where populations can stop and produce more dispersers) and non-breeding (through which the population can move but not reproduce) habitat; and
- **Species specific traits:** values used to parameterise the dispersal kernels that underly the movement calculations. The particulars of dispersal kernel choice and parameterisation is discussed in each chapter.

Once these are provided the landscape is converted to a resistor network via the dispersal kernel and a voltage applied from the source to the target causes current to flow – predominantly through the routes of lowest resistance. Circuit theory calculations evaluate and describe network connectivity through three metrics: Conductance, Flow and Power.

**Table 1.1: McRae circuit theory and Condatis.** A Comparison of the core architecture of McRae style circuit theory (Circuitscape) and Condatis

| <b>Network/ circuit concept</b> | <b>Usage in McRae circuit analogy</b>   | <b>Usage in Condatis circuit analogy</b>  |
|---------------------------------|---|---|
| <b>Nodes</b>                    | Nodes are placed in matrix cells over the entire landscape. Often, breeding habitat cells are assigned 0 resistance and used as sites to ‘inject’ current, but their effect on movement is not examined.  | Nodes are placed only in breeding habitat cells.  |
| <b>Resistors</b>                | Resistors are placed between spatially adjacent nodes (usually 4 or 8 neighbours)   | Resistors are placed between all nodes  |
| <b>Resistance</b>               | Resistance values are defined by cell values in a resistance surface (usually a raster) – it is assumed that dispersing individuals are more likely to take steps in a low-resistance direction than a high-resistance one. In this sense, the resistance represents the behavioural response of individuals to the landscape as they travel. | Resistance values are determined by a distance-dependent colonisation kernel, which defines how quickly an entire breeding population at one cell could seed a new population at the habitat in another cell. As such, the kernel approximates the average outcome of many individual dispersal events, which would have taken many different paths through the matrix. |
| <b>Current through a node</b>   | Represents the relative likelihood of dispersers passing through a particular cell on the landscape. Calculated by linear solvers using Kirchoff’s and Ohm’s laws   | Represents the relative likelihood that a particular habitat cell was colonised by ancestors of the populations that successfully reach the target – i.e. that the cell was used as a stepping stone in the range expansion. Calculated by linear solvers using Kirchoff’s and Ohm’s laws   |
| <b>Sources</b>                  | Where breeding populations exist and thus dispersal events start. Cell(s) in the network where voltage is applied or current is injected. User defined; can be existing habitat cells or cells adjacent to the network  | Where range expansion starts – user can define this as existing habitat cells or cells adjacent to the network. At these cell(s), voltage is fixed and high.  |
| <b>Ground</b>                   | Cell(s) in the network acting as ground. User defined; can be existing habitat cells or cells adjacent to the network. Additional resistors can be connected to ground to represent the potential mortality of dispersers.  | The place(s) where range expansion will be deemed successful (termed ‘target’ cells). User can define these as existing habitat cells or cells adjacent to the network. At these cell(s), voltage is fixed and low, causing current to flow from the source(s).   |

### 1.8.1.1 Conductance

Conductance (or ‘Circuit conductance’) is a representation of the overall connectedness of the network and is a property of the entire landscape. Hodgson et al. (2012) showed that conductance is highly correlated with the speed of a range expansion which starts at the source and ends at the target. High conductance is indicative of a source and target that are well connected. Indeed, using historical empirical moth colonisation data Hodgson et al. (2022) showed that landscapes with higher conductance were those that had faster colonisation times during range expansion.

The conductance between a source and a target is calculated by  $K = \mathbf{V} \times \mathbf{c}_{\text{target}}$ , where  $\mathbf{V} = \mathbf{M}^{-1} \mathbf{c}_{\text{source}}$ .  $\mathbf{M}$  is a  $N \times N$  matrix with elements  $M_{ij} = \delta_{ij} \sum_l c_{jl} - c_{ij}$ , where  $c$  is the single step colonisation rate (calculated by the dispersal kernel and the inverse of resistance) between any two cells,  $i$  and  $j$  index the  $N$  intermediate cells,  $l$  indexes the  $N$  patches together with the source and target, and  $\delta_{ij} = \begin{cases} 1, & i = j \\ 0, & i \neq j \end{cases}$ .  $\mathbf{c}_{\text{source}}$  and  $\mathbf{c}_{\text{target}}$  are vectors of length  $N$  of colonisation rate values between each intermediate cell and the source or target. Should there be multiple target or source cells the contributions from each are simply added together to produce  $c_{\text{target},i}$  and  $c_{\text{source},i}$ .

### 1.8.1.2 Flow

Flow is a property of individual habitat cells and describes the relative importance of each cell to overall landscape connectivity, the loss of conductance that would occur if a cell was lost from the network relates to its flow value (Hodgson et al., 2016). Areas of habitat with high flow are good indicators of places to conserve in order to protect connectivity.

Given the design of the network each cell in the circuit is held at a particular potential ( $v_i$  for the  $i^{\text{th}}$  cell in vector  $\mathbf{V}$ ). The current flowing between any two cells  $i$  and  $j$  is calculated as  $c_{ij}(v_j - v_i)$ . The amount of current into cell  $i$  from cells with a higher potential is strictly equal to the current out to cells with a lower potential – also known as Kirchhoff’s first law. The ‘flow’ metric is given by summing these inward (or outward) currents.

### *1.8.1.3 Power*

Power is a property of the imaginary links between two cells of habitat and defines the strain that link is under. Links with high power represent regions of relatively high resistance along a high flow route (Hodgson et al., 2016), such links are called ‘bottlenecks’ and identify those that are constraining the speed of range expansion. Creating or restoring habitat around bottlenecks would likely yield large increases in conductance.

Electrical power is defined as  $P = \frac{qV}{t}$  where  $q$  is the charge moved and  $V$  is the voltage, because  $I = \frac{q}{t}$ , where  $I$  is the current, it follows that  $P = IV$ . Therefore, in circuits constructed by Condatis the power of the link joining cells  $i$  and  $j$  is given by  $P_{ij} = c_{ij}(v_j - v_i)^2$ .

## *1.9 Research objectives*

The overall aim of this thesis is to improve how we plan ecological networks to take into account long-distance connectivity and ensure they continue to support nature in the long term. Specifically, this overarching aim is represented in the following themes of each chapter:

**Chapter 2** – Improving our understanding of how to protect connectivity by examining the extent to which existing protected area networks conserve habitat patches important to connectivity;

**Chapter 3** – Evaluating if current conservation practice is improving long-distance connectivity through studying recent conservation projects;

**Chapter 4** – Developing a new method to aid conservation planners in deciding where to create habitat to improve long-distance connectivity; and

**Chapter 5** – Exploring the use of connectivity metrics in conservation around the world to understand if they are used, and what conservation results from their use.

# Chapter 2 Habitat patches providing South-North connectivity are under-protected in a fragmented landscape

This chapter was published in Proceedings of the Royal Society B as:

Travers, T.J., Alison, J., Taylor, S.D., Crick, H.Q. and Hodgson, J.A., 2021. Habitat patches providing south–north connectivity are under-protected in a fragmented landscape. Proceedings of the Royal Society B, 288(1957), p.20211010.

Note in the publication J. Alison and I are recorded as joint first authors with equal contributions to the study. J. Alison carried out initial Condatis analysis to generate the flow values of cells of priority habitat networks that were used as the core dataset, reviewed drafts and assisted in addressing reviewer comments. I conducted the statistical analysis, including converting cell flow values to patch flow values, wrote the first draft of the paper, addressed comments from co-authors and addressed reviewer comments during the publication process.

The paper has been modified for inclusion in this thesis to avoid repetition of methodology.

*“I feel that as long as the Shire lies behind, safe and comfortable, I shall find wandering more bearable”*

- Frodo Baggins

## *2.1 Abstract*

As species' ranges shift to track climate change, conservationists increasingly recognise the need to consider connectivity when designating protected areas (PAs). In fragmented landscapes, some habitat patches are more important than others in maintaining connectivity, and methods are needed for their identification. Here, using the Condatis methodology, I model range expansion through an adaptation of circuit theory. Specifically, I map 'flow' through 16 conservation priority habitat networks in England, quantifying how patches contribute to functional South-North connectivity. I also explore how much additional connectivity could be protected via a connectivity-led protection procedure. I find high-flow patches are often left out of existing PAs; across 12 of 16 habitat networks, connectivity protection falls short of area protection by 13.6% on average. I conclude that the legacy of past protection decisions has left habitat-specialist species vulnerable under climate change. This situation may be mirrored in many countries which have similar habitat protection principles. Addressing this requires specific planning tools that can account for the directions species may shift. My connectivity-led reserve selection procedure efficiently identifies additional PAs that prioritise connectivity, protecting a median of 40.9% more connectivity in these landscapes with just 10% increase in area.

## *2.2 Introduction*

Species can be hampered in their ability to shift ranges as an adaptation to climate change (Lenoir et al., 2020) where there are synergistic negative impacts of anthropogenic land use (Mora et al., 2007; Riggio et al., 2020). We need to safeguard species' ability to respond to climate change by incorporating regional and national connectivity into conservation planning (Isaac et al., 2018). Many studies look at how easily individuals can traverse landscapes (Littlefield et al., 2017; Koen et al., 2019), but modelling landscape connectivity across one or few generations is unlikely to predict long-term, large-scale responses to climate change. Studies need to assess multi-generational connectivity; i.e. whether there is enough habitat in the right places to facilitate long-distance range shifts. Landscape-scale decision making is crucial to deliver climate-resilient landscapes (Keeley et al., 2018), and losing habitat patches from critical regions between current and projected ranges will hamper species' range expansion – potentially causing extinction (Thomas et al., 2004).

Recently, we have seen a global shift towards promoting functionally connected networks, typified by Aichi biodiversity target 11 (Secretariat of the Convention on Biological Diversity, 2011). National examples of this include the UK Government's plan to develop a nationwide Nature Recovery Network to protect, restore and connect the country's wildlife sites (DEFRA, 2018). Such initiatives cause stakeholders to reconsider where to prioritise conservation of priority habitats. For both pragmatic and strategic reasons, conservation may have historically favoured larger patches over small ones, thus avoiding fragmented regions (Hernández-Ruedas et al., 2014; Hill et al., 2018). However, there remains active debate on the value of several small patches for species richness, versus one contiguous patch of the same size (Fletcher et al., 2018; Fahrig, 2019). Simulations of species persistence and expansion, using simple metapopulation models, highlight the strengths and weaknesses of different habitat creation strategies. In general, aggregation strategies are good for facilitating metapopulation persistence but not for range expansions,

because large gaps are left between habitat aggregations in the direction of range advance (Ovaskainen, 2002; Hodgson et al., 2011).

Safeguarding habitats in protected areas (PAs) is a widespread, cost-effective tool for biodiversity conservation (James et al., 1999). Many studies have demonstrated the representation of species' projected future ranges in existing PA networks (Hannah et al., 2007). Others have shown existing PAs may facilitate species' range expansions by supporting high abundances of, and preferential colonisation by, range-expanding species (Gillingham et al., 2015). However, colonisation does not necessarily lead to successful range expansions, and an important subset of species are failing to shift their ranges (Pearce-Higgins et al., 2017). If protection was lost in patches critical to reaching the projected range, even more species could be vulnerable, and up to now the protection of such critical patches has generally not been prioritised. Following intensive research, software can now incorporate connectivity in relation to climate change into the decision-making process (Nuñez et al., 2013; Anderson et al., 2016; Keeley et al., 2018; Dickson et al., 2019). Work is ongoing to put connectivity science into practice, and incorporate connectivity in a nuanced, 'climate-wise' context (Keeley et al., 2018; Williams et al., 2020). To that end, tools to identify and protect habitat patches that are crucial for range expansion need to be developed and disseminated.

Successful inclusion of connectivity in conservation decision-making also depends on legal and ecological context. In England, a 2006 Act of Parliament (Natural Environment and Rural Communities Act 2006) provides for the conservation of listed priority habitats and species (Reporting and Group, 2007). Specifically, legally recognised priority habitats, from lowland meadows to blanket bog, are platforms to protect c.1,000 priority species. Priority habitats are ecologically distinct from one another, providing for unique subsets of priority species including threatened and specialist plants, fungi, birds, beetles, butterflies, moths and several other taxa (Webb et al., 2010). Some species depend on multiple priority habitats, but protection, restoration and conservation decisions are likely to consider each



habitat individually. Beyond priority habitats, conservation practice in England now emphasises building a “coherent and resilient ecological network”, and ensuring that wildlife sites are “joined up” (Lawton et al., 2010). During contemporary climatic warming, South-North range shifts have been widely documented in England among many species (Webb et al., 2010). In recent decades those species undertaking range shifts have disproportionately colonised PAs, highlighting their key role in protecting habitats – even in species’ potential future ranges (Thomas et al., 2012).

Here, I use connectivity analysis to inform decision-making within the constraints of a specific policy context. I assess the capacity of England’s protected areas to secure long-distance connectivity in 16 national conservation priority habitat networks. I define habitat networks as assemblages of patches of a given priority habitat type, because priority habitats receive distinct legal recognition and underpin planning decisions in England, and are highly ecologically distinct, providing for unique subsets of priority species. I use Condatis (Hodgson et al., 2012; Hodgson et al., 2016), a landscape-scale decision-support software, to identify habitat patches (i.e. contiguous clumps of habitat) critical to long-distance connectivity and range expansion under climate change. Condatis uses circuit theory to efficiently calculate how quickly a species could reach a specified target location from a specified source. It has mathematical similarities to, but key conceptual differences from, the circuit theory models used by other landscape ecologists (McRae et al., 2008): one link in the Condatis network represents a population sending colonists to an empty patch to found a new population (not a disperser stepping between one cell and its neighbour). Crucially, if a patch in Condatis has high “flow”, it is located on one of the likeliest routes for range expansion between the source and the target (Hodgson et al., 2016).

To better understand and conserve priority habitats under climate change, I ask: (i) To what extent are high-flow habitat patches represented in England’s current PA network? (ii) How is the protection and/or high-flow status of habitat patches related to their area? (iii) How much extra network connectivity could be conserved through targeted conservation of

high-flow habitat patches? I use generalised linear models to explore relationships between the flow, size and protection status of patches across priority habitat networks. I rank unprotected habitat patches based on their contribution to long-distance connectivity, and strategically add them to the PA network to demonstrate how targeted conservation could efficiently increase connectivity for a given increase in PA coverage.

## 2.3 Methods

### 2.3.1 **Data preparation:**

Spatial data for the Priority Habitat Inventory (PHI), Sites of Special Scientific Interest and National Nature Reserves (SSSIs and NNRs, henceforth collectively PAs) in England were downloaded from the Natural England Open Data Geoportal (Natural England, 2019). Polygons of England were downloaded from the Ordnance Survey (OS) OpenData Boundary-Line Layer (Ordnance Survey, 2019).

The PHI represents a broad range of semi-natural habitat types identified as the most threatened and requiring conservation action under the UK Biodiversity Action Plan. These data were all originally in vector format. The PHI polygons were converted to a 50 m raster using ArcMap 10.6, with cell values corresponding to the habitat type of the polygon their centroid intersected. Where cells intersected polygons of multiple habitat types, the rarest took precedence. I merged (1) upland and lowland calcareous grassland habitat types and (2) upland heathland, lowland heathland, and mountain heathland and willow scrub habitat types (Table 2.1) because of functional similarity between them. The minimum mapping unit of the PHI is 0.1 ha, whilst the raster resolution equates to 0.25 ha. Therefore, it is unavoidable that a small number of habitat patches will have been lost in the rasterization process. However, I consider it unlikely to be so prevalent that it significantly influenced the findings (mean area lost = 1.8%; Table A.1).

To consistently represent the colonisation process across both large and small patches, Condatis works best with a raster of habitat cells at the finest resolution that will not overwhelm the RAM available (more information in Appendix A). For the 16 habitat networks in this study, the feasible analysis resolution was 2 km for deciduous woodland due to its large extent (Table 2.1) and 1 km for all other priority habitat types. Thus, habitat cells for the Condatis network (as defined in the next section) were derived by aggregating a 50 m resolution raster using the ‘*rgdal*’ (Bivand et al., 2019) and ‘*raster*’ (Hijmans, 2019)

packages in R 3.5.0 (R Core Team, 2019), converting the sum of 50 m habitat cells to a proportional cover.

**Table 2.1: Habitats.** Habitats initially included in the study in descending order of area

| Habitat                             | Code     | Area (ha) |
|-------------------------------------|----------|-----------|
| Deciduous Woodland                  | wood     | 736511    |
| Heathland*                          | heath    | 285475    |
| Blanket Bog                         | blbog    | 230950    |
| Coastal Floodplain Grazing Marsh    | marsh    | 217556    |
| Calcareous Grassland†               | cgrass   | 71075     |
| Mudflats                            | mudfl    | 61261     |
| Salt Marsh                          | saltm    | 34111     |
| Lowland Meadows                     | lmead    | 21174     |
| Lowland Fens                        | lowfens  | 20294     |
| Traditional Orchard                 | orchard  | 16023     |
| Lowland Dry Acid Grassland          | agress   | 15179     |
| Maritime Cliff and Slope            | cliff    | 13348     |
| Coastal Sand dunes                  | dunes    | 10227     |
| Upland Flushes, Fens and Swamps     | upfens   | 10005     |
| Purple Moor Grass and Rush Pastures | pastures | 9105      |
| Lowland Raised Bog                  | lrbog    | 7814      |
| Coastal Vegetated Shingle           | shingle  | 3985      |
| Reedbeds                            | reeds    | 3136      |
| Upland Hay Meadow                   | hay      | 2439      |
| Saline Lagoons                      | lagoons  | 1360      |
| Limestone Pavement                  | pavement | 1268      |
| Calaminarian Grassland              | calam    | 297       |

\*Heathland network formed of Lowland Heathland (56418 ha), Upland Heathland (227646 ha), and Mountain Heaths and Willow Scrub (1411 ha)

†Calcareous Grassland network formed of Lowland (61856 ha) and Upland (9219 ha) Calcareous Grassland.

### **2.3.2 Condatis settings**

The underlying theory and calculations of the Condatis method are outlined in the introduction (see Section 1.8). Here I describe the dispersal kernel used to generate resistance values between cells of breeding habitat, and parameterisation.

#### **2.3.2.1 Dispersal kernel**

The dispersal kernel implemented in this study was the negative exponential dispersal kernel. This kernel was used in the development of the Condatis method (Hodgson et al., 2012; Hodgson et al., 2016), and closely approximates the short-distance movements that dominate the metapopulation dynamics underpinning Condatis theory (Hanski, 1998; Baguette, 2003), due to its focus on multi-generational movements. The negative exponential dispersal kernel takes the form

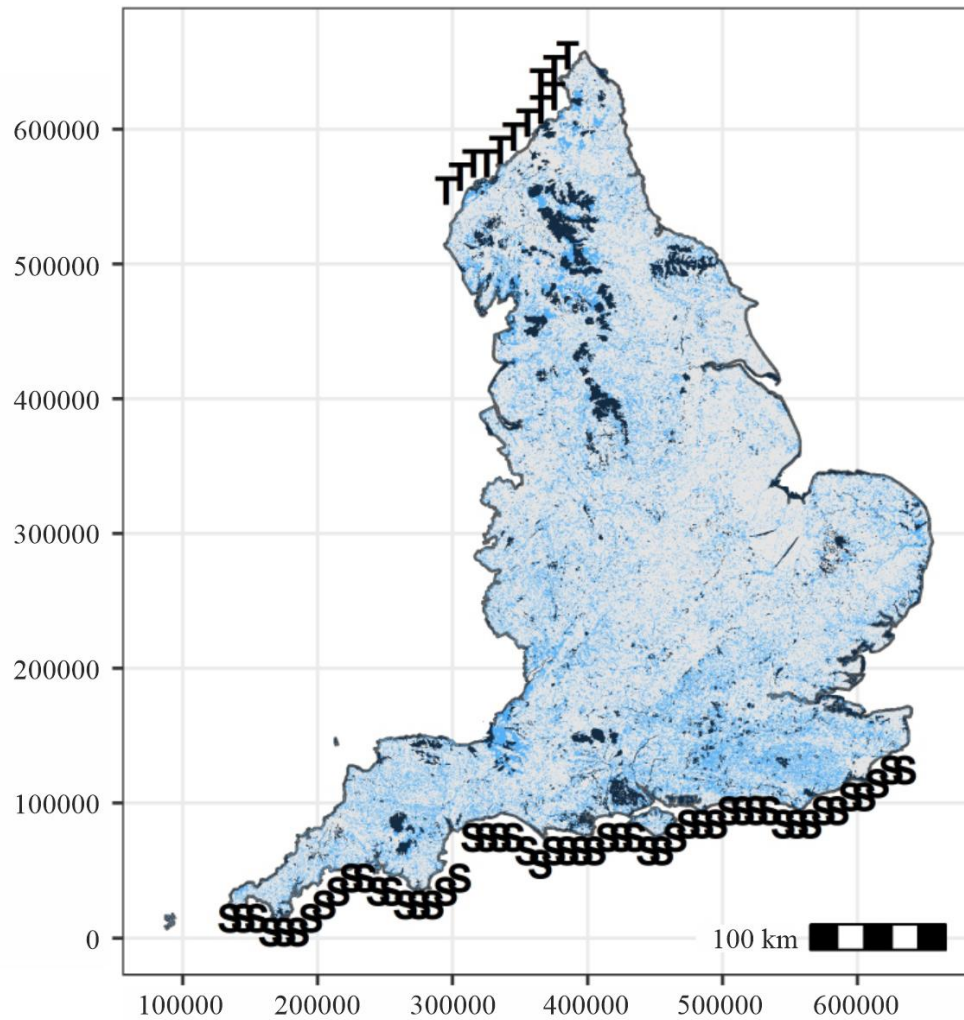
$$p_i p_j R \cdot \frac{\alpha^2}{2\pi} \cdot \exp(-\alpha d_{ij}), \quad \text{Equation 2.1}$$

where  $p$  is the area of habitat in each cell,  $R$  is reproductive rate,  $2/\alpha$  is mean dispersal distance,  $d_{ij}$  is the distance between cells  $i$  and  $j$ . The  $p$  and  $R$  values determine the number of dispersers leaving and arriving in the cells. The distribution of dispersers declines with distance according to this kernel.

#### **2.3.2.2 Parameterisation**

I ran Condatis for each of the 16 priority habitat networks and three exemplar mean dispersal distances. I did not attempt to make exact species-specific predictions; instead, I focussed on habitat networks as platforms for conservation actions, using traits and processes relevant for multiple species. For the mean dispersal distance trait ( $2/\alpha$ ; eqn. 2.1), 2, 4, and 8 km options were run, aiming to represent a broad range of plant, fungi, vertebrate and invertebrate species specialised to each priority habitat network. While many relevant species likely have dispersal abilities of less than 2km, Condatis calculations encountered rounding errors if the average dispersal was several orders of magnitude lower than the largest gap in the network (See Appendix A). Reproductive rate ( $R$ ; Eqn 2.1) was fixed at

100 throughout, equating to the production of one emigrant per hectare. This was not based on specific data, but is plausible for a medium-bodied vertebrate, or an invertebrate with a low population density. Varying R would not have affected the relative performance of networks and patches, which were the focus of this study, because R modulates all flow and conductance values in proportion. I identified sources and targets for Condatis on the premise that species are adjusting their ranges to higher latitudes (Lenoir et al., 2020). Thus, a 10 km raster file was produced with sources along the south coast of England, and targets along the northern border with Scotland (Fig. 2.1).



**Figure 2.1: Habitat distribution, sources and targets.** Spatial distribution of all habitats used in the analysis defined as protected (dark blue) and unprotected (light blue). Source (S) and target (T) cells used as an input to Condatis. Coordinates correspond to the Ordnance Survey (OS) British National Grid (measured in metres).

### **2.3.3 Patch flow and protection assignment:**

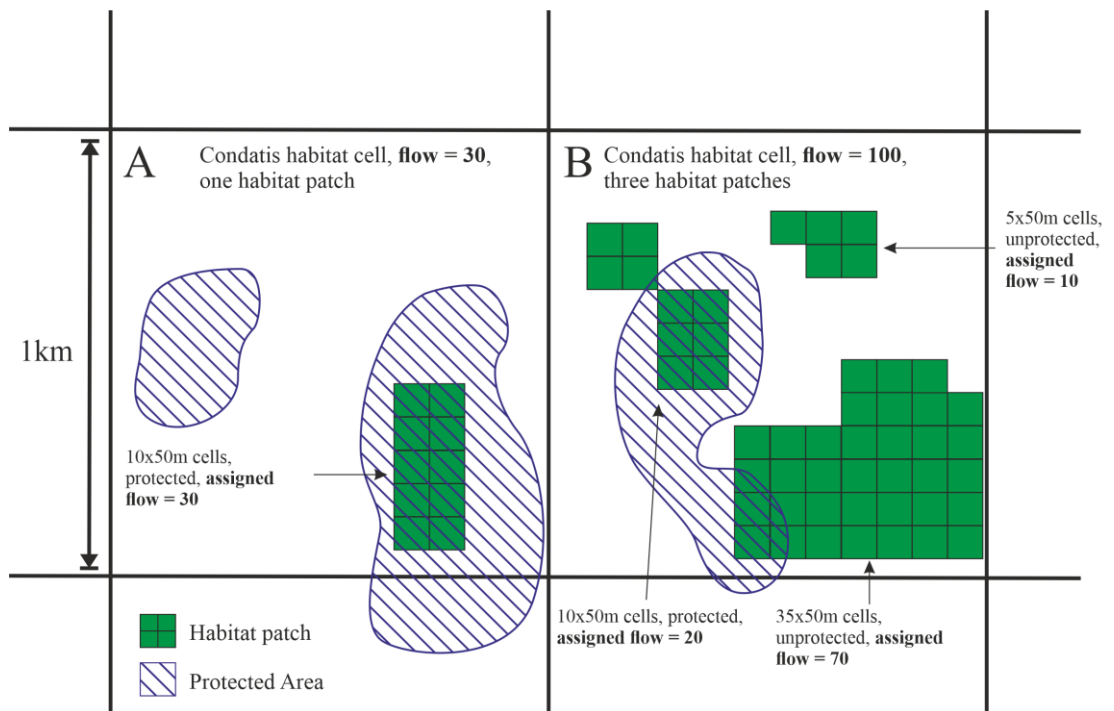
For each habitat network and dispersal option, results were returned as a raster of flow across habitat cells at 1 km resolution (2 km for deciduous woodland). Protection decisions are normally made for habitat patches. Therefore, within each 50 m habitat raster I identified patches as contiguous clumps of grid cells that share an edge and/or vertex – a Moore neighbourhood. These patches were assigned flow values of the 1 km or 2 km habitat cell they intersected. Where a habitat cell contained more than one patch, flow was divided in proportion to the patches' areas (Fig. 2.2). Then, for patches that intersected multiple habitat cells, flow assignments were summed. A geometric average of flow was taken for each habitat patch across the three analysed dispersal distances. The rank of each patch in terms of flow (its 'flow rank') was taken to represent its importance to connectivity. Finally, each patch was classified as 'protected' if more than 50% of its area was covered by PAs. The resulting dataset included protection status and the flow rank of each habitat patch across a range of dispersal abilities.

### **2.3.4 Statistical analysis:**

All statistical analysis was conducted using R 3.5.0 (R Core Team, 2019). Graphics and maps were produced in R using 'ggplot2' (Wickham, 2016). Linear regression analysis was performed to investigate the relationship between log-transformed total habitat network area and conductance. Comparison of protected and unprotected patches was completed for each habitat network through generalised linear modelling using a binomial distribution, including log-transformed area and flow rank as covariates. Prior to inclusion in the model, flow rank was standardised and centralised such that values fell between -0.5 and 0.5. The relationship between patch size and flow was analysed using Kendall Rank-order correlations. The degree of fragmentation of each habitat network was assessed using the GISfrag metric (Ripple et al., 1991). More contiguous patches, with large amounts of interior habitat, would have had high values, representing a low degree of fragmentation. To investigate the impact of flow-led patch selection on connectivity protection, I imagined



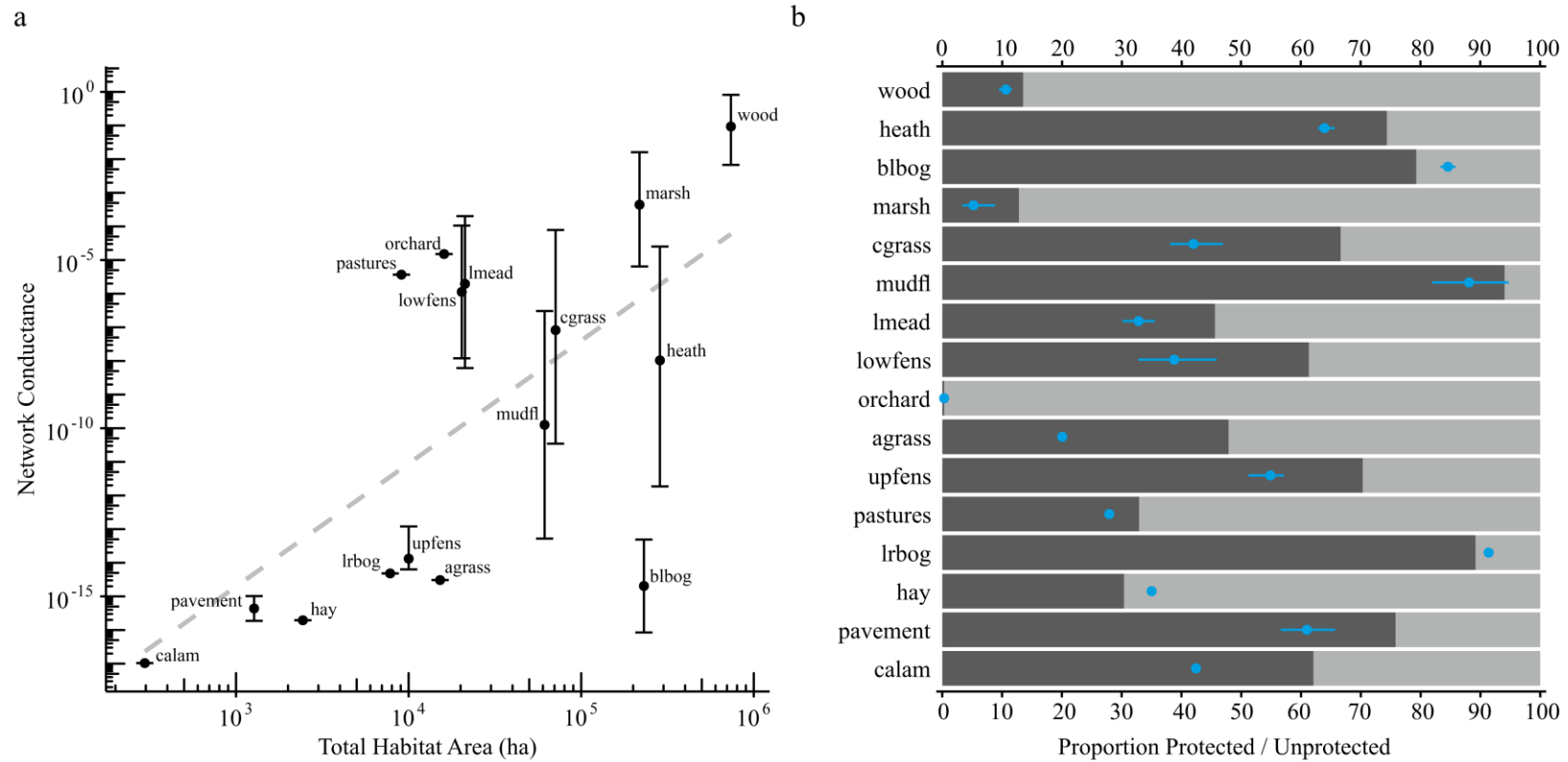
three different protection investment levels: a 1%, 10% and 25% increase in the proportion of each habitat network that is protected. Unprotected habitat patches were ranked by flow before being added to the PAs in descending order (highest flow first), until each of the three imagined protection investment levels were met.



**Figure 2.2: Proportional flow assignment.** Two 1 km habitat cells from a hypothetical Condatis run, including coverage of habitat (green pixels) and protected areas (PAs, blue polygons). Cell A contains 10×50 m<sup>2</sup> of habitat within one patch and had a flow of 30 in the Condatis output. Cell B contains 50×50 m<sup>2</sup> of habitat across three patches and had a flow of 100. Each patch is assigned flow in proportion to its area, and is assigned as “protected” if >50% of its area is covered by PAs.

## 2.4 Results

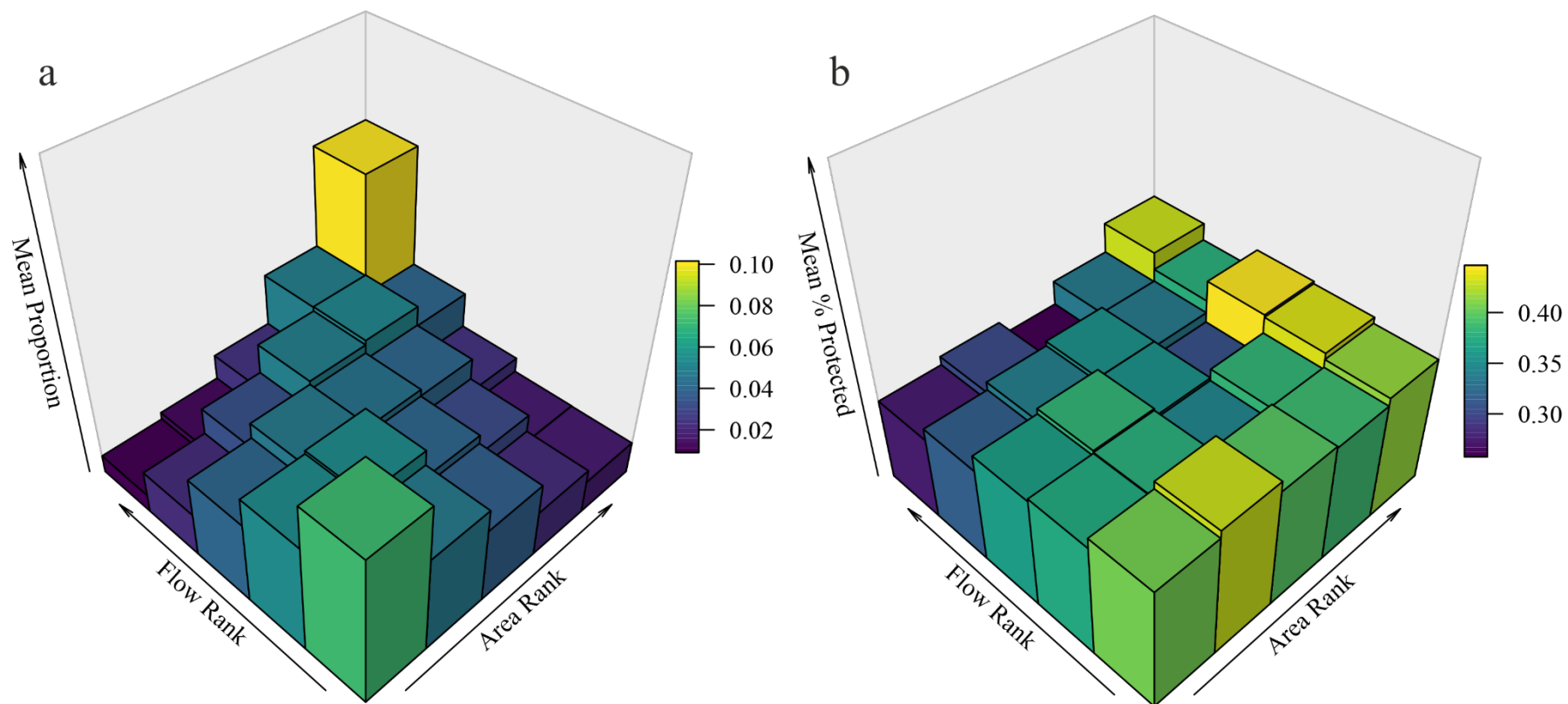
The networks of priority habitat in England range in extent from >0.7 M ha (deciduous woodland) to 296 ha (calaminarian grassland), cover 13.1% of England's land (1.7 million hectares total; Table 2.1), and are highly fragmented (median patch size 0.75 ha; Table A.1). Six habitat networks (salt marsh, maritime cliff and slope, coastal sand dunes, coastal vegetated shingle, saline lagoons, and reedbeds) were spatially distributed such that they could not be analysed as electrical circuits at the scales and resolutions used in the study (see Appendix A). Of the remaining habitat networks, those covering a larger area facilitated significantly faster speeds of range expansion (Regression of log conductance on log-transformed area;  $\beta = 3.655$ , 95% CI [1.371, 5.940],  $R^2 = 0.371$ ,  $F_{1, 14} = 9.493$ ,  $p = 0.0073$ ; Fig. 2.3a). Habitat networks also varied widely in the extent to which they are currently protected, ranging from 0.3% (traditional orchard) to 94% (mudflats), with a mean of 53.5% (Fig. 2.3b). Although the majority of habitat area was protected in most of the habitat networks (Fig. 2.3b), most patches were unprotected (Table. A.2). This was possible because within each habitat network protected patches were, on average, larger than unprotected patches (overall protected mean area 20.98 ha [n = 32,253]; overall unprotected mean area 3.58 ha [n = 287,737]; Table A.1), and tended to be less fragmented (protected GISfrag = 258.84, unprotected GISfrag = 84.84; Table A.1). Proportionally, protection of flow was generally lower than protection of area; in 12 of the 16 habitat networks, flow protection was, on average, 13.6% lower than area protection. The proportion of flow protected matched or exceeded the proportion of area protected in the remaining four habitat networks (blanket bog [+5.28%], traditional orchard [+0.01%], lowland raised bog [+2.19%], and upland hay meadow [+4.60%]; Fig. 2.3b).



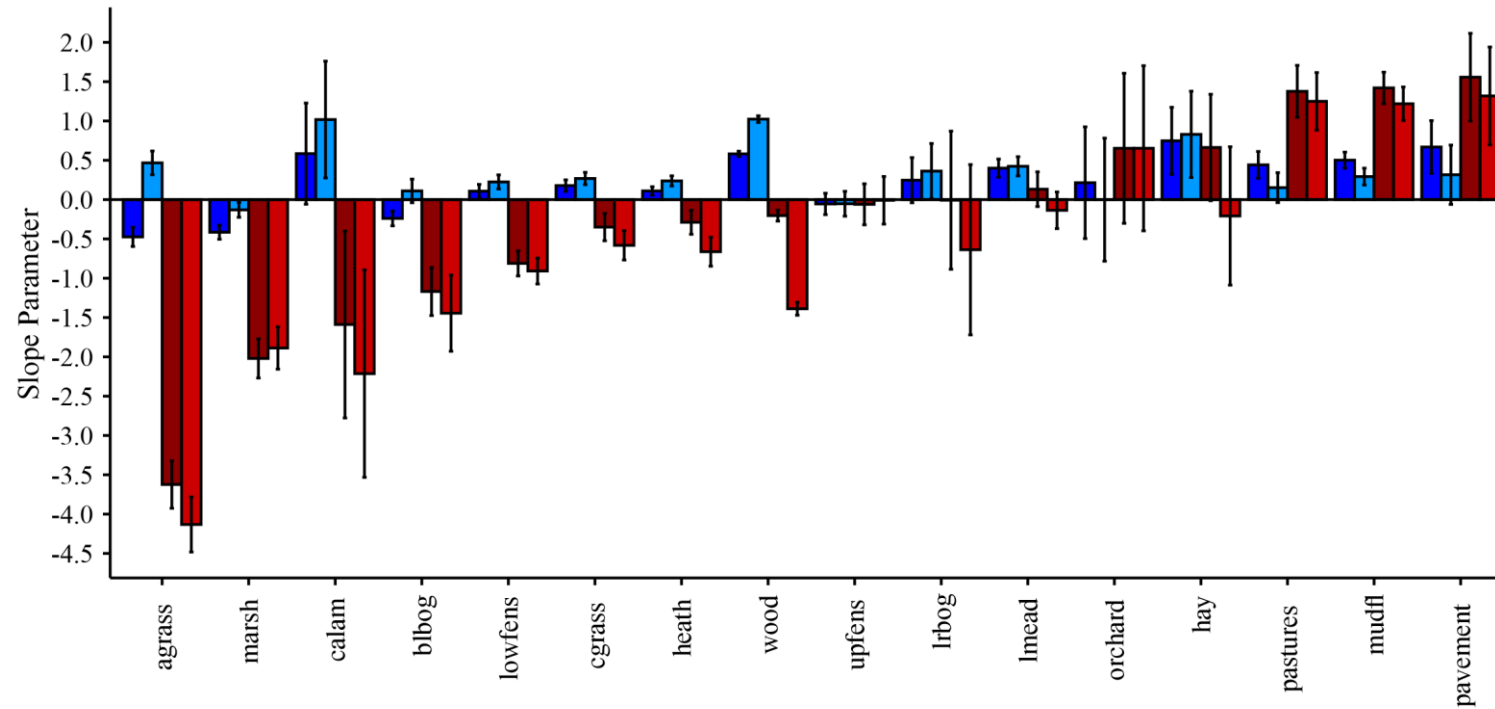
**Figure 2.3: Area, conductance and protection levels of 16 priority habitat networks in England.** (a) relationship between total habitat area and network conductance, with linear regression (dashed grey line). (b) Proportion of habitat area protected (dark grey) and the proportion of total flow that is protected (blue) in each habitat. Points represent geometric means across up to three modelled dispersal distances, while error bars show the range. Habitats are arranged in descending order of total area.

Larger patches of a given habitat network generally had higher flow. Kendall rank order correlations showed weak to moderate positive correlations between patch size and patch flow in most habitat networks (Table A.1; overall  $\tau = 0.309$ ). However, small patches can contribute disproportionately to connectivity; there is wide variation in patch flow values among patches with low area (Fig. 2.4a; Fig. A.1). Of the top 10% of patches for flow in each habitat network, an average of 13.8% were patches with an area of  $\leq 1$  ha (Table A.2).

Given a tendency for larger patches to have higher flow, and to be more often protected, one might expect flow to be well protected. Two results help to show why this is not the case. Firstly, among patches that have below-average area, protection level clearly declines with increasing flow (Fig. 2.4b; Fig. A.2). Secondly, GLMs that include flow as a predictor of protection indicate that flow has generally negative effects, and those that include both area and flow as predictors of protection status show even more negative effects of flow (Fig. 2.5; Table A.3). Effects of patch area in these GLMs tends to be positive, and to become more positive when flow is included as a predictor. Just three habitat networks are exceptions, where the model shows positive effects on protection attributed to both the predictors area and flow (Fig. 2.5; Table A.3).

