Informing nature recovery in England by analysing “bottlenecks” in broad habitats

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Foreword

A key aspect of Defra's 25 Year Plan for the Environment and the Environment Act 2021 is the delivery of a national Nature Recovery Network (NRN) to protect and restore wildlife in our countryside. The basis of any nature network is provided by a set of core sites in which the conservation of biodiversity is the primary purpose (Crick et al., 2020). However, connectivity between such sites and other parts of the network is a key issue that helps to confer resilience to environmental pressures and change. It can promote the exchange of individuals between habitat patches, ensuring genetic diversity and the repopulation of patches that have lost a species due to some chance or extreme event. Connectivity can take many forms, e.g. physical corridors (structurally connected) or small patches of habitat ('stepping stones') that occur between larger patches (functionally connected). Further, areas which may not currently contain features of conservation interest may need protecting to enhance connectivity – we need to be able to identify these, so that they can recognised as potentially important parts of the NRN.

The Condatis decision support tool developed by the University of Liverpool (http://wordpress.condatis.org.uk/) is designed to identify sites that are important for connectivity and for identifying where "bottlenecks" occur that restrict connectivity. This Research Project explores the applicability and utility of Condatis for identifying key areas for improving ecological connectivity at national and local scales.

The project has developed some new ways of analysing, classifying and presenting the results from Condatis that will improve its usefulness for practitioners. The study provides a set of case studies at both national and local scales for three broad exemplar habitats that demonstrate the utility of this approach. The results at the national scale will be used to inform national conservation planning for the NRN and Local Nature Recovery Strategies. The individual case study results are already being used to inform the development of the Nature Recovery Projects which took part, as well as providing useful information to the others which might adopt the approach in their planning.

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Executive summary

To fulfil the Nature Recovery Network's commitment to delivering better-connected habitat networks at the national scale, it is important to target restoration in strategic sites where it will have the greatest impact on ecological connectivity. Restoration could be prioritised nationally but it will always be delivered by teams working locally. Action has been started through several initiatives, including the landscape-scale Nature Recovery Projects (NRPs) funded by Defra and Natural England.

In this study, we aimed to identify key areas where connectivity “bottlenecks” occur (where connectivity is restricted) at the national scale in England and assess the extent to which these areas match with bottlenecks identified in three focal NRPs for three broad habitats: grassland, heathland and wetlands.

We used the decision support tool Condatis to identify bottleneck areas. We modelled the movement of generic species with moderate-low (1 km) and moderate-high dispersal abilities (3.4 km) across the landscape in four possible directions (north-south, east-west, northeast-southwest and northwest-southeast). We developed a scoring system applicable across different landscapes and spatial scales, that allowed us to categorise bottlenecks into severe, major and minor and to rank the areas within these categories.

We produced national maps of the most significant bottlenecks in the three broad habitats. We suggest that these maps are used alongside other relevant spatial information (e.g. topographic, infrastructure, or land use maps), to help identify sites where restoration to improve connectivity is feasible.

We estimate that severe bottleneck areas of the three broad habitats cover 7.3% of land and are mostly concentrated in the Midlands. We identified fewer and mostly minor bottlenecks in NRP areas because habitat availability and connectivity were better in these areas than the national average. The project areas are relatively small in a national context (13,490 - 62,070 ha; 0.1% - 0.5% of England’s land area), so their chance of overlapping a major or severe bottleneck (if they had been randomly selected) was low. Additionally, these areas were not chosen with a specific remit to address nationally significant gaps to secure habitat networks.

There are some advantages and disadvantages of running Condatis analyses at the national and local scales. National analyses set an important context which can inform every local area and show options that species have for using alternative routes through the networks. However, they face computational limitations in the modelling of short-distance dispersers (<1km). In contrast, local analyses can be run at a finer spatial resolution and can consider shorter dispersal abilities. They can inform on the functioning of local habitat networks, but may not provide a long-term, large-scale perspective.

We recommend modelling at an intermediate scale such as region, county, or several ‘landscape character areas’, to get an overview of multi-generation movement potential, and to set local priorities in that context. Initiatives such as the Local Nature Recovery Strategies which focus on mapping key areas for restoration at county-level scales, could find this approach highly informative.

To maximise the benefit of this study, further work would usefully include engaging with the NRP and LNRS teams to help them with the use of the project’s spatial outputs. We could also further test how our bottleneck scoring system works in different contexts.

Contents

Introduction

The Nature Recovery Network (NRN), a major commitment outlined in the UK Government's 25-Year Environment Plan (Defra, 2018), aims to restore and link up natural habitats so that wildlife can thrive while fostering human well-being and generating nature-based solutions. This involves providing 500,000 hectares of additional wildlife-rich habitat that links existing protected sites and landscapes. The spatial prioritisation of recovery sites at the local scale is essential to fulfilling this commitment effectively and efficiently. This has been recently addressed with the launch of the Nature Recovery Projects (NRPs). The NRPs are multi-partnership endeavours funded by Natural England and Defra to put in place targeted restoration actions at the local scale, each covering c. 10,000 ha.

The connectivity of habitats can be greatly improved by creating or restoring habitats in 'bottleneck' areas and forming functional habitat networks. Bottlenecks are gaps that impede the movement of species through landscapes due to the lack of suitable habitat, affecting their ability to respond to environmental changes, such as climate change. Providing information on bottleneck occurrence can help inform the prioritisation of restoration sites at different spatial scales.

Condatis is a decision support tool to identify the best locations for habitat creation and restoration to facilitate long-distance multi-generation shifts across fragmented landscapes (Hodgson et al., 2022). This connectivity approach is particularly relevant given the pressure many species are under due to climate change. We used Condatis to identify connectivity bottlenecks in three of England's broad habitat classes: grasslands, heathlands and wetlands, nationally and within the boundaries of three NRPs.

Aim

In this study, we aimed to provide information to support nature recovery plans in England by analysing bottleneck occurrence in three broad habitats. To achieve this we set the following objectives:

1. To provide a spatial output ready for use in conservation. We aimed to map bottleneck areas that can be used by practitioners as a broad spatial indication of priority zones to improve habitat connectivity at the national scale.
2. To develop a methodology for scoring bottlenecks. To maximise habitat connectivity with limited restoration opportunities it is essential to identify the most important areas that could facilitate species movement in a landscape. Therefore, we aimed to develop a scoring system, consistent across different landscapes and spatial scales, to facilitate the recognition of severe bottleneck areas.
3. To understand how identified national bottleneck areas relate to a sample of current NRPs.

4. To assess the utility of bottleneck information within NRPs. We collaborated with three local teams to evaluate how the bottleneck area maps and bottleneck scoring system could be used at different stages of project development.

Methods

National habitats and Nature Recovery Projects

Broad habitats

We focused our bottleneck analyses on three currently available habitat classes relevant to the NRPs which were to be included in the study: seminatural grasslands, heathlands and wetlands (Figure 1a), and hereafter, broad habitats. We defined these broad habitats based on the latest Natural England Priority Habitats Inventory (PHI), a spatial dataset that describes the geographic location and extent of 25 habitats identified as being the most threatened and requiring conservation action under the UK Biodiversity Action Plan in England (Natural England, 2022).

The PHI map is made up of polygons where one or more than one priority habitat is recorded to occur. The constituent habitats that we included within the three broad habitats are listed in Table 1. Since some classes shared a habitat of interest, there is some overlap among these broad habitats.