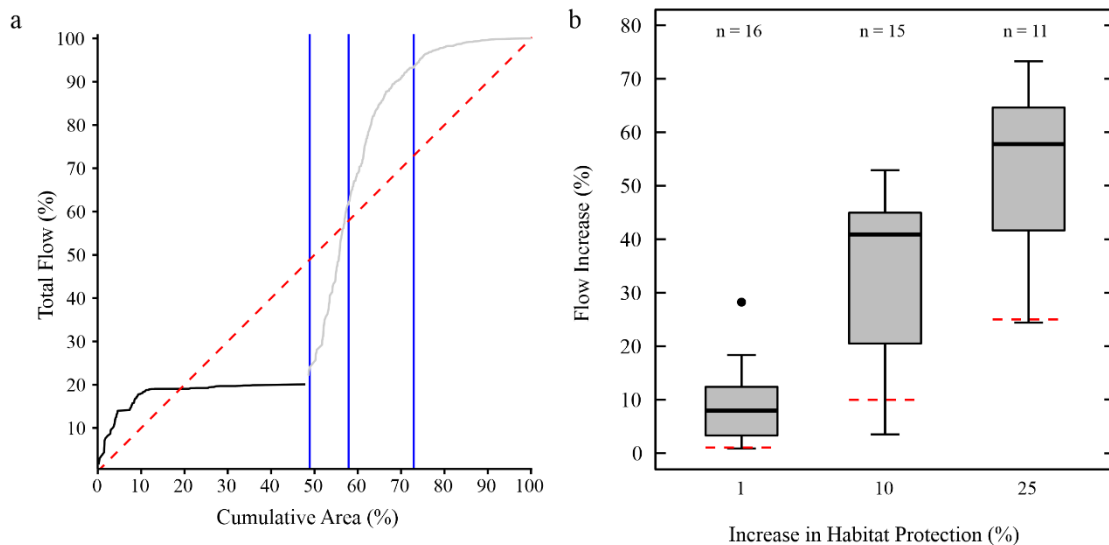


**Figure 2.4: Area - flow relationship and its protection.** Rank correlations between patch area and flow; ties are assigned random rank. (a) 5x5 3D histogram (yellow = high, purple = low) showing the mean proportion of patches, across all habitats, falling into each bin. (b) ranked patch area against ranked flow, showing the mean proportion of patches in each bin that are protected (yellow = high, purple = low), across all habitats. Habitat by habitat plots are available in Fig. A.2.



**Figure 2.5: Estimates of the effects of patch flow (red) and area (blue) on protection.** Parameters for the effect of area and flow on protection in isolation (dark), and together in the same model (light). Habitats are presented in order from lowest to highest flow parameter. Parameter estimates for each habitat area derived from generalised linear models. Error bars represent 95% CIs.

In my scenarios, in which additional high-flow habitat patches were protected, increases in the proportion of flow protected were almost always greater than increases in the proportion of habitat area protected (Fig. 2.6). In a few cases disproportionate improvements to overall flow protection were not possible due to insufficient unprotected high-flow patches: specifically, coastal floodplain grazing march (when adding 1%, 10% and 25%), blanket bog (adding 10%), and lowland raised bog (adding 10%). However, most connectivity conservation gains were highly disproportionate to the areas of habitat selected for protection. Across all habitat networks, increasing the coverage of PAs by 1%, 10% and 25% resulted in respective median increases of 8.0%, 40.9% and 57.8% flow protection (Fig. 2.6b).



**Figure 2.6: Flow protection increases after flow-led patch selection.** (a) Proportion of flow protected against area of habitat protected (black) and the resulting increase in flow conserved after adoption of flow-led patch selection (grey) for lowland dry acid grassland (chosen as the highest respondent to 25% increase in protection). Data sorted by patch flow in descending order, 1:1 trend line (red) and lines indicating 1%, 10% and 25% increases in area (blue). (b) The increase in flow protection for a 1%, 10% and 25% increase in PA for all habitats after adopting flow-led patch selection. Proportional increase denoted in red, outliers calculated as  $1.5 \times IQR$ .

## 2.5 Discussion

Here, I highlight that the connectivity of the fragmented networks studied is vulnerable, because patches critical for species range expansions are under-protected. Crucially, I found that, for the majority of habitat networks, protection is biased away from high flow patches (Fig. 2.5); median rate of protection of patches in each habitat network is 44.5%, but drops to 37.5% when considering only patches above the 90<sup>th</sup> percentile for flow. This absence of designation increases the likelihood of degradation or destruction of habitat patches, which is expected to severely impact network connectivity.

### 2.5.1 Patterns of under-protection

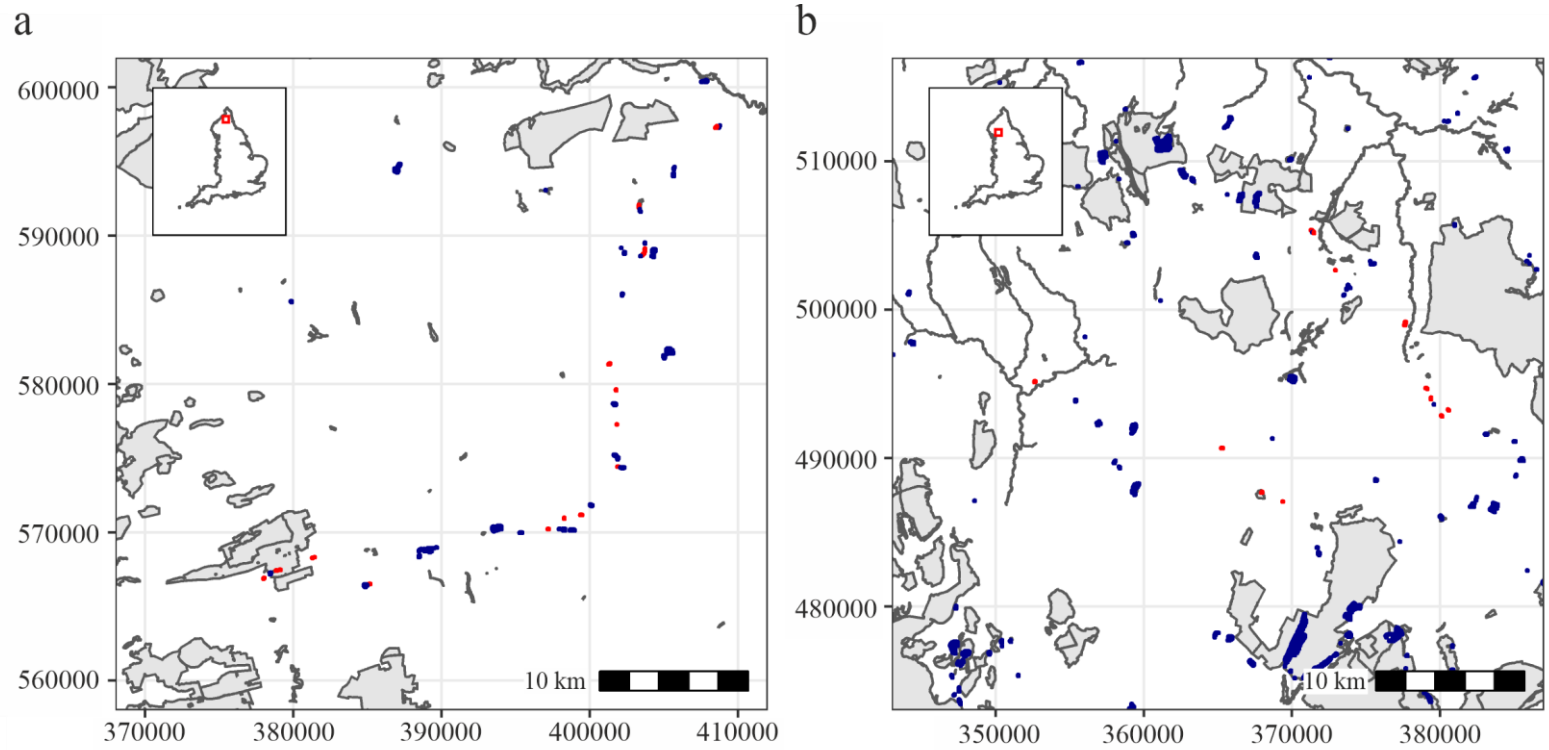
Previous research has established that for the majority of countries, PA connectivity is lacking (Saura et al., 2018). However, species will not directly respond to PA connectivity *per se*; it is the connectivity of the entire habitat network, whether or not protected, which affects the reproduction and dispersal of species, and is critical for range expansion under climate change (Gillingham et al., 2015). Unlike previous work, I investigate patch connectivity and patch protection independently. Thus, I contribute ecological realism by focusing not on PA connectivity, but the connectivity of the habitat networks that PAs conserve. I identify the important routes a wide variety of species may take, using simplified dispersal assumptions, as they shift ranges from South to North in reaction to climate change, regardless of protection status (Fig. A.3). In this way I identify a critical oversight in the design of England's PA network.

Patches that happen to be strategically located to act as South-North stepping stones (Fig. 2.7) may be small and may lack other attributes that were important for past PA designation. I found that existing protected areas tended to be biased towards low-flow patches for most habitat networks, despite also being biased towards large patches. This is surprising, because large patches typically have higher flow (Fig. 2.4a). The preferential protection of large patches over small is not a new finding (Hill et al., 2018). However, that



those same patches typically contribute more to connectivity, and yet connectivity is still under-represented, indicates a disconnect between past protection decisions and those needed to facilitate range shifts. Consequently, the capacity of the landscape to facilitate species' reaction to climate change, particularly those habitat specialists who already find it more difficult to expand (Fartmann et al., 2021), is vulnerable.

The patterns I observe in protection are probably not unique to England, given similar biases and lack of PA connectivity have also been evidenced in other regions (Hernández-Ruedas et al., 2014; Ward et al., 2020). I propose that comparable network vulnerabilities elsewhere probably result from similar habitat protection principles – and practical considerations – to those known in my study region (Joppa and Pfaff, 2009). For example, reserve selection might actively favour aggregation because, under a stable climate, species persistence is expected to be higher in aggregated networks than fragmented ones (Moilanen and Wintle, 2006). However, passive processes could also be at play. In the UK, many PAs arose from 'Rothschild's Reserves' (Lawton et al., 2010), the selection criteria of which included "*areas of land ... which retain primitive conditions and contain rare and local species liable to extinction*" (Evans, 2002). This led to reserves being clustered in areas of low economic and agricultural development, especially in the North and the uplands (Shwartz et al., 2017), a phenomenon not limited to the UK (Joppa and Pfaff, 2009). Furthermore, while climate change was not an issue of the time, it is unlikely any form of connectivity was a factor in historical designation decisions, given the growth of PAs in the UK has often occurred without consideration of their wider context (Gaston et al., 2006).



**Figure 2.7: Small patches acting as stepping stones.** Small habitat patches with flow values in the top 10% (red) positioned in such a way that they act as stepping stones between other areas of habitat (blue) and protected areas (grey), in (a) calcareous grassland and (b) lowland fens. Coordinates correspond to the Ordnance Survey (OS) British National Grid (measured in metres).

## **2.5.2 Applications in conservation**

I do not envisage contribution to connectivity – represented here as flow – to be the sole criterion to prioritise protection. Patches that contribute little to connectivity are often crucial to sustain metapopulations (Hanski, 1998). However, I argue that flow should form part of a nuanced prioritisation process, accounting for land use changes, habitat quality, climate suitability, and landscape connectivity (Shwartz et al., 2017). Nevertheless, considering the extent to which high-flow areas have been overlooked, it would not be unreasonable to ring-fence some future PA resources to specifically promote connectivity. Note particularly that flow distribution across patches is highly skewed (on average 31.2% of patches contained 75% of the flow), so future selection of high-flow patches by chance, or by a moderately correlated proxy such as area, is unlikely. By contrast, targeted patch selection on the basis of flow could be very efficient. For example, between 2014 and 2019 terrestrial PAs in the UK increased by 11,200 ha (JNCC, 2019); my analyses show that the addition of 714.25 ha, 438.50 ha and 3544.50 ha to lowland dry acid grassland, purple moor grass and rush pasture, and calcareous grassland PAs (representing 5% increases in protected area) would yield 15.6%, 33.1% and 33.5% gains in flow protection respectively. Such increases in connectivity protection are an urgent requirement if we are to help build more resilient networks for nature in the face of climate change (IPCC, 2014).

As connectivity ascends the conservation agenda, I demonstrate the potential for efficient conservation of climate-resilient landscapes. I show that the inclusion of a connectivity measure into the planning process can facilitate the identification of patches important to climate change connectivity, resilience, and adaptation. In most habitat networks studied here, substantial gains in connectivity protection can be made for relatively small increases in PA coverage (Fig. 2.6b). Only for a small number of habitat networks were proportional connectivity gains less than the proportional increase in area. In these instances, either a strong correlation existed between area and flow, or existing protection coverage was high, such that the majority of high-flow patches were already protected

(Table A.2). Saura et al. (2018) identified that targeted designation of PAs to enhance connectivity was many countries' most pressing priority for meeting PA conservation goals. The flow metric described here provides potential for proactive safeguarding of connected habitats and stepping-stones, allowing conservation planners to target their designation and conservation activities to achieve substantial increases in connectivity protection. This could help to meet targets outlined in legislation such as the UK's 25 year environment plan (DEFRA, 2018) and the EU's biodiversity strategy, or international commitments, including the upcoming Post-2020 global biodiversity framework (Secretariat of the Convention on Biological Diversity, 2020b).

### **2.5.3 Limitations**

My study uses cutting-edge methods to quantify protection of long distance, multi-generational habitat connectivity. My approach has limitations, but also clear avenues for progression. For example, I analyse 16 priority habitat networks individually, based on the UK Biodiversity Action Plan. Some species are of course reliant on multiple habitat types, and to differing extents, so future work could analyse composite networks of associated habitats used by different subsets of generalist species. However, a more comprehensive assessment might not show any additional crucial patches that had been missed in analyses of individual habitats. Furthermore, if actions increased connectivity for individual priority habitat networks, the connectedness of the composite networks they form part of would also improve. The assumption of a homogeneous matrix is another limitation, and may lead Condat's to overestimate the importance of some regions for those species that are hindered by landscape barriers. However, this assumption reduces the computational burden of evaluating connectivity, which is itself a major limitation (Moilanen, 2011), whilst still maintaining the principles of isolation by resistance (McRae, 2006). Another limitation is that while my choice of sources and targets follow the general trend of species moving away from the equator, it does not consider that climate refugia may be found at higher altitudes or different aspects. Furthermore, although the negative exponential kernel at the core of my

analysis has been tried-and-tested for modelling animal movements, it may be a poor function for plant dispersal; for example, some studies suggest that log hyperbolic secant or exponential power probability density functions would be more appropriate (Bullock et al., 2017). Finally, due to my focus on habitats, the scale at which most conservation actions happen, I made use of theoretical species. It would be beneficial to validate my findings empirically with data from species that have already shifted ranges, as has been done with Condatis' conductance metric (Hodgson et al., 2022). However, data are not always available, while conservation guidance is needed immediately; many range shifts are ongoing, or have yet to start (Pearce-Higgins et al., 2017).

#### **2.5.4 Conclusions**

My study quantifies how South-North connectivity is currently conserved within PAs across fragmented habitat networks, using England as an exemplar for application to other countries or regions. Although PAs tend to contain larger patches, which usually contribute more flow, they under-represent connectivity in the majority of habitats studied. The scientific community has been emphasising the importance of incorporating connectivity into the planning process for at least 30 years (Keeley et al., 2019), but the connectedness of habitats remains vulnerable to degradation and loss. I have shown that patches important to long distance connectivity can be easily identified, allowing the proportion protected to be greatly increased with minimal additional resources. The decision-making tools demonstrated here help enable the change in conservation planning needed to protect the permeability of landscapes, allowing species to track changing climate and preventing extinction.

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# **Chapter 3 Landscape-scale conservation projects achieve climate change-relevant connectivity increases no better than random**

*“Understanding must move with the flow  
of the process, must join it and flow with  
it.”*

- Reverend Mother

### *3.1 Abstract*

In response to climate change and biodiversity loss, many governments plan to develop large functional habitat networks. Key to this is connectivity, allowing species to shift ranges to follow their climatic niche. However, the ability of large-scale conservation projects to achieve landscape-scale connectivity goals has seen little study. Here, I attempt such an analysis. I collated parameters for 157 plant and animal species, and used the Condatis methodology to model connectivity in the habitat networks affected by five projects at local, regional, and national scales. I then compared changes in connectivity to that expected given the amount of habitat created or restored through the projects. Although connectivity improved in every instance, I find 71.3% of increases were less than what would be expected if habitat had been added at random. Furthermore, my analyses show such improvements tended to occur at local scales, suggesting range shifts, occurring at regional and national scales, will not have benefitted. These results indicate that long-distance connectivity requires specific consideration at the planning stage if we are to allow species to adapt to their changing environment. Condatis offers one way to facilitate such a consideration, and could ensure connectivity projects result in widely connected landscapes.



## 3.2 Introduction

In response to the continuing decline of nature worldwide (IPBES, 2019), many governments and regulatory organisations have produced plans to establish far reaching, interconnected habitat networks (DEFRA, 2018; European Union, 2020; DeFazio, 2021). Modern conservation needs to consider biodiversity decline and climate change in tandem (Pettorelli et al., 2021). Therefore, functional ecological networks must support both local and long-distance connectivity, facilitating movement between habitat patches to support metapopulations (Hanski, 1998), and more substantial movements such as those allowing species to follow climate niches and adapt to climate change (Parmesan, 1996).

In England, the Government has laid out a 25-year Environment Plan (25YEP; DEFRA, 2018) that includes, as a key component, the development of a national Nature Recovery Network (NRN). This is based on the ideas of Lawton et al. (2010) for a “*coherent ecological network in England to help counter habitat loss and fragmentation, and declining habitat quality*”. To that end, the 25YEP includes provision to create and restore 500,000 ha of new conservation priority habitat, restore 75% of protected sites on land to favourable condition, and to support work to increase woodland cover. It also aims to build resilience and adaptation to climate change, including improving the connectivity between wildlife sites. However, given the large-scale changes in climate suitability for many species (Pearce-Higgins et al., 2017), there is also a need to consider the issue of long-distance connectivity within that structure.

Meeting the ambitious targets of establishing habitat networks of that ilk will require evidence-based actions. Unfortunately, historically this has not been the case; the tools we use need adjustment to account for contemporary issues such as anthropogenic climate change (Reside et al., 2018), many of our strategies seem to be based on belief systems (Pressey et al., 2017), and peer-reviewed science often takes a back seat in the decision-making process (Sutherland and Wordley, 2017; Kadykalo et al., 2021). Nowhere are these shortfalls more apparent than in the continued trend of missed biodiversity targets worldwide

(Secretariat of the Convention on Biological Diversity, 2010, 2020a; Hawkins et al., 2019; European Environment Agency, 2020).

However, tools are available to aid conservation planners design connected networks (Keeley et al., 2021), and recent attention has been paid to developing methods that can consider connectivity over the distances required for species to undertake range shifts (Hodgson et al., 2012; Hodgson et al., 2016). It seems likely that the use of these tools, particularly those specific to long-distance connectivity, could be vital to ensure that the connectivity goals at the core of new international targets, like the post-2020 biodiversity framework (Secretariat of the Convention on Biological Diversity, 2020b), are met, and functionally connected habitat networks established. Yet, while these tools have been used to investigate the state of connectivity in protected areas (Saura et al., 2017), or how we can incorporate connectivity into conservation planning (Williams et al., 2020), they are rarely, if ever, used to scrutinise the ability of conservation projects to achieve connectivity goals. Information vital for assessing the conservation planning methods likely to be implemented within future policy objectives such as the NRN.

I explore this issue by considering how a suite of landscape-scale conservation projects in England impacted connectivity. In the Kent Downs a series of large scale agri-environment projects have focused on the creation of wildflower-rich grassland through arable reversion. Elsewhere, following the influential review by Lawton et al. (2010), twelve Nature Improvement Areas (NIAs) were established to develop a new approach to nature conservation at a landscape-scale aiming to not only enhance biodiversity, but also ecosystem services with social and economic objectives (Collingwood Environmental Planning, 2015). These projects provide a good model with which to investigate long-distance connectivity, within the proposed Nature Recovery Network, because the latter will include large areas for biodiversity at its core (DEFRA, 2018). The NIAs included a focus on improving local connectivity, but their success in this regard could not be established when the projects were completed (Collingwood Environmental Planning, 2015), although one

study has been published subsequently for one of the NIAs (Hunter-Ayad and Hassall, 2020). Nevertheless, improving connectivity within the bounds of a conservation area does not necessarily translate to the scales over which range shifts occur. The impacts these projects have had on facilitating movement through their bounds, in the wider landscape, and at the national scale remains unclear. An analysis of which could indicate whether specific measures to account for climate change relevant connectivity are required.

Here, in to my knowledge the first study of its type, I assess how modern large-scale conservation projects affect connectivity relevant to climate change, using a subset of recent projects in England as a case study. I use Condatis (Hodgson et al., 2012; Hodgson et al., 2016), a landscape-scale, multi-generational connectivity assessment tool, parameterised with a representative assemblage of British plant and animal species, to identify how connectivity changed as a result of the studied projects across three spatial scales: local, regional, and national. To fully understand the overall improvement, I ask: (i) How has the network “conductance” changed at each spatial scale? (ii) are the changes seen better or worse than expected given the amount of habitat created/restored? And (iii) what might be the underlying drivers for the changes I see?

## 3.3 Methods

### 3.3.1 The Condatis model

The underlying theory and calculations of the Condatis method is outlined in the introduction (Section 1.8), here I describe the dispersal kernel used to generate resistance values between cells of breeding habitat. Definition of dispersal distances and reproductive rates are described in later sections.

#### 3.3.1.1 Dispersal kernels

Dispersal kernels are used to calculate the reciprocal resistance between cells  $i$  and  $j$  - the colonisation rate – which underpins Condatis metric calculations. Previously, studies using Condatis, including the preceding chapter, have implemented single parameter negative exponential dispersal kernels in the form

$$p_i p_j R \cdot \frac{\alpha^2}{2\pi} \cdot \exp(-\alpha d_{ij}), \quad \text{Equation 3.1}$$

where  $p_i$  and  $p_j$  are the area of breeding habitat within cells  $i$  and  $j$ ,  $R$  is the reproductive rate,  $2/\alpha$  is the mean dispersal distance governing the slope of the dispersal kernel (Fig. B.1a), and  $d_{ij}$  is the Euclidean distance between cells  $i$  and  $j$ .

However, while suitable for animal dispersal, the negative exponential kernel insufficiently captures the “fat-tailed” nature of plant dispersal; an exponential power function performs better in this regard (Bullock et al., 2017). Therefore, to properly represent plant species I calculated reciprocal resistances using a kernel in the form

$$p_i p_j R \cdot \frac{b}{2\pi a^2 \Gamma(2/b)} \cdot \exp\left(-\frac{d_{ij}^b}{a^b}\right), \quad \text{Equation 3.2}$$

where  $p_i$ ,  $p_j$ ,  $R$ , and  $d_{ij}$  are defined as above.  $\Gamma(y) = \int_0^\infty x^{y-1} e^{-x} dx$  is the Gamma function,  $a$  and  $b$  are species specific traits governing the shape and scale of the kernel (Fig.

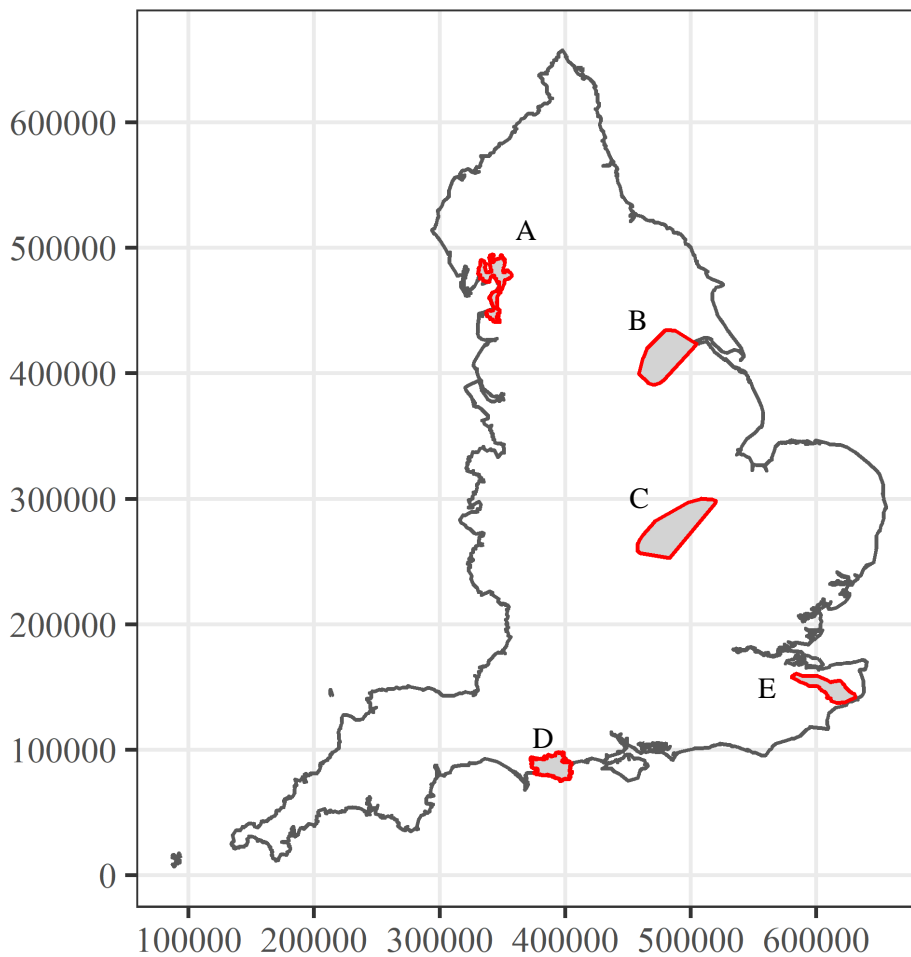
B.1), and are identified through measurement of seed densities over incremental distances from the originating plant (Bullock et al., 2017).

### **3.3.2 Data sources and preparation**

Spatial data for the priority habitat inventory (PHI) were downloaded from the Natural England Open Data Geoportal (Natural England, 2019). Polygons of England were downloaded from the Ordnance Survey (OS) OpenData Boundary-line Layer (Ordnance Survey, 2019).

For focal projects I chose NIAs and the Kent Downs Project (KDP). All projects were contacted in 2018 requesting spatial data of conservation that had been undertaken. Where possible this was requested to include; the project boundary, the location and spatial extent of plots of habitat creation or restoration, and descriptions of habitats created or restored. Five projects responded to my requests; Nene Valley (NV), Wild Purbeck (WP), Morcambe Bay Limestone and Wetlands (MB), Humberhead Levels (HL), and KDP (Fig. 3.1).

Habitat descriptions included within the data provided did not always align with those of the PHI. Where necessary I assigned habitats to the PHI they would likely form a network with, given the description provided, underlying geology and ecological similarity (Table 3.1). Pre- and post-project habitat networks, between which conductance, flow and bottlenecks could be compared, were defined using different subsets of the data provided. Pre-project networks consisted of the relevant PHI habitat, with patches created over the course of the study projects removed using ArcMap 10.6 (ESRI, 2018), patches of habitat noted to have been “restored” or “managed” will likely have improved in quality over the course of the project, and were therefore marked as poor-quality habitat (such that they only contribute half their area in Condatis calculations). Post-project networks comprised all habitat patches, with those previously marked as “restored” or managed” no longer labelled as poor quality.



**Figure 3.1: Location of projects included in the analysis.** Spatial situation of the projects included in the analysis: A) Morcambe Bay, B) Humberhead Levels, C) Nene Valley, D) Wild Purbeck, E) Kent Downs Projects. Coordinates correspond to the Ordnance Survey (OS) British National Grid (measured in metres)

**Table 3.1: Projects and habitats.** Projects included in the study, their focal habitats, and PHI network they were assigned.

| <b>Project</b>            | <b>Habitat Description</b>           | <b>PHI</b>                           | <b>Code</b> |
|---------------------------|--------------------------------------|--------------------------------------|-------------|
| Nene Valley (NV)          | Coastal floodplain and grazing marsh | *                                    | CFPGM       |
|                           | Lowland meadows                      | *                                    | LMEAD       |
|                           | Reedbeds                             | *                                    | RBEDS       |
| Wild Purbeck (WP)         | Heathland                            | Heath                                | HEATH       |
|                           | Wet grassland                        | Coastal floodplain and grazing marsh | CFPGM       |
|                           | Rough grassland                      | Coastal floodplain and grazing marsh | CFPGM       |
|                           | Acid grassland                       | Lowland dry acid grassland           | LDAGR       |
|                           | Wet rush grassland                   | Purple moor grass and rush pasture   | PMGRP       |
|                           | Calcareous grassland                 | *                                    | CAGRA       |
| Morecambe Bay (MB)        | Limestone grassland                  | Calcareous grassland                 | CAGRA       |
|                           | Neutral grassland                    | Lowland meadow                       | LMEAD       |
|                           | Wet meadow                           | Coastal floodplain and grazing marsh | CFPGM       |
|                           | Fen                                  | Lowland fens                         | LFENS       |
|                           | Lowland raised bog                   | *                                    | LRBOG       |
|                           | Rush pasture                         | Purple moor grass and rush pasture   | PMGRP       |
|                           | Wet grassland                        | Coastal floodplain and grazing marsh | CFPGM       |
| Humberhead Levels (HL)    | Neutral Grassland                    | Lowland meadow                       | LMEAD       |
|                           | Fen                                  | Lowland fens                         | LFENS       |
|                           | Lowland raised bog                   | *                                    | LRBOG       |
|                           | Reedbeds                             | *                                    | RBEDS       |
|                           | Species rich grassland               | Calcareous grassland                 | CAGRA       |
| Kent Downs Projects (KDP) |                                      |                                      |             |

\* Denotes instances where the habitat description and PHI were aligned

Spatial data was largely provided in vector format. These were converted to 50 m rasters using ArcMap 10.6. The minimum mapping unit of the PHI is 0.1 ha, whilst raster cells with a resolution of 50 m equate to 0.25 ha, thus, due to the nature of rasterisation some of the smallest patches will have been lost in the conversion process. However, it was considered unlikely to have occurred to such a degree to significantly influence the findings of this study. To accurately represent the colonisation process across habitat patches of varying size, Condati works best with a raster of habitat cells at the finest resolution that will not overwhelm the available RAM (See Appendix A). For analysis at the national and regional scale (defined in Section 1.3.4 below) this resolution was determined to be 1 km, while at the local scale this was 1 ha. Accordingly, habitat cells were aggregated using the “*rgdal*” (Bivand et al., 2019) and “*raster*” (Hijmans, 2019) packages in R 3.6.3 (R Core Team, 2019), converting the sum of 50 m habitat cells to proportional cover.

### **3.3.3 Species data**

Species were chosen to comprise a representative assemblage of British species, which the projects may benefit. In total 157 species were included in the study, 89 animal species (17 mammals, 5 reptiles, 4 amphibians, 5 insects, and 58 birds), and 68 plant species (7 graminoids, 50 herbs, 2 shrubs, and 9 trees) representing a broad range of dispersal abilities, growth forms, and dispersal syndromes.

#### **3.3.3.1 Animals**

To implement the negative exponential dispersal kernel (eqn. 1) I required the mean dispersal distance and the reproductive rate of the species in question. The PanTheria (Jones et al., 2009) and Amniote (Myhrvold et al., 2015) databases (subset to include species native and/or currently occurring in the British Isles) formed the foundation of the animal trait dataset. I found that reproductive rate ( $R$ ) is rarely recorded in the literature. Therefore, assuming  $R$  can be calculated from the number of females that survive to adulthood and the number of offspring raised to adulthood over their lifetime, I estimated  $R$  as



$$R = \text{Female}_{sur} \cdot \text{Offspring}, \quad \text{Equation 3.3}$$

where

$$\text{Female}_{sur} = (\text{PD} \cdot \text{SR})(\text{Sur}_l \cdot \text{Sur}_j) \quad \text{Equation 3.4}$$

$$\text{Offspring} = (\text{CS} \cdot \text{CY}) \sum_{n=0}^{\infty} \text{Sur}_a^n, \quad \text{Equation 3.5}$$

where  $PD$  is population density,  $SR$  is sex ratio,  $\text{Sur}_l$ ,  $\text{Sur}_j$  and  $\text{Sur}_a$  are larval, juvenile and adult survival rates,  $CS$  is clutch size,  $CY$  is clutches  $\text{yr}^{-1}$ , and  $n$  is age. Summing the geometric series in Eqn. 3.5 leads to

$$\text{Offspring} = (\text{CS} \cdot \text{CY}) \left( \frac{1}{1 - \text{Sur}_a} \right) \quad \text{Equation 3.6}$$

The species dataset was supplemented for missing trait values via a systematic search of the literature using the terms "*dispersal ability*", "*species dispersal*", "*dispersal distance*", "*long distance dispersal*", "*survival*", and "*population density*" in combination with the scientific name of the species of interest. Notably, insects were absent from the databases, so a secondary literature search was conducted to garner data on this broad class of animals. Occasionally, maximum dispersal was reported rather than mean. In these instances, the mean dispersal distance was estimate from the maximum using the formula  $(\text{max}) = F \cdot (\text{mean})$ , where  $F$  was estimated from species in the same class for which I had both mean and maximum dispersal figures. Where survival data was not available, a base rate of 0.5 was used. Population density for bird species were calculated via breeding bird survey data included within Newson et al. (2008).

### 3.3.3.2 Plants

Data on plant dispersal was acquired through databases provided in Tamme et al. (2014) and Bullock et al. (2017), edited and supplemented following the same method as the animal data above. Reproductive rate ( $R$ ) was estimated from seed bank densities (usually reported at  $\text{m}^2$ ), or, if available, propagule counts where the figure closest to the originating

plant was taken as  $R$ . Standardised  $a$  and  $b$  (eqn 3.2) values provided within Bullock et al. (2017) were assigned to each plant species given their traits (Table 3.2), unless specific values were available for the species in question.

**Table 3.2: Plant dispersal data.**  $a$  and  $b$  values for the exponential power function grouped by growth form and dispersal mode, and subdivided by seed mass or plant height (adapted from Bullock et al. 2017)

| Growth form | Dispersal mode              | $a$                  | $b$    |
|-------------|-----------------------------|----------------------|--------|
| Herb        | Ant                         | 0.5281               | 1.2762 |
|             | 0.7 – 8 mg                  | $2.5 \times 10^{-6}$ | 0.1888 |
|             | 10 – 36 mg                  | 0.3726               | 1.1615 |
| Herb        | Ballistic (all 10 mg & 1 m) | 0.0917               | 0.6349 |
| Herb        | Wind + appendage            | $4.7 \times 10^{-5}$ | 0.2336 |
|             | 1 – 3.5 m                   | $1 \times 10^{-8}$   | 0.1423 |
|             | 0.1 – 0.8 m                 | 0.003                | 0.3454 |
| Herb        | Wind no appendage (all 1 m) | $4.2 \times 10^{-6}$ | 0.2069 |
| Graminoid   | Wind no appendage           | $3.0 \times 10^{-8}$ | 0.1597 |
|             | 1.75 – 3 m                  | 31.985               | 1.0141 |
|             | 0.06 – 0.65 m               | $1 \times 10^{-8}$   | 0.1549 |
| Shrub       | Ant                         | 0.1716               | 0.594  |
|             | 7 – 9 mg                    | 0.1915               | 0.6272 |
|             | 29 – 40 mg                  | 0.268                | 0.6568 |
| Shrub       | Vertebrate                  | $1 \times 10^{-8}$   | 0.1339 |
|             | 0.2 – 3 mg                  | $1 \times 10^{-8}$   | 0.1161 |
|             | 31 – 69 mg                  | $1 \times 10^{-8}$   | 0.1264 |
|             | 5000 – 10500 mg             | 0.0008               | 0.3122 |
| Tree        | Rodent                      | 0.1507               | 0.4171 |
|             | 195 – 950 mg                | 2.0615               | 0.6538 |
|             | 2420 – 18800 mg             | 0.3212               | 0.5035 |
| Tree        | Vertebrate                  | $1 \times 10^{-8}$   | 0.1246 |
|             | 0.3 – 15.1 mg               | $1 \times 10^{-8}$   | 0.1288 |
|             | 31 – 180 mg                 | $1 \times 10^{-8}$   | 0.1237 |
|             | 200 – 800 mg                | $1 \times 10^{-8}$   | 0.1238 |
|             | 1000 – 113700 mg            | 1.8875               | 0.341  |
| Tree        | Wind + appendage            | 0.5602               | 0.4289 |
|             | 30 – 46 m                   | 1.3437               | 0.4654 |
|             | 5 – 15 m                    | 2.7825               | 0.8346 |

### **3.3.4 Source and target definition**

#### **3.3.4.1 Local scale**

At a local scale the spatial distribution of habitat will dictate the directionality of a dispersing population. As such, specifying sources along a North-South axis, as is the general trend found in the literature (Hickling et al., 2006; Mason et al., 2015), would likely result in an oversimplification of the movement of species. Instead, voltage maps generated from a Condat analysis of national level pre-project habitat maps using dispersal of 2 km and reproductive rate of 100 were used to estimate the directionality of movements. Recall that, similarly to how electrical current flows from areas of high potential to low, a simulated population expands from cells with high voltage to those with low. Sources and targets were defined in each habitat network for each project as the closest 10% of boundary cells to the habitat cell with the highest and lowest voltage respectively (Fig. 3.2a).

#### **3.3.4.2 Regional scale**

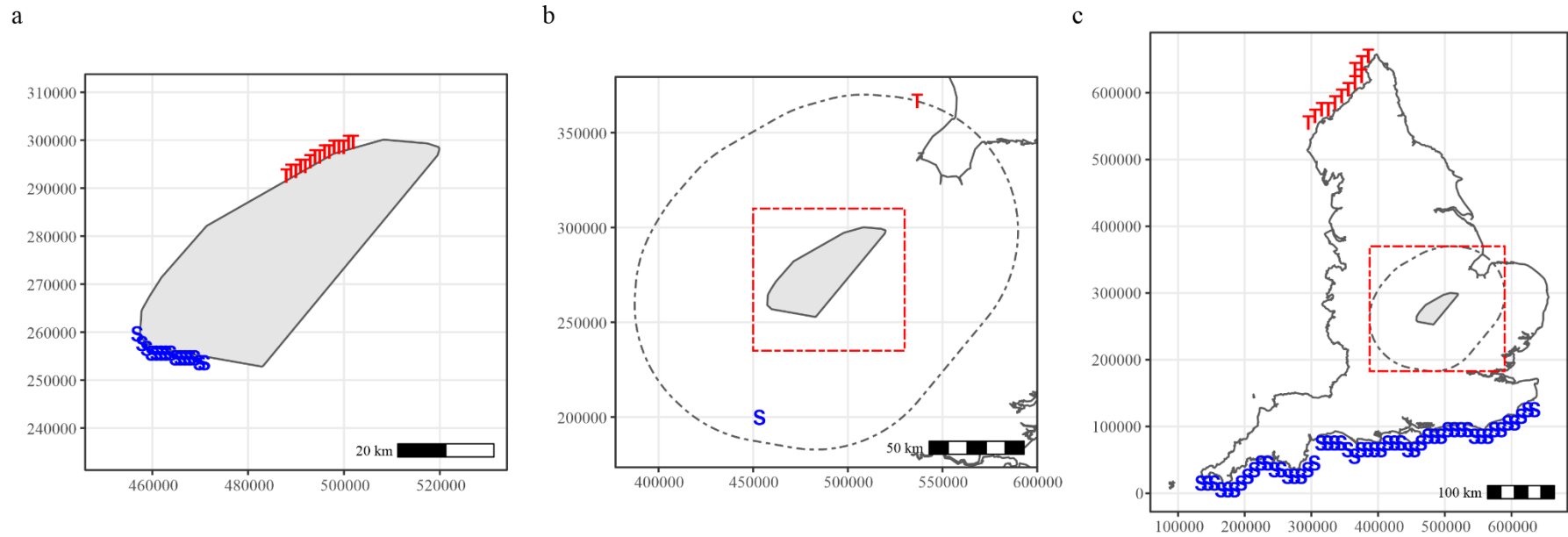
It is highly unlikely that the adjustment of ranges will occur in a single or even several generations. Therefore, in this transient period areas of habitat able to support large populations will be particularly important not only for viability, but to also produce propagules facilitating continued forward progress (Lawson et al., 2012). These areas (henceforth “nodes”) will likely constitute sources and targets on an intermediate scale between the local and national.

Nodes were identified through metapopulation capacity  $\lambda_M$  (Hanski and Ovaskainen, 2000).  $\lambda_M$  is defined as the leading eigenvalue of matrix  $\mathbf{M}$ , consisting of elements  $m_{ij} = \exp(-\alpha d_{ij})A_i A_j$  for  $j \neq i$  and  $m_{ii}=0$ , where  $2/\alpha$  is the mean dispersal distance,  $d_{ij}$  is the distance between patches  $i$  and  $j$ , and  $A$  is the area of each patch. The contribution of patch  $i$  to  $\lambda_M$  is given by  $\lambda_i = x_i^2 \lambda_M$ , where  $x_i^2$  is the square of the  $i^{\text{th}}$  element of the leading eigenvector of matrix  $\mathbf{M}$ . Nodes within each habitat network were defined by subdividing England into 20 km squares, and highlighting the 1 km habitat cell with the highest  $\lambda_i$  in each 20 km  $\times$  20 km region.

The voltage maps described above were used to assign voltage values to nodes. The closest node outside a 50 km buffer around the project with voltage higher than the highest within the project boundary were selected as a source, and the node outside of the buffer with a lower voltage than that of the lowest within the project was assigned as a target. Finally, the furthest Euclidean distance between source or target and the project boundary was used to create the area defined as the ‘region’ (Fig. 3.2b).

#### *3.3.4.3 National scale*

On a national scale I assigned sources and targets following the predominant poleward trend (Hickling et al., 2006; Mason et al., 2015), positioning sources along the southern coast of England, and targets along the northern border with Scotland (Fig. 3.2c).



**Figure 3.2: Source and target definition.** Example locations of sources (S) and targets (T) in the lowland meadow network around the Nene Valley NIA (grey) at (a) local, (b) regional, and (c) national scales. Red dashed boxes indicate the extent of the previous map, black dashed line shows the extent of the area considered to be the 'region' as described in text. Coordinates correspond to the Ordnance Survey (OS) British National Grid (measured in metres)

### **3.3.5 Statistical analysis**

All statistical analysis was completed using R 3.6.3 (R Core Team, 2019), graphics were produced in “*ggplot2*” (Wickham, 2016) and “*sf*” (Pebesma, 2018) packages.

Simply establishing an increase in conductance, and the magnitude of that increase, would insufficiently evaluate the effect of the conservation works of each project, because conductance will always increase when habitat is added to a network and the amounts of habitat added differed between projects. Hodgson et al. (2016) found that, in idealised cellular landscapes, when habitat cells are added at random, conductance increases proportionally to the number of cells squared, a pattern which may hold in real habitats (see Fig. 2.3a in the previous chapter).

I calculated the increase in conductance expected for the amount of habitat added (henceforth “baseline conductance increase” or “BCI”) by following this rule of thumb; squaring the proportional increase in habitat area. This figure, which controls for the area of habitat created, was used as the yardstick by which the success of each project’s habitat creation/restoration activities was evaluated. Conductance increases were split into five categories depending on their proportion of BCI: comparable ( $\pm 10\%$ ), positive ( $110\% < x \leq 150\%$ ) or negative ( $50\% \leq x < 90\%$ ), and highly positive ( $>150\%$ ) or highly negative ( $<50\%$ ). For summation purposes, species were grouped based upon their mean dispersal ability into “poor” ( $<1\text{km}$ ), “moderate” ( $1\text{km} < x < 10\text{km}$ ), and “good” ( $>10\text{km}$ ) dispersers. The underlying causality of conductance increases compared to BCI was investigated through the use of flow and bottleneck distribution maps. These identify any change in the importance of areas of habitat to connectivity as a result of the conservation works, as well as the importance of the patches added, and if the habitat creation/restoration has addressed the major constraints to movement. Bottlenecks were defined as the 20 links with the highest power (described in Section 1.8).

### 3.4 Results

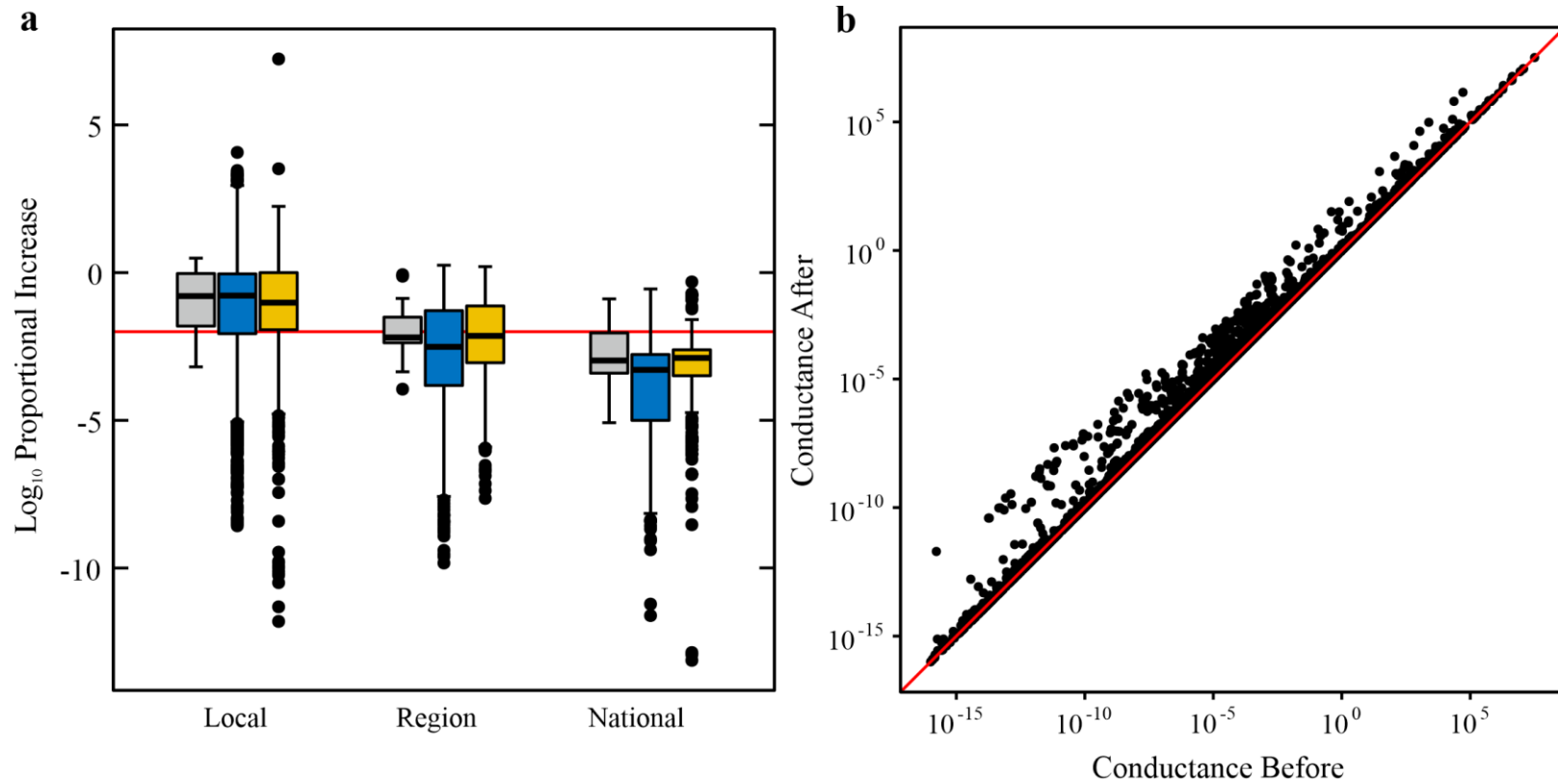
The five projects included in the analysis are located across the length of England, and encompass a total extent of 221390.9 ha (Fig. 3.1). In these projects, habitat creation, restoration and enhancement were undertaken for nine priority habitats with an area totalling 8190.3 ha (2580.4 ha created, 5563.9 ha restored; Table 3.3). Conservation actions in the five areas varied from HL, which undertook the most extensive conservation activities covering a total area of 2344.6 ha, to NV, where conservation covered 171.2 ha. The most diverse range of habitats were incorporated at MB where conservation was undertaken across seven habitats, whilst KDP was least diverse in its output, focusing efforts entirely on calcareous grassland habitats (Table 3.3).

Every project had a positive effect on conductance at every spatial scale studied. However, the magnitude of the conductance increase differed significantly between spatial scales ( $H = 1246.3, df = 2, p < 0.001$ ; Fig. 3.3a). This trend was consistent for both animals and plants, but conductance increases did not differ significantly between kingdoms ( $U = 2157167, p = 0.573$ ). The greatest median proportional increase in conductance for animals was noted in the calcareous grassland habitat at KDP at the local and regional scales (local = 2577.9%; regional = 108.4%), and in the reed bed habitat at HL at the national scale (11.8%). For plants the largest median increases were reported in calcareous grassland at KDP for the local scale (3881.5%), lowland raised bog at MB for the regional scale (129.9%), and reed bed at HL at the national scale (19.3%). A summary table is available in appendix B (Table B.1).

**Table 3.3: Project activities.** Summary of habitat creation and restoration undertaken across the five projects included in the analysis. All figures reported in ha.

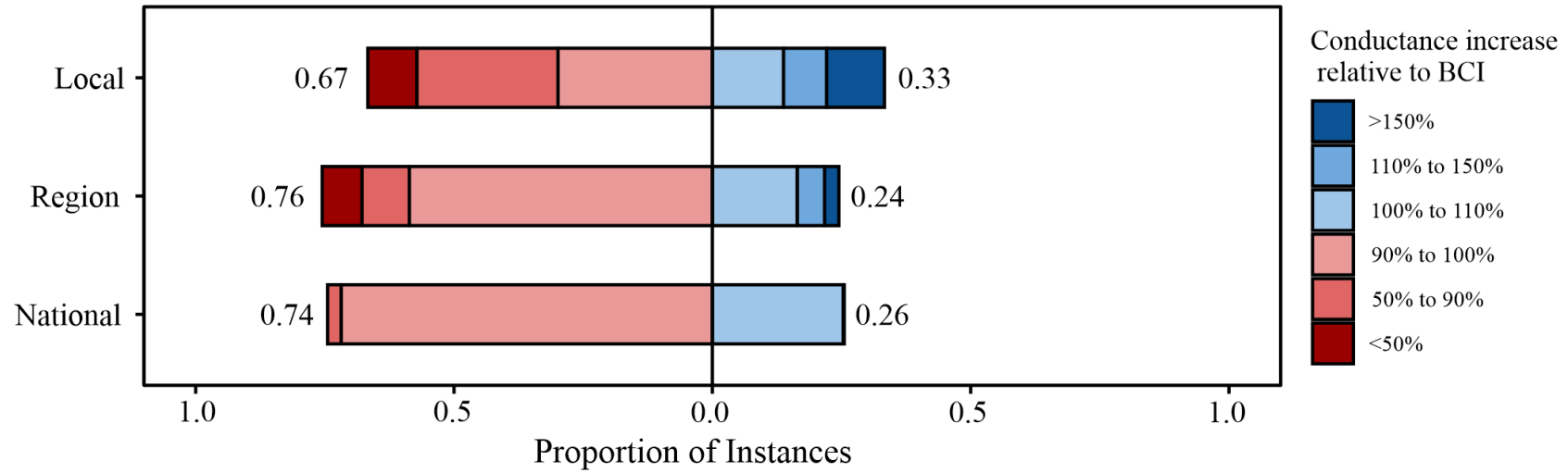
| Habitat        | Project |          |         |          |         |          |         |          |         |          |
|----------------|---------|----------|---------|----------|---------|----------|---------|----------|---------|----------|
|                | HL      |          | KDP     |          | MB      |          | NV      |          | WP      |          |
|                | Created | Restored | Created | Restored | Created | Restored | Created | Restored | Created | Restored |
| Cagra          | -       | -        | 1575.3  | 721.6    | -       | 568.9    | -       | -        | -       | 46.0     |
| Cfpgm          | 107.0   | 16.0     | -       | -        | 0.7     | 462.2    | -       | 30.2     | 30.2    | 13.1     |
| Heath          | -       | -        | -       | -        | -       | -        | -       | -        | -       | 1068.0   |
| Ldagr          | -       | -        | -       | -        | -       | -        | -       | -        | 152.5   | 406.5    |
| Lmead          | 12.3    | -        | -       | -        | -       | 15.9     | 18.5    | 118.5    | -       | -        |
| Rbeds          | 184.4   | 172.0    | -       | -        | 1.2     | -        | -       | 4.0      | -       | -        |
| Pmgrp          | -       | -        | -       | -        | 253.0   | -        | -       | -        | -       | 14.2     |
| Lfens          | 10.7    | 75.0     | -       | -        | 130.9   | 110.6    | -       | -        | -       | -        |
| Lrbog          | -       | 1767.2   | -       | -        | 103.7   | -        | -       | -        | -       | -        |
| <b>Totals</b>  | 314.4   | 2030.2   | 1575.3  | 721.6    | 489.5   | 1157.6   | 18.5    | 152.7    | 182.7   | 1547.8   |
| <b>Overall</b> | 2344.6  |          | 2296.9  |          | 1647.1  |          | 171.2   |          | 1730.5  |          |





**Figure 3.3: Conductance before and after conservation.** a) Boxplots of the proportional increases in area (grey) and conductance for animal (blue), and plant (yellow) species at the local, regional and national scales – note the proportional increase in area decreases because the projects could only effect change within their bounds and so the area affected remains the same despite the spatial scale of the analysis increasing. For visualisation, variables were  $\text{log}_{10}$  transformed, outliers calculated as  $1.5 \times \text{IQR}$ , red line indicates a 1% increase. b) Before and after conductances for all species, habitats, and spatial scales on a  $\text{log}_{10}$  scale, with  $f(x) = y$  line (red).

The majority (71.3%) of conductance increases were less than BCI, a pattern that holds when looking at the three spatial scales individually (Fig. 3.4). However, in most cases increases were still comparable to BCI, with 65.4% of conductance increases falling between 90% and 110% of BCI. Broad variation existed in both plants and animals with some species performing far worse and better than BCI. However, this variation was not seen at all spatial scales – at the national scale almost all conductance increases were comparable to BCI (Fig. 3.4). When considering only results in the highly positive category (>150%,  $n = 271$ ), I found that the majority occurred at the local scale (Fig. 3.4), for poor dispersers (Fig. B.2), and in landscapes whose pre-project conductance were in the bottom 25% (Fig. B.3). In 73.4% of scenarios where conductance increases were positive or highly positive (>110% BCI,  $n = 527$ ), at least one of the top 20 bottlenecks in the pre-project network had been addressed by the conservation works.



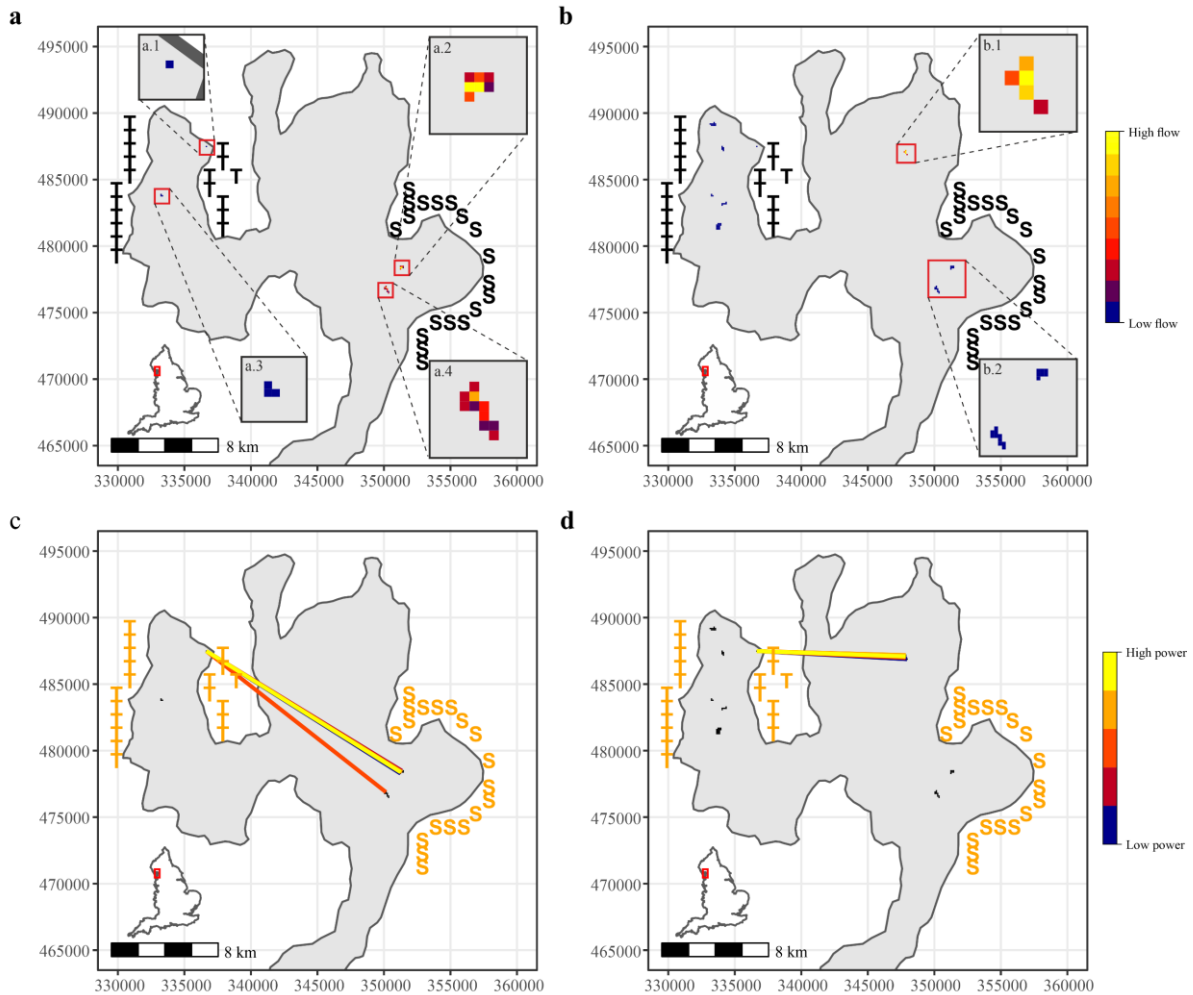
**Figure 3.4: Performance against BCI.** Barplot detailing the proportion of instances where conductance increases were greater (blue) or less (red) than BCI at each spatial scale. Sample sizes for local, region and national spatial scales were 2055, 1518 and 945 respectively. Each result was grouped depending on the magnitude of that under or over performance relative to BCI, and is indicated by the shade

### *3.5 Discussion*

Here, I have studied five landscape-scale conservation projects to explore their influence on climate change relevant connectivity at local, regional, and national scales. It is inevitable that habitat connectivity, measured by conductance, will increase as a result of habitat creation and restoration (Hodgson et al., 2012), but I found that these increases were generally small – less than 1% (Fig. 3.3a). Strategically placed habitat creation can increase conductance to a far greater extent than if habitat was added at random (Hodgson et al., 2016), even when the amount of habitat added is low (See chapter 2). In the projects studied, however, the majority of conductance increases were comparable to the increase in conductance expected for the amount of habitat added (baseline conductance increase; BCI), although generally below it (Fig. 3.4). Kuempel, Chauvenet and Possingham (2016) found that protected area increases linked to AICHI target 11 were not implemented strategically, increasing protection equality – a measure of the ecological representation within PA networks (Barr et al., 2011) – at a similar level to random. The present results echo this, implying that even in projects directly established from the recommendations of a review advocating joining a nation’s landscape (Lawton et al., 2010) connectivity could have been considered more judiciously.

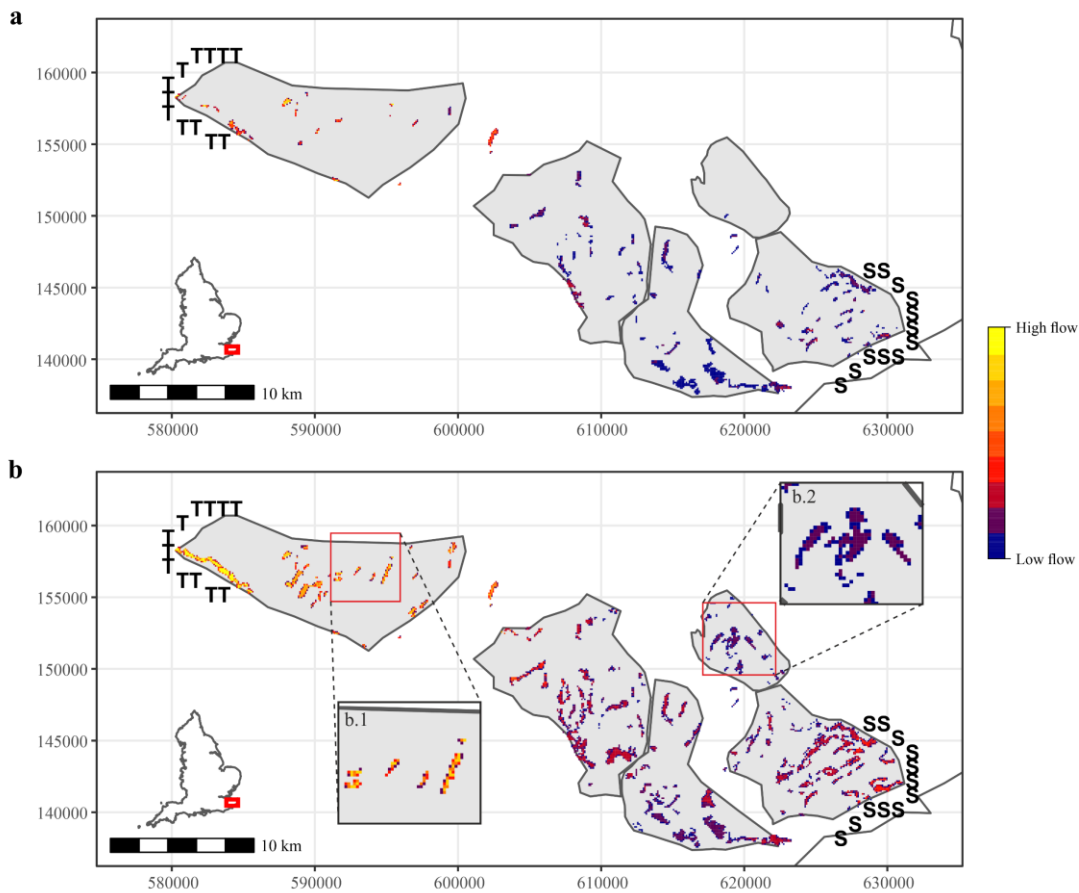
There are a number of reasons the studied projects may have led to connectivity increases comparable to BCI. Firstly, national-scale connectivity maps were not readily available, or did not exist, at the time the projects were being planned. It is also unlikely that the computing power needed to handle datasets of the size required to produce national-scale evaluations of connectivity would have been at the disposal of the individual projects at the time of their inception. Furthermore, long-distance connectivity of the type I measure here was not a consideration for any of the projects, the majority of which focused on local connectivity, often employing simplified metrics such as distance-based methods or principles of increasing site area (Collingwood Environmental Planning, 2015).

Nevertheless, within local settings, while connectivity within the sites may have been improved (Hunter-Ayad and Hassall, 2020), connectivity through the sites only increased similarly to BCI. The majority (84.6%) of instances where conductance increases were substantially greater than BCI occurred at the local scale (Fig. 3.4), but largely for dispersal-limited species (Fig. B.2), or where the landscape was so impermeable beforehand that any addition of habitat would likely have resulted in significant increases in connectivity. This is well illustrated by the results of poor dispersing animals (mean dispersal < 1 km) in purple moor grass and rush pasture habitat in Morecambe Bay (Fig. 3.5), where a single habitat patch produced a median conductance increase of 155-times BCI. However, in reality connectivity increases tend not to benefit poorly dispersing species (Donaldson et al., 2016), and facilitating species' ability to adapt to climate change will require planning that considers large spatial scales. If projects focusing on local connectivity regularly could not garner improvements at that scale greater than BCI, we should be concerned about their ability to do so at the scales necessary to plan for and accommodate range shifts. These results support this concern (Fig. 3.4), indeed, in only two instances were national scale improvements positive or highly positive, one of which resulted from the creation of habitat at the site of a bottleneck for national connectivity. The use of specific connectivity tools may have enabled the identification of further such opportunities.



**Figure 3.5: Morecambe Bay NIA impacts on purple moor grass and rush pasture habitat and poor dispersing animals.** Maps highlighting the changes in flow distribution (a, b), and location and strength of bottlenecks (c, d) in the pre-project (a, c) and post-project (b, d) purple moor grass and rush pasture habitat network at Morecambe bay NIA when modelling poor dispersing animal species. A single habitat patch (inset b.1) completely changes the flow distribution (see flow values for patches in insets a.2, a.4 and b.2) and location of bottlenecks (identified by lines in c and d). Flow and power scores represent geometric means across all species included, which were then standardised such that the maximum of each was 1. The project boundary (grey), and source (S) and target (T) locations are also shown. Coordinates correspond to the Ordnance Survey (OS) British National Grind (measured in metres).

In a number of instances high conductance increases were still comparable, or lower, than BCI due to large amounts of additional habitat being located away from high flow routes. For instance, in the local calcareous grassland network at KDP conductance increases for a third of all animal species were lower than BCI (median = 44.6%), despite the actual conductance increase being substantial (median = 744.5%; Fig. 3.6). One could therefore ask; is equivalency to random a poor result? The answer likely comes down to a question of spatial scale. At the local scale equivalency could mean population viability has improved in tandem with long-distance connectivity, due to increased habitat availability. Increasing population viability has the added benefit of promoting connectivity through ensuring populations are stable enough to produce dispersers to carry out range shifts (Hodgson et al., 2009). Some suggest it is a pre-requisite to range shifts (Mair et al., 2014), and particularly important in regions of high anthropogenic disturbance, where ongoing population losses can occur as a result of insufficient supplementation of individuals (Lenoir et al., 2020). However, when studying national or regional scales we start to consider the distances over which range shifts occur, rather than movements within metapopulations. Here, the focus shifts to identifying how we can facilitate movement between areas that can support viable populations, such as linking areas of low climate trajectories, or climate refugia. At these scales equivalency to BCI likely indicates a missed opportunity to improve connectivity.



**Figure 3.6: High connectivity increase but poor performance compared to BCI in calcareous grassland habitat at Kent Downs Projects following conservation actions.** Maps depicting the change in flow distribution in the pre-project (a) and post-project (b) calcareous grassland network at Kent Downs Projects for species with high conductance increases that were identified as being worse than random. Note that much of the habitat added to the west of the project has high flow (inset b.1). However, the gains in long-distance connectivity garnered is offset by the majority of habitat to the east of the project, which has low flow (inset b.2), and is therefore adding little additional connectivity. The figure includes the location of the project (grey), habitat, and sources (S) and targets (T). Flow was geometrically averaged between the species included. Coordinates correspond to the Ordnance Survey (OS) British National Grind (measured in metres).



### **3.5.1 Limitations**

In this study, I used the Condatis method to investigate the effect of landscape-scale projects on climate change relevant connectivity. Condatis' conductance metric is one specific type of connectivity, and was not the focus of the individual projects, nor was it available at the time these projects were planned. However, as the most recent large conservation projects of their type, their methods will likely be exemplars when future projects are being designed. This analysis was relatively exploratory, and there are a number of potential avenues for adaptation and advancement of the method. At the regional scale my source and target choice were based upon assuming that core areas of habitat with high persistence, which I termed 'nodes', provided staging posts during any species' range expansion. Introducing climate refugia datasets (Suggitt et al., 2014; Maclean and Duffy, 2019) to further pare down source and target choice would add further ecological realism. In addition, I chose to analyse each habitat individually. While this is suitable when modelling populations of habitat specialists, and follows the legislation of the UK which tends to use priority habitats as platforms for conservation legislation (Natural Environment and Rural Communities Act 2006), it is likely that the majority of species are not restricted to a single habitat when moving through landscapes. Consulting with habitat specialists to build networks of core and associated habitats would provide a more holistic assessment of long-distance connectivity.

### **3.5.2 Conclusions**

This study quantifies the impact that recent large-scale conservation projects had on climate change relevant connectivity over three spatial scales, using a representative assemblage of British plant and animal species as exemplars. Despite connectivity being a cornerstone of many of the projects' establishment, I found that, for the majority of populations modelled, increases in connectivity were equivalent to the baseline connectivity increase given the amount of habitat area that was added, even at the spatial scales considered by the projects. I propose that, while this may mean species persistence has

increased in tandem with connectivity at the local scale, it is of concern at the larger spatial scales over which climate change driven movements will occur. The evidence here highlights that just as the absence of consideration in protected area designation lead to under-protection of connectivity (See Chapter 2), conservation projects that do not consider long-distance connectivity are unlikely to garner potential improvements of relevance to climate change adaptation. Such potential improvements can only be attained by enhanced and well-targeted conservation efforts (Pörtner et al., 2021). Connectivity metrics can provide such a resource and, at a time when conservation targets have been routinely missed, could ensure connectivity projects result in better connected landscapes.

# **Chapter 4 Where to create habitat for connectivity? A procedure to bridge gaps in habitat networks**

*“Ah, the outdoors. I visited that mythical  
place once”*

- *Shallan Davar*

## *4.1 Abstract*

Current conservation policy has the ambition to establish large connected habitat networks. This will often require considerable habitat restoration or creation. Systematic conservation planning is a common tool used by practitioners to plan large projects, but until recently it has proven difficult to incorporate connectivity. Even now its implementation often fails to consider how to improve connectivity through habitat creation/restoration, instead focusing on where to conserve to protect connectivity. In this study, I strive to develop a novel method to allow planners to consider gaps in habitat networks that might be acting as barriers to species moving through them. I modify the Condatis assessment method to develop three habitat adding algorithms which evaluate where to create habitat for connectivity improvement on three separate and distinct principles. The routines spatially prioritise where to create habitat based on the amount that can be created, where creation is possible, and the traits of the species of interest. To investigate the utility of these algorithms I compare the change in connectivity they generate in a variety of landscape structures and in a national-scale case study to random placement of habitat. My methods show promising results, producing considerable increases in connectivity across a wide variety of landscape structures and dispersal abilities. These routines can help practitioners examine more than just where to conserve when considering connectivity in conservation plans to deliver policy such as England's Nature Recovery Network.

## *4.2 Introduction*

Connectivity is important to multiple ecological processes from local scale behaviours such as foraging, to wholesale shifts in where species occur as a result of climate change (McGuire et al., 2016). However, this important landscape characteristic has been severely negatively impacted by habitat fragmentation and loss resulting from anthropogenic activities (Haddad et al., 2015). In response to this, and the concurrent trend of declining biodiversity worldwide (IPBES, 2019), governmental bodies have enacted policy to promote the development of large-scale interconnected habitat networks (DEFRA, 2018; European Union, 2020; DeFazio, 2021; Environment Act 2021) and signed international treaties that include targets for connectivity enhancement (Secretariat of the Convention on Biological Diversity, 2020b). At the same time, non-governmental organisations have invested in large-scale initiatives to promote, protect and enhance connectivity.

Clearly, there is a need and willingness to act. However, doing so will put further strain on a system where the appetite for conservation already exceeds the resources available (Butchart et al., 2010). Therefore, it is imperative that actions maximise the benefits to biodiversity (Cook et al., 2017). To that end, conservation planners frequently need to juggle multiple, not always complementary, policy directives, while simultaneously addressing the biodiversity benefits, threats, and economic considerations of a suite of actions over multiple spatial scales. Now, they must also weave connectivity into this complex tapestry.

Systematic conservation planning (SCP) is a discipline developed to aid practitioners in such decisions in an evidence-based and transparent way (Margules and Pressey, 2000). Since its inception at the turn of the 21<sup>st</sup> century SCP has become ever more popular amongst academics, governments, and conservation organisations. Despite legitimate concerns surrounding the insufficient reporting of outcomes (McIntosh et al., 2018), it remains preferable to the predominantly expert opinion-based approach of the past (Sutherland et al., 2004) which was neither transparent nor repeatable (Drescher et al., 2013).

In England, the government is committed to establishing a Nature Recovery Network (NRN; DEFRA, 2018), a nationwide coherent ecological network, through local stakeholder driven plans called Local Nature Recovery Strategies (LNRSs). As a catalyst, the 25-year environment plan (25YEP; DEFRA, 2018) includes provision to create and restore 500,000 ha of habitat, restore 75% of protected sites on land to favourable condition, and to support work to increase woodland cover. These are all habitat creation and restoration activities. Given SCP has core concepts that align with the NRN (Crick et al., 2020) and has shown promise in speculative studies designing an NRN (Smith et al., 2022), it is plausible that SCP will be used in the planning process.

Historically, connectivity and restoration have been difficult to include within the SCP structure. Connectivity is multifaceted and requires different considerations at, for instance, different spatial scales (Tischendorf and Fahrig, 2000). More recently, however, progress has been made to facilitate evaluation of connectivity either directly within SCP programs (Lehtomäki and Moilanen, 2013; Daigle et al., 2020), or through other techniques which can then inform SCP (Correa Ayram et al., 2016). The majority of those methods promote conservation of areas facilitating movement by assessing the present landscape conditions. However, doing so neglects to consider the second route of action available to address connectivity – restoration of areas impeding movement through targeted habitat creation. Restoration will only grow in importance as our landscapes continue to degrade (WWF, 2020), and is of relevance here in light of the habitat creation provisions included in modern conservation policy. Habitat creation and restoration is inherently a local scale action, but through systematic identification of barriers to dispersal these local actions can have benefits at much larger extents (Baldwin et al., 2012). Methods to address connectivity systematically in restoration do exist (McRae et al., 2012; Torrubia et al., 2014; Hodgson et al., 2016). However, while offering important contributions, these either fail to consider where habitat creation is actually possible, or do not add habitat iteratively. Iterative habitat addition is particularly important at times when conservation resources are stretched (Butchart et al.,

2010), as it increases the efficiency of conservation actions. A connectivity evaluation is an assessment of a habitat network at a fixed point in time. However, there is the possibility that bridging the gaps highlighted in that evaluation might not require all the habitat a conservation project could create. A single measurement of connectivity could not identify such cases. Adding habitat iteratively, and then recalculating connectivity distribution, would allow a model to detect and react to changes where conservation is most needed. This could potentially maximise the benefits a particular amount of conservation could have and ensure that local scale actions have far reaching impacts.

Here, using England's NRN as a backdrop, I attempt to extend the Condatis methodology (Hodgson et al., 2012; Hodgson et al., 2016) to provide landscape planners with exact locations for habitat creation to address major barriers to long-distance dispersal. The Condatis connectivity decision support tool is mentioned in Natural England best practice (Crick et al., 2020), and therefore its use seems plausible when designing an NRN. I develop three algorithms that add habitat to networks based on different principles, and test them over a series of neutral landscapes of differing habitat structures and a national scale example to demonstrate their applicability at the extents an NRN will function.

To understand the capabilities of these methods I ask: (i) Do the adding algorithms generate conductance increases better than random? (ii) Are there situations in which one method is better suited than the others? (iii) How important is it to parameterise the model with the correct dispersal parameter? Finally, I conclude with a number of recommendations for the best way to implement these methods into the landscape planning process as England moves towards developing an NRN.

## 4.3 Methods

### 4.3.1 Dispersal kernels

As in Chapter 3, the Condatis model employed in this chapter uses both the negative exponential dispersal and exponential power kernels for modelling animal and plant dispersal respectively. The negative exponential dispersal kernel takes the form

$$p_i p_j R \cdot \frac{\alpha^2}{2\pi} \cdot \exp(-\alpha d_{ij}), \quad \text{Equation 4.1}$$

where  $p_i$  and  $p_j$  are the area of breeding habitat within cells  $i$  and  $j$ ,  $R$  is the reproductive rate,  $2/\alpha$  is the mean dispersal distance governing the slope of the dispersal kernel (Fig. B.1a), and  $d_{ij}$  is the Euclidean distance between cells  $i$  and  $j$ . The Exponential power kernel takes the form

$$p_i p_j R \cdot \frac{b}{2\pi a^2 \Gamma(2/b)} \cdot \exp\left(-\frac{d_{ij}^b}{a^b}\right), \quad \text{Equation 4.2}$$

where  $p_i$ ,  $p_j$ ,  $R$ , and  $d_{ij}$  are defined as above.  $\Gamma$  is the Gamma function (defined as  $\Gamma(y) = \int_0^\infty x^{y-1} e^{-x} dx$ ),  $a$  and  $b$  are species specific traits governing the shape and scale of the kernel (Fig. B.1b), and are identified through measurement of seed densities over incremental distance from the originating plant.

### 4.3.2 Condatis adding routine and sub-algorithms

Four adding algorithms are used in the analysis. Flow, Time-to-Cross, and Distance are each examined as prospective tools to aid conservationists, while Random is employed as a control. Each algorithm is an extension of the original Condatis method (Hodgson et al., 2012; Hodgson et al., 2016), which uses circuit theory to model multi-generational movements through a habitat network. The algorithms described in this section require the same parameters as the core Condatis method with four additions (Table 4.1). Once these



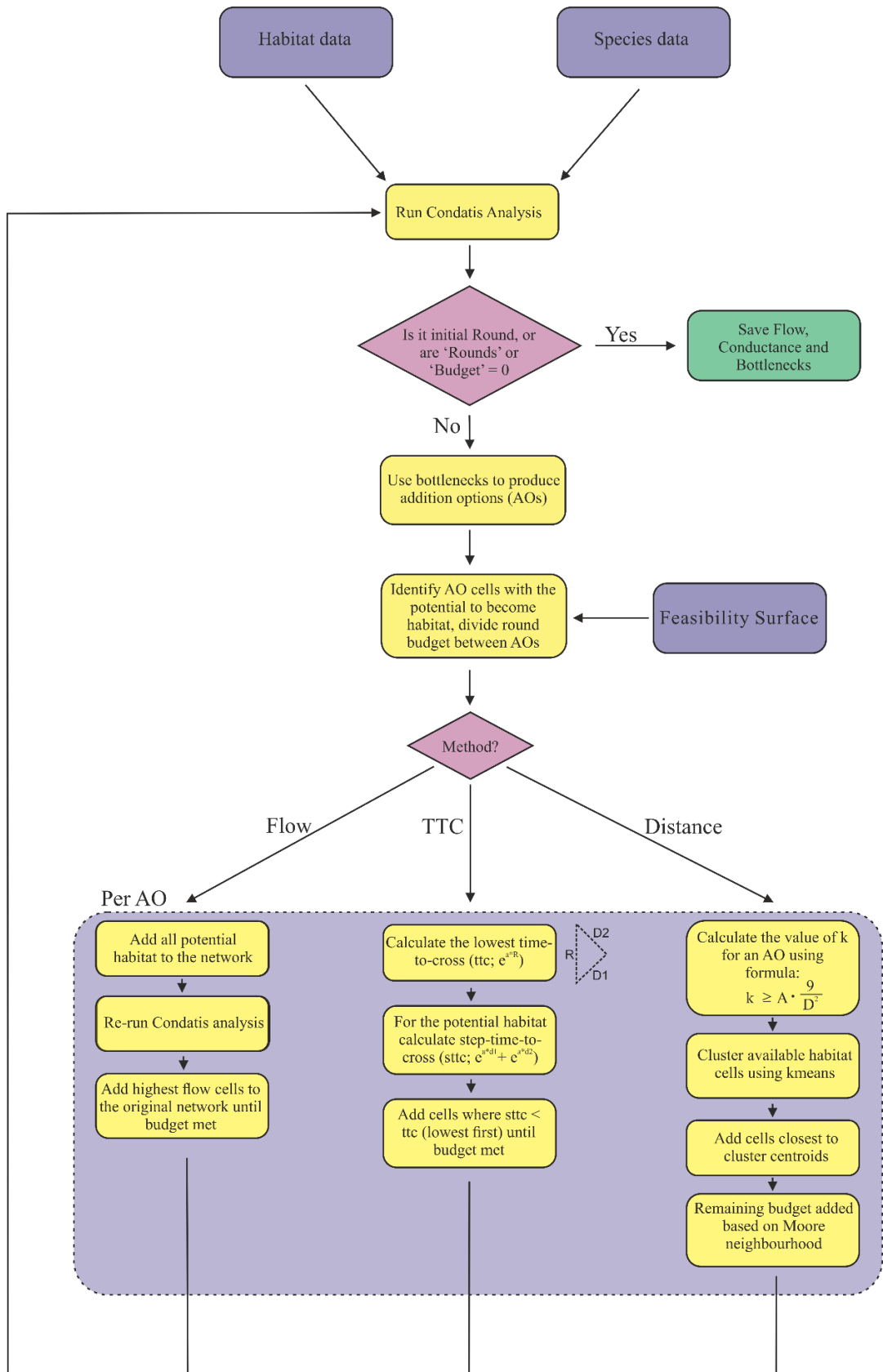
parameters have been defined, the locations for habitat creation best suited to improve connectivity can be calculated.

**Table 4.1: Parameters required for Condatis analysis.**

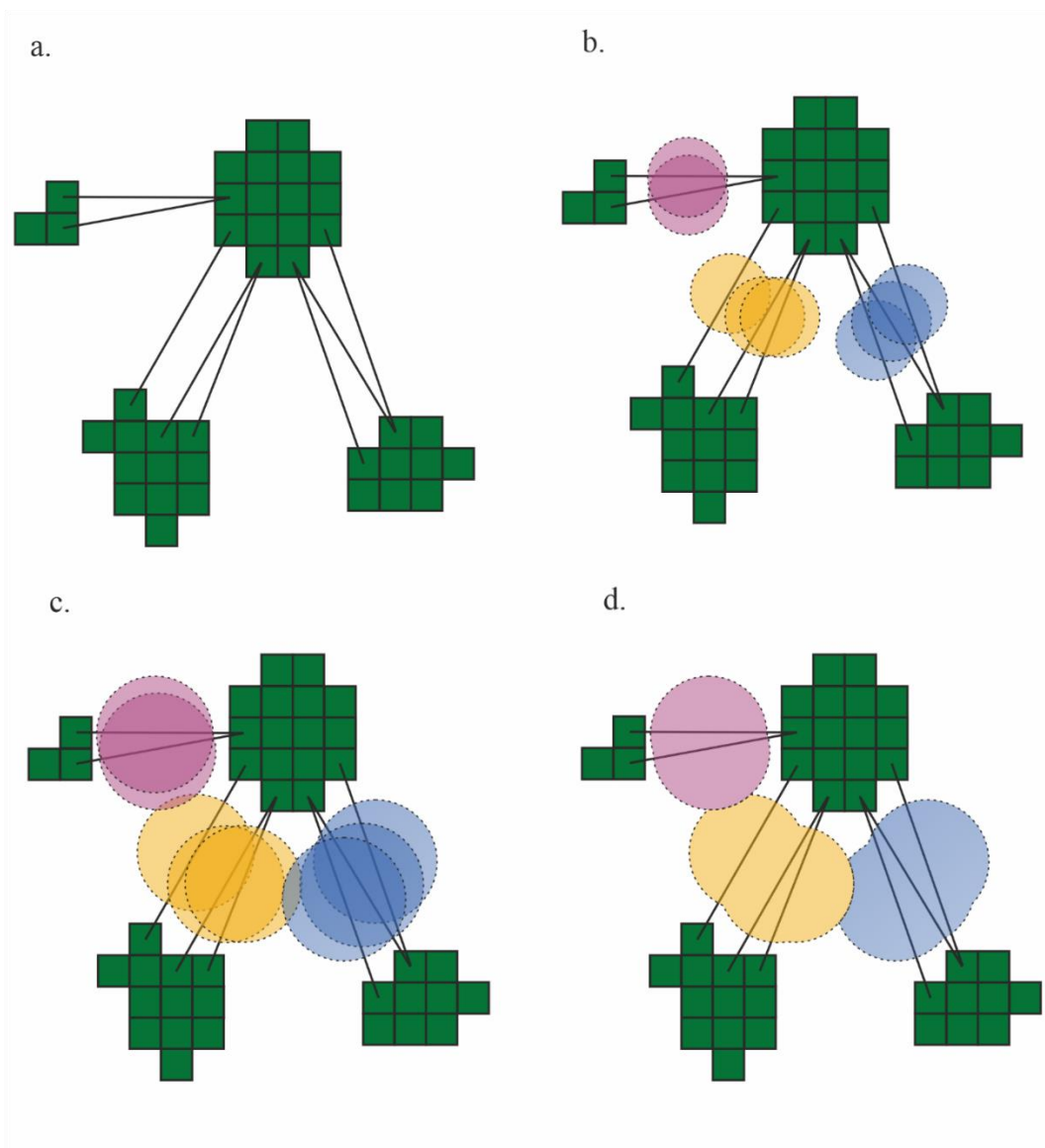
| <b>Parameter</b>     | <b>Description</b>  |
|----------------------|---|
| Habitat              | The distribution of breeding habitat the dispersing population can colonise and use to generate further dispersers. Usually in raster format. |
| Feasibility Surface* | A raster outlining where habitat can be created.  |
| Source               | The area(s) from which the population begins to move  |
| Target               | The area(s) where, once colonised, range expansion will be deemed successful  |
| Dispersal            | The mean dispersal distance of the population being modelled  |
| Fecundity (R)        | The reproductive rate of the population being modelled, controls the number of dispersers produced from occupied habitat per km <sup>2</sup>  |
| Power threshold*     | Controls the number of links between habitat cells that Condatis returns as bottlenecks   |
| Budget*              | The amount of habitat the algorithms can add to the network.  |
| Rounds*              | The number of iterations over which the habitat budget is spent   |

\* Parameters not required for base Condatis analysis

The three experimental algorithms (Flow, Time-to-Cross, and Distance – See following Sections) are implemented as steps within an overall routine which remains the same (illustrated as a flow chart in Fig. 4.1); the random algorithm differs substantially. This overall routine proceeds as follows: The habitat budget is added over ten rounds, in each round Condatis evaluates the connectivity of the existing habitat network and identifies the major bottlenecks. Major bottlenecks are found by calculating the total power of all links in the network (see Section 1.8), before ordering links by their power and finding those whose cumulative power represents the proportion defined by the power threshold parameter (Table 4.1). Next, the areas within which the algorithms look to place habitat are defined. To do this the central point of each bottleneck is located and a buffer established around it equal to 20% of the bottleneck's length. Buffers that overlap are grouped and extended by a further 20% before being merged (Fig. 4.2). These merged areas (henceforth 'addition options'; AOs) are assigned a value equalling the summed powers of their constituent bottlenecks, this enables prioritisation of the most important regions. This two-step process ensures only bottlenecks in close proximity to one another form an AO, preventing the possibility of elongated AOs being established (e.g. a combination of purple, yellow, and blue in Fig. 4.2). AOs are then rasterised, and masked with the feasibility surface and existing habitat layer so only cells where habitat creation can occur remain. With the AOs defined, the algorithm divides the habitat budget for that round proportionally amongst AOs based on their power, and the placement of new habitat cells within each AO follows one of the algorithms described in the following sections. Any 'unspent' habitat budget is divided amongst the remaining rounds, and a new round begins (Fig. 4.1). Undertaking addition over rounds allows the algorithms to account for, and react to, any shift in connectivity distribution that may occur as a consequence of habitat placement.



**Figure 4.1: Flow diagram of the three experimental algorithms with the overarching adding routine.** Inputs (dark blue), outputs (green), steps involved (yellow), decision points (pink)



**Figure 4.2: Generation of addition options (AOs) from bottlenecks.** Bottlenecks (lines) between habitat cells (green) are identified (a). The central point of each bottleneck is buffered by 20% of the length of the bottleneck and overlapping buffers are grouped (b; grouping signified by colour). The buffers are extended by a further 20% (c), and finally buffers in the same group are merged (d). Producing AOs in this way enables habitat addition to be more targeted by ensuring only buffers from bottlenecks in close proximity to one another form an AO.

#### 4.3.2.1 Flow

The Flow algorithm presumes that the best places to create habitat are those that Condatis would identify as carrying the highest current flow (most important to connectivity; see Section 1.8), if they were already habitat. Here, all AO cells are temporarily added to the habitat network and Condatis flow analysis undertaken. The cell budget for that round is divided amongst the AOs, and the algorithm adds the cells with the highest flow to the habitat network until the budget is met (Fig. 4.3a).

#### 4.3.2.2 Time-to-Cross

Time-to-Cross works on the principles outlined in Hodgson et al., (2012). The time to colonise a habitat patch from another (henceforth Time-to-Cross; TTC) can be calculated by  $e^{\alpha d}$  for the negative exponential kernel, or  $e^{d^b/a^b}$  for the exponential power kernel, where  $d$  is the distance between the two habitat areas,  $\alpha$  is the species' typical dispersal distance, and  $a$  and  $b$  are species-specific traits controlling the shape and scale of the exponential power kernel. If a stepping-stone is placed at some intermediary position, the time to colonise one habitat area from the other via the stepping stone (henceforth Step-Time-to-Cross; STTC) can be calculated as  $e^{\alpha d_s} + e^{\alpha d_t}$  or  $e^{d_s^b/a^b} + e^{d_t^b/a^b}$ , where  $d_s$  and  $d_t$  are the distance between each area of habitat and the stepping-stone respectively. Usually, stepping-stones placed directly in the centre of the bottleneck will achieve the minimum possible STTC, but importantly there will be a number of combinations of  $d_s$  and  $d_t$  where  $STTC < TTC$ .

In the TTC algorithm  $d$  is defined as the mean length of the constituent bottlenecks for each AO, and  $d_s$  and  $d_t$  are the distances from each cell in the AO to the closest bottleneck end. The algorithm then adds the number of cells allocated to that round with the lowest STTC, where  $STTC < TTC$  (Fig. 4.3b).

#### 4.3.2.3 Distance

The Distance algorithm attempts to increase resilience to habitat loss by creating multiple moderately sized habitat patches, while still improving connectivity through

reducing the maximum inter-patch distances within the AO. I decided to reduce the inter-patch distance by approximately threefold (in each round). Other levels of reduction could have been chosen (and this variable can be easily changed within the code), but I judged that a third would produce spacing intermediate between the above-described Flow and TTC algorithms. The number of patches ( $k$ ) needed to reduce the inter-patch distance below this threshold will vary depending on the area of the AO and length of the bottlenecks. Thus, the value of  $k$  was calculated via the formula:

$$\sqrt{\frac{A}{k}} \leq \frac{D}{3}, \quad \text{Equation 4.3}$$

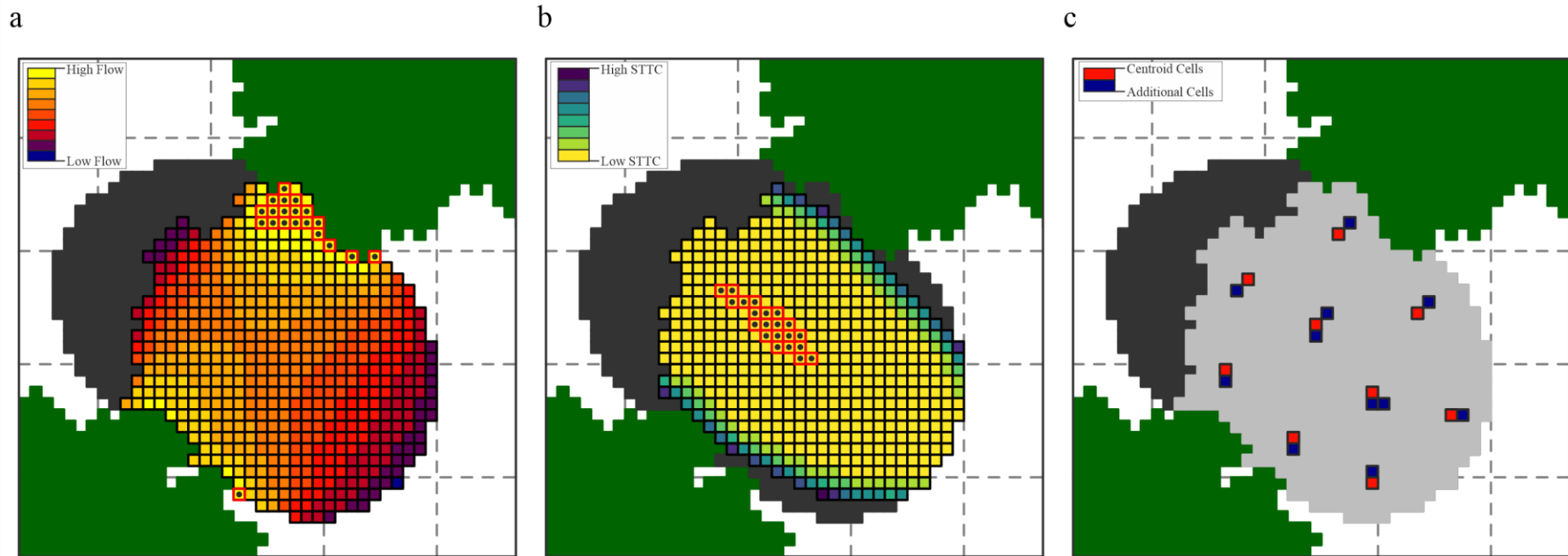
which can be rearranged to

$$k \geq A \cdot \frac{9}{D^2}, \quad \text{Equation 4.4}$$

where  $A$  is the area of the AO, and  $D$  is the mean length of bottlenecks constituent to the AO. k-means clustering is then carried on the AO cells using the lowest integer that satisfies equation 4.4, and the cell closest to the centroids of the  $k$  clusters are added to the habitat network. k-means clustering is employed because it enables patches to be placed evenly throughout the AO regardless of its shape. Finally, any remaining budget for that round is distributed among the centre cells and added via Moore neighbourhood (Fig. 4.3c)

#### 4.3.2.4 Random

To provide a measure with which to compare the above methods, a fourth algorithm adds cells randomly to the network. Here, no Condatis analysis is carried out to define regions of interest; instead, cells are simply randomly added to the habitat network according to the feasibility surface, until the budget has been reached.



**Figure 4.3: Example of experimental adding algorithms.** Here Condatis analysis was conducted over a simple theoretical landscape (Green = habitat), with the source along the south and target along the north. The resulting AO was evaluated by each algorithm, all were given a budget of 20 cells to add to the network. Dark grey cells are those not considered for addition due to the feasibility surface, and where  $STTC > TTC$  in b. **A) The Flow Algorithm** - Flow scores for the AO cells and the highest flow cells which are added to the network (red outline with black dot). **B) The TTC Algorithm** - STTC scores for each AO cells, and the cells with the lowest STTC which are added to the network (red outline with black dot). **C) The Distance Algorithm** - Here all available cells in the AO (light grey) were grouped into  $k$  clusters (9 on this occasion), and the cells closest to the centroid of each cluster (red) were added to the network. The remaining 11 cells (blue) were added based on the Moore neighbourhoods around the 9 central cells.

### **4.3.3 Algorithm testing**

The experimental algorithms were tested and compared through their improvements to the speed of range expansion (as measured by conductance) and computation time. They were parameterised using a range of realistic species trait values, and run over a series of neutral landscapes of varying characteristics, and in a real-world national-scale example.

#### **4.3.3.1 Neutral landscapes**

Neutral landscape models (NLMs) are regularly used in the development of novel landscape metrics (Turner and Gardner, 2015). Within NLMs, fractal landscapes have a long history of use in ecology because their inherent autocorrelation results in realistic habitat patterns. For example, since their introduction in the 1980s, fractal maps have been employed to model the degree of spatial dependence of actual landscapes (Palmer, 1992), how landscape fragmentation affects population and community dynamics (With et al., 1997), and the spread of invasive species (Lavorel and Chesson, 1995) to name but a few.

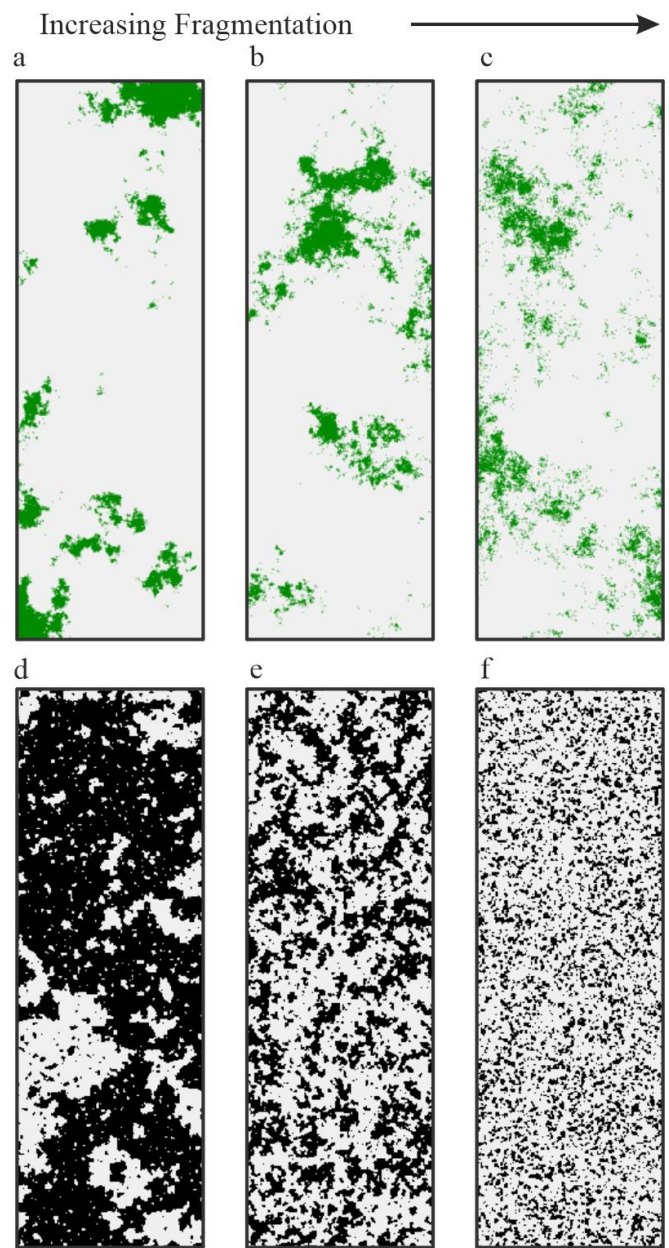
I used the ‘*NLMR*’ package (Sciaini et al., 2018) to produce NLMs that could be grouped into three categories depending on their degree of fragmentation: Coarse, Medium, and Fine (Fig. 4.4). Habitats were produced via fractal Brownian motion (FBM) using the ‘*nlm\_fbm*’ function. The fractal dimension ( $D$ ) can be varied to alter the autocorrelation of the landscapes; low values result in negatively correlated rough maps, and high values positively correlated smooth maps. Continuous two-dimensional surface fractals were generated on a 200×600 grid, where  $D$  was defined as 0.95 (Coarse; Fig. 4.4a), 0.65 (Medium; Fig. 4.4b), or 0.35 (Fine; Fig. 4.4c). The continuous variables were then classified into 10 discrete classes, the first which, assigned a value of 1, denoted habitat, and others were given a value of 0 to represent non-habitat. Therefore, each neutral landscape consisted of 12,000 habitat cells.

To produce feasibility surfaces I used a random cluster algorithm using the ‘*nlm\_randomcluster*’ function of the *NLMR* package (Sciaini et al., 2018). I chose this as it



produces less fragmented distributions than FBM algorithms and seem more akin to the distributions of geological substrates which can govern the feasibility of habitat creation in real-world situations. Three parameters control the shape of patches produced by the random cluster algorithm.  $P$  defines the proportion of cells randomly selected to form clusters,  $ai$  controls the proportion of cells assigned as a habitat and the number of  $ai$  values defined governs the number of habitat types in the landscape, and  $n$  defines the neighbourhood structure used to create patches. I produced feasibility surfaces on a 200×600 grid, where  $n = 4$  (von Neumann neighbourhood), and  $P$  and  $ai$  varied for coarse (0.58, 0.5; Fig. 4.4d), medium (0.5, 0.4; Fig. 4.4e), and fine (0.25, 0.25; Fig. 4.4f) landscapes. Cells were assigned a value of 1 to identify where habitat could be created, and 0 where it was not possible. This produced feasibility surfaces with approx. 24%, 40% and 60% habitat availability in fine, medium and coarse respectively (feasibility cell counts are available in Table C.1).

Four replicates were created of each habitat and feasibility surface class, and I employed all pairwise combinations in the analysis to give 144 landscapes over which the conductance increases and computation times of the algorithms were tested (Fig. 4.4; Fig. C.1-2).



**Figure 4.4: Neutral landscapes.** Example habitat maps (a:c), and feasibility surfaces (d:f) created by the FBM and random cluster algorithms. Autocorrelation reduces (fragmentation increases) moving from left to right, with coarse ( $D = 0.95$ , a;  $P = 0.58$ , d), medium ( $D = 0.65$ , b;  $P = 0.5$ , e), and fine ( $D = 0.35$ , c;  $P = 0.25$ , f).

#### 4.3.3.2 *Real-world example*

The algorithms were also tested at a national scale, due to their potential application in designing projects such as Local Nature Recovery Strategies and the Nature Recovery Network in England.

##### **Habitat data**

Calcareous grassland in England was chosen to provide a real-world example due to its broad distribution and history of use by range expanding species (Hill et al., 1999). The spatial extent was downloaded via the Priority Habitat Inventory available on Natural England's Geo-portal (Natural England, 2019), converted to a 50 m raster using Arc Map 10.7 (ESRI, 2018), and aggregated to a resolution of 500 m using the *'rgdal'* (Bivand et al., 2019) and *'raster'* (Hijmans, 2019) packages in R 4.0.5 (R Core Team, 2019), converting the sum of the 50 m habitat cells to a proportional cover. A resolution of 500 m was identified as the finest resolution that could be analysed given the RAM available.

##### **Feasibility surface**

The national feasibility surface was created by extracting geological substrates associated with calcareous soils (chalk and limestone) from the Geology Digimap (EDINA Digimap, 2008), identified from the "*ROCK\_D*" variable within that dataset. Further detail was added by removing areas covered by urban development and open water, as identified through land-use maps downloaded from EIDC (Rowland et al., 2017). The spatial data was converted to a raster of the same resolution of the habitat data using the same process described above.

##### **Parameterisation**

Due to my interest in the performance of the underlying methods, rather than how the landscapes facilitate movement for any particular focal species, I chose to use generalised trait values representative of poor, moderate and good dispersers. These generalised dispersal abilities were chosen from distributions of a broad range of species

collated in the previous chapter (see Chapter 3): 10th and 90th percentiles, and mean to represent poor, good, and moderate dispersers respectively for plant and animal species. The 20th percentile was later chosen for poor animal species as the 10th represented such a low dispersal ability that the neutral landscapes could not be evaluated. The mean dispersal abilities for plants, given the exponential power dispersal kernel, were calculated as

$$a \cdot \frac{\Gamma(3/b)}{\Gamma(2/b)},$$

where  $\Gamma$  is the gamma function (defined as  $\Gamma(y) = \int_0^{\infty} x^{y-1} e^{-x} dx$ ). The plant species whose mean dispersal were closest to the desired dispersal abilities were used to derive  $a$  and  $b$  values (those controlling the shape and scale of the kernel). Thus, for animals mean dispersals of 591 m, 4.71 km, and 14.36 km were selected to represent poor, moderate and good dispersing species, while plant  $a$  and  $b$  values were  $2.5 \times 10^{-7}$ ,  $1.0 \times 10^{-8}$ , and 0.56, and 0.1888, 0.1423, and 0.429 respectively – equating to mean dispersals of 172m, 4.343 km and 27.232 km.

Fecundity ( $R$ ) modulates all Condatis metrics in proportion, and would not influence the performance of the algorithms. Therefore, it was not deemed necessary to further complicate the study by varying this parameter. Thus,  $R$  was fixed at 100 throughout, which equates to the production of approximately 1 disperser  $\text{ha}^{-1}$ .

The power threshold, determining which bottlenecks are identified and therefore where the algorithms will look to create habitat, was set to 0.5. This equates to selecting bottlenecks whose summed power equals half of the total power of all links in the network.

The ‘Budget’ available to the adding routines was defined as 5% of the habitat network area, based on the draft post-2020 CBD targets (CBD, 2020). In the national example, the full area recommended under the post-2020 targets going towards connectivity may seem unrealistic. However, for calcareous grassland this would equate to only 3619 ha. Meanwhile the 500,000 ha of priority habitat creation provisioned under the 25YEP

(DEFRA, 2018) is equivalent to approximately 29% of all priority habitats. Nevertheless, I also conducted a second ‘resource restricted’ scenario, where 30% of the post-2020 area was used amounting to 1086 ha; a similar area to the habitat created or restored through arable reversion under England’s Environmental Stewardship Scheme.

I identified sources and targets in the neutral landscapes at the extremities of the y-axis. In the national examples these were positioned along the southern coast of England, and northern border with Scotland respectively; following the trend of species adjusting their ranges away from the equator (Lenoir et al., 2020).

#### **4.3.4 Statistical analysis**

All statistical analysis was conducted using R 4.0.5 (R Core Team, 2019). The ability of the algorithms to produce greater conductance increases was investigated using exact binomial tests, where success was defined as the conductance change caused by an algorithm being greater than that caused by random addition. There is a paucity of data regarding the dispersal abilities of many species of conservation interest, especially at the landscape scale (Fagan and Calabrese, 2006). Therefore, when attempting to consider connectivity, planners must often use generalised dispersal figures or best-guesses. As such, the sensitivity of the algorithms in these circumstances was examined by calculating the change in conductance for poor and good dispersers generated when an algorithm modifies the landscape using the moderate dispersal value. The resulting increase in conductance was compared to that garnered by landscapes modified using the “true” dispersal value.

## 4.4 Results

### 4.4.1 Conductance increases

Of the 3456 individual runs conducted in this study, the algorithms were able to evaluate connectivity and add habitat in 3088 (89.4% success rate). Of the 368 in which connectivity measures could not be obtained, likely due to issues with floating point arithmetic (see Appendix A), the majority occurred either when modelling poor animal dispersers (68.5%), or for the TTC algorithm (47.6%).

#### 4.4.1.1 Neutral landscapes

In neutral landscapes consisting of 10% habitat coverage adding an additional 5% of habitat by selecting cells at random led to an overall median increase in conductance of 1.003 (min < 1.001, max = 1.404) in plants, and 1.545 (1.049,  $6.229 \times 10^8$ ) in animals. Using any one of my three algorithms, which add habitat based on a landscape's bottlenecks, led to sharper improvements overall (Table 4.2). Exact binomial tests to measure the likelihood of success (defined as the conductance change caused by the algorithm being greater than that caused by random addition) found that in all but one instance the algorithms resulted in significantly higher conductance increases than random (Table 4.3). When comparing algorithms to one another I found that the Flow algorithm tended to yield higher conductance increases compared to random than TTC and Distance algorithms for moderate and good plant dispersers, and good animal dispersers in all landscape subcategories (Fig. 4.5). However, as the dispersal ability of the species studied decreased so did Flow's performance relative to the others. For moderate and poor dispersing animal species, and poor dispersing plant species Distance or TTC matched or exceeded conductance increases yielded by the Flow algorithm. However, this relatively poor performance of the Flow algorithm was not observed in "fine" landscapes for poor dispersing animals, and "medium" landscapes for poor dispersing plants. Distance and TTC algorithms can provide improvements of the highest magnitude in situations where increases in connectivity are perhaps of most conservation importance, due to the difficulty with which poor dispersing species may

spread without intervention. For animals, the Distance algorithm performed better than TTC for poor dispersers, but especially for moderate dispersers where TTC occasionally performed worse than random. However, for moderate dispersers in “coarse” landscapes and poor dispersers in “fine” landscapes the two algorithms functioned similarly (Fig. 4.5a). In plants TTC led when Flow did not (Fig. 4.5b).

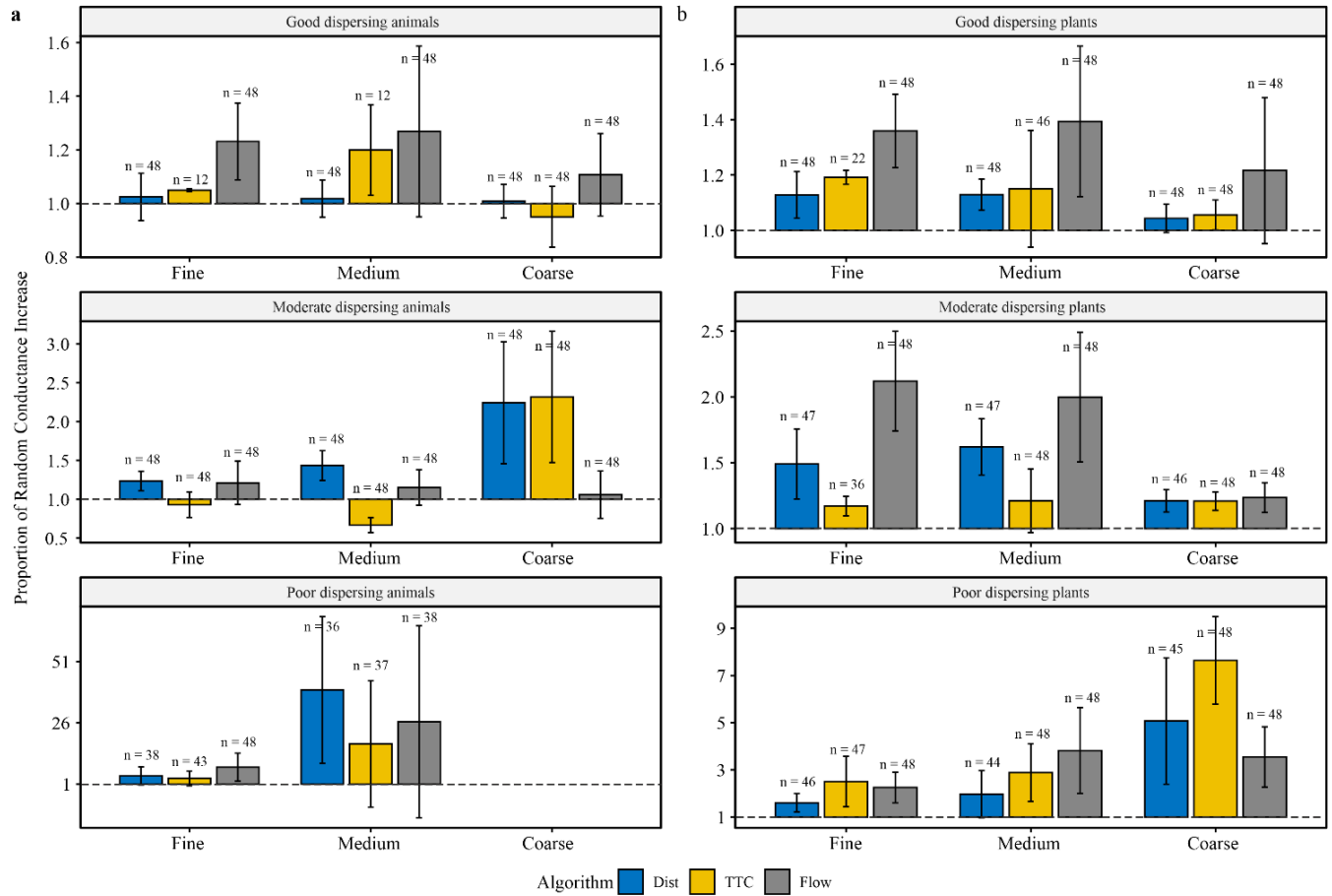
**Table 4.2: Algorithm conductance changes.** Proportional change in conductance produced by each algorithm for animal and plant species. *n* refers to the number of successful runs for that algorithm (max = 432).

| Kingdom | Algorithm | n   | Median proportional conductance change | Minimum proportional conductance change | Maximum proportional conductance change | IQR    |
|---------|-----------|-----|--|---|---|--------|
| Animal  | Dist      | 362 | 1.959                                  | 1.022                                   | $1.301 \times 10^{10}$                  | 11.558 |
|         | Flow      | 374 | 1.818                                  | 1.074                                   | $1.638 \times 10^{10}$                  | 6.670  |
|         | Rand      | 374 | 1.545                                  | 1.049                                   | $6.229 \times 10^8$                     | 6.226  |
|         | TTC       | 296 | 1.584                                  | 1.001                                   | $1.123 \times 10^{10}$                  | 28.011 |
| Plant   | Dist      | 419 | 1.380                                  | 1.004                                   | 76.447                                  | 0.734  |
|         | Flow      | 432 | 1.911                                  | 1.019                                   | 226.449                                 | 2.302  |
|         | Rand      | 432 | 1.003                                  | < 1.001                                 | 1.404                                   | 0.009  |
|         | TTC       | 391 | 1.331                                  | 1.002                                   | 82.480                                  | 1.626  |

**Table 4.3: Results of exact binomial tests** measuring the likelihood of a conductance change resulting from an algorithm being greater than that caused by random addition.

| <b>Kingdom</b> | <b>Algorithm</b> | <b>Landscape</b> | <b>n</b> | <b>Probability of success (95 CI)</b> | <b>p – value</b> |
|----------------|------------------|------------------|----------|---------------------------------------|------------------|
| Animal         | Dist             | Fine             | 96       | 0.813 (0.720, 0.885)                  | < 0.001          |
|                |                  | Medium           | 132      | 0.758 (0.675, 0.828)                  | < 0.001          |
|                |                  | Coarse           | 134      | 0.851 (0.779, 0.906)                  | < 0.001          |
|                | TTC              | Fine             | 96       | 0.657 (0.552, 0.750)                  | 0.003            |
|                |                  | Medium           | 97       | 0.412 (0.313, 0.517)                  | 0.104            |
|                |                  | Coarse           | 103      | 0.602 (0.501, 0.697)                  | 0.048            |
|                | Flow             | Fine             | 96       | 0.802 (0.708, 0.876)                  | < 0.001          |
|                |                  | Medium           | 134      | 0.851 (0.779, 0.906)                  | < 0.001          |
|                |                  | Coarse           | 144      | 0.944 (0.894, 0.976)                  | < 0.001          |
| Plant          | Dist             | Fine             | 139      | 1 (0.974, 1)                          | < 0.001          |
|                |                  | Medium           | 139      | 1 (0.974, 1)                          | < 0.001          |
|                |                  | Coarse           | 141      | 1 (0.974, 1)                          | < 0.001          |
|                | TTC              | Fine             | 144      | 1 (0.975, 1)                          | < 0.001          |
|                |                  | Medium           | 142      | 1 (0.974, 1)                          | < 0.001          |
|                |                  | Coarse           | 105      | 1 (0.966, 1)                          | < 0.001          |
|                | Flow             | Fine             | 144      | 1 (0.975, 1)                          | < 0.001          |
|                |                  | Medium           | 144      | 1 (0.975, 1)                          | < 0.001          |
|                |                  | Coarse           | 144      | 1 (0.975, 1)                          | < 0.001          |

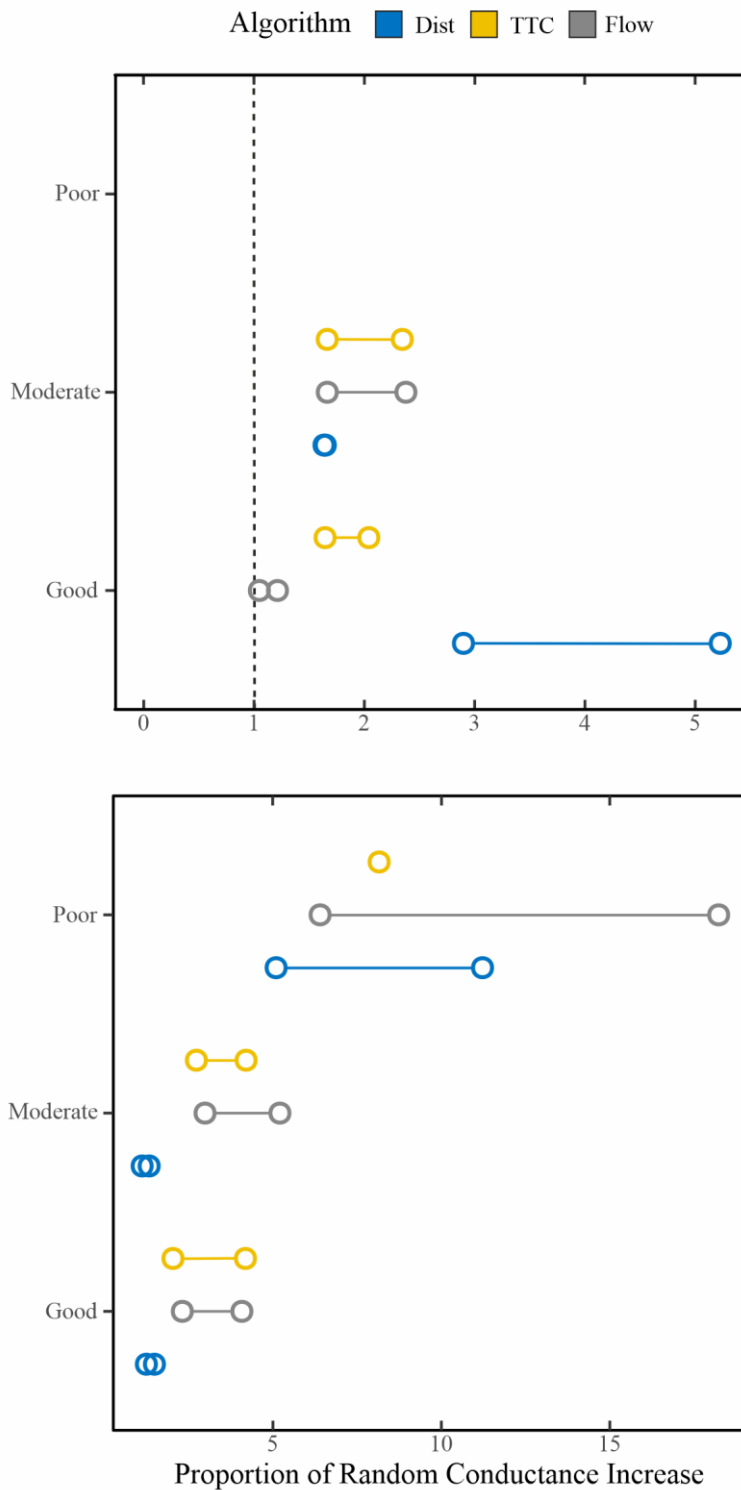




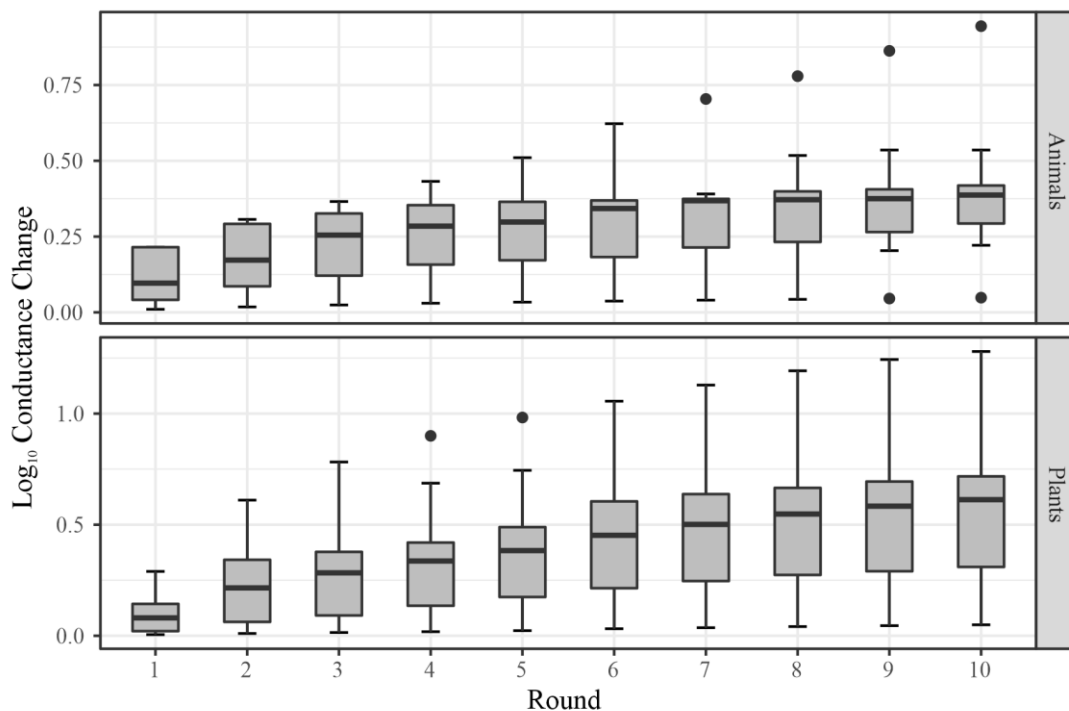
**Figure 4.5: Algorithm performance compared to random in neutral landscapes.** The median increase in conductance produced by each algorithm as a proportion of the conductance increase resulting from random addition. Results are grouped by landscape and dispersal distance for animal (a) and plant (b) species. Label denotes sample size (max = 48), error bars represent median absolute deviation.

#### *4.4.1.2 National example*

In national landscapes no algorithm was able to analyse the network with poor dispersing animals as the input parameter. However, for moderate and good dispersing species all algorithms outperformed random (Fig. 4.6), in some instances, such as for poor dispersing plants, considerably so (median proportion of random conductance increases of 8.16, 12.32, 8.15, for Distance, Flow and TTC respectively). In animal species, TTC and Flow performed best, and comparably to one another, for Moderate dispersers. However, Distance performed better for good dispersing species, with flow performing far closer to random (median proportion 1.13). In plants there was a steady decline in algorithm performance compared to random as dispersal ability increased (Fig 4.6b; median proportion 8.15 [Poor], 2.86 [Moderate], 2.17 [Good]). Scrutinising conductance increases per round, I found that the magnitude of the connectivity gains generally reduced as round number increased (Fig. 4.7). However, there are exceptions where habitat created in later rounds resulted in substantial spikes in conductance increase, or lasting increases in the rate of conductance change (Fig. C3 - 5).



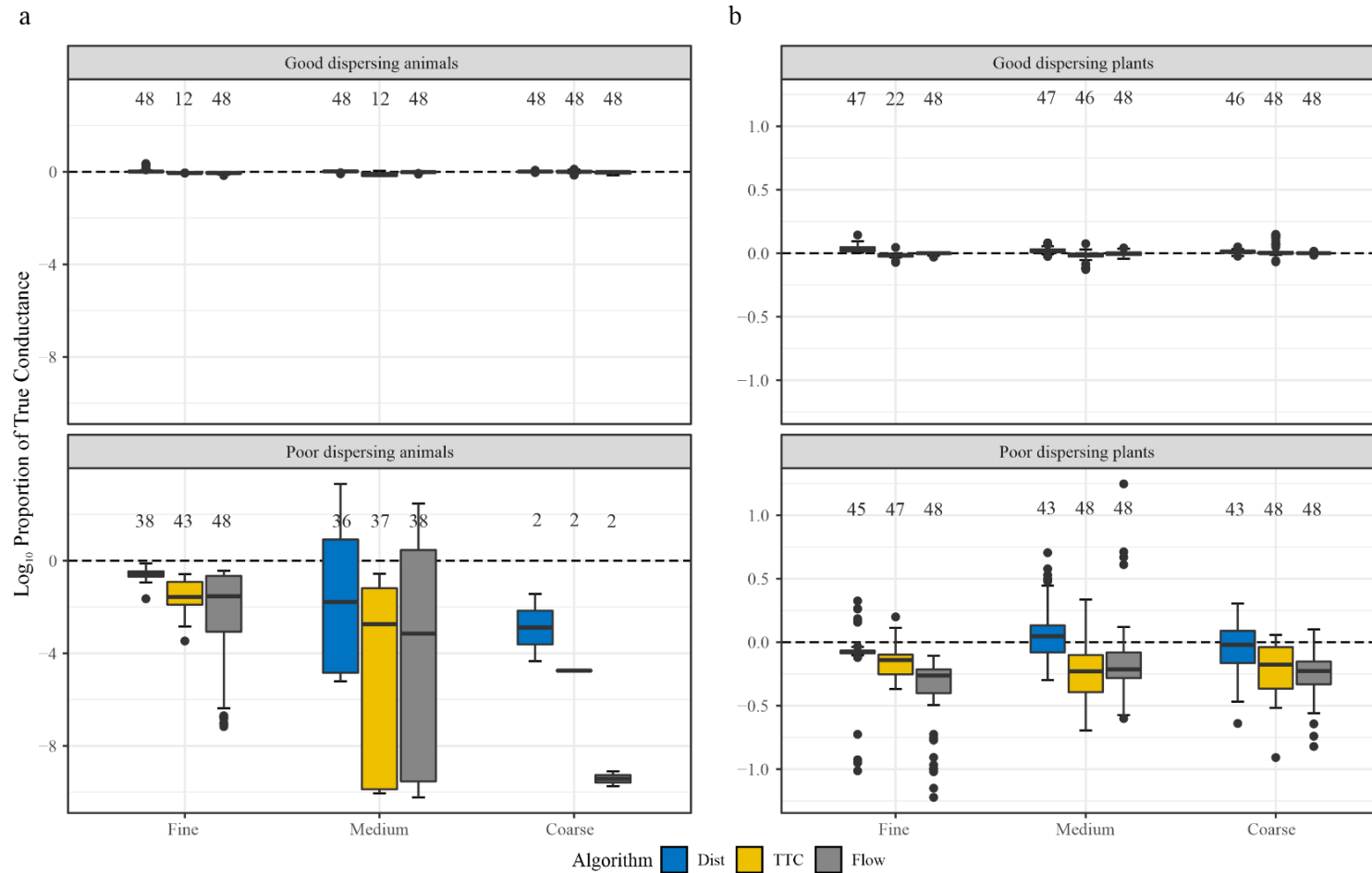
**Figure 4.6: Algorithm performance compared to random in the national landscape.** The increase in conductance produced by each algorithm as a proportion of the conductance increase resulting from random addition for low (left symbol) and high (right symbol) budget scenarios in animal (a) and plant (b) species. Results grouped by dispersal distance.



**Figure 4.7: Per round conductance increases in the national landscape.** Boxplots of round conductance as a proportion of initial conductance for animal and plant species (random algorithm results excluded). Values were  $\log_{10}$  transformed for visualisation purposes.  $n = 12$  (animal),  $n = 17$  (plant), outliers are calculated as  $1.5 \times \text{IQR}$ .

#### 4.4.2 Sensitivity to parameterisation

When modelling good and poor dispersers over landscapes modified by algorithms parameterised with moderate dispersal, I noted good dispersers experienced comparable conductance increases to those resulting from the algorithms using the “true” dispersal figure (Fig. 4.8). In contrast, poor dispersers generally experienced lower conductance increases than if the “true” dispersal had been used; overall median proportion of 0.217, 0.022 and 0.018 for Distance, TTC and Flow algorithms respectively in animals, 0.867, 0.695, 0.578 in plants. However, there were a number of instances where landscapes yielded conductance increases far exceeding those created using the “true” dispersal; maximum of 2076-fold increases in conductance for distance algorithm in the medium landscape (Fig. 4.8a).



**Figure 4.8: Sensitivity of algorithms to generalised dispersal distance.** Boxplots of increases in conductance produced by algorithms parameterised with moderate dispersal as a proportion of the conductance increase yielded when the algorithms use the bespoke dispersal value for animals (a) and plants (b). Label denotes sample size (max = 48), for visualisation purposes values were log<sub>10</sub> transformed.

### **4.4.3 Computation time**

The algorithms differed considerably in their computation time. The TTC and Distance algorithms took similar times to compute across both the neutral (network size = 12000 cells, cells added = 600) and national landscapes (network size = 13636 cells, cells added = 682 cells [high budget] or 225 cells [low budget]) with a median time taken of 4597 and 4485 seconds respectively. The flow algorithm took far longer to modify the landscapes with a median time of 11703 seconds.

## *4.5 Discussion*

The emphasis placed on connected landscapes in modern conservation policy (DEFRA, 2018; European Union, 2020; DeFazio, 2021; Environment Act 2021), the limited resources available (Butchart et al., 2010), and the growing understanding for the need to accommodate connectivity in our natural landscapes will necessitate some systematic measurement in our conservation planning procedures. However, the majority of tools utilised to do so focus on preservation and are unable to consider how habitat creation/restoration may affect connectivity to direct efforts to best effect. In this study I attempt to develop a set of algorithms capable of filling this planning gap.

Previous work has recommended the placement of habitat in the centre of areas identified as barriers to dispersal (Hodgson et al., 2012) and developed iterative procedures to place single cells of habitat following that rule (Hodgson et al., 2016). However, it may not always be possible to place habitat at the centre of bottlenecks, and, while producing substantial improvements in connectivity, iteratively placing individual cells does not scale well as you approach the size of networks needed to consider range expansion. The routine described here, which utilises three algorithms that direct habitat creation/restoration on different principles, represents an important expansion on that previous work that addresses these issues. It inherits the efficiencies and clarity of Condatis' conductance and flow metrics (See Section 1.8), but is also capable of providing exact locations of where to create habitat to best improve connectivity given where habitat can be created. Furthermore, it strives to produce habitat patch sizes and configurations that could be used by dispersing species and does so by employing Hodgson et al.'s (2016) powerful iterative method in a less computationally taxing way.

### **4.5.1 Algorithm performance**

In neutral landscapes the algorithms showed promise, yielding considerable connectivity improvements. Typically, a random configuration of habitat should be better for

conductance than a clumped one (Hodgson et al., 2012), and here the random algorithm generated an approximately 150% increase in conductance on average. Yet, the Flow, TTC and Distance algorithms almost always resulted in greater still conductance increases.

The results from the national scale examples reveal some interesting differences between the algorithms. For good dispersing animals Flow and TTC performed substantially worse than Distance. This highlights a weakness of these two methods in low resistance networks; networks through which a population could already traverse with relative ease – as the good dispersing animal species could. When resistance is low, links between cells of habitat will be under relatively uniform strain, and a large proportion will be included before their sum power exceeds the defined threshold parameter for identifying bottlenecks. The resulting AOs, in which the algorithms look to place habitat, can be extremely large – 25,431 km<sup>2</sup> in the above instance amounting to ~19.5% of the total area of England. In areas of such size the tendency of TTC and Flow to place single large habitat patches, or to add to existing patches (Fig. 4.3), becomes detrimental to their goals, while Distance and Random, which place many stepping-stones, fare better. Nevertheless, I argue that such instances reflect a network without need for connectivity improvement, and resources may be better spent on another more dispersal limited population or in another network entirely. In plants, I note the opposite pattern to animals, with Distance performing comparably to random (Fig. 4.6). I suggest that this is likely a result of the different dispersal kernel utilised for plant modelling. The fat-tailed nature of the exponential power kernel increases the likelihood of long-distance dispersal events (Bullock et al., 2017). Therefore, in this study plant populations are able to cross larger gaps than animal species. As such, the placement of a single patch, or adding to existing patches, is more likely to result in a gap being bridged, while placing many stepping stone patches would likely result in some redundancy.

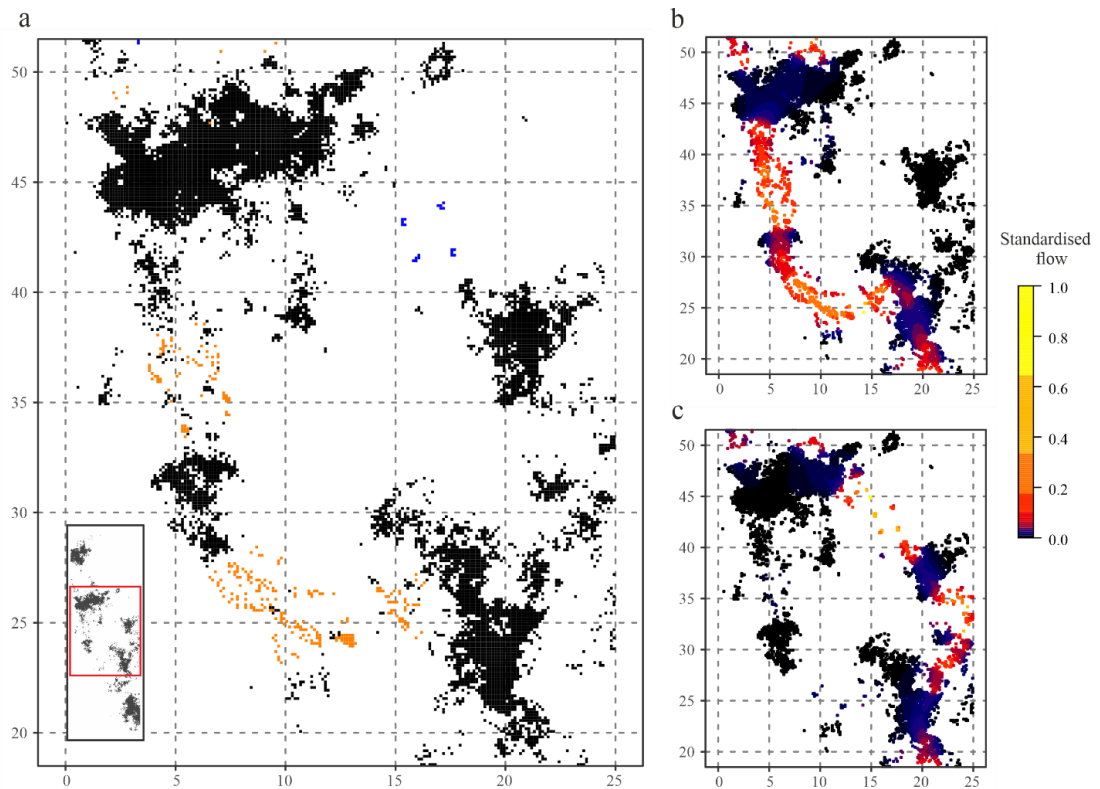
It is difficult to identify if any one algorithm is “best”; they each have strengths and weaknesses. If conductance increase is the sole qualifier, one could argue that Flow performed best in this analysis. However, habitat structure varies; in instances where the



population modelled is dispersal limited, and/or the landscape analysed is coarse in nature TTC and Distance garner the greatest improvements (Fig. 4.5). One must also consider the temporal and computational demands of the differing methods. Over the landscapes modelled in this analysis, which are moderate in size, consisting of approximately 12,000 cells of habitat, Distance and TTC took 4484.4 and 4597.4 seconds to compute on average, while Flow took nearly three times as long (median time = 11702.9 s). This is unsurprising given the Flow's requirement of twice the sets of computations to be completed (Fig. 4.1). Similarly, as Condatis measures connectivity between all pairwise combinations of habitat units, adding all possible habitat during this intermediary step can lead to considerable increases in the number of calculations that must occur – the addition of a single cell to a network of  $n$  cells requires an additional  $n$  calculations. Therefore, the above disparities would likely only increase with the size of the networks and number of rounds, and/or as resistance of the network decreases (due to lower resistance networks producing larger AOs). I note this in my own findings, where Flow's calculation time increased with dispersal ability in the national scale example (animals: 3877 and 3666 seconds [moderate], 9428 and 8976 [good]; plants: 6914 and 6743 [poor], 16868 and 20266 [moderate], 14172 and 19696 [good]).

Modulating the dispersal parameter can lead to results with potentially useful applications. When modelling connectivity for good dispersing species through landscapes modified for those with a moderate dispersal ability, I found that all algorithms are relatively tolerant to incorrect dispersal definition (Fig. 4.8). I suggest that this is because reducing the distance between areas of habitat in such a way that benefits dispersal-limited species will not hinder, and may still benefit, those more capable of dispersing; conductance always increases alongside habitat area (Hodgson et al., 2012). However, when dispersal ability was overestimated all algorithms tended to yield substantially smaller conductance increases than if the bespoke conductance was used. The pitfalls of overestimating dispersal ability are most evident in animal species, likely due to the capacity that plant species have for long-

distance dispersal as noted previously. Interestingly, there were occasions where modifying the landscape using an overestimated dispersal distance parameter led to substantially greater conductance increase than if the “true” dispersal had been used. Here, large gaps that would have been insurmountable, and therefore not a consideration, using the actual lower dispersal figure could be addressed. Where such gap closures resulted in shorter routes becoming available, the speed with which a population could move from source to target, and consequently conductance, increased (Fig. 4.9). Such examples evidence the benefits of considering a spectrum of dispersal traits when contemplating conservation action, as has been suggested previously (e.g Brodie et al., 2015; Khosravi et al., 2018; Williams et al., 2020).



**Figure 4.9: Example of alternate routes provided by consideration of different dispersal distances.** a) Habitat created through the Distance algorithm using moderate and poor dispersal distances were placed in drastically different locations (Habitat created using poor dispersal = Orange, Moderate dispersal = Blue). Consideration of dispersal distances other than that specifically targeted can result in substantial improvements to connectivity. In this example, where conductance was modelled for a poor disperser but the network was modified for a moderate disperser, a gap in the network that would not have been considered for habitat creation with a poor dispersal distance was addressed. The resulting landscape enabled poor dispersing species to now cross that gap. The change in flow distribution for a poor-dispersing population between the landscape modified specifically for poor dispersers (b) and for moderate dispersers (c) illustrates this. The population could move from source to target via a shorter alternative route, additionally less of the budget was needed which could then be spent elsewhere, resulting in a conductance increase 2076 times the size of that generated using the bespoke dispersal distance. For plotting purposes cell flow values have been standardised to fall between 0 and 1.

## **4.5.2 Applications for conservation planning**

Condatis can help conservation practitioners make informed decisions on where to protect to conserve connectivity, through flow maps (see Chapter 2), and now, through the methods I describe here, where to prioritise for habitat restoration or creation. My process of pre-determining regions in which to consider placing habitat via the bottleneck function in the Condatis methodology, before further screening options via a feasibility surface, lend themselves to large-scale conservation planning in particular. This represents a significant improvement in computational efficiency to the Zonation style dropping procedure proposed by Hodgson et al., (2016), and the distinct procedures by which the three algorithms place habitat allows for more nuance than simply considering the centre of bottlenecks. Finally, the iterative nature of this process facilitates the identification of rounds where adding further habitat begins to offer minimal benefits (Fig. 4.7, Fig C.3-5), allowing resources to be allocated elsewhere, where they may be of more use.

Connectivity analysis at national and larger scales is computationally demanding, and is often conducted over coarse spatial data. Theoretically, the underlying Condatis method means evaluations at these spatial scales can be carried out at a finer resolution than other connectivity tools (see Section 1.8), but to a large extent this ability is determined by the hardware available to the end user. As such, realistically, national scale studies and larger will still have to be undertaken at a relatively coarse resolution. Therefore, I propose further studies could investigate the application of a two-step procedure. First, areas for creation/restoration at a national scale are identified and then second evaluation is conducted over the smaller regions identified in step one, allowing fine scale analysis and more precise prioritisation of where to restore/create.

I also think these methods could be of particular use in urban settings. Large urban spaces are a significant barrier to many dispersing species, and the spatial constraints in such areas necessitate stringent planning when designing structures such as urban greenways (Lynch, 2018). The evidence suggests that contemporary urban green spaces, such as green

roofs (Braaker, Ghazoul, et al., 2014) can be of importance to connectivity, especially due to the prohibitive spatial demands required for corridors. The tendency of the methods outlined here to produce stepping stone features lend themselves to such situations.

This framework has clear benefits, but parameterisation requires careful consideration. As I have shown, different dispersal values can lead to strikingly different results when all other variables are maintained. The results here imply that it is usually better to enact connectivity improvements based upon underestimations of dispersal than overestimations (Fig. 4.8). However, I acknowledge that there are occasions where overestimation can be surprisingly beneficial. Therefore, where possible, it is sensible to consider a spectrum of dispersal traits - a recommendation I am not alone in making (Brodie et al., 2015; Khosravi et al., 2018; Williams et al., 2020). Yet, if time or computational constraints mean only one analysis can be performed, I would counsel caution not to overestimate the dispersal ability of the species in question. Furthermore, definition of the power threshold value will also require careful thought, and should be chosen in such a way that accounts for the spatial structure of the network and the dispersal values being modelled. I am not aware of a way to pre-determine the optimal threshold value, and therefore some trial and error will be necessary.

### **4.5.3 Further steps**

I can see a number of avenues in which these algorithms, or the methods I employed in my analysis could be built upon or adapted to improve their performance, or applicability to different circumstances. Firstly, the feasibility surface I used was fairly rudimentary, and could be improved with the use of data such as land-ownership, land-use, existing habitat, topology, and protection status. Next, budgetary constraints on conservation actions should be a consideration within prioritisation not after (Balmford et al., 2000). Currently, these algorithms do so by defining the area of habitat that can be created. However, it is unlikely that habitat creation costs will be uniform across landscapes. Land-cost data could be easily incorporated into the Flow and TTC algorithms by selecting cells on highest flow or lowest

crossing time per monetary unit (Torrubia et al., 2014). This would only require the additional input of a cost per land unit layer and the budget parameter could then represent a fiscal rather than spatial budget. Finally, in this analysis I measured connectivity between two general locations, southern and northern extents of the landscapes. Conservationists may not only be interested in movements between two points, instead wishing to address bottlenecks throughout the area being analysed. In these instances, one could carry out multiple analyses using sources and targets that vary in their locale (e.g. East to west, South-east to North-west, South to North, South-west to North-east), before consolidating results.

#### **4.5.4 Conclusion**

In this study I have attempted to further the Condatis method to not only measure long-distance connectivity in habitat networks, but to also suggest where habitat creation might be of most benefit to improving the connectedness of the landscape. These methods require relatively simple inputs, are computationally efficient, such that large networks can be analysed, and produce easy-to-interpret outputs complementary to SCP procedures. There is a need to improve the connectedness of our landscapes, and recent policy often includes considerable habitat provision to facilitate those improvements. However, as it stands many conservation projects do not lead to connected landscapes (see Chapter 3). I find the algorithms described here are able to yield results significantly better than random, across a range of dispersal abilities and habitat structures. I propose that the methods described herein constitute an important tool for conservation planners, enabling clear description of where to consider habitat creation to best improve long-distance connectivity and ensure efficient conservation action. The methods thus allow long-distance connectivity to be more easily considered, improving the resilience of landscapes, and helping species adapt to their changing environment.

# Chapter 5 The use and usefulness of connectivity metrics

*“There is nothing like looking, if you want to find something. You certainly usually find something, if you look, but it is not always quite the something you were after.”*

- Thorin Oakenshield

## *5.1 Abstract*

Connectivity metrics and tools will be vital in achieving the resilient and coherent habitat networks that national legislation and international targets seek to create. However, there has been no investigation of their use in driving conservation action/delivery. Here I attempt to conduct such an assessment by exploring how conservation projects that seek to improve connectivity assess it and what that assessment leads to. I found information on 89 individual conservation projects which constituted a total of 100 connectivity analyses. While I find some evidence of diverse usage of connectivity tools, over 40% of connectivity assessments did not use a connectivity metric, instead relying on expert opinion, joining of topographical features, or, in some cases, not considering connectivity at all and using a surrogate such as increasing habitat coverage. My ability to draw firm conclusions on the use of connectivity tools in modern conservation was hindered, however, by the difficulty with which information on conservation projects could be obtained. As has been suggested previously, the thoroughness of conservation reporting needs improvement. I conclude by discussing why such a large portion of projects may not be using connectivity tools and put forward three priorities to tackle scepticism in connectivity metrics and increase the uptake in future projects.



## *5.2 Introduction*

Reducing habitat loss and fragmentation, and increasing habitat connectivity are important strategies to aid in nature's recovery and halt the decline of biodiversity worldwide (Taylor et al., 1993; Haddad et al., 2015; Isaac et al., 2018; Hilty et al., 2019), especially in the face of anthropogenic climate change due to the wholesale shifts of populations it drives (Parmesan, 1996; Chen et al., 2011; Lenoir et al., 2020). The importance of this strategy is recognised at national and international levels through legislation (Bai et al., 2018; DEFRA, 2018; European Union, 2020; DeFazio, 2021; Environment Act 2021), and targets past, present and future (CBD, 2011; OSPAR, 2020; CBD, 2021; IPCC, 2022). All of which include habitat creation and protection, explicitly stating that efforts should be made to produce resilient and coherent ecological networks.

Key to this effort will be delivery of conservation action based upon coordinated spatial planning. Conservation actions are typically a local scale endeavour undertaken with the guidance of local experts, but to produce habitat networks planning will be necessary at scales and complexities beyond the scope of expert opinion alone (Martin et al., 2012). As such, much intellectual effort has been expended over the past two decades to develop methods and tools capable of evaluating the connectedness of habitat networks and identify places important to connectivity, or where improvements to connectivity might be necessary (Calabrese and Fagan, 2004; Kindlmann and Burel, 2008; Correa Ayram et al., 2016; Keeley et al., 2021).

A recent study specifically considering connectivity conservation plans found they generally do lead to conservation outcomes (Keeley et al., 2019). However, beyond examining if it influenced the implementation of those plans, the study did not explore trends in connectivity evaluation methods. Indeed, to my knowledge there has been no study specifically investigating how connectivity has been evaluated in conservation projects that aim to increase connectivity. Understanding how, when and what connectivity measurement tools are used in conservation is of importance because the suite of connectivity tools

available represents a diverse resource pool that could be being under-utilised, or, if connectivity tools are used in situations they were not designed for, mis-used. Here, I explore existing peer-reviewed studies of conservation plans, databases of connectivity conservation projects and search the literature. By doing so I attempt to answer the questions: What connectivity metrics are used in connectivity projects? and What are the outcomes of those projects?

### 5.3 Methods

I identified conservation projects by (1) searching online databases such as Conservation Corridor and the Centre for Large Landscape Conservation; (2) searching the academic and grey literature for reviews of conservation plans and projects; and (3) through *ad hoc* discovery while researching projects from the preceding sources. The projects needed to meet three criteria to qualify for inclusion within this study. First, they needed to have an aim of improving habitat connectivity, be it the sole purpose of the project or one of a multitude of targets. Whether connectivity was considered in terms of animal movement, gene flow, or other types of ecological connectivity did not matter. Secondly, the projects needed to have the intention of producing a tangible effect, rather than being a wholly speculative study. Lastly, only projects whose documentation could be found in English were included.

Once a potentially suitable project was identified a targeted search was conducted of the academic and grey literature to find the method of connectivity analysis. These methods were classified into eight categories (Table 5.1). Placement of projects into these categories was straightforward for the most part. However, deciding where to place projects that utilised systematic conservation planning software or principles like ‘comprehensiveness’ and ‘representativeness’ was more complicated. In these instances, I tried to identify what data were included within the model to direct actions. If these data were not available, it was assumed that connectivity had not been included, due to the historic difficulty of including it within SCP procedures because of the diverse considerations needed to account for connectivity’s multifaceted nature (Tischendorf and Fahrig, 2000). The outcomes of the projects were placed into four categories for simplicity of analysis: ‘evidence production’, generating connectivity-based resources for use in future planning or conservation; ‘protection’, direct purchasing of land by the project or project activities leading to statutory designation of an area; ‘restoration/creation’, creating or restoring areas of habitat to improve connectivity; and ‘other’, reported outcomes that did not fall into the above categories.

Outcomes were identified through the literature found for each project, particularly final project reports. A list of projects included in the analysis as well as the literature from which information was obtained is provided in the supplementary materials (Appendix D).

This search strategy does not constitute a full systematic review; indeed conducting one would have been beyond the resources of this study. However, I consider it more closely represents the information that is readily available to conservation planners and practitioners who may be seeking examples of what has worked in the past to help guide their actions.

**Table 5.1: Definitions of connectivity assessments used in the analysis.**

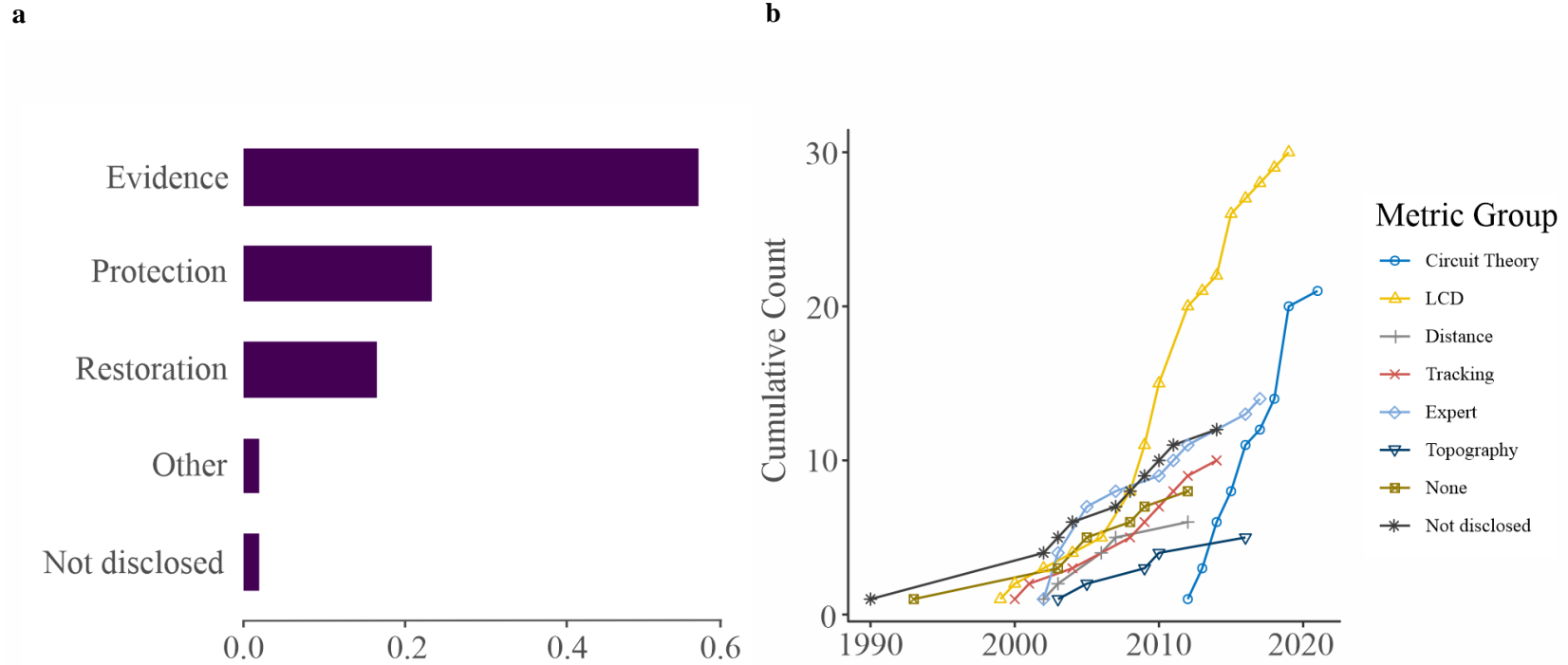
| <b>Connectivity assessment</b> | <b>Count</b> | <b>Definition</b>   | <b>Example tool/metric/method</b>                       |
|--------------------------------|--------------|---|---|
| Circuit theory                 | 21           | Analogue the movement of species or populations through a landscape to the flow of current through an electrical circuit        | Circuitscape  |
| Least Cost                     | 30           | Utilise a cost surface representation of the landscape to find the single path that has the lowest accumulated cost to traverse | CostDistance  |
| Distance                       | 6            | Use the distance between two points, or the dispersal ability of a species to describe how connected areas are                  | Incidence function model                                |
| Tracking                       | 10           | Identify connectivity through the examination of tracking data, through telemetry from tracking collars, camera traps etc.      | Tracking collar GPS data                                |
| Expert opinion                 | 15           | Tap into the knowledge of experts, either of a particular species or the study area, to identify areas that should be connected |   |
| Topography                     | 6            | Use maps to identify similar features that should be connected  | Increasing permeability between mountain ranges         |
| None                           | 8            | Do not specifically measure connectivity, instead assume it was increased based on a conservation action                        | Increasing the area of habitat present in the landscape |
| Not disclosed                  | 12           | Did not state how connectivity was measured, or could not be obtained   |   |

## *5.4 Results*

In total I was able to find reference to 89 individual conservation projects with a specific aim of improving connectivity. The earliest project started in 1990 and the latest in 2021. Of these, 32 occurred in North America, 17 in Asia, 13 in Oceania, 12 in Africa, 11 in Europe, 3 in South America, and 1 in the Arctic. Within these 89 projects I found reference to 100 connectivity assessments. Of these, 63 included a specific measure of connectivity (defined as those using circuit theory, least cost and distance based metrics or direct observations of movements such as tracking data), 26 forwent the use of connectivity metrics in favour of expert opinion, topography, or no connectivity assessment (e.g. simply increasing the area of habitat present in the network and stating that as a result connectivity had likely increased), and the remaining 11 did not disclose how connectivity was assessed (Table 5.1).

### **5.4.1 What are the outcomes of connectivity projects?**

The majority of projects (57.4%) cited evidence creation for use in future planning or conservation as a core outcome of their work (Fig. 5.1a). Of the projects included in the study, 38.6% resulted in some form of physical conservation intervention, comprising 22.8% that resulted in the protection of important areas of habitat, and 15.8% that created or restored habitat in some form or another. Other outcomes reported by the projects included training and the establishment of a conservation lease program. Two of the projects did not disclose what work came of their analysis.

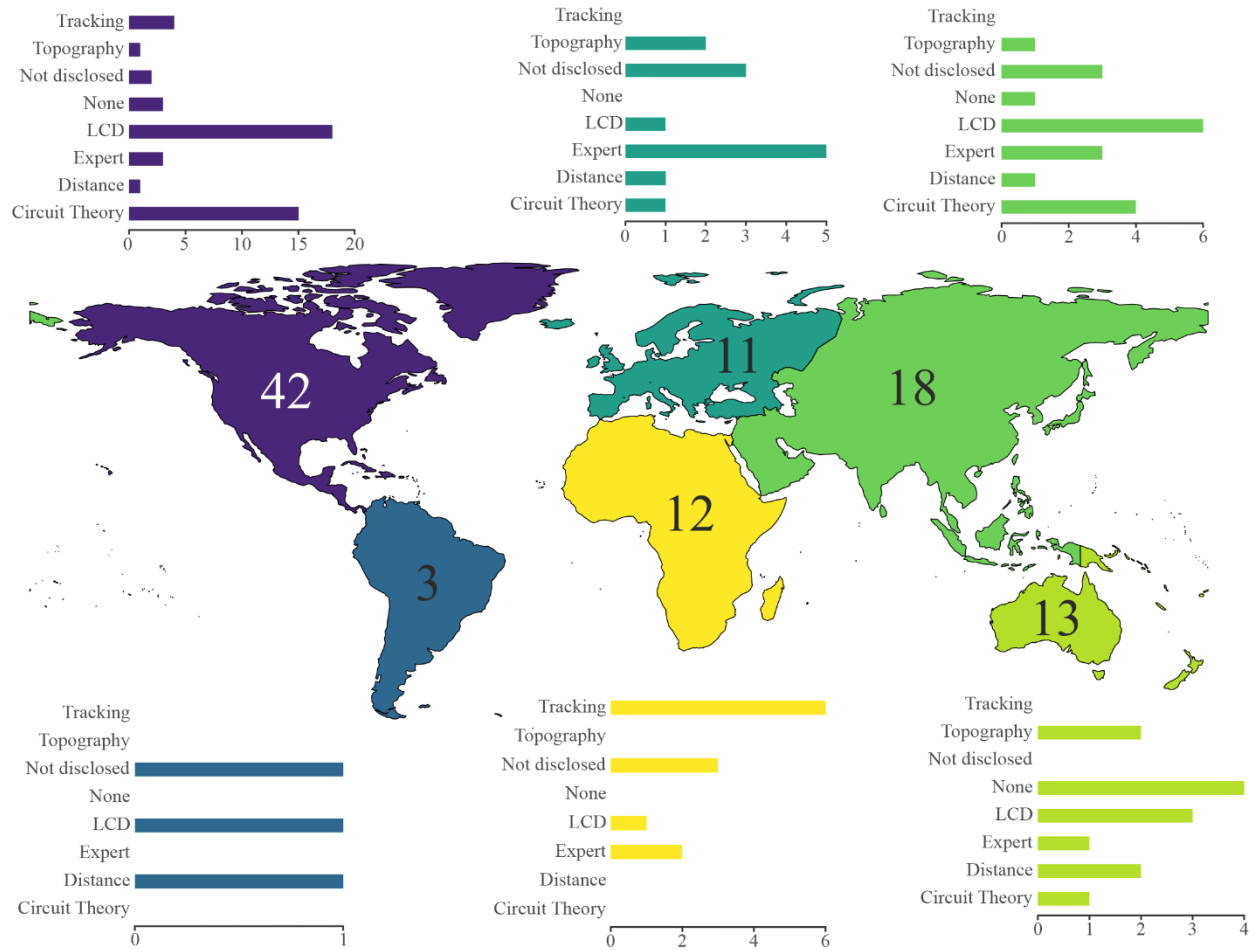


**Figure 5.1: Outcomes of connectivity projects and metrics of use.** (a) Bar plot detailing the output categories as a proportion of the projects included within the analysis. ‘Other’ consists of two projects describing ‘Training’ and ‘conservation lease program’ as outputs. (b) The cumulative number of projects using a connectivity metric type conducted between 1990 and 2021.

## **5.4.2 What connectivity metrics are used in connectivity projects?**

The methods used to assess connectivity were varied, ranging from joining similar topographical features through to utilising complex connectivity models. Since their respective underlying theory was first published in the literature, it appears least cost and circuit theory quickly became the most commonly used methods to assess connectivity in conservation (Fig. 5.1b), equating to 27.8% and 19.4% of methods used in projects included in this study respectively, and 28.3% and 43.8% when only including projects since their first usage. However, this was not consistent across all regions, with the prevailing method of assessment changing depending on where the project was undertaken (Fig. 5.2). For instance, while circuit theory and least cost were favoured in North America and Asia, expert opinion was the most used method in the connectivity analyses of Europe, and tracking data in African projects (Fig. 5.2).

Delving deeper to look at specific tools or metrics used to measure connectivity, I found that only two of the 25 analyses that used circuit theory did not use Circuitscape (Shah and McRae, 2008) or some extension of it such as Omniscape (Landau et al., 2021). Contrastingly, analyses using least cost methods were more diverse with a total of 11 different tools or metrics implemented. The most popular of these were CorridorDesigner (Majka et al., 2007), and the CostDistance and Least Cost Corridor Analysis functions of the ArcGIS spatial analysis toolkit, which represented 24%, 12% and 12% of analyses respectively. Linkage Mapper (McRae and Kavanagh, 2011) was another popular tool, utilised in six analyses, that uses both circuit theory and least cost methods.



**Figure 5.2: Geographic trends in connectivity metric usage.** The number of connectivity assessments for each continent and bar graphs of the connectivity metrics utilised within those assessments. Note that sums in the bar charts may not align with the number of connectivity assessments because some used multiple metrics in their analysis of connectivity.



## *5.5 Discussion*

Over the last two decades there has been extensive development in tools to measure and assess connectivity (Calabrese and Fagan, 2004; Kindlmann and Burel, 2008; Correa Ayram et al., 2016; Keeley et al., 2021). However, to my knowledge there has been little study of what connectivity tools are actually used for conservation and what results from their use. Identifying answers to those questions could be valuable to evaluate best practice. Here, I have attempted such a study.

### **5.5.1 The use of metrics and outcomes**

Overall, the metrics used to assess connectivity were generally based upon least cost or circuit theory (Fig. 5.1b). Distance based methods were not utilised as often as one might expect given their importance when connectivity measurements first entered the conservation sphere. One plausible explanation is that the connectivity projects I identified were largely of a regional scale or smaller and distance-based methods are now typically applied at larger scales, hence their frequent use in global analyses (Santini et al., 2016; Saura et al., 2017; Saura et al., 2018; Ward et al., 2020). However, distance-based measures also prove useful in landscapes where the delineation between habitat and non-habitat is well defined, such as those covered by urban development or intensive agriculture (Keeley et al., 2021). Therefore, another explanation could be that projects utilising these measures were disproportionately missed. Distance-based connectivity measures were some of the first to enter the literature (Kindlmann and Burel, 2008), as such projects using them may be older and thus the presence of documentation online is less likely.

When looking at conservation outcomes, the majority (57.4%) of projects lead to the production of evidence (Fig. 5.1a). This should not be surprising because evidence production precludes conservation action in most circumstances. However, in 48 of 58 instances citing evidence production it was the only output I could identify. Producing evidence is important, but the existence of a “knowledge – action” gap is already well-

established in conservation (Knight et al., 2008; Buxton et al., 2021), the perpetuation of which is in conflict with the fundamental aspect of successful conservation; translating sound information to action.

### **5.5.2 Under-reporting of methods**

The scope and depth of this study was severely curtailed by the difficulty with which I was able to acquire details on connectivity assessment methods. Yet, that in itself is a result worthy of further discussion. I was able to identify 89 conservation projects for inclusion in the study, but many more were excluded through lack of data. The road to details on connectivity assessment, where it existed, was paved with dead hyperlinks, unarchived reports, and ambiguity, such as stating that connectivity had been measured but not giving further detail, or providing maps showing the results of connectivity analysis but not expanding on how they were generated. As a result, even in instances where information was available it was often difficult to attribute work to specific projects. The majority of information sources I identified could be considered “grey literature” and these results parallel previous research commenting on the difficulty associated with accessing methodological details, particularly outside of the peer-reviewed literature (Knight et al., 2008; Sinclair et al., 2018).

In the face of this difficulty, previous work has relied on responses to questionnaires (Sinclair et al., 2018; Keeley et al., 2019), but doing so was beyond the scope of this study. Nevertheless, the success of such methods relies upon receiving responses and the responders correctly recalling what happened on projects that may have taken place decades in the past (Gillham, 2011). These factors can combine to result in a substantial reduction in data. For instance, Keeley et al. (2019) reported a 41.4% response rate in their study, this certainly still represents a considerable yield of information, but is substantially less than if details had been recorded in the first place.

There has been, and continues to be, a shift in legislation and targets towards creating resilient and coherent ecological networks (Bai et al., 2018; DEFRA, 2018; European Union, 2020; DeFazio, 2021; Environment Act, 2021). Therefore, now perhaps more than ever, scrutiny of the methods used to deliver conservation focusing on connectivity is needed. Scrutiny that is not possible if we do not know what those methods are. I echo the sentiments of other researchers before me when I say that reporting of connectivity analysis and any resulting conservation activities has been insufficient and needs to be addressed (Sutherland et al., 2004; Knight et al., 2008; Rands et al., 2010; Sinclair et al., 2018; Bowgen et al., 2022). Clearly, demanding a level of methodological reproducibility akin to peer review for grey literature would be needlessly restrictive. Yet, conservation projects are how we, as conservationists, put our theories to the test, understanding the methods that led to successful outcomes will be vital to successful conservation.

### **5.5.3 Considerations for connectivity assessment development**

The literature is full of new and innovative tools for connectivity modelling that can aid conservation planners make local scale decisions within the context of large-scale habitat networks (Correa Ayram et al., 2016; Keeley et al., 2021). We know that connectivity conservation plans regularly lead to conservation outcomes (Keeley et al., 2019), but we do not know how connectivity is assessed in those plans. Therefore, we also do not know if those innovative tools are put to use and if they lead to delivery of conservation and attaining connectivity targets. Previous research found that methodological advancements led to the development of globally used prioritisation tools (Sinclair et al., 2018), and the findings here suggest a similar process has occurred in the connectivity literature, with circuit theory, least-cost and distance-based metrics used throughout the world. Yet, stakeholders still appear sceptical of connectivity metrics when compared to direct observations or expert opinion, with practitioners commenting that “*A single animal*

*movement path could be more compelling than the output of the most sophisticated model”* (Keeley et al., 2019). Indeed, despite the use of tools in a large proportion of projects, I found 43.5% of evaluations of connectivity were based on expert opinion, tracking data, joining of topographical features, or did not use any measure of connectivity directly, such as stating that connectivity had increased because the amount of habitat present in the network had increased.

Scepticism of connectivity tools from conservation practitioners is understandable, but how can we tackle it? A portion of projects will have occurred prior to the development of connectivity metrics, but this is the case for only two of the those included in this study. Validation is a particular area of concern amongst practitioners when it comes to connectivity tools and is still an emerging field with many tools yet to be evaluated in this way (Thurfjell et al., 2014; Koen et al., 2014; Wade et al., 2015; Marrotte et al., 2017). Furthermore, the dearth of dispersal data with which to parameterise projects (Fagan and Calabrese, 2006; Travis et al., 2013) has resulted in the use of generic species in many connectivity analyses, which is at odds with the highly species-specific nature of dispersal. Yet, some of this hesitancy may be due to unfamiliarity with methods for connectivity assessment. Movement data, when it is available, is tangible and easily understood, while the outputs of connectivity models can seem abstruse at first. Granted, connectivity metrics may not be necessary in every connectivity assessment, but unfamiliarity should not be a barrier to their use where they could be of help. I propose three important paths towards breaking these barriers.

First, we need to conduct more testing on the metrics we have. We need to validate tools with real world data and test to properly ascertain how metrics react to different changes in landscape structure and configuration. For instance, measures based on graph theory may be able to model the change in connectivity when increasing the size of existing patches, but not the reduction in connectivity caused by the loss of a linkage in the network, because connectivity isn't considered between a patch and every other patch as it is in

techniques such as circuit theory (see Section 1.5). Validation would give practitioners confidence in the outputs of connectivity tools, and break down this principal barrier to their use.

Next, the proliferation of connectivity metrics and tools could be a barrier in itself. Not only does an overabundance of options lead to indecision (Iyengar and Lepper, 2000; Haynes, 2007), but the ever more diffuse methods of connectivity measurement make it difficult for practitioners to develop the technical skills to use them. This compounds when we consider the recommendation to implement more than one connectivity tool in connectivity analysis (Keeley et al., 2021). Therefore, I would also argue that, where possible, further development in connectivity methods should try to build upon existing tools already used in conservation. Doing so would amass familiarity in their outputs and usage among stakeholders and practitioners through consistent exposure, perhaps promoting uptake and tackling the sentiment noted in Keeley et al. (2019). That is not to say that innovation should be stifled, simply that innovation packaged in a familiar way might be included more readily into conservation practice. If methodological advancement necessitates the generation of a new tool, then that new tool should certainly be created. For instance, ConScape (van Moorter et al., 2022) builds upon least cost and circuit theory through the inclusion of randomised shortest paths, which allows the assumption of the mover's knowledge of their surroundings to be considered on a continuum, rather than simply the two extremes of complete knowledge or total absence – a frequent criticism of both circuit theory and least cost methods (McClure et al., 2016). Yet, in doing so, ConScape still builds upon established methods by integrating functionalities of the existing software packages Confor (Saura and Torné, 2009) and Circuitscape (Shah and McRae, 2008). Condatis is another example, it takes methodological advancements of circuit theory and adapts them to relax the data requirements so the powerful circuit theoretic interpretation of the landscape can be applied at larger scales to model range shifts.

Certainly, I am also not implying that least cost or circuit theory should be the basis of all connectivity assessment; circumstance will dictate which tool is appropriate. For instance, the results here suggest tracking data was the favoured method of connectivity measurement in projects undertaken in Africa (Fig. 5.2). This may be because the migrations of megafauna were a primary concern. These movements occur along regular routes, therefore tracking data, which represents the actual movements undertaken by individuals, and least-cost methods, which include a consideration of an individual's knowledge of its surrounds, are natural choices. Whereas, methods like circuit theory, which assume that the mover has no knowledge of its surrounds would be less appropriate (McClure et al., 2016). Therefore, I propose that the production and dissemination of something akin to a taxonomic key to be a pressing need for connectivity metrics. A key would help practitioners navigate the options they have available and decide which tool is suitable in their instance. Examples of components to consider are:

- **Data requirements/complexity:** The data available to a practitioner may rule out certain connectivity tools, such as those that require data to produce cost-surfaces, and model complex population and evolutionary dynamics like Rangesifter (Bocedi et al., 2014);
- **Computational requirements:** The computational requirements of some models may be prohibitive depending on the facilities available to the practitioner. Furthermore, all connectivity models, to differing extents, make concessions to reduce the computational requirements. The type of concession made, such as Condatis' representation of the matrix, should also be a consideration in model choice;
- **Connectivity type:** Measures of connectivity differ in their capability to model structural, functional or landscape connectivity;
- **Landscape structure:** Connectivity tools that are able to determine the effect of losing a habitat patch on the overall connectivity of the landscape and those that

recommend where to place or protect stepping stones may be more appropriate in highly fragmented landscapes. These capabilities that would be less necessary when modelling largely intact wild areas;

- **Spatial scale:** the spatial scale at which connectivity is modelled changes the processes that need to be considered and therefore the model utilised. For instance, modelling at local scales may favour individual-based models or those that incorporate population dynamics, but these methods that may be less applicable to larger-scales due to modelling movements between, rather than within, metapopulations;
- **Type of movement:** As mentioned previously modelling range shifts, migrations and natal dispersal require different considerations that not all connectivity measures are capable of; and
- **Desired output:** Some connectivity tools are able to provide options of specific areas to undertake conservation (see Chapter 4), or general areas to target conservation, while others provide statistics, such as Condatis' conductance, to enable the comparison between different conservation options.

This work has been attempted in the past (Calabrese & Fagan, 2004; Kindlmann & Burel, 2008; Keeley et al., 2021), but even the most recent of these, while fairly comprehensive, does not consider factors such as data requirements. The points above regarding testing, validation and consolidation of methods would help facilitate the production of a comprehensive and clear key. Such a resource would enable conservation practitioners to make informed choices, guiding them through the sea of options presented in the connectivity measurement sphere.

#### **5.5.4 Conclusions**

Here, I attempted to identify which connectivity metrics are used for connectivity enhancement through conservation planning and what their use leads to. I find that while connectivity metrics are used, there is still a heavy reliance on simplistic analogues and

expert opinion, with some projects not measuring connectivity directly at all. However, my ability to draw meaningful conclusions was curtailed by the difficulty with which methodologies of conservation projects could be found. Past studies have identified some hesitancy to use connectivity tools from conservationists and the evidence presented here paints a similar picture. I suggest that this could be alleviated through testing and validating models to establish confidence in their outputs, increasing familiarity by reducing the proliferation of individual connectivity tools, and producing a taxonomic key of connectivity metrics to ensure the right tool is chosen for the job. Substantial conservation efforts will be needed to meet the targets and initiatives focused on producing coherent and resilient ecological networks. Appropriate measurement of connectivity will be an important factor, and through the above steps, might be more readily implemented. However, we also need to ensure that conservation methods are better recorded. This would allow us to identify what works in conservation as we continue to aid nature's recovery from anthropogenic pressures.



# Chapter 6 General Discussion

*“It's the questions we can't answer that teach us the most. They teach us how to think.”*

- Kvothe

## *6.1 Summary of findings and significance*

Connectivity is of importance to a vast array of ecological processes such as recovery from disturbance (Altermatt et al., 2011; Oliver et al., 2013) and preventing inbreeding (Keller and Waller, 2002). Now, with the advent of anthropogenic climate change, connectivity is playing a crucial role in species adaptation by facilitating range shifts (Parmesan, 1996; Lenoir et al., 2020). In the face of habitat loss and fragmentation, a key conservation stratagem is providing and restoring large scale ecological networks (Hilty et al., 2019; Hilty et al., 2020). The importance placed on this strategy is reflected in legislation and targets at both national and international levels. Concurrently, there has been an escalation in the development of diverse tools that allow conservationists to evaluate and plan conservation to reach these goals. One such area is through the evaluation of the connectedness of our landscapes (Calabrese and Fagan, 2004; Kindlmann and Burel, 2008; Correa Ayram et al., 2016; Keeley et al., 2021). The aim of this thesis was to fill existing knowledge gaps to allow long-distance connectivity, of the type necessary to facilitate species' adaptation to climate change, to be considered in the conservation planning process. Over the course of four chapters I examined how protected areas conserve habitat patches important to connectivity; scrutinised recent conservation projects to determine whether our current methods improve long-distance connectivity; developed a new method to aid in directing where to create habitat to improve long-distance connectivity; and explored the use of connectivity metrics in conservation. Following these avenues of research, I highlighted potential shortfalls in our existing methodologies and provided examples of how we might be better able to plan conservation to provide habitat networks that aid nature's recovery in the face of anthropogenic climate change.

### **6.1.1 Chapter 2: Habitat patches providing South-North connectivity are under-protected in a fragmented landscape**

I found that in 12 of 16 habitat networks I studied, connectivity was under-protected. I observed that despite patch protection favouring larger patches, which are typically more important to connectivity, existing protected areas (PAs) appeared biased towards low-flow patches. This finding indicates a disconnect between past protection decisions and those needed to facilitate climate adaptation through range shifts. I posited that comparable network vulnerabilities likely exist in the PA networks of other nations due to the similarity of habitat protection principles around the world. To accompany this finding, I produced evidence that substantial gains in connectivity protection can easily be made for little addition to the overall area of the protected area estate. By selecting habitat patches based on flow, I was able to capture important, often small, connectivity patches and protected on average 40.9% more connectivity with just a 10% increase in area.

Previous studies exploring connectivity and the PA estate have done so in the context of joining individual, existing PAs (Santini et al., 2016; Saura et al., 2017; Saura et al., 2019). However, though important, PA connectivity per se is not necessarily the only route to explore. It is the connectivity of the habitat patches those PAs serve to protect that affects the reproduction and dispersal pivotal to climate change adaptation. In this chapter I took inspiration from measures of functional connectivity, which consider the experiences of the mover, and included the species' perspective in an analysis of PA networks. By investigating patch protection and connectivity independently from one another, I added further ecological realism to PA network evaluations. As such, I was able to go beyond the consideration of the disconnection between our PA networks, and say that what connectivity there is remains vulnerable because PAs inadequately conserve it.

### **6.1.2 Chapter 3: Landscape-scale conservation projects achieve connectivity increases relevant to climate change no better than random**

I presented an assessment of how modern conservation projects effected connectivity relevant to climate change. I found that, in the majority of instances (71.3%), connectivity improved less than would be expected given the amount of habitat that had been added – the Baseline Conductance Increase (BCI). I put forward that this result suggests that even in projects established from recommendations to connect a nation’s landscape, connectivity could have been more judiciously considered. There were a few instances where connectivity gains substantially outstripped BCI. Yet, the majority of these instances occurred at spatial scales that would not necessarily benefit climate change adaptation. I drew parallels between the underrepresentation of connectivity in the PA network and the shortfalls of conservation projects – both of which arose from failure to consider long-distance connectivity. I concluded by stating that connectivity improvements relevant to climate change are likely only attainable via well-targeted conservation efforts. Connectivity metrics are poised to provide this and should be utilised in future conservation to ensure connectivity projects lead to connected landscapes.

Much of the legislation and targets associated with modern conservation focus on providing large-scale and connected ecological networks. However, while studies have shown that connectivity conservation plans are regularly utilised (Keeley et al., 2019) or that conservation projects have improved connectivity within the bounds of the project (Hunter-Ayad and Hassall, 2020), none have examined the ability of conservation projects to promote connectivity in the wider-landscape. This study does so and provides further evidence that conservation is unlikely to deliver wide-reaching connectivity without proper consideration, a finding that is particularly timely due to the extensive habitat creation and restoration activities on the horizon.

### **6.1.3 Chapter 4: Where to create habitat for connectivity?** **A procedure to bridge gaps in habitat networks**

I developed a new method of identifying specific places to create habitat to best improve connectivity. I outlined promising results, which highlighted the ability of the algorithms to produce considerable increases in connectivity across a variety of landscape structures and for species with a range of dispersal abilities. Although there were a small number of instances where the algorithms performed comparably to random habitat placement, these occurred in habitat networks with a lower priority for connectivity improvement. I concluded with a section outlining suitable applications of the method in conservation planning, and further considerations for its improvement.

Existing methods to systematically address connectivity in restoration planning exist (McRae et al., 2012; Torrubia et al., 2014; Hodgson et al., 2016), but the method I present builds upon them in important ways. First, I incorporate a “feasibility” surface that can be generated from a variety of different data and allows for confidence that where the model suggests, action can be taken. Next, I build upon Hodgson et al.’s (2016) powerful iterative adding routine, making it more computationally efficient such that it can be applied over large scales more readily. Finally, the different methods by which my algorithms add habitat allow flexibility in the size, shape and arrangement of habitat patches that are created, and recommend specific places to act rather than general regions (McRae et al., 2012), parcels of land (Torrubia et al., 2014), or individual cells (Hodgson et al., 2016). As a result, the tool I have produced is well placed to aid conservation planners address major gaps that exist in our fragmented habitat networks in an economical and accurate way.

#### **6.1.4 Chapter 5: The use and usefulness of connectivity metrics**

I presented findings from an evaluation of 89 individual conservation projects, with a specific aim of improving connectivity, that took place between 1990 and 2021. I showed that just over a third (38.6%) of the projects included in the study resulted in some form of “on the ground” action. Interestingly, while least cost and circuit theory-based models now dominate connectivity assessment methods, 43.5% of the analyses I identified did not use a specific measure of connectivity. I also noted a disappointing lack of reporting on the methods of connectivity assessment in conservation projects, and added my voice to the chorus of researchers calling for improvement in the reporting of conservation outcomes and methods. I finished by discussing the evidence of scepticism from practitioners and stakeholders regarding connectivity metrics that others had reported, and outlined three suggestions that might increase uptake; testing and validation, reduction in unnecessary proliferation of connectivity tools, and the production of decision trees to help practitioners chose the right tool for the job.

While recent research has explored the implementation of connectivity plans (Keeley et al., 2019), to my knowledge there had been no study in specifically how connectivity is assessed in conservation plans. Much intellectual effort has been expended in the production and development of connectivity assessment tools, and it has remained unclear how widespread their use is, what they are used for, and what comes from their use. The study I presented represents a step towards gathering this information, sheds light on some reasons why connectivity tools might not be used by conservation planners that could benefit from them and highlights that connectivity analyses are not immune from the reporting paucity that blights much of conservation.

## 6.2 *Synthesis*

### 6.2.1 **Weaving climate change-relevant connectivity into conservation planning**

The findings of this thesis provide evidence for the need to specifically consider long-distance connectivity in our planning processes and have implications for how we do so in both designation and conservation.

#### 6.2.1.1 *Protected areas*

Considering the protected area (PA) estate, it is well established that PAs throughout the world are disconnected (Saura et al., 2017; Saura et al., 2018; Saura et al., 2019; Williams et al., 2022). However, Chapter 2 also highlights their failure to include areas most important to long distance connectivity. Well-connected PA networks that work for a multitude of species will require strategically placed PAs. Furthermore, investment in new designations to cope with climate change has been, and continues to be, a pressing concern (Hannah et al., 2007; Elsen et al., 2020; Williams et al., 2022). Naturally, we will need to protect the eventual end points of range shifts, but we also need to protect land that helps facilitate those shifts. I have shown that, unfortunately, previous guiding principles have inadvertently selected against such land (Chapter 2). Including connectivity into the designation process has become more feasible with the rise in use of techniques such as Systematic Conservation Planning, which can now employ least cost and circuit theory measures for more complex representations of connectivity (Lehtomäki and Moilanen, 2013; Daigle et al., 2020). However, while these may help join PAs, they typically are not suitable for considering connectivity over distances relevant to climate change adaptation. I provide evidence of Condatis' capability in supplementing designation planning to provide that context and highlight the relatively small increases to the PA estate needed to drastically improve the protection of long-distance connectivity in our habitat networks. This is particularly timely given the substantial PA area increases on the horizon (IUCN, 2021). My work has been undertaken in terrestrial systems, but the objectives, methods and analyses

employed in marine spatial prioritisation are strikingly similar (Virtanen et al., 2020).

Therefore, I think it plausible that these same methods hold equal promise at sea as on land. PAs are not solely responsible for safeguarding the ability of habitat networks to facilitate range shifts and, similarly, are not the only conservation activities that can be guided by the topics covered in this thesis. Other Effective area-based Conservation Measures (OECMs; IUCN-WCPA Task Force on OECMs, 2019) are defined by the IUCN as areas outside of PAs that are governed and managed in ways that achieve positive and sustained long-term outcomes for conservation. OECMs include a broad spectrum of activities, adding further tools to the conservation arsenal and will be invaluable in places where designation is not viable, or palatable, and at a time where the rigidity of traditional statutory designations is misaligned with the dynamism of conservation in a changing world (Dudley et al., 2018; Lázaro et al., 2021; Bailey et al., 2022).

### *6.2.1.2 Beyond*

Considering conservation activities outside of PAs, Chapter 3 highlights that, in the absence of a measure of long-distance connectivity, conservation projects are unlikely to lead to connected landscapes. Biodiversity is not constrained by geopolitical borders and its proper conservation will require thinking beyond them too (Kark et al., 2015; Runting et al., 2015). The need for conservation across international borders is well-established (Vasiljević et al., 2015). However, it is no less important at a sub-national level where conservation plans are also usually subdivided. For example, in England the Nature Recovery Network (DEFRA, 2018) will be produced through a series of Local Nature Recovery Strategies (LNRSSs) arranged such that they cover the entirety of England (Environment Act, 2021). To establish a national ecological network, we need to ensure that individual projects think of their positioning in the “big picture”. The results from Chapter 3, which studies projects that can be considered precursors to LNRSSs, indicate that as it stands they might not serve conductivity on a larger spatial scale. Historically, connectivity models have struggled to provide exact locations of where restoration with the aim of improving connectivity should



be undertaken. Chapter 4 advances progress towards this objective by providing an example that works across a variety of dispersal abilities and landscape structures, and is economical enough in its data requirements to feasibly see application at the scales needed to consider climate change adaptation.

Other studies have suggested conservation focused on increasing the size and aggregation of existing patches would be more beneficial to connectivity conservation, and recommended that this should happen prior to attempting to increase connectivity itself (Hodgson et al., 2009; Mair et al., 2014). I question a sequential recommendation, that one action should be a pre-requisite of the other, especially in the context of connectivity. Yes, we need stable populations capable of producing dispersers necessary for range shifts, which increasing the area of core habitat may well support (Hodgson et al., 2011), but what use are dispersers if they have no route by which to disperse? Indeed, this paradigm of increasing core habitat area is now challenged by recent findings that increases in the “clumpiness” of habitats slows climate-driven changes in community redistributions (Fourcade et al., 2021), and that the spatial configuration of habitat is potentially more important to the speed of range shifts than simply the amount of habitat (Hodgson et al., 2022). My findings that areas whose designation leads to substantial increases in connectivity protection (Chapter 2) and patches created by algorithms specifically designed to maximise connectivity (Chapter 4) were often small in size, further supports those results. Future study could disentangle the influences of increased connectivity between habitat patches and simply an increase in area of habitat through the examination of the species area relationship. This typically follows a power law with an exponent of  $< 1$  (Fischer, 2000), a deviation from that trend may signify the positive impact connectivity has had over and above the amount of habitat that has been added. Nevertheless, the urgency with which conservation related to climate change adaptation needs to be implemented (Morecroft et al., 2019) strengthens my argument that increasing the amount and connectedness of habitat needs to occur in parallel rather than series; especially, because even now empirical evidence to support many claims made

regarding what types of conservation action lead to successful adaptation is lacking (Newson et al., 2014; Bowgen et al., 2022). It is unlikely that either action will consistently be best in any situation, and a balance will need to be struck in individual circumstances. The best route to find that balance is through the use of proper planning considering the differing spatial scales over which connectivity can act, the population and landscape in question, and through constant re-evaluation of progress towards clearly defined goals (Morecroft et al., 2012; Isaac et al., 2018; Morecroft et al., 2019). Connectivity tools, such as the methods I demonstrate here, will prove a valuable part of that procedure and aid in ensuring we protect biodiversity into an uncertain future.

## **6.2.2 Barriers to doing so**

As Chapter 5 touches upon, there are still a number of barriers to the inclusion of long-distance connectivity, and connectivity in general, in conservation planning that need to be addressed: barriers related to Data, Uncertainty, and Reporting.

### ***6.2.2.1 Dispersal data***

The use of connectivity tools has traditionally been limited by the barrier to entry posed by data. Advancements in remote sensing techniques are increasing the availability of habitat spatial data and leading to higher resolution and accuracy. Yet, dispersal data remains difficult to obtain, particularly at the landscape scale, where it typically derives from small samples sizes (Fagan and Calabrese, 2006; Travis et al., 2013).

If we want our analyses to reflect the species-specific nature of dispersal, then accurate and diverse dispersal data is an important resource. Fortunately, there have been promising developments in recent years. For instance, tracking technology has advanced to produce smaller and more complex hardware that can facilitate the collection of ‘lifetime’ data, with an increased resolution of datapoints and for a broader range of species (Kays et al., 2015). Not only could this tracking data help us deduce the dispersal abilities of species and help counter the biases in tracking data that may have accumulated from not being able to detect

the longest distance movements, but also define suitable resistance values for different habitat types. However, before this can be of use we will need to untangle and differentiate between actual dispersal activity and movements related to resource use because there are often substantial differences in habitat association that species exhibit between the two movement types (Elliot et al., 2014; Gastón et al., 2016; Jackson et al., 2016). Prospecting, movements between breeding sites within which an individual does not currently breed, often occurs before dispersal (Reed et al., 1999) and could prove useful as a marker for dispersal in tracking data. Alternatively, the movements of individuals through unfamiliar environments following species reintroduction/releases could provide another opportunity to gather information on dispersal (Driezen et al., 2007). In addition to its use to parameterise connectivity tools, sufficient dispersal data will be invaluable in the development of appropriate and accurate dispersal kernels to utilise within those connectivity tools, as illustrated for plants by Bullock et al. (2017).

Databases have also been in development that provide useful resources, both those of individual studies, or larger more global datasets including Movebank (Wikelski et al., 2022; Kays et al., 2022) for tracking data and Pantheria (Jones et al., 2009) for life history and dispersal figures. In the context of climate change-relevant connectivity, we should not overlook the effect climate change will have on dispersal, both directly and indirectly (Travis et al., 2013) – for instance, through selection pressures towards longer dispersing morphs (Hill et al., 1999; Simmons and Thomas, 2004). However, acquiring dispersal data of such morphs would be difficult and I question if conservation mechanisms could move quickly enough to put such data to use in time for it to be effective. Furthermore, the conservative approach of using dispersal of normal morphs, leading to underestimation would be preferable to the overestimation that may occur from poorly inferred improvements to dispersal ability as a result of climate change.

### 6.2.2.2 *Uncertainty*

As discussed in Chapter 5 there still seems to be some scepticism surrounding connectivity models (Keeley et al., 2019). Within that chapter, I discussed the need for validation, reducing the proliferation and redundancy of connectivity models, and decision trees. However, validation warrants further discussion due to its relative rarity (Walpole et al., 2012; Thurfjell et al., 2014; Koen et al., 2014; Wade et al., 2015; Marrotte et al., 2017) and importance in highlighting the suitability of connectivity models to direct conservation efforts.

Many aspects of models require validation (Sargent, 2013), including the conceptual basis of the model, computerisation, and operation. Here, I will focus on validation of the output of models – operational validation – because conceptual validation of models, that the underlying theory upon which they are based is sound, and computerisation, that the model has been correctly implemented in whatever programming language it has been written in, should have occurred at the point of peer review, prior to being released for use by the wider conservation community.

There are many facets of operational validation (Sargent, 2013), but the techniques applicable to connectivity are predictive validity, historical validity, face validity and comparison to other models. It seems sensible that combinations should be utilised to properly validate a connectivity model's output. Predictive and historical validity require substantial data, so only one will be used in most circumstances, but comparison and face validity – namely comparing outputs with other models and checking with experts – do not. Indeed, it is already suggested that more than one connectivity model should be used to inform conservation (Keeley et al., 2021). However, in isolation face validation is likely weak at best (Wade et al., 2015), especially if, as is often the case, expert opinion was also used to parameterise the model. Similarly, comparisons to other models can only be considered independent, and therefore offer strong validation, if they differ significantly in their methodology. For instance, it would not be surprising if outputs from models based on

circuit theory and least cost converged, given that they would both be constrained by the same cost surfaces (Wade et al., 2015).

Thus, predictive or historical validation offer us the best route to evidence the suitability of connectivity models. Where the outputs of connectivity models are validated in this way they can utilise data from a variety of sources such as inferential data, occurrence data or path data (Wade et al., 2015). Validations using inferential data include vehicle collisions (Koen et al., 2014; Laliberté and St-Laurent, 2020) and genetic similarity (McRae and Beier, 2007; Short Bull et al., 2011; Dickson et al., 2019). However, because movement is inferred we cannot validate patch utilisation between data points. Additionally, while genetic data is dependent on the movement and successful breeding of individuals (i.e. when dispersal is successful) there is a time delay associated with it as genetic distances change gradually. Therefore, barriers can take some generations to detect (Landguth et al., 2010). Occurrence data such as presence/absence (Chardon et al., 2003; Verbeylen et al., 2003), camera traps (LaPoint et al., 2013), aerial observation (Osipova et al., 2019), and museum specimens (Jackson et al., 2012) have all been used to validate connectivity models. However, they also require extremely high survey effort to not miss fast moving populations and suffer from uneven sampling intensity (Wade et al., 2015), while methods such as aerial detection are likely only successful for megafauna. Telemetry data is now possible at such point resolution that we can map actual dispersal paths, and has been used in a broad range of studies to validate least cost and circuit theory methods (Pullinger and Johnson, 2010; Poor et al., 2012; Koen et al., 2014; Braaker, Moretti, et al., 2014; McClure et al., 2016; Bond et al., 2017; Zeller et al., 2018). However, not only is this sort of data sparse for the time being, as described previously, but determining preferential usage of areas of the landscape requires multiple paths over a long period of time (Wade et al., 2015). Furthermore, in order to properly validate model outputs, sufficient data would be needed to ensure that a subset of the dataset, or preferably a wholly independent dataset, could be set aside for these purposes, given, as stated above, telemetry's usefulness in parameterising

connectivity models. However, this requirement for independent data further exacerbates the data requirements.

Up to this point many of the data sources I have discussed are unlikely to be suitable in the context of measuring range shifts. For instance, a range shift is a multi-generational occurrence and as such telemetry data, which tracks the individual, will not capture it. One could collect tracking data over multiple generations of a population undergoing a range shift, but by the time the data necessary to validate a model had been collected the shift would have already occurred. In short, we would have missed our opportunity to act. Historical validation through historical occurrence data likely holds the key to validating connectivity models for range shifts. Indeed, it has previously seen use in vulnerability models (Wheatley et al., 2017), and recently Hodgson et al. (2022) used historical occurrence data of moth species to validate Condatis' conductance metric, showing that landscapes with high conductance lead to faster colonisation in range-expanding species.

### *6.2.2.3 Reporting and evaluation*

There are a multitude of reports calling for conservation practice to be informed by science (Sutherland et al., 2004; Pullin et al., 2004; Knight et al., 2008; Sunderland et al., 2009; Sinclair et al., 2018; Kadykalo et al., 2021). Yet, equally important is conservation practice informing science through highlighting what works in practice and what does not. However,, this is muddled by the fact there is no one definition of what success looks like (Dilling et al., 2019). Without systematic reporting, outcome evaluation becomes extremely difficult (Wamukota et al., 2012), and there remains a distinct lack of reporting around conservation outcomes (Knight et al., 2008; Wamukota et al., 2012; Wiersma and Sleep, 2016; Mair et al., 2018; Sinclair et al., 2018). Connectivity conservation projects are not an exception (see Chapter 5). Startlingly, there is evidence that the interest in producing these reports is declining rather than growing (Wiersma and Sleep, 2016; Mair et al., 2018). Reporting of project failures is particularly lacking (Sutherland et al., 2004; Sunderland et al., 2009; Bottrill et al., 2011; Catalano et al., 2018; Godet and Devictor, 2018), a cause for

concern given the numerous issues associated with exclusively using success as a guide such as overconfidence, over sampling errors, incorrect attribution of causality and reduced motivation to search for alternatives (Catalano et al., 2018). Platforms exist specifically for the dissemination of field evidence like the *Conservation Evidence* journal, its sister website *Conservation Evidence* (Sunderland et al., 2009) and the *Journal of Conservation Science and Practice* (Schwartz et al., 2019). Yet, academic evidence is mostly utilised by academics rather than practitioners and a search of the conservation evidence database shows that of the 14 actions explicitly mentioning connectivity, eight have no studies associated with them and a further five lack conclusive evidence (Conservation Evidence, 2022). Conservation is being undertaken, so why is this not being reported or evaluated?

Evaluation requires indicators with which to measure the effectiveness of our actions (Pearce-Higgins et al., 2022), but currently, at least in the context of climate change adaptation, these are sorely lacking (Morecroft et al., 2019; Wilson et al., 2020). Generalised impacts such as abundance, extinction risk and ecosystem service provision can be helpful to measure the efficacy of an overall ensemble of conservation actions; if those traits remain constant in the face of a changing environment one can infer our actions are working (Pearce-Higgins et al., 2022). However, through such measures we cannot make inferences on the performance of specific policies or interventions. Baselines against which to measure improvement are an important component of evaluation but one that poses an issue due to the likelihood that new measures will miss previous impacts (Papworth et al., 2009). Historical data could be useful in this context, but there is no guarantee that the past is a good predictor of the future (Layton-Matthews et al., 2020). In order to return the natural world to a pre-anthropogenic impacted state such baselines are required but one could question if such an aim is feasible. In any event, I think improvement against even an intermediary baseline will be helpful in indicating if conditions are reacting favourably to an action.

I posit that models have an important role to play in establishing baselines and evaluation. While changes in occurrence or abundance of species assemblages can be more informative overall (Siriwardena et al., 2019), we cannot dismiss the paucity of existing data as noted earlier. Furthermore, sustained survey effort would be required over a lengthy period to generate the necessary data and accommodate the understanding that adaptation is a continuous process (Stein et al., 2013). The implementation of such a scheme is often impractical in the face of short-term funding and opportunities for action (Curzon and Kontoleon, 2016). Additionally, it may take decades or centuries for ecological processes to recover from anthropogenic degradation (Watts et al., 2020) and the events we are trying to build resilience against may not occur for many years (IPCC, 2012). Therefore, in situations where it seems our actions have no effect, it could simply be that too little time has passed to measure a change. Yet, waiting for physical evidence is not an option because, as I argued earlier, it may take so long to gather that the evidence will no longer be useful in guiding actions. Instead, we can turn to models to act as an intermediary to steer action while collecting empirical evidence (Watts et al., 2020). Metapopulation models are already used in this way and models such as Condatis are similarly well placed for connectivity (Synes et al., 2016). However, for this application it is even more imperative that the issues surrounding uncertainty and data are addressed.

A lack of reporting has been attributed to practitioners not documenting field experiences and experiments in such a way that can be included in a journal (Sunderland et al., 2009) and, in other cases, insufficient time and monetary investment required to produce manuscripts (Curzon and Kontoleon, 2016). While still more suggest the lag time between plan initiation and implementation increases difficulty in achieving publication (Mair et al., 2018). Yet, despite these barriers, evaluations may be being carried out but just not published or made available. Curzon and Kontoleon (2016) interviewed conservation practitioners and noted existing reviews or evaluations are unlikely to give an accurate assessment of what is actually happening because they focus on academically-oriented sources or readily available



reports. If evaluations are ongoing it is good news but not if they take place behind closed doors. Reporting is at the core of the scientific method and not doing so, especially in regards to failure, leaves scope for unintentional duplication of unsuccessful actions (Mace et al., 2000), which constitutes a waste of resources that are already in short supply (Butchart et al., 2010). Furthermore, evaluation enables us to identify potential conflicts between conservation objectives that can mean certain actions have a detrimental rather than positive effect (Morecroft et al., 2019) – reforestation is a prime example (Veldman et al., 2019). This is especially relevant in the context of the current trends in legislation and targets, which will lead to an acceleration in conservation activity. If we are to meet the challenges nature faces, we need conservation that works in practice, the identification of which is reliant on conservationists in all settings reporting what works and what does not.

### *6.3 Conclusions*

Connectivity holds importance at every life history stage of an organism, from natal dispersal to migratory movements. The scientific community has known this for some time, yet the evidence shows this has not been reflected in our conservation actions. The research laid out within this thesis uses England as an exemplar to add to that evidence base. It highlights shortfalls in the abilities of past conservation actions to facilitate connectivity over scales relevant to species adaptation to climate change. Protected area networks are not just disjointed, as others have shown, but that they do not protect areas of habitat vital to connectivity at national scales. Additionally, while recent conservation projects may have increased connectivity with their boundaries, they have not been able to improve connectivity through them and in their surroundings better than if habitat was added at random. This thesis also provides evidence for the value in connectivity metrics specifically designed to account for connectivity over these distances. Condatis was able to add substantial amounts of connectivity protection to protected area networks for a comparably small investment in habitat area. Meanwhile, extensions to the Condatis method, developed here, were able to highlight specific areas where habitat creation would be most beneficial to

long-distance connectivity. Yet, none of this matters if connectivity tools are not used by practitioners. Shifting to look at connectivity tools in general, this thesis reveals that, while they are used, a considerable portion of connectivity projects still forgo the use of metrics, and practitioners still exhibit scepticism towards what they consider “black boxes”. Therefore, there is a pressing need to grow the body of evidence validating connectivity models with empirical data, better explain how they are best used, and actually report what methods lead to conservation successes and, perhaps more importantly, missteps.

We find ourselves custodians of nature at a particularly turbulent and dynamic ecological period. Wholesale shifts in community structures are occurring due to climate change and are expected to increase in extent. Ensuring that species are able to adapt will require providing extensive and well-connected ecological networks. Connectivity tools such as Condatis can play a key part in producing and protecting such networks, helping biodiversity not just weather anthropogenic pressures but recover from them.

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# Supplementary Materials

## *Appendix A – Chapter 2 supporting information*

### **Computational Limitations:**

#### Sparsely distributed habitats and floating-point arithmetic

In the text I refer to six habitat networks that could not be analysed as electrical circuits. This is likely be due to limitations in how computers handle floating points, termed floating point arithmetic (Goldberg, 1991). When numbers get sufficiently small, which is likely when quantifying the rates of colonisation in sparsely spatially distributed habitat networks, a computer can no longer accurately represent them in 32 or 64 bits, and its ability to carry out calculations with them is compromised, leading to rounding errors termed arithmetic underflow.

#### Trade-off between spatial scale or resolution and memory

No matter the computational power available, it is likely that a trade-off will need to occur between the spatial scale of the analysis, and the resolution of the input habitat data.

Condatis uses a standard linear solver to simultaneously solve  $N$  equations in the process of calculating resistance, conductance and flow. As one can imagine, the number of equations to solve can quickly escalate as the size of the landscape increases; adding a single cell to a network of  $n$  cells adds  $2n$  new links to be calculated. Thus, as the area analysed is increased or the resolution of the habitat raster increases, so too does the number of cells and links, lengthening computation time. It is important to find a balance that suits the study's needs and computational resources. As a general rule of thumb, calculations begin to slow down at around 20,000 habitat cells (empty cells are discounted) on a standard desktop computer.

### **References:**

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**Table A.1: Area – Flow correlations.** Patch size, fragmentation (Higher GISfrag = less fragmented), and Kendall rank-order correlation between area and flow of habitats included in the analysis (all significant at  $p < 0.001$ ).

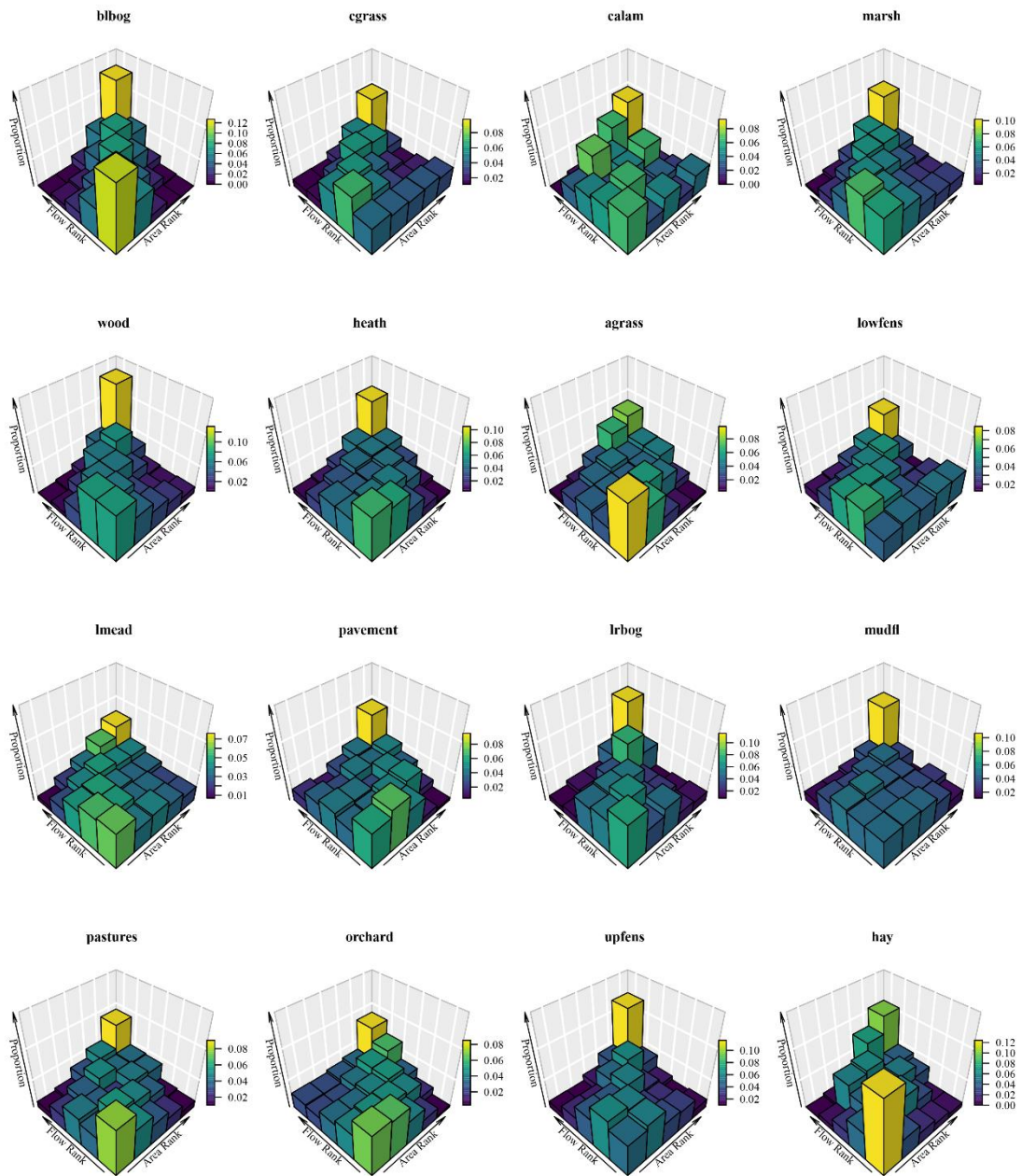
| <b>Habitat</b>  | Total area<br>(ha) | No. of<br>patches | Area lost<br>due to<br>rasterization<br>(ha) | Median<br>patch area<br>(ha) | Proportion<br>of patches<br>protected | Mean area of<br>protected<br>patches (ha) | Mean area of<br>unprotected<br>patches (ha) | Protected<br>GISfrag | Unprotected<br>GISfrag | Patch area:flow<br>correlation |
|-----------------|--------------------|-------------------|--|------------------------------|---------------------------------------|---|---|----------------------|------------------------|--------------------------------|
| <b>wood</b>     | 737191             | 244948            | 22596.80                                     | 0.75                         | 0.04                                  | 9.63                                      | 2.72  | 77.59                | 60.70                  | 0.481                          |
| <b>heath</b>    | 285850.5           | 8245              | 1863.60                                      | 1                            | 0.51                                  | 50.96                                     | 17.99                                       | 189.65               | 158.95                 | 0.345                          |
| <b>blbog</b>    | 230898             | 2218              | 60.50  | 2.25                         | 0.58                                  | 141.90                                    | 51.56                                       | 288.78               | 208.82                 | 0.603                          |
| <b>marsh</b>    | 217731             | 9728              | 2225.50                                      | 1.75                         | 0.11                                  | 26.84                                     | 21.85                                       | 95.12                | 93.22                  | 0.345                          |
| <b>cgrass</b>   | 71051.25           | 7205              | 177.20                                       | 1.25                         | 0.33                                  | 19.75                                     | 4.9   | 144.83               | 69.53                  | 0.27                           |
| <b>mudfl</b>    | 61378              | 5494              | 252.90                                       | 0.5                          | 0.62                                  | 16.94                                     | 1.75  | 223.64               | 69.44                  | 0.271                          |
| <b>lmead</b>    | 21213.75           | 4775              | 230.30                                       | 1.75                         | 0.29                                  | 6.93                                      | 3.41  | 77.55                | 64.22                  | 0.227                          |
| <b>lowfens</b>  | 20319              | 7726              | 619.03                                       | 0.5                          | 0.47                                  | 3.43                                      | 1.92  | 70.32                | 60.86                  | 0.179                          |
| <b>orchard</b>  | 16047.25           | 18755             | 921.70                                       | 0.5                          | >0.01                                 | 0.90                                      | 0.86  | 52.32                | 53.29                  | 0.312                          |
| <b>agrass</b>   | 15214.75           | 3319              | 257.90                                       | 1                            | 0.43                                  | 5.11                                      | 4.19  | 88.68                | 70.21                  | 0.371                          |
| <b>upfens</b>   | 10008.75           | 2919              | 186.50                                       | 0.5                          | 0.59                                  | 4.07                                      | 2.50  | 96.19                | 76.64                  | 0.367                          |
| <b>pastures</b> | 9085.5             | 2943              | 134.50                                       | 1.25                         | 0.11                                  | 4.99                                      | 2.60  | 72.92                | 61.68                  | 0.305                          |
| <b>lrbog</b>    | 7817.75            | 251               | 61.5   | 1.75                         | 0.55                                  | 50.89                                     | 7.42  | 161.41               | 83.67                  | 0.41                           |
| <b>hay</b>      | 2438.75            | 621               | 22.90  | 2.5                          | 0.22                                  | 5.41                                      | 3.51  | 61.31                | 59.54                  | 0.461                          |
| <b>lpave</b>    | 1272.5             | 693               | 58.90  | 0.5                          | 0.58                                  | 2.40                                      | 1.06  | 58.14                | 53.58                  | 0.322                          |
| <b>calam</b>    | 296                | 150               | 7.00   | 0.5                          | 0.46                                  | 2.66                                      | 1.39  | 67.79                | 54.36                  | 0.223                          |
| <b>Overall</b>  | 1707814            | 319990            | 29676.73                                     | 0.75                         | 0.10                                  | 20.98                                     | 3.58  | 258.84               | 84.84                  | 0.309                          |

**Table A.2: Small patch representation.** Representation of small ( $\leq 1$  ha) habitat patches in the entire network, and the top 10% and 1% of patches for flow.

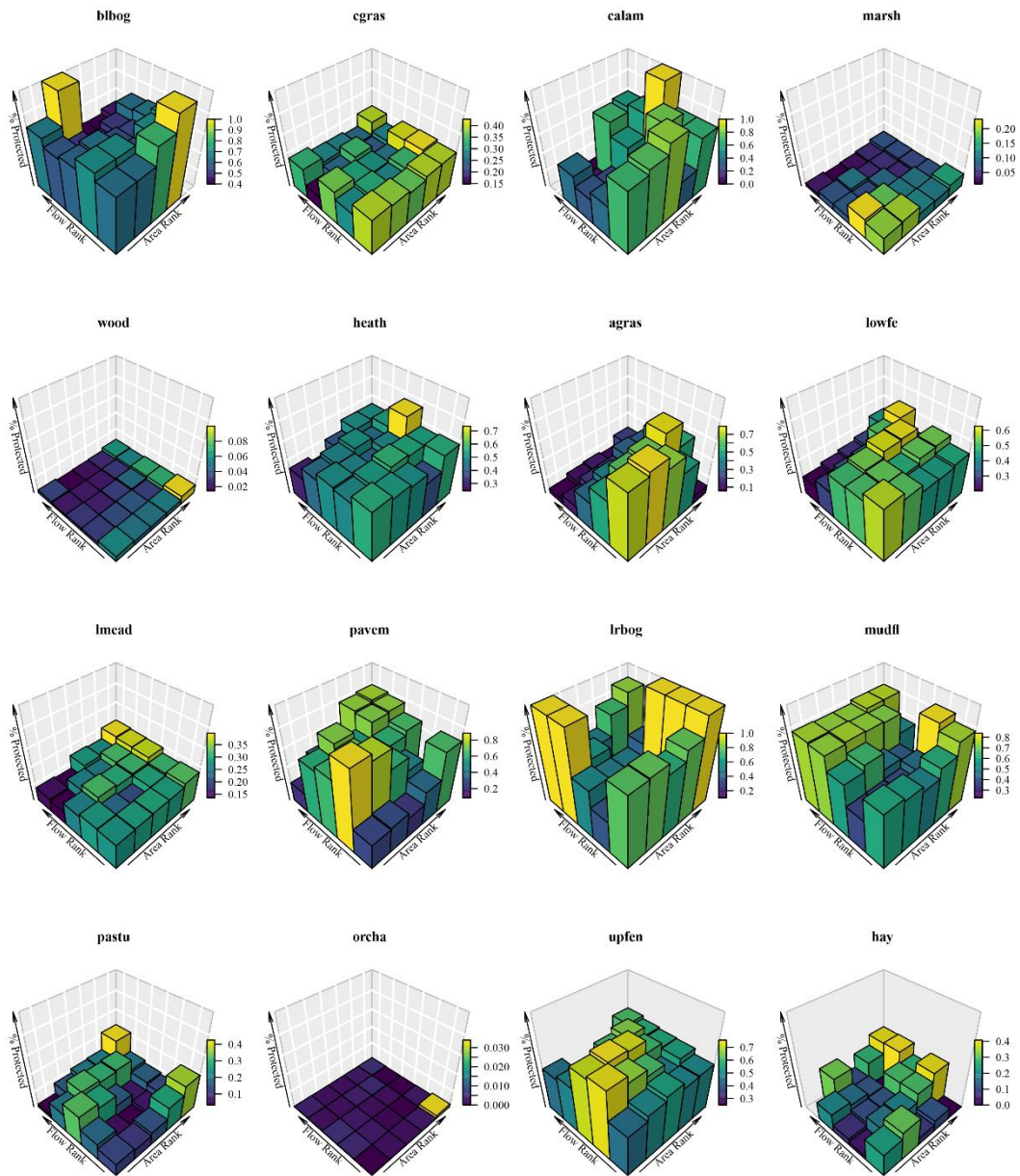
| <b>Habitat</b>  | Proportion of small patches ( $\leq 1$ ha) | Proportion protected in top 10% | Proportion of top 10% small | Proportion of small protected in top 10% | Proportion of top 1% protected | Proportion of top 1% small | Proportion of small in top 1% protected |
|-----------------|--|---------------------------------|-----------------------------|--|--------------------------------|----------------------------|---|
| <b>blbog</b>    | 0.378                                      | 0.428                           | 0.009                       | 1.000                                    | 0.739                          | 0.000                      | -                                       |
| <b>cgrass</b>   | 0.450                                      | 0.370                           | 0.114                       | 0.232                                    | 0.438                          | 0.003                      | 0.000                                   |
| <b>calam</b>    | 0.620                                      | 0.467                           | 0.000                       | -  | 0.500                          | 0.000                      | -                                       |
| <b>marsh</b>    | 0.408                                      | 0.061                           | 0.037                       | 0.000                                    | 0.020                          | 0.000                      | -                                       |
| <b>wood</b>     | 0.580                                      | 0.065                           | 0.033                       | 0.016                                    | 0.163                          | 0.000                      | -                                       |
| <b>heath</b>    | 0.475                                      | 0.475                           | 0.089                       | 0.082                                    | 0.627                          | 0.005                      | 0.000                                   |
| <b>aggrass</b>  | 0.507                                      | 0.166                           | 0.066                       | 0.091                                    | 0.206                          | 0.000                      | -                                       |
| <b>lowfens</b>  | 0.635                                      | 0.336                           | 0.273                       | 0.238                                    | 0.269                          | 0.021                      | 0.188                                   |
| <b>lmead</b>    | 0.343                                      | 0.299                           | 0.069                       | 0.091                                    | 0.292                          | 0.002                      | 0.000                                   |
| <b>lpave</b>    | 0.675                                      | 0.571                           | 0.357                       | 0.280                                    | 0.429                          | 0.029                      | 0.000                                   |
| <b>lrbog</b>    | 0.394                                      | 0.846                           | 0.000                       | -  | 1.000                          | 0.000                      | -                                       |
| <b>mudfl</b>    | 0.747                                      | 0.813                           | 0.218                       | 0.825                                    | 0.946                          | 0.006                      | 1.000                                   |
| <b>pastures</b> | 0.444                                      | 0.278                           | 0.139                       | 0.024                                    | 0.167                          | 0.000                      | -                                       |
| <b>orchard</b>  | 0.784                                      | 0.005                           | 0.606                       | 0.004                                    | 0.000                          | 0.065                      | 0.000                                   |
| <b>upfens</b>   | 0.652                                      | 0.541                           | 0.202                       | 0.424                                    | 0.567                          | 0.021                      | 0.667                                   |
| <b>hay</b>      | 0.208                                      | 0.381                           | 0.000                       | -  | 0.571                          | 0.000                      | -                                       |
| <b>Overall</b>  | 0.578                                      | 0.058                           | 0.047                       | 0.017                                    | 0.149                          | 0.002                      | 0.000                                   |

**Table A.3: Parameter estimates.** Full parameter estimates of the generalised linear models used to show the effects of patch flow and area on protection.

| Habitat  | Parameter                | Area model |            |         | Flow Model |            |          | Area/flow model |            |         |
|----------|--------------------------|------------|------------|---------|------------|------------|----------|-----------------|------------|---------|
|          |                          | Estimate   | Std. Error | z       | Estimate   | Std. Error | z        | Estimate        | Std. Error | z       |
| blbog    | Intercept                | 0.442      | 0.049      | 9.037   | 0.339      | 0.044      | 7.754    | 0.289           | 0.055      | 5.238   |
|          | Log <sub>10</sub> (area) | -0.239     | 0.047      | -5.063  | -          | -          | -        | 0.110           | 0.075      | 1.473   |
|          | Flow Rank                | -          | -          | -       | -1.169     | 0.153      | -7.641   | -1.444          | 0.242      | -5.965  |
| cgrass   | Intercept                | -0.731     | 0.026      | -27.875 | -0.704     | 0.025      | -28.079  | -0.752          | 0.027      | -28.297 |
|          | Log <sub>10</sub> (area) | 0.173      | 0.036      | 4.781   | -          | -          | -        | 0.264           | 0.039      | 6.752   |
|          | Flow Rank                | -          | -          | -       | -0.350     | 0.087      | -4.022   | -0.585          | 0.093      | -6.287  |
| calam    | Intercept                | -0.095     | 0.170      | -0.557  | -0.163     | 0.168      | -0.972   | -0.038          | 0.179      | -0.214  |
|          | Log <sub>10</sub> (area) | 0.584      | 0.322      | 1.817   | -          | -          | -        | 1.018           | 0.371      | 2.741   |
|          | Flow Rank                | -          | -          | -       | -1.586     | 0.594      | -2.669   | -2.213          | 0.660      | -3.356  |
| marsh    | Intercept                | -2.021     | 0.034      | -60.187 | -2.260     | 0.037      | -61/266  | -2.214          | 0.039      | -56.734 |
|          | Log <sub>10</sub> (area) | -0.418     | 0.045      | -9.358  | -          | -          | -        | -0.133          | 0.047      | -2.815  |
|          | Flow Rank                | -          | -          | -       | -2.020     | 0.124      | -16.242  | -1.891          | 0.134      | -14.109 |
| wood     | Intercept                | -3.167     | 0.010      | 303.109 | -3.126     | 0.010      | -310.263 | -3.212          | 0.011      | 297.516 |
|          | Log <sub>10</sub> (area) | 0.579      | 0.017      | 34.048  | -          | -          | -        | 1.019           | 0.021      | 48.513  |
|          | Flow Rank                | -          | -          | -       | -0.203     | 0.040      | -5.831   | -1.383          | 0.041      | -33.644 |
| Heath    | Intercept                | -0.003     | 0.023      | -0.112  | 0.21       | 0.022      | 0.960    | -0.034          | 0.023      | -1.428  |
|          | Log <sub>10</sub> (area) | 0.109      | 0.027      | 4.067   | -          | -          | -        | 0.235           | 0.032      | 7.309   |
|          | Flow Rank                | -          | -          | -       | -0.288     | 0.076      | 3.774    | -0.658          | 0.092      | -7.150  |
| agress   | Intercept                | -0.258     | 0.035      | -7.271  | -0.365     | 0.040      | -9.189   | -0.399          | 0.041      | -9.790  |
|          | Log <sub>10</sub> (area) | -0.479     | 0.061      | -7.877  | -          | -          | -        | 0.466           | 0.075      | 6.181   |
|          | Flow Rank                | -          | -          | -       | -3.624     | 0.151      | -23.982  | -4.149          | 0.175      | -23.682 |
| lowfens  | Intercept                | -0.108     | 0.023      | -4.671  | -0.124     | 0.023      | -5.423   | -0.098          | 0.023      | -4.195  |
|          | Log <sub>10</sub> (area) | 0.104      | 0.043      | 2.412   | -          | -          | -        | 0.222           | 0.045      | 4.947   |
|          | Flow Rank                | -          | -          | -       | -0.811     | 0.080      | -10.146  | -0.913          | 0.082      | -11.071 |
| lmead    | Intercept                | -0.988     | 0.036      | -27.455 | -0.887     | 0.032      | -27.864  | -0.993          | 0.036      | -27.324 |
|          | Log <sub>10</sub> (area) | 0.395      | 0.058      | 6.864   | -          | -          | -        | 0.417           | 0.061      | 6.834   |
|          | Flow Rank                | -          | -          | -       | 0.132      | 0.110      | 1.199    | -0.124          | 0.116      | -1.063  |
| lpave    | Intercept                | 0.434      | 0.084      | 5.174   | 0.338      | 0.079      | 4.278    | 0.389           | 0.085      | 4.552   |
|          | Log <sub>10</sub> (area) | 0.669      | 0.168      | 3.987   | -          | -          | -        | 0.315           | 0.189      | 1.673   |
|          | Flow Rank                | -          | -          | -       | 1.559      | 0.279      | 4.278    | 1.320           | 0.311      | 4.243   |
| lrbog    | Intercept                | 0.076      | 0.141      | 0.539   | 0.184      | 0.127      | 1.450    | 0.027           | 0.148      | 0.180   |
|          | Log <sub>10</sub> (area) | 0.247      | 0.144      | 1.719   | -          | -          | -        | 0.364           | 0.176      | 2.069   |
|          | Flow Rank                | -          | -          | -       | -0.012     | 0.439      | -0.028   | -0.643          | 0.542      | -1.187  |
| mudfl    | Intercept                | 0.593      | 0.031      | 19.365  | 0.505      | 0.028      | 17.753   | 0.568           | 0.031      | 18.403  |
|          | Log <sub>10</sub> (area) | 0.502      | 0.051      | 9.795   | -          | -          | -        | 0.290           | 0.054      | 5.411   |
|          | Flow Rank                | -          | -          | -       | 1.421      | 0.100      | 14.214   | 1.234           | 0.107      | 11.547  |
| pastures | Intercept                | -1.428     | 0.049      | -29.428 | -1.415     | 0.048      | -29.663  | -1.428          | 0.049      | -29.038 |
|          | Log <sub>10</sub> (area) | 0.435      | 0.085      | 5.120   | -          | -          | -        | 0.143           | 0.095      | 1.508   |
|          | Flow Rank                | -          | -          | -       | 1.377      | 0.165      | 8.341    | 1.257           | 0.183      | 6.880   |
| orchard  | Intercept                | -5.748     | 0.159      | -36.204 | -5.865     | 0.139      | -42.298  | -5.817          | 0.172      | -33.777 |
|          | Log <sub>10</sub> (area) | 0.239      | 0.347      | 0.687   | -          | -          | -        | 0.038           | 0.383      | 0.098   |
|          | Flow Rank                | -          | -          | -       | 0.653      | 0.477      | 1.368    | 0.607           | 0.517      | 1.174   |
| upfens   | Intercept                | 0.371      | 0.038      | 9.672   | 0.375      | 0.038      | 9.956    | 0.371           | 0.039      | 9.624   |
|          | Log <sub>10</sub> (area) | -0.056     | 0.068      | -0.823  | -          | -          | -        | -0.052          | 0.079      | -0.656  |
|          | Flow Rank                | -          | -          | -       | -0.060     | 0.131      | -0.459   | -0.016          | 0.151      | -0.105  |
| hay      | Intercept                | -1.567     | 0.138      | -11.393 | -1.273     | 0.098      | -13.033  | -1.596          | 0.152      | -10.515 |
|          | Log <sub>10</sub> (area) | 0.748      | 0.213      | 3.510   | -          | -          | -        | 0.829           | 0.274      | 3.022   |
|          | Flow Rank                | -          | -          | -       | 0.664      | 0.338      | 1.962    | -0.207          | 0.440      | -0.471  |

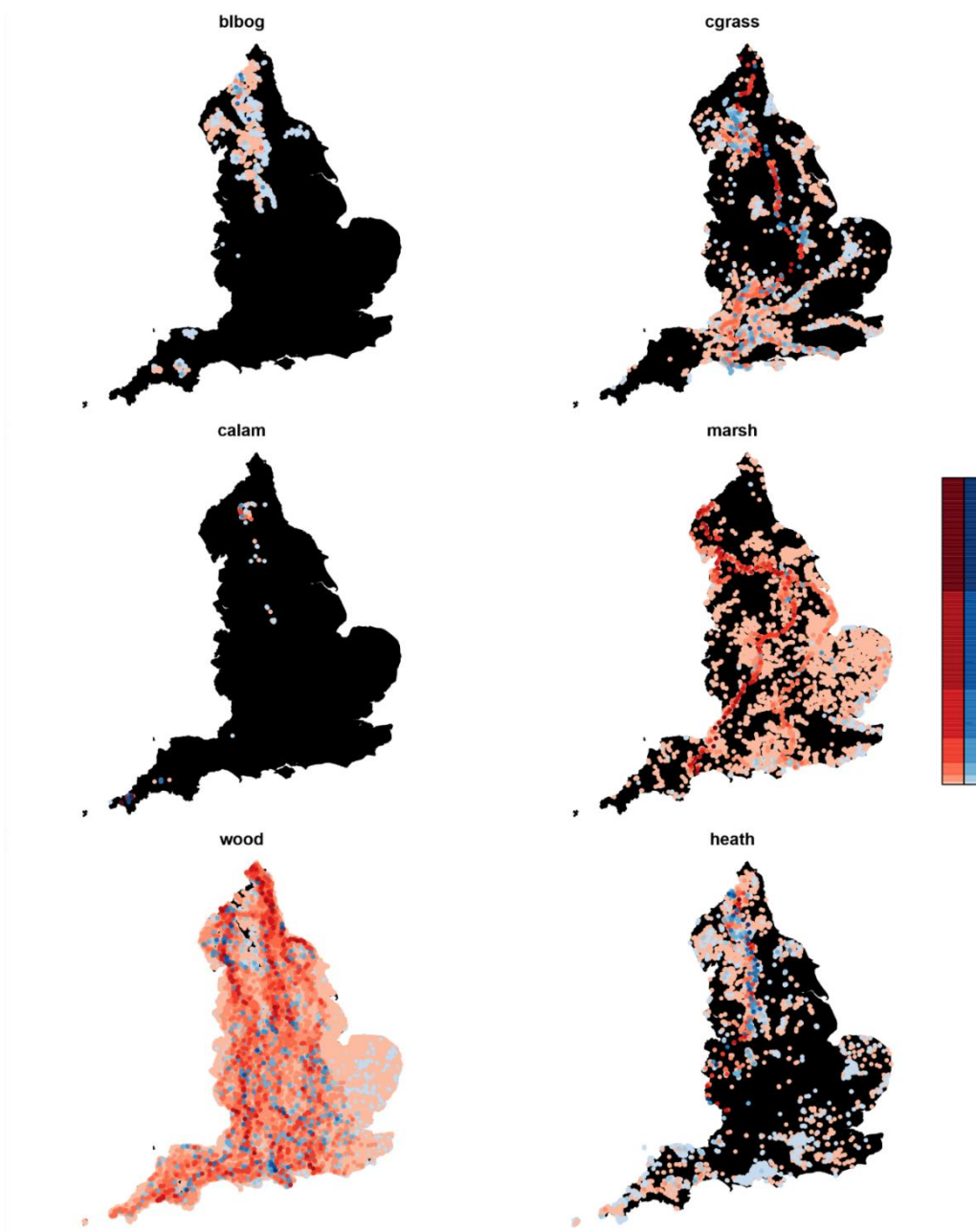


**Figure A.1: Habitat separated area – flow relationship.** 5x5 3dhistogram (yellow = high, purple = low) showing proportion of patches in each habitat falling into each bin.

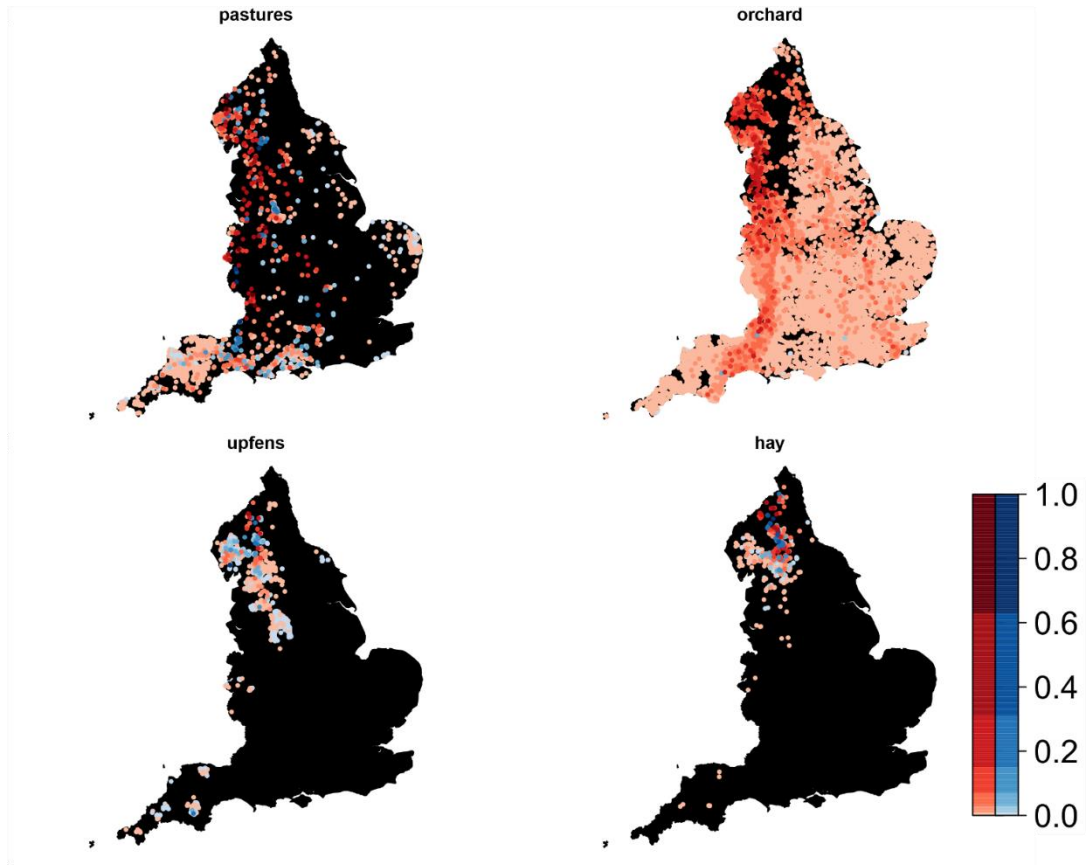


**Figure A.2: Habitat separated Area-Flow Protection.** Ranked patch area against ranked flow for each habitat, showing the proportion of patches in each bin that are protected (yellow = high, purple = low).



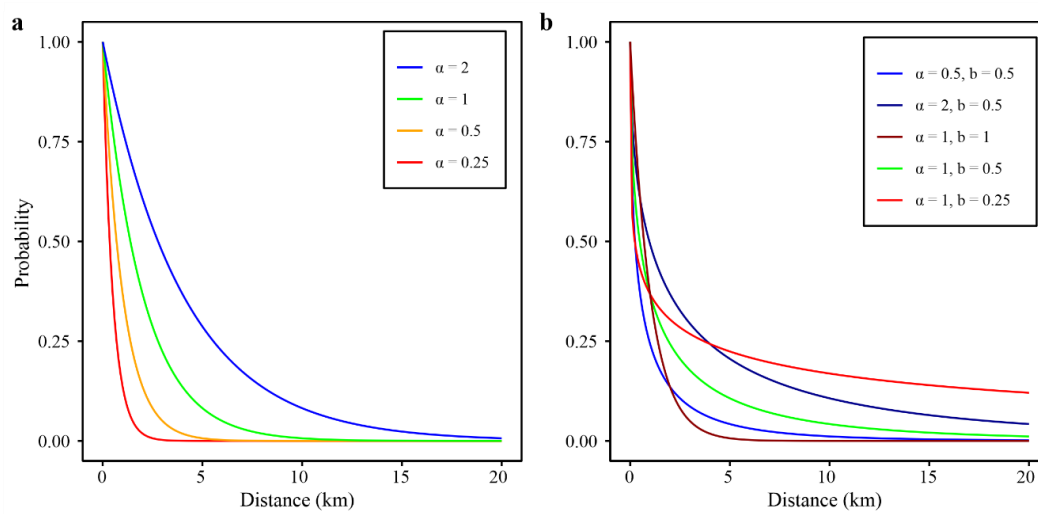




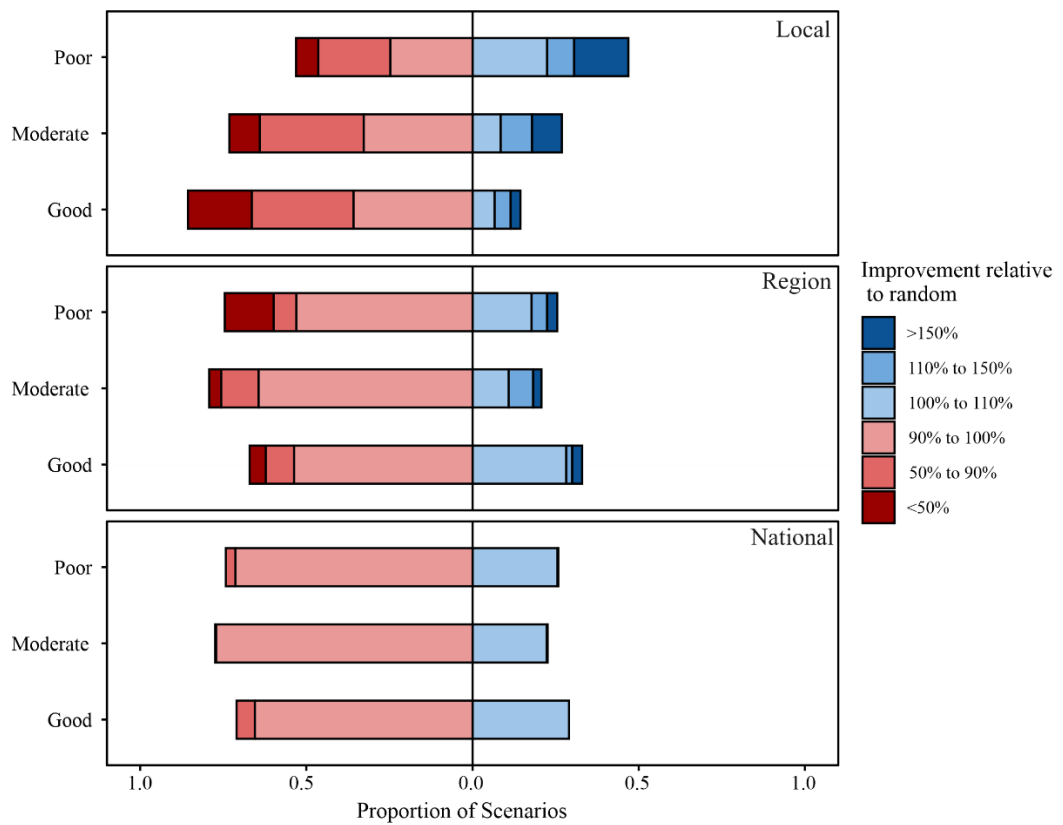


**Figure A.3: Habitat separated Flow distributions.** Flow scores for each habitat for protected (blue) and unprotected (red) patches, standardised such that 1 = the maximum in each panel. Flow was geometrically averaged across the three dispersal distances prior to plotting.

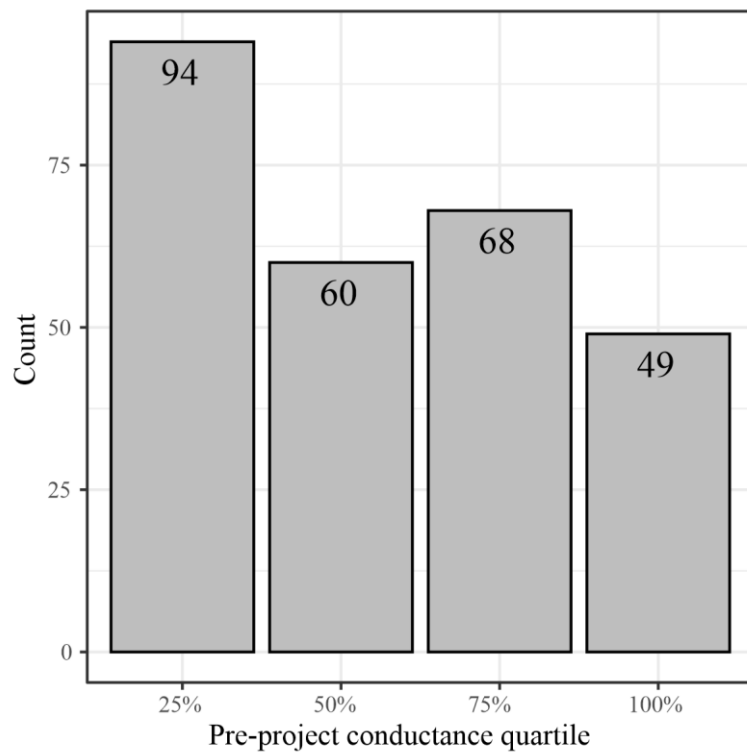
## Appendix B – Chapter 3 supporting information



**Figure B.1: Dispersal kernels.** Representation of the negative exponential (a) and exponential power (b) dispersal kernels used in the analysis. Line colour indicates the effect of different parameter values on the shape of the function. Note that in both kernels  $a$  controls the slope, and for exponential power,  $b$  controls the ‘fatness’ of the tail.



**Figure B.2: Per dispersal performance against BCI.** Barplots detailing the proportion of instances where conductance increases were greater (blue) or less (red) than BCI for each dispersal group at each spatial scale, shade denotes the magnitude of performance relative to BCI



**Figure B.3: Highly positive conductance increases.** Counts of “Highly Positive” conductance increases in each quartile of pre-project conductance. Networks with the lower starting conductances more often yield conductance increases far exceeding BCI.

**Table B.1: Conductance increases.** Median proportional conductance increases, BCI, and median performance vs BCI grouped by kingdom, project, habitat and spatial scale.

| Kingdom | Project | Habitat | Spatial Scale | n  | Median proportional conductance increase | BCI      | Median Conductance increase as proportion of BCI |
|---------|---------|---------|---------------|----|--|----------|--|
| animal  | hl      | cfpgm   | local         | 75 | 1.768924                                 | 1.05232  | 1.680974   |
| animal  | hl      | cfpgm   | national      | 39 | 1.000689                                 | 1.001035 | 0.999655   |
| animal  | hl      | cfpgm   | region        | 41 | 1.000008                                 | 1.00823  | 0.991845   |
| animal  | hl      | lfens   | local         | 61 | 1.120269                                 | 1.5629   | 0.716789   |
| animal  | hl      | lfens   | national      | 33 | 1.000512                                 | 1.004792 | 0.99574  |
| animal  | hl      | lfens   | region        | 67 | 1.002288                                 | 1.032238 | 0.970986   |
| animal  | hl      | lmead   | local         | 58 | 1.040615                                 | 1.137592 | 0.914753   |
| animal  | hl      | lmead   | national      | 45 | 1.001118                                 | 1.001203 | 0.999915   |
| animal  | hl      | lmead   | region        | 56 | 1.002132                                 | 1.008469 | 0.993716   |
| animal  | hl      | lrbog   | local         | 74 | 1.935159                                 | 3.730788 | 0.5187   |
| animal  | hl      | lrbog   | national      | 11 | 1.000519                                 | 1.274935 | 0.784761   |
| animal  | hl      | lrbog   | region        | 10 | 1.000306                                 | 1.285216 | 0.778318   |
| animal  | hl      | rbeds   | local         | 71 | 1.251118                                 | 6.452976 | 0.193882   |
| animal  | hl      | rbeds   | national      | 10 | 1.117599                                 | 1.177469 | 0.949154   |
| animal  | hl      | rbeds   | region        | 39 | 1.005074                                 | 3.444148 | 0.291821   |
| animal  | knrn    | cagra   | local         | 80 | 26.77852                                 | 16.71457 | 1.602107   |
| animal  | knrn    | cagra   | national      | 24 | 1.000002                                 | 1.053307 | 0.949393   |
| animal  | knrn    | cagra   | region        | 77 | 2.083728                                 | 3.07875  | 0.67681  |
| animal  | mb      | cagra   | local         | 78 | 1.374518                                 | 1.431666 | 0.960082   |
| animal  | mb      | cagra   | national      | 31 | 1.000227                                 | 1.008075 | 0.992215   |
| animal  | mb      | cagra   | region        | 50 | 1.000088                                 | 1.047562 | 0.954682   |
| animal  | mb      | cfpgm   | local         | 79 | 1.043706                                 | 1.024966 | 1.018284   |
| animal  | mb      | cfpgm   | national      | 39 | 1.000643                                 | 1.002117 | 0.998529   |
| animal  | mb      | cfpgm   | region        | 56 | 1.000329                                 | 1.012375 | 0.988102   |
| animal  | mb      | lfens   | local         | 67 | 1.933263                                 | 4.562164 | 0.42376  |
| animal  | mb      | lfens   | national      | 33 | 1.002755                                 | 1.018238 | 0.984794   |
| animal  | mb      | lfens   | region        | 54 | 1.028326                                 | 1.092578 | 0.941192   |
| animal  | mb      | lmead   | local         | 75 | 1.513572                                 | 1.347258 | 1.123446   |
| animal  | mb      | lmead   | national      | 46 | 1.001633                                 | 1.00079  | 1.000843   |
| animal  | mb      | lmead   | region        | 52 | 1.003133                                 | 1.011675 | 0.991557   |
| animal  | mb      | lrbog   | local         | 54 | 1.273229                                 | 1.272351 | 1.00069  |
| animal  | mb      | lrbog   | national      | 10 | 1.000027                                 | 1.030754 | 0.97019  |
| animal  | mb      | lrbog   | region        | 43 | 1.733202                                 | 1.05203  | 1.647484   |
| animal  | mb      | pmgrp   | local         | 64 | 7.581557                                 | 13.82314 | 0.548468   |
| animal  | mb      | pmgrp   | national      | 26 | 1.002487                                 | 1.00582  | 0.996687   |
| animal  | mb      | pmgrp   | region        | 62 | 1.03826                                  | 1.063193 | 0.97655  |
| animal  | mb      | rbeds   | local         | 65 | 1.008172                                 | 1.016    | 0.992296   |
| animal  | mb      | rbeds   | national      | 11 | 1.00142                                  | 1.00063  | 1.00079  |
| animal  | mb      | rbeds   | region        | 41 | 1.000623                                 | 1.01173  | 0.989022   |
| animal  | nv      | cfpgm   | local         | 68 | 1.149435                                 | 1.030732 | 1.115164   |
| animal  | nv      | cfpgm   | national      | 39 | 1.000422                                 | 1.000144 | 1.000278   |

| Kingdom | Project | Habitat | Spatial Scale | n  | Median proportional conductance increase | BCI      | Median Conductance increase as proportion of BCI |
|---------|---------|---------|---------------|----|--|----------|--|
| animal  | nv      | cfpgm   | region        | 55 | 1.000624                                 | 1.001327 | 0.999298   |
| animal  | nv      | lmead   | local         | 70 | 1.697527                                 | 2.023023 | 0.839104   |
| animal  | nv      | lmead   | national      | 46 | 1.000795                                 | 1.007191 | 0.99365  |
| animal  | nv      | lmead   | region        | 35 | 1.00228                                  | 1.033766 | 0.969542   |
| animal  | nv      | rbeds   | local         | 64 | 1.128206                                 | 1.451589 | 0.777221   |
| animal  | nv      | rbeds   | national      | 9  | 1.003438                                 | 1.00134  | 1.002096   |
| animal  | nv      | rbeds   | region        | 34 | 1.026983                                 | 1.010046 | 1.016769   |
| animal  | wp      | cagra   | local         | 69 | 1.001392                                 | 1.031206 | 0.971088   |
| animal  | wp      | cagra   | national      | 29 | 1.000003                                 | 1.00065  | 0.999353   |
| animal  | wp      | cagra   | region        | 74 | 1.00004                                  | 1.002052 | 0.997992   |
| animal  | wp      | cfpgm   | local         | 79 | 1.000136                                 | 1.017474 | 0.982959   |
| animal  | wp      | cfpgm   | national      | 39 | 1.000005                                 | 1.000143 | 0.999862   |
| animal  | wp      | cfpgm   | region        | 52 | 1.000086                                 | 1.00088  | 0.999207   |
| animal  | wp      | heath   | local         | 79 | 1.000089                                 | 1.001292 | 0.998799   |
| animal  | wp      | heath   | national      | 29 | 1  | 1.000017 | 0.999984   |
| animal  | wp      | heath   | region        | 37 | 1.000119                                 | 1.000228 | 0.999892   |
| animal  | wp      | ldagr   | local         | 76 | 2.101269                                 | 3.920672 | 0.535946   |
| animal  | wp      | ldagr   | national      | 21 | 1.000468                                 | 1.047136 | 0.955433   |
| animal  | wp      | ldagr   | region        | 50 | 1.025027                                 | 1.244013 | 0.823968   |
| animal  | wp      | pmgrp   | local         | 70 | 1.000222                                 | 1.095766 | 0.912807   |
| animal  | wp      | pmgrp   | national      | 27 | 1.000002                                 | 1.001618 | 0.998387   |
| animal  | wp      | pmgrp   | region        | 63 | 1.093797                                 | 1.012832 | 1.079939   |
| plant   | hl      | cfpgm   | local         | 19 | 5.3773                                   | 1.05232  | 5.109945   |
| plant   | hl      | cfpgm   | national      | 17 | 1.001263                                 | 1.001035 | 1.000228   |
| plant   | hl      | cfpgm   | region        | 16 | 1.00003                                  | 1.00823  | 0.991866   |
| plant   | hl      | lfens   | local         | 24 | 1.066945                                 | 1.5629   | 0.68267  |
| plant   | hl      | lfens   | national      | 43 | 1.001983                                 | 1.004792 | 0.997204   |
| plant   | hl      | lfens   | region        | 25 | 1.004642                                 | 1.032238 | 0.973265   |
| plant   | hl      | lmead   | local         | 15 | 1.017027                                 | 1.137592 | 0.894017   |
| plant   | hl      | lmead   | national      | 16 | 1.001523                                 | 1.001203 | 1.00032  |
| plant   | hl      | lmead   | region        | 22 | 1.000872                                 | 1.008469 | 0.992467   |
| plant   | hl      | lrbog   | local         | 52 | 2.000009                                 | 3.730788 | 0.536082   |
| plant   | hl      | lrbog   | national      | 13 | 1.121564                                 | 1.274935 | 0.879704   |
| plant   | hl      | lrbog   | region        | 8  | 1.085778                                 | 1.285216 | 0.844822   |
| plant   | hl      | rbeds   | local         | 32 | 1.011362                                 | 6.452976 | 0.156728   |
| plant   | hl      | rbeds   | national      | 4  | 1.19292                                  | 1.177469 | 1.013123   |
| plant   | hl      | rbeds   | region        | 14 | 1.033213                                 | 3.444148 | 0.299991   |
| plant   | knrn    | cagra   | local         | 34 | 39.81493                                 | 16.71457 | 2.38205  |
| plant   | knrn    | cagra   | national      | 6  | 1.000352                                 | 1.053307 | 0.949725   |
| plant   | knrn    | cagra   | region        | 57 | 1.074647                                 | 3.07875  | 0.349053   |
| plant   | mb      | cagra   | local         | 31 | 1.472952                                 | 1.431666 | 1.028838   |
| plant   | mb      | cagra   | national      | 10 | 1.000183                                 | 1.008075 | 0.992171   |
| plant   | mb      | cagra   | region        | 43 | 1.00721                                  | 1.047562 | 0.96148  |
| plant   | mb      | cfpgm   | local         | 59 | 1.038823                                 | 1.024966 | 1.01352  |

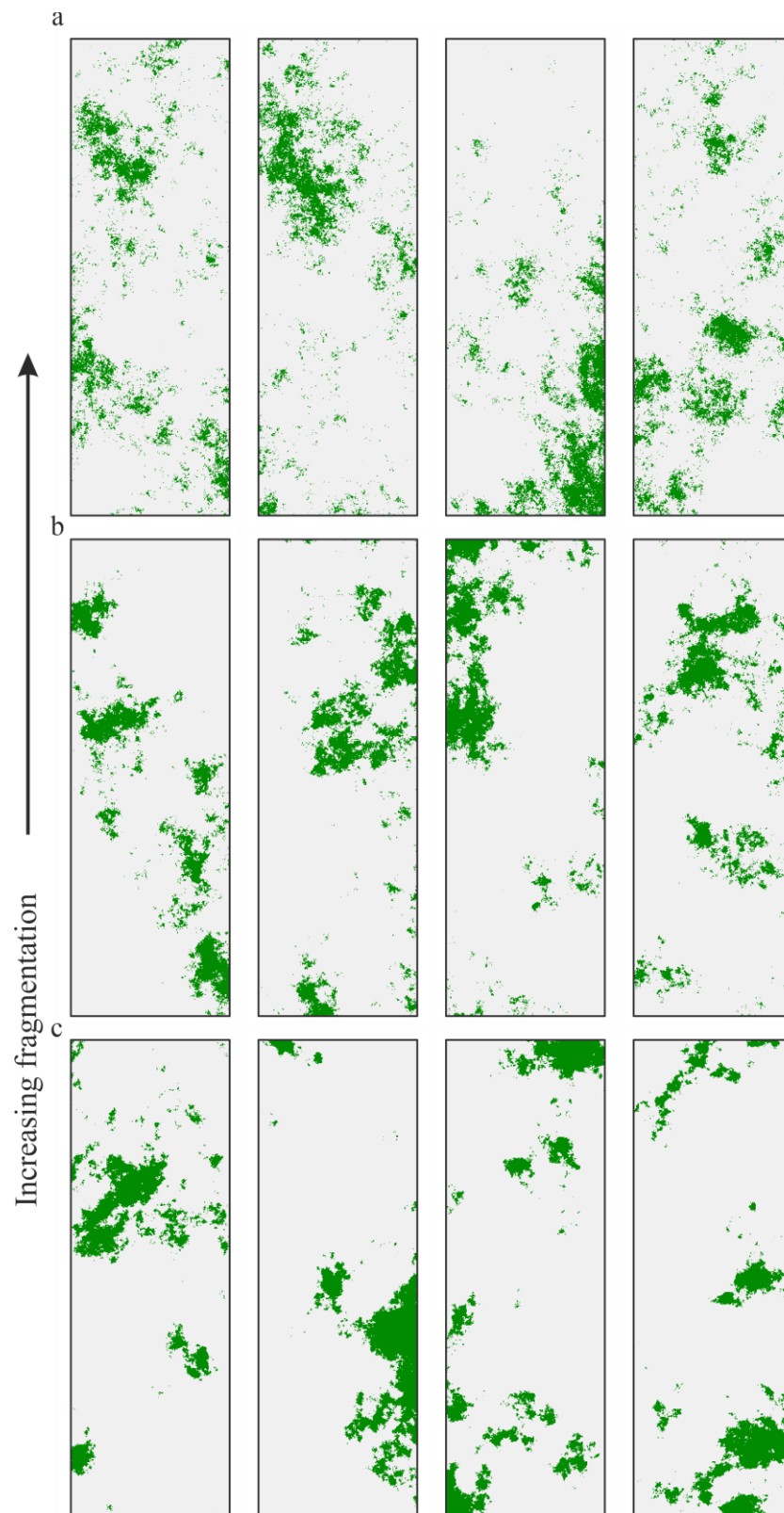


| Kingdom | Project | Habitat | Spatial Scale | n  | Median proportional conductance increase | BCI      | Median Conductance increase as proportion of BCI |
|---------|---------|---------|---------------|----|--|----------|--|
| plant   | mb      | cfpgm   | national      | 17 | 1.000834                                 | 1.002117 | 0.998719   |
| plant   | mb      | cfpgm   | region        | 21 | 1.000983                                 | 1.012375 | 0.988748   |
| plant   | mb      | lfens   | local         | 23 | 2.684714                                 | 4.562164 | 0.588474   |
| plant   | mb      | lfens   | national      | 44 | 1.00454                                  | 1.018238 | 0.986547   |
| plant   | mb      | lfens   | region        | 23 | 1.06591                                  | 1.092578 | 0.975592   |
| plant   | mb      | lmead   | local         | 13 | 1.677971                                 | 1.347258 | 1.245471   |
| plant   | mb      | lmead   | national      | 22 | 1.001466                                 | 1.00079  | 1.000676   |
| plant   | mb      | lmead   | region        | 22 | 1.002412                                 | 1.011675 | 0.990844   |
| plant   | mb      | lrbog   | local         | 16 | 1.218001                                 | 1.272351 | 0.957284   |
| plant   | mb      | lrbog   | national      | 10 | 1.01045                                  | 1.030754 | 0.980302   |
| plant   | mb      | lrbog   | region        | 12 | 2.299299                                 | 1.05203  | 2.185583   |
| plant   | mb      | pmgrp   | local         | 16 | 16.64379                                 | 13.82314 | 1.204052   |
| plant   | mb      | pmgrp   | national      | 17 | 1.001311                                 | 1.00582  | 0.995517   |
| plant   | mb      | pmgrp   | region        | 24 | 1.052082                                 | 1.063193 | 0.98955  |
| plant   | mb      | rbeds   | local         | 20 | 1.007733                                 | 1.016    | 0.991864   |
| plant   | mb      | rbeds   | national      | 6  | 1.002026                                 | 1.00063  | 1.001395   |
| plant   | mb      | rbeds   | region        | 11 | 1.003433                                 | 1.01173  | 0.991799   |
| plant   | nv      | cfpgm   | local         | 25 | 1.066013                                 | 1.030732 | 1.034229   |
| plant   | nv      | cfpgm   | national      | 16 | 1.000505                                 | 1.000144 | 1.000361   |
| plant   | nv      | cfpgm   | region        | 24 | 1.000738                                 | 1.001327 | 0.999411   |
| plant   | nv      | lmead   | local         | 17 | 1.729335                                 | 2.023023 | 0.854827   |
| plant   | nv      | lmead   | national      | 17 | 1.000703                                 | 1.007191 | 0.993558   |
| plant   | nv      | lmead   | region        | 16 | 1.002109                                 | 1.033766 | 0.969378   |
| plant   | nv      | rbeds   | local         | 28 | 1.129813                                 | 1.451589 | 0.778328   |
| plant   | nv      | rbeds   | national      | 5  | 1.001292                                 | 1.00134  | 0.999952   |
| plant   | nv      | rbeds   | region        | 12 | 1.041675                                 | 1.010046 | 1.031315   |
| plant   | wp      | cagra   | local         | 43 | 1.022969                                 | 1.031206 | 0.992013   |
| plant   | wp      | cagra   | national      | 9  | 1.000004                                 | 1.00065  | 0.999354   |
| plant   | wp      | cagra   | region        | 42 | 1.000951                                 | 1.002052 | 0.998902   |
| plant   | wp      | cfpgm   | local         | 37 | 1.020687                                 | 1.017474 | 1.003158   |
| plant   | wp      | cfpgm   | national      | 16 | 1.000002                                 | 1.000143 | 0.99986  |
| plant   | wp      | cfpgm   | region        | 15 | 1.000014                                 | 1.00088  | 0.999135   |
| plant   | wp      | heath   | local         | 34 | 1.000383                                 | 1.001292 | 0.999092   |
| plant   | wp      | heath   | national      | 10 | 1.000006                                 | 1.000017 | 0.999989   |
| plant   | wp      | heath   | region        | 21 | 1.000283                                 | 1.000228 | 1.000055   |
| plant   | wp      | ldagr   | local         | 22 | 8.141402                                 | 3.920672 | 2.076532   |
| plant   | wp      | ldagr   | national      | 34 | 1.001296                                 | 1.047136 | 0.956224   |
| plant   | wp      | ldagr   | region        | 19 | 1.008799                                 | 1.244013 | 0.810923   |
| plant   | wp      | pmgrp   | local         | 19 | 1.00004                                  | 1.095766 | 0.91264  |
| plant   | wp      | pmgrp   | national      | 16 | 1.000014                                 | 1.001618 | 0.998398   |
| plant   | wp      | pmgrp   | region        | 23 | 1.122305                                 | 1.012832 | 1.108085   |

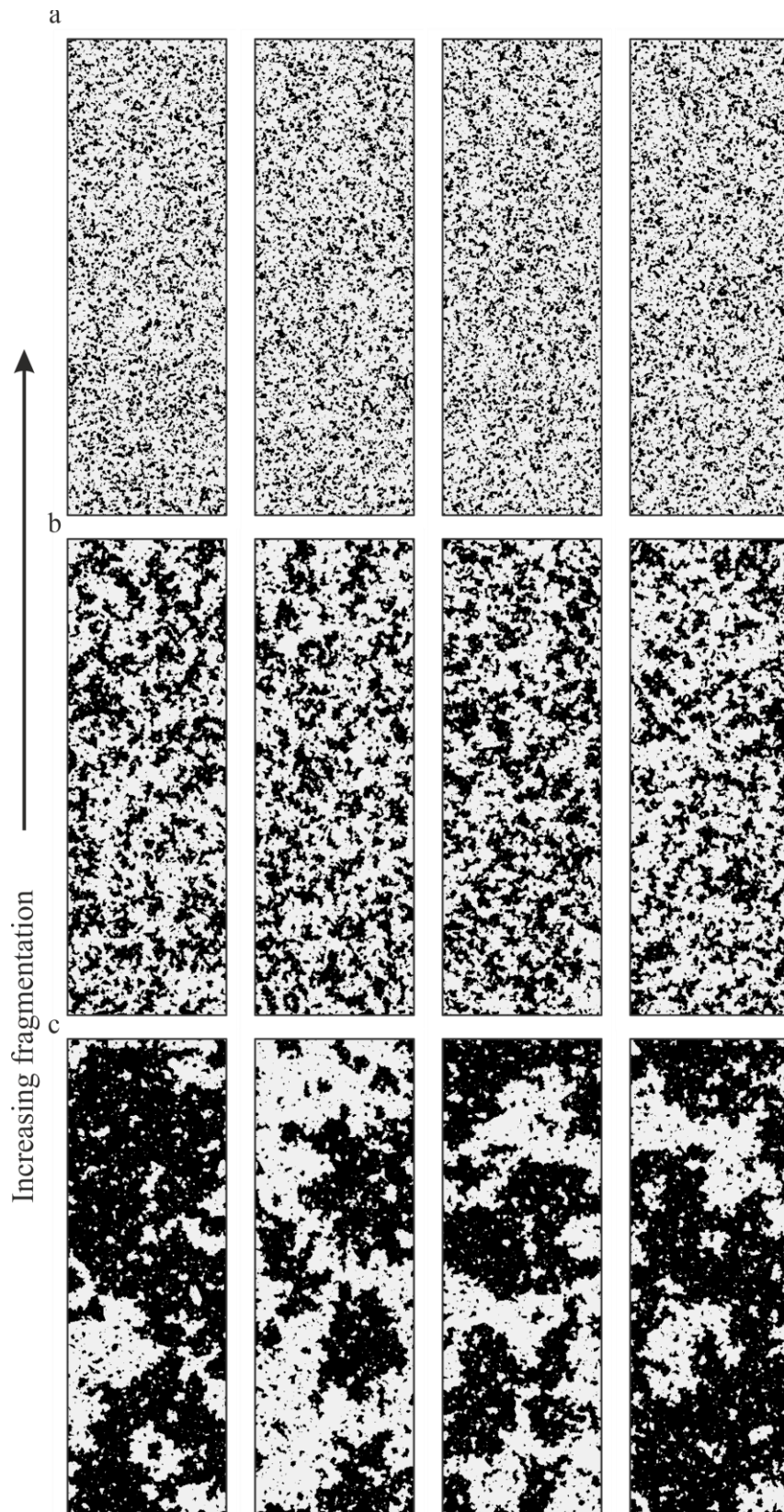
*Appendix C – Chapter 4 supporting information*

**Table C.1: Cell counts** in each feasibility surface used the analysis.

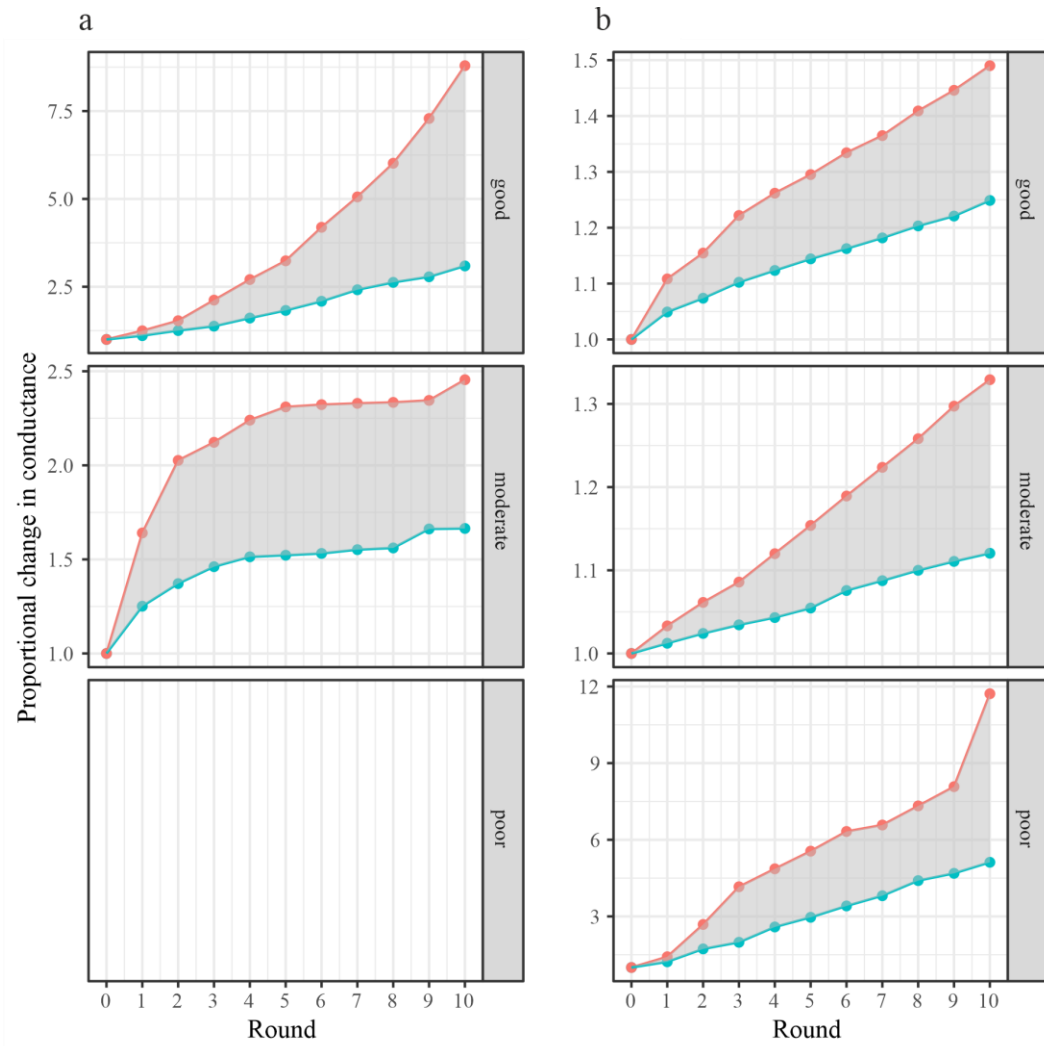
| <b>Replicate</b> | <b>Fine</b> | <b>Medium</b> | <b>Coarse</b> |
|------------------|-------------|---------------|---------------|
| <b>1</b>         | 29,456      | 49,830        | 82,709        |
| <b>2</b>         | 29,234      | 47,188        | 51,940        |
| <b>3</b>         | 29,252      | 51,321        | 66,537        |
| <b>4</b>         | 29,467      | 46,281        | 80,403        |



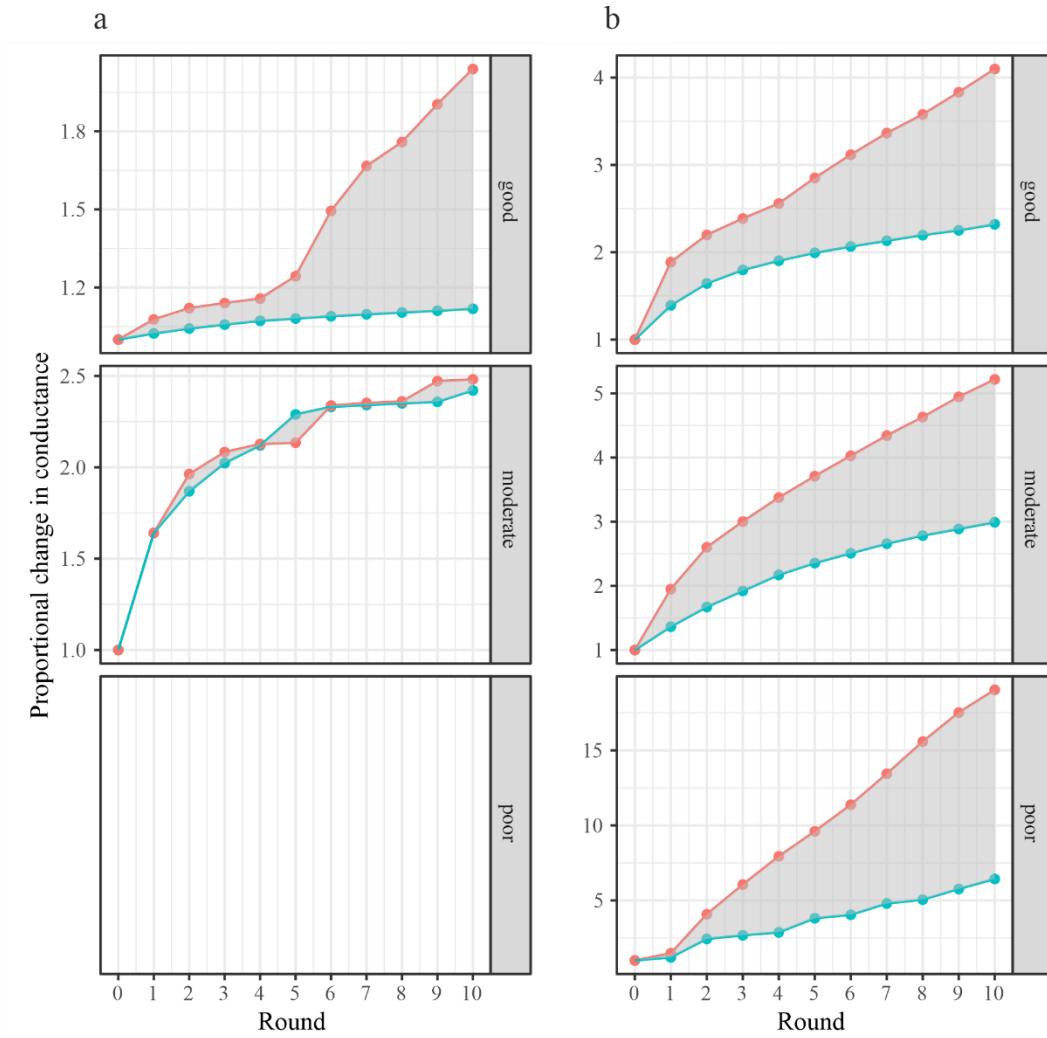
**Figure C.1: Neutral landscapes.** The habitat maps used to test the algorithms, created using fractal brownian motion from the NLMR r package. Autocorrelation decreases from top to bottom with fine (a;  $D = 0.35$ ), medium (b,  $D = 0.65$ ), and coarse (c;  $D = 0.95$ ) landscapes and their replicates



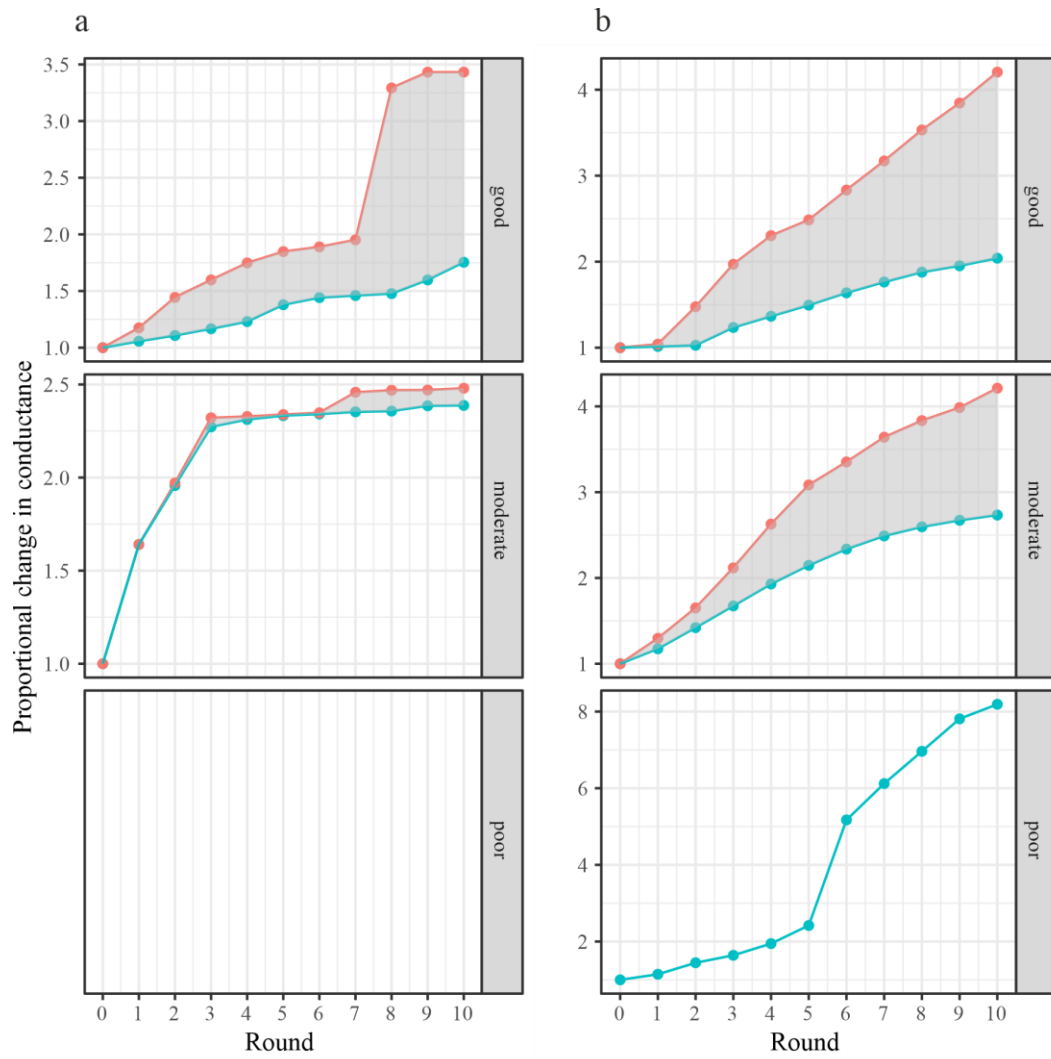
**Figure C.2: Feasibility surfaces.** The feasibility surfaces used in the study, created using random cluster algorithm from the NLMR *r* package. Autocorrelation decreases from top to bottom, with fine (a;  $P = 0.25$ ,  $ai = 0.25$ ), medium (b;  $P = 0.5$ ,  $ai = 0.4$ ), and coarse (c;  $P = 0.58$ ,  $ai = 0.5$ ) landscapes and their replicates.



**Figure C.3: Distance round performance.** Per round conductance increases generated by the Distance algorithm in the national scale example for animal (a) and plant (b) species.



**Figure C.4: Flow round performance.** Per round conductance increases generated by the flow algorithm in the national scale example for animal (a) and plant (b) species.



**Figure C.5: TTC round performance.** Per round conductance increases generated by the TTC algorithm in the national scale example for animal (a) and plant (b) species

## Appendix D – Chapter 5 supporting information

**Table D.1: Information on Projects used in Chapter 5.**

| Region | Project   | Start Year | Connectivity assessment  | Connectivity assessed? | Assessment Year | Metric            | Connectivity assessment group | On the ground or evidence?  | Found via                  | Ref           |
|--------|---|------------|--|------------------------|-----------------|-------------------|-------------------------------|---|----------------------------|---------------|
| Africa | Kilimanjaro Landscape                                       | 2009       | Identified migration corridors for elephants, presumably through radio tracking or similar but doesn't actually say, Annual report mentions the use of 'historic' migration corridors.   | Y                      | 2009            | None              | Not disclosed                 | On the ground action: Conservation lease programme for landowners | Grey literature            | 1, 2, 3       |
| Africa | Kavango zambezi transfrontier conservation area             | 2011       | The Integrated development plan mentions work carried out in 2011 which I believe is the referenced study. Confirmation that the priority wildlife dispersal corridors were established via telemetry studies.   | Y                      | 2011            | Tracking data     | Tracking                      | On the ground action: Protected areas community engagement        | Databases, Grey literature | 1, 4, 5, 6    |
| Africa | Kwazulu-natal and eastern cape climate adaptation corridors | 2011       | They state in their report that terrestrial data was limited, so delineation of the corridors relied heavily on expert knowledge. They attempted to identify corridors that met the criteria for a "good" corridor outlined in the referenced report.  | Y                      | 2011            | None              | Expert                        | Evidence  | Academic literature        | 50, 51        |
| Africa | Futi corridor in Lumbombo Transfrontier Conservation area   | 2011       | Research has been done studying telemetry data from elephants. A 2008 study used Marxan to highlight where new core areas should be lines up eerily similar to the actual designated area this was also done in partnership with Mozambique, South Africa and Swaziland.   | Y                      | 2008            | Tracking data     | Tracking                      | On the ground action: Protected area                              | Academic literature        | 7, 8, 9       |
| Africa | Albertine rift  | 2000       | Used ArcGIS add-on Corridor Designer to analyse where would be beneficial to place corridors. The most recent conservation plan, and the studies that led up to it, made use of species distribution models, particularly Marxan Maximum entropy model to suggest areas for new PAs, but this doesn't appear to consider landscape connectivity. | Y                      | 2010            | Corridor Designer | Least Cost                    | Evidence  | Databases, Grey literature | 1, 10, 11, 12 |
| Africa | kilombero valley  | 2016       | Identified the Rupia-East corridor by using information from 2000 surveys which involved wildlife movement surveys answered by locals about animal sightings (elephants). Also makes note of 2009 surveys which used transect surveys, questionnaires and satellite data.  | Y                      | 2009            | Tracking data     | Tracking                      | On the ground action: Protected Area                              | Databases, Grey literature | 1, 13, 14     |
| Africa | Selous - Nissa Wildlife Corridor                            | 2000       | Made use of radio tracking of elephant migration routes between 2000 and 2003.   | Y                      | 2000            | Tracking data     | Tracking                      | On the ground action: Protected areas                             | Academic literature        | 26, 30        |
| Africa | Cape Town Municipal Biodiversity Network                    | 2016       | Used Marxan and C-Plan, connectivity was incorporated in a couple of ways. First, experts were asked to identify potential corridors, and then the boundary length modifier of MARXAN was used to Minimise habitat fragmentation.  | Y                      | 2016            | None              | Expert                        | Evidence  | Ad hoc                     | 67            |
| Africa | Northern Rangelands Trust                                   | 2004       | Connectivity between reserves measured using telemetry data  | Y                      | 2004            | Tracking data     | Tracking                      | Evidence  | Databases                  | 84, 85        |



| Region           | Project  | Start Year | Connectivity assessment   | Connectivity assessed? | Assessment Year | Metric                       | Connectivity assessment group | On the ground or evidence?           | Found via                  | Ref            |
|------------------|--|------------|---|------------------------|-----------------|------------------------------|-------------------------------|--------------------------------------|----------------------------|----------------|
| Africa           | Northern Tanzania Rangelands Initiative              | 2008       | Rangeland reports refer to corridors being identified, but I cannot find any information on how these corridors were identified. The Nature Conservancy is involved, so it is plausible that circuitscape would be used, but I can't know for certain and none of the Africa summary reports on the nature conservancy website shed light on this either.   | Unknown                | 2008            | Unknown                      | Not disclosed                 | Evidence, training etc.              | Databases                  | 86             |
| Africa           | Ruaha-katavi Landscape                               | 2014       | No information available on how these corridors were identified, or how it was determined that connectivity was improved for elephants.   | Unknown                | 2014            | Unknown                      | Not disclosed                 | Evidence                             | Databases                  | 87,88          |
| Africa           | Gambella Region                                      | 2014       | Migratory routes were assessed using radio telemetry data.  | Y                      | 2014            | Tracking data                | Tracking                      | Evidence                             | Databases                  | 89             |
| Arctic/Antarctic | ArcNet   | 2017       | While Marxan was used to establish the network of PACs the migration bottleneck data was not included in this, instead to be used in a separate analysis that the technical document does not explain. It appears that migration bottlenecks were identified via visual analysis of maps and expert opinion.  | Y                      | 2017            | None                         | Expert                        | Evidence                             | Databases                  | 95, 96, 97, 98 |
| Asia             | Sahyadri-konkan corridor                             | 2013       | Circuitscape analysis was used, based upon previously calculated probability of occupancy models, the results from the circuitscape analysis were then used to direct camera trapping exercises to confirm their use by tigers, dholes and leopards. In July 2020 the Indian government designated the tillari conservation reserve, which is 29.53sq km and is located directly where circuitscape analysis showed connectivity was vulnerable.  | Y                      | 2013            | Circuitscape                 | Circuit Theory                | On the ground action: Protected area | Ad hoc                     | 15             |
| Asia             | Central India tiger landscape                        | 2014       | In 2014 The National Tiger Conservation Authority in collaboration with the Wildlife Institute of India published a report which mapped out 32 major corridors across the country which are protected under a Tiger conservation plan and law. These corridors were identified using Circuitscape and LCP methodology. Later, The Wildlife Institute of India published a subsequent atlas of connective links and pinch points at a far finer scale for the use of planners and conservation practitioners that also made use of updated Circuitscape tools. | Y                      | 2014            | Circuitscape                 | Circuit Theory                | Evidence                             | Databases                  | 20, 21         |
| Asia             | Thailand's forest complexes                          | 2013       | Implemented MaxEnt to find habitat areas that would be important to key species, and then used Corridor Designer Program V0.2 to identify appropriate wildlife corridors using a least-cost modelling technique. I can't find any information about implementation of these plans.  | Y                      | 2013            | Corridor Designer            | Least Cost                    | Evidence                             | Databases, Grey literature | 1, 16          |
| Asia             | Biodiversity Conservation Corridors Initiative (BCI) | 2006       | It seems that most of the places where chosen through expert opinion after consulting GIS habitat layers, species distributions, camera traps etc, but the tenasserim corridor in Thailand actually commissioned study by the wildlife conservancy, which used least cost modelling via corridor designer to highlight where would be best to carry out restoration/enhancement works.  | Y                      | 2005, 2008      | Corridor Designer            | Expert, Least Cost            | On the ground action: Protected area | Databases                  | 17, 18, 19     |
| Asia             | Sarawak Wildlife Corridors                           | 2015       | They used Linkage mapper to find corridor routes between protected areas and then used circuit scape to assess the different configurations.  | Y                      | 2015            | Linkage mapper, Circuitscape | Least Cost, Circuit Theory    | Evidence                             | Academic literature        | 31             |

| Region | Project                               | Start Year | Connectivity assessment  | Connectivity assessed? | Assessment Year | Metric                | Connectivity assessment group | On the ground or evidence?   | Found via           | Ref      |
|--------|---------------------------------------|------------|--|------------------------|-----------------|-----------------------|-------------------------------|--|---------------------|----------|
| Asia   | Kanha-Pench Corridor                  | 2010       | Use of the corridor has been evaluated via on the ground surveys. The WWF report references an unpublished report that identified a number of critical linkages in the corridor, but this is not, as far as I can tell, available. It appears that the corridor itself was identified by nature of it being a large intact area of forest, the WWF report says that no systematic effort has been carried out to identify the exact boundary or area of this corridor. | N                      | 2010            | None                  | Not disclosed                 | On the ground action: Wildlife underpasses built   | Academic literature | 72       |
| Asia   | Terai arc Landscape                   | 2001       | Connectivity evaluated using a GIS-based cost-distance model. They treated protected areas as sources and then used a Cost-distance function in ArcInfo/grid to create dispersal cost grids between them.  | Y                      | 2004            | Not Disclosed         | Least Cost                    | Evidence and On the ground: restoration, protection  | Academic literature | 74,75,76 |
| Asia   | Transboundary Manas Conservation Area | 2011       | A 2019 project used Circuitscape to evaluate the connectivity between tiger populations in the region and protected areas, using Human Footprint Index to map the resistance surface. A previous project modelled connectivity in the region as shown in the 2015 WWF report, but record of that work cannot be found.   | Y                      | 2019            | Circuitscape          | Circuit Theory                | Evidence for upcoming conservation planning and in drafting of indicative conservation plan for all forest complexes managed in the region | ad hoc              | 78, 79   |
| Asia   | Tenasserim corridor project           | 2006       | A WCS report titled "Restoring Tenasserim corridor for living connectivity" outlines the use of corridor designer which is a least cost pathway method, looks like this work was conducted in 2009.  | Y                      | 2009            | Corridor Designer     | Least Cost                    | Action: Habitat restoration and creation   | Databases           | 77       |
| Asia   | Amur Green Belt                       | 2008       | Aside from mention that all areas are linked via waterways no actual analysis of connectivity can be found.  | N                      | 2008            | NA                    | None                          | Evidence, On the ground action   | Databases           | 90, 91   |
| Asia   | Central forest spine                  | 2005       | Linkages between important forest complexes were identified through supporting information like road kills, human-wildlife conflict, and importance of forest biodiversity value. Biodiversity experts were ten consulted to finalise the linkages.  | Y                      | 2005            | None                  | Expert advice                 | Evidence   | Academic literature | 156      |
| Asia   | Central Asia Econet                   | 2003       | Design of the ECONET involved the incorporation of multiple layers of spatial data including landcover, species distribution etc. A layer called "Integrated map of corridors" is included, however these corridors are identified by joining lines of similar topographical features rather than any specific measure of connectivity.  | N                      | 2003            | None                  | Topography                    | Evidence, On the ground action: Designation, restoration etc   | Databases           | 92, 93   |
| Asia   | Sikhote-alin Russia                   | 2015       | Study used the CostDistance tool for GIS.  | Y                      | 2015            | CostDistance          | Least Cost                    | Evidence   | Databases           | 94       |
| Asia   | Halmahera/Northern Sulawesi           | 2005       | In the report the nesting sites were evaluated via, connectivity was defined as access with three levels. The levels of connectivity were defined as varying extents of the nest site boundary that were contiguous with forest.   | Y                      | 2007            | Distance based metric | Distance                      | On the ground: Habitat Protection  | Databases           | 99, 100  |
| Asia   | National Elephant Corridors Project   | 2005       | It is unclear how corridors were identified. The report states that corridor boundaries were delineated based on structural and functional connectivity, but does not elaborate on this. From the text it seems like this might have simply been a visual analysis of forest cover and terrain with expert consultation.   | Y                      | 2005            | None                  | Expert, Topography            | Evidence and On the ground: protection   | Databases           | 101      |

| Region    | Project  | Start Year | Connectivity assessment  | Connectivity assessed? | Assessment Year | Metric                | Connectivity assessment group | On the ground or evidence?                          | Found via           | Ref            |
|-----------|--|------------|--|------------------------|-----------------|-----------------------|-------------------------------|---|---------------------|----------------|
| Asia      | Jordan Rift Valley                                 | 2007       | Report states that one of the criteria for selecting the seven PAs was ecosystem connectivity, but does not state how this was assessed  | Unknown                | 2007            | Unknown               | Not disclosed                 | On the ground: protection                           | Databases           | 102            |
| Asia      | Kangchenjunga Landscape                            | 2002       | Six corridors were identified in 2002 and further corroborated with GIS tools in 2005. However, I can't find any information on how these corridors were identified, or what tools were used to corroborate them.  | Unknown                | 2002            | unknown               | Not disclosed                 | Evidence, On the ground                             | Databases           | 103, 104       |
| Australia | The great eastern ranges Initiative (formerly A2A) | 2006       | The 2007-2011 report says that they carried out a desk-top analysis of connectivity priorities such as, biological values (such as regional distinctiveness), connectivity need (discontinuity in connectedness), conservation and social opportunity, and program contribution. The 2010 report states that their approach is based on systematic conservation planning. In the 2011 - 2015 report they outline that they used two different approaches depending on the level of assessment (whole GER region or for each area identified by that GER assessment) they both seem like SCP methods that don't include a specific connectivity metric. Drielsma et al., 2009 state that one of the methods used to service the GER initiative was "link analysis" which is a sort of least cost path model | Y                      | 2009            | Spatial Links Tool    | Least Cost                    | Action Habitat restoration and creation             | Academic literature | 46, 47, 48, 49 |
| Australia | Gondwana Link                                      | 2002       | The project makes use of MCAS-S software, which is a decision support tool, to determine where to act first. This includes a very basic assessment of connectivity such as proximity to other habitat or riparian habitat.   | Y                      | 2002            | Distance based metric | Distance                      | On the ground: Habitat creation / restoration       | Databases           | 32, 33, 34     |
| Australia | Grampians to Pyrenees Biolink                      | 2016       | Looks like they used a map that was created as part of the great eastern ranges project.   | Y                      | 2009            | Spatial Links Tool    | Least Cost                    | NA  | Academic literature | 29             |
| Australia | Nature Links                                       | 2003       | Naturelinks is/was a framework to guide conservation action by government and non-governmental organisations and the community.  | N                      | 2003            | None                  | None                          | Evidence  | Academic literature | 33, 35         |
| Australia | Tasmania East Coast Conservation corridor          | 2005       | The 2012 report that seems to propose the east coast conservation corridor makes lots of mentions to connectivity, but I cannot see where this has been actually assessed. In the section on conservation planning they again note that connectivity is important, but do not state how they assessed it. It seems they use the CAR approach (Comprehensive, adequate and representative reserve system) which is a SCP approach.  | N                      | 2005            | None                  | Not disclosed                 | Evidence and On the ground: restoration, protection | Grey literature     | 52, 53, 54     |
| Australia | Habitat 141  | 2005       | Habitat 141 carries out the Conservation Action Planning framework established by the Nature Conservancy, but gathering from the 2015 CAP they don't include aspects of connectivity into this. The framework identifies conservation assets, the viability of those and the risks to them and then develops actions and objectives to counter those.  | N                      | 2005            | None                  | None                          | On the ground: Protection, creation, restoration    | Academic literature | 33, 36         |
| Australia | Midlandscapes                                      | 2008       | They made use of GAP CLoSR analysis which uses LCP. Looks like they modelled specific species, but it's really hard to find details on it.   | Y                      | 2008            | GAP CLoSR             | Least Cost                    | On the ground: Restoration                          | Academic literature | 33, 37         |

| Region    | Project   | Start Year | Connectivity assessment   | Connectivity assessed? | Assessment Year | Metric   | Connectivity assessment group | On the ground or evidence?  | Found via                  | Ref       |
|-----------|---|------------|---|------------------------|-----------------|--|-------------------------------|---|----------------------------|-----------|
| Australia | Territory Eco-link  | 2009       | Seems to just have identified gaps between existing protected areas, via visual analysis.   | N                      | 2009            | None   | Topography                    | Evidence<br>On the ground: Protection                                     | Academic literature        | 33, 34    |
| Australia | Pilbara Corridors   | 2012       | No specific connectivity assessment appears to have been made. Connectivity was promoted by reducing loss of ground cover through implementing Ecologically sustainable grazing management plans.   | N                      | 2012            | None   | None                          | Evidence  | Databases                  | 113       |
| Australia | Wild Eyre   | 2007       | A priority habitat map was produced through a SCP process which included an analysis of connectivity via circuit theory.  | Y                      | 2013            | Current flow analysis in Connectivity Analysis Toolkit | Circuit Theory                | On the ground: restoration  | Databases                  | 114       |
| Europe    | Open Borders for Bears between Romanian and Ukrainian Carpathians | 2012       | From a WWF presentation it appears that they used a mixture of the corridor designer from Maxent and then cross referenced this with telemetry data.  | Y                      | 2012            | Corridor designer                                      | Least Cost                    | Evidence  | ad hoc                     | 45        |
| Europe    | Pan-European ecological network                                   | 2002       | Corridors between core areas identified through the use of known migration routes, forest density, mountain ranges, rivers, expert consultation, comparison with existing national networks.  | Y                      | 2002            | None   | Expert                        | Evidence  | Academic literature        | 44        |
| Europe    | NIA   | 2012       | Basic measurements of connectivity used for the most part, such as principles of increasing the size of habitat patches, or (as an example) reduction in the number of weirs along a river. One project, Humberhead levels, appears to have used a distance based metric (negative exponential dispersal kernel) similar to the Incidence Function Model, and others used models that highlight areas that are resilient to climate change etc. | Y                      | 2012            | Custom Incidence Function Model                        | Distance                      | On the ground: Habitat creation / restoration                             | ad hoc                     | 82, 83    |
| Europe    | ECONAT  | 2010       | The ecological network appears to have been established largely through mapping techniques, rather than the implementation of any core metric.  | Y                      | 2010            | None   | Expert                        | NA  | Academic literature        | 27        |
| Europe    | COREHABS to Bear Connect  | 2015       | 2019 study used Circuitscape to model potential movement routes across the Carpathians, and how current infrastructure projects may sever them.   | Y                      | 2019            | Circuitscape   | Circuit Theory                | Evidence  | Databases, Grey literature | 1, 80, 81 |
| Europe    | Utrechtse heuvelrug   | 2004       | No material available on how they decided where to located the bridges  | Unknown                | 2004            | Unknown  | Not disclosed                 | On the ground: Defragmentation by construction of wildlife road crossings | Databases, Grey literature | 1, 115    |
| Europe    | ALPBIONET2030   | 2016       | Their connectivity assessment is based on the evaluation of a number of input layers including land use, environmental protection, population pressure, fragmentation and topography, as well as consultation with experts. The program used is called Joint Ecological Continuum Analysing and Mapping Initiative (JECAMI) and seems to be a sort of SCP type program.   | Y                      | 2016            | None   | Expert Opinion, Topography    | Evidence  | Ad hoc                     | 117       |
| Europe    | Caucases Ecoregon   | 2007       | The Ecoregional conservation plan for the Caucasus identifies conservation and bridging landscapes; the purposes of both are to reduce fragmentation and promote connectivity. The additional reports included with the reports appear to reflect that these were identified through expert consultation using the concept of Key Biodiversity Areas and identifying large undisturbed or less disturbed ecosystems.                            | Y                      | 2007            | None   | Expert                        | Evidence  | Databases                  | 118, 119  |

| Region        | Project  | Start Year | Connectivity assessment  | Connectivity assessed? | Assessment Year  | Metric  | Connectivity assessment group            | On the ground or evidence?  | Found via           | Ref        |
|---------------|--|------------|--|------------------------|------------------|---|--|---|---------------------|------------|
| Europe        | Netzwek Naturwald  | NA         | Uses the outputs of a former alps project called ECONNECT to identify important stepping stones. This project was a precursor to ALPBIONET2030 and therefore uses the same software.   | Y                      | Not disclosed    | None  | Expert Opinion, Topography               | Not disclosed   | Databases           | 120        |
| Europe        | ECONET Kostroma  | 2003       | Aside from mention in the IUCN guidelines I cannot find any material on the project. Wageningen university website mentions that GIS, and map analysis were undertaken but does not explain further.   | Unknown                | 2003             | unknown   | Not disclosed                            | Evidence, on the ground protection  | Databases           | 1, 116     |
| Europe        | Rewilding Europe   | 2011       | A number of the projects mention corridors, however they do not provide information on how these corridors were identified.  | Unknown                | 2011             | unknown   | Not disclosed                            | On the ground restoration   | Databases           | 121        |
| North America | The Conservation Lands Network                                       | 2006       | In their 2.0 report released in 2019 they implemented a measure of connectivity in the mix thanks to The Nature Conservancy.   | Y                      | 2019             | Omniscape   | Circuit Theory                           | On the ground: protection of sites  | Academic literature | 28         |
| North America | 12 Rivers Conservation Initiative                                    | 2014       | Mapped overlapping priority areas identified by combining the terrestrial resilience and region flow datasets from The Nature Conservancy and the Index of Ecological integrity from the Designing Sustainable Landscapes Project  | Y                      | 2014             | Circuitscape                                      | Circuit Theory                           | On the ground: protection of sites  | Academic literature | 22         |
| North America | St Lawrence lowlands, Montreal Canada                                | 2017       | Selected 14 focal species and assessed species specific habitat quality and resistance maps through the use of a multi metric approach developed in Rayfield et al., 2016.   | Y                      | 2017             | Circuitscape, Equivalent connectivity             | Circuit Theory, Least Cost               | On the ground actions: protection of sites  | ad hoc              | 23         |
| North America | Arizona counties wildlife connectivity assessment                    | 2004       | Used least cost pathways to describe the cost of moving through areas between core areas of habitat.   | Y                      | 2006             | Least Cost Corridor Analysis                      | Least Cost                               | On the ground actions: Wildlife bridges etc   | Academic literature | 24,25      |
| North America | South-eastern Ecological Framework                                   | 2002       | Linkages between Hubs are identified via physical ecological connections such as; Riparian (along rivers), upland (along similar altitudes) and habitat (similar habitats). They use cost surfaces and run a least cost path model to find links between the hubs in question.   | Y                      | 2002             | GIS Least cost Path tool                          | Least Cost                               | Evidence and on the ground actions: Used by federal highway administration to find alternate routes for the I69 | Academic literature | 38         |
| North America | Florida Ecological Network/ Florida greenways                        | 1991       | Linkages between Hubs are identified via physical ecological connections such as; Riparian (along rivers), upland (along similar altitudes) and habitat (similar habitats). They use cost surfaces and run a least cost path model to find links between the hubs in question.   | Y                      | 2000             | GIS Least cost Path tool                          | Least Cost                               | Evidence and on the ground actions (if we consider the Florida wildlife corridor act)                           | Academic literature | 39, 40, 41 |
| North America | California Essential Connectivity Project                            | 2010       | Linkages between Natural Landscape Blocks are identified via LCP modelling, where a "resistance surface" is used to identify how difficult dispersers would find it to move through different areas of the landscape   | Y                      | 2010             | Specific Tool Not Disclosed                       | Least Cost                               | Evidence  | Ad hoc              | 42, 43     |
| North America | New Mexico Highlands Wildlands                                       | 2003       | Used expert opinion to design and revise the network before using a conservation planning software called SITES to create the final network. The software was asked to incorporate stepping stones for focal species, but these stepping stones appear to have been identified via area, rather than any specific measure of connectivity. | Y                      | 2003             | None  | Expert                                   | Evidence and Action?  | Databases           | 55         |
| North America | Rocky mountain wild (part of the Southern Rockies Wildlands network) | 2003       | Initial report carried out in 2003 by the wildlands network used expert opinion to design and revise the network before using a conservation planning software called SITES to create the final network. The software was asked to incorporate stepping stones for focal species, but these stepping stones appear to have been            | Y                      | 2003, 2006, 2019 | Initially none, then custom IFM, now Circuitscape | Expert Opinion, Distance, Circuit Theory | Evidence  | Databases           | 56,57,58   |

| Region        | Project   | Start Year | Connectivity assessment  | Connectivity assessed? | Assessment Year | Metric                       | Connectivity assessment group | On the ground or evidence?                               | Found via                  | Ref                |
|---------------|---|------------|--|------------------------|-----------------|------------------------------|-------------------------------|--|----------------------------|--------------------|
|               |   |            | identified via area, rather than any specific measure of connectivity.   |                        |                 |                              |                               |  |                            |                    |
|               |   |            | In 2006 they were making use of graph theory and least cost distances to inform highways agencies of the important wildlife linkages across the state of Colorado.   |                        |                 |                              |                               |  |                            |                    |
|               |   |            | Since then rocky mountain wild have moved on and their most recent work (2019) makes use of circuitscape.  |                        |                 |                              |                               |  |                            |                    |
| North America | staying connected initiative  | 2009       | The 8 priority linkages at the core of the SCI were identified from the 2 countries 1 forest project which used SCP methods that assigned irreplaceability and vulnerability scores to planning units (2009). Within those linkages SCI and its partners use GIS LCD analysis to identify critical areas of fine-scale connectivity (2012). Other studies use tracking data and circuitscape (2014).   | Y                      | 2012, 2014      | Not disclosed, circuitscape  | Least Cost, Circuit Theory    | Evidence and Action: Protection and creation/restoration | Databases, Grey literature | 59, 60             |
| North America | Quabbin to Cardigan Partnership   | 2003       | The 8 linkages (and 1 new linkage in 2020 are: Catskills to the Adirondacks, Green Mountains to Hudson Highlands, Tug Hill to Adirondacks, Taconics to Green Mountains, Northern Greens to Canada, Worcester's to NEK, NEK Northern NH to Maine, Three Borders, and Chignecto Isthmus  | Y                      | 2018            | Circuitscape                 | Circuit Theory                | Evidence   | Databases                  | 61                 |
| North America | Appalachian Corridor  | 2002       | Their website includes the latest map and outlines that connectivity corridors were identified least-cost GIS processing using The Nature Conservancy's permeability data.   | Unkown                 | 2002            | Unknown                      | Not disclosed                 | Action: Protection                                       | Databases                  | 62                 |
| North America | Appalachian Corridor  | 2002       | Material available on their website advises that the approach landowners targeted by their "Ecological network analysis", but there is no information on what this is  |                        |                 |                              |                               |  |                            |                    |
| North America | Cold Hollow to Canada   | 2008       | A "story map" on their website outlines that they make use of the 2016 Nature Conservancy flow maps. These are maps produced from Circuitscape.  | Y                      | 2016            | Circuitscape                 | Circuit Theory                | Action: Protection                                       | Databases                  | 63,64              |
| North America | Two countries one forest  | 2002       | In 2008 they issued a document identifying key areas warranting protection based on ecological importance and vulnerability. This drew together work from the nature conservancy, and wildlands project, as well as their own work looking at human impact on areas. MAXAN was then employed to identify important ecological features for a variety of conservation goals, those areas appearing consistently were identified as key areas. | Y                      | 2008, 2019      | None, Circuitscape           | None, Circuit Theory          | Evidence   | Databases                  | 65,66              |
| North America | California Central Coast District of Caltrans Wildlife Corridor and Connectivity plan | 2014       | In 2019 they updated their work, using the maps produced by the Nature Conservancy in 2016 for "resilient connected landscapes" which make use of circuitscape.  |                        |                 |                              |                               |  |                            |                    |
| North America | California Central Coast District of Caltrans Wildlife Corridor and Connectivity plan | 2014       | The connectivity assessments used in the analysis were: California Essential Habitat Connectivity: LCPBay Area Critical Linkages: Least Cost Corridor in GIS Central Coast conservation network design: LCP Central valley conservation network design Least Cost Corridor in ArcGIS.  | Y                      | 2014            | Least cost Corridor Analysis | Least Cost                    | Evidence   | Academic literature        | 42, 68, 69, 70, 71 |
| North America | Sierra Nevada Foothills Connectivity  | 2015       | Used Least cost corridor analysis to identify connectivity for a variety of species throughout the study area, then collated these into 246 wildlife linkages connectivity 198 landscape blacks that provided habitat for at least seven and up to 26 focal species.   | Y                      | 2015            | Least cost Corridor Analysis | Least Cost                    | Evidence   | Academic literature        | 73                 |

| Region        | Project  | Start Year | Connectivity assessment  | Connectivity assessed? | Assessment Year        | Metric  | Connectivity assessment group        | On the ground or evidence?                       | Found via                  | Ref                           |
|---------------|--|------------|--|------------------------|------------------------|---|--------------------------------------|--|----------------------------|-------------------------------|
| North America | Wildlands network  | 1991       | Reports have been produced in which connectivity is measured using Circuitscape and its add-on Linkage mapper.   | Y                      | 2015                   | Circuitscape, Linkage Mapper, Connectivity Analysis Toolkit | Circuit Theory, Least Cost           | Evidence   | Databases                  | 122, 123, 124                 |
| North America | The red desert to hoback mule deer corridor (Wyoming Migration initiative) | 2012       | Use GPS data from tacking collars, using the software migration mapper to analyse the data and identify corridors from that.   | Y                      | 2012                   | Tracking data   | Tracking                             | Evidence   | Databases, Grey literature | 1, 125,                       |
| North America | Mayacamas to Berryessa Wildlife corridor project                           | 2016       | Landscape and Riparian connectivity assessed with Linkage Mapper   | Y                      | 2016                   | Linkage Mapper, circuitscape                                | Least Cost, Circuit Theory           | Evidence   | Databases                  | 126                           |
| North America | Boreal songbird initiative   | 2003       | Number of reports and their website state that 50% of land should be conserved in large interconnected protected areas, but no information is available to say if a connectivity analysis as been completed.   | N                      | 2003                   | None  | None                                 | Evidence   | Databases                  | 127, 128                      |
| North America | Yellowstone to Yukon (Y2Y)   | 1993       | Linkage mapper used to map connectivity across Canada-US trans-border region, which lead to conservation works the demonstrably increased connectivity in the region (130, 131).   | Y                      | 1993, 2005, 2010, 2018 | Presence models based on habitat , Linkage mapper, tracking | Least Cost, Circuit Theory, tracking | Evidence, on the ground: protection, restoration | Databases, Grey literature | 129, 130, 131 , 132, 157, 158 |
| North America | Algonquin to Adirondacks collaborative (A2A)                               | Unknown    | A number of connectivity assessments have been conducted in the region by different organisations. Early identifications of the corridor (1999) used a Cost Path Analysis based on producing a cost surface and finding routes on minimal cost. More recent studies largely appear to involve the use of circuitscape although many of the cited reports appear to only be provided on the A2A website, which does not currently work. | Y                      | 1999, 2021             | Avenue Program, Circuitscape                                | Least Cost, Circuit Theory           | Evidence, on the ground: protection, restoration | Databases                  | 132, 133                      |
| North America | Connect the Connecticut  | 2014       | In the design of their landscape conservation design approach they used the Nature Conservancy datasets which were produced using Circuit theory.  | Y                      | 2016                   | Circuitscape  | Circuit Theory                       | Evidence   | Databases                  | 134                           |
| North America | Connect the Coast  | 2019       | The project used Linkage mapper to identify wildlife corridors for 11 focal species.   | Y                      | 2019                   | Linkage Mapper  | Least Cost, Circuit Theory           | Evidence   | Databases                  | 135                           |
| North America | Sky island alliance  | 2001       | Mapping of wildlife pathways appears to have been based on tracking data that is continually updated.  | Y                      | 2001                   | Tracking data   | Tracking                             | Evidence, On the ground: restoration, protection | Databases                  | 136                           |
| North America | Transborder Grizzly Bear Project   | 2004       | Used radio tracking data and multiple regression models to predict grizzly bear habitat usage and identify four important linkage zones bisecting a Highway in the region.   | Y                      | 2008                   | Tracking data   | Tracking                             | Evidence   | Databases                  | 137, 138                      |
| North America | Sonoma Valley Wildlife Corridor  | 2012       | Used data from a previous 2010 study that used the GIS add-on FunnConn to identify important linkages in the Mayacamas Mountains.  | Y                      | 2012                   | FunnConn  | Least Cost                           | Evidence, on the ground: Protection              | Databases                  | 139                           |
| North America | Washington connected landscapes Project                                    | 2007       | Used species specific dispersal data and environmental data to produce cost surfaces, and then to the weighted average of Least cost corridor analysis results for each of the different dispersal inputs to produce an overall state map. Subsequent ecoregional analysis was conducted using Linkage Mapper.   | Y                      | 2010, 2012             | CostDistance, Linkage Mapper                                | Least Cost, Circuit Theory           | Evidence   | Databases                  | 140, 141                      |

| Region          | Project  | Start Year | Connectivity assessment   | Connectivity assessed? | Assessment Year | Metric   | Connectivity assessment group | On the ground or evidence?              | Found via                  | Ref                |
|-----------------|--|------------|---|------------------------|-----------------|--|-------------------------------|---|----------------------------|--------------------|
| North America   | Massachusetts Critical Linkages Project                          | 2012       | Used randomised Least-cost paths to find a number of low-cost paths that might be used by terrestrial wildlife to move between areas of habitat. Used Graph theory to evaluate the importance of each area of habitat to regional connectivity. Finally, Saura and Pascual-Hortal's Probability of connectivity index was used to assess connectivity of the landscape as a whole.  | Y                      | 2012            | Custom LCP method, Probability of Connectivity | LCP                           | Evidence                                | Academic Literature        | 153, 154           |
| North America   | Northern Rockies: Great Migrations and Crucial Corridors Program | 2012       | Their key linkage areas were identified through a ranking process after input from biologists on the important linkage areas for their focal species.   | Y                      | 2012            | None   | Expert advice                 | Not disclosed                           | Academic literature        | 155                |
| North America   | SC wildlands   | 2000       | Resulted in the creation of the CorridorDesigner GIS addon as well as a number of documents outlining the linkage zones across California.  | Y                      | 2008            | Corridor designer                              | Least Cost                    | Evidence                                | Databases                  | 142, 143, 144, 145 |
| Pacific Islands | The Coral Triangle   | 2003       | Initial delineation of seascapes was done via expert advice, latter reorganisation done following further expert advice that involved identifying areas where connectivity within the seascape is higher than connectivity with the surroundings. Connectivity was assessed via examination of current patterns.  | Y                      | 2003            | None   | Expert advice, topography     | Evidence                                | Databases                  | 105                |
| Pacific Islands | Micronesia challenge   | 2006       | The initial planning report in 2006 makes mention that the % goals must strive for "appropriate representation of habitat/structure (considering connectivity and replication). However, not all constituent members carried out an assessment of connectivity. Republic of Palau report states that no connectivity assessment was conducted in designation process. While the federated states of Micronesia appear to have included a connectivity value in their MARXAN analysis, the value was based on distance of reef to mangroves. Guam does not appear to have conducted a connectivity analysis. No information available on Marshall Islands. | Y                      | 2006            | Distance based metric                          | Distance                      | On the ground: Protection               | Databases                  | 106, 107, 108, 109 |
| Pacific Islands | Vatu-i-Ra Land/Seascape  | 2010       | Report cited in Fiji's National Biodiversity Strategy and Action Plan identified forest blocks that could function as corridors based on those that span a range of elevations.   | N                      | 2010            | None   | Topography                    | Evidence                                | Databases                  | 110, 111, 112      |
| South America   | Jaguar Corridor initiative                                       | 2010       | Used expert opinion to build a resistance surface and then produced a map of corridors using Corridor analysis in GIS, between Jaguar Conservation Units which were identified in 1999.   | Y                      | 2010            | CostDistance                                   | Least Cost                    | Evidence, on the ground                 | Databases, Grey literature | 1, 146, 147        |
| South America   | Corridors for Life, Brazil                                       | 2002       | The location of corridors was guided by a 'Dream map', no information on the methods utilised to create this map although from viewing it appears corridors follow rivers.  | Unknown                | 2002            | unknown  | Not disclosed                 | On the ground: restoration and creation | Databases, Grey literature | 1, 148             |
| South America   | Paraguay Atlantic Forest Biological Corridor                     | 2003       | Creation of the conservation landscape was undertaken using a spatial conservation planning approach, they used fragmentation and distance to rivers and PAs within this. In the cited document they say the identified main and secondary corridors between core habitat areas via the biodiversity conservation potential map that was produced.  | Y                      | 2003            | Distance based metric                          | Distance                      | Evidence                                | Databases                  | 149                |
| Central America | Mesoamerican Biological Corridor                                 | 1990       | No clear assessment of connectivity outside of the original work revolving around jaguars which Sought to link high quality nodes   | Unknown                | 1990            | unknown  | Not disclosed                 | Evidence                                | Academic literature        | 150, 151, 152      |



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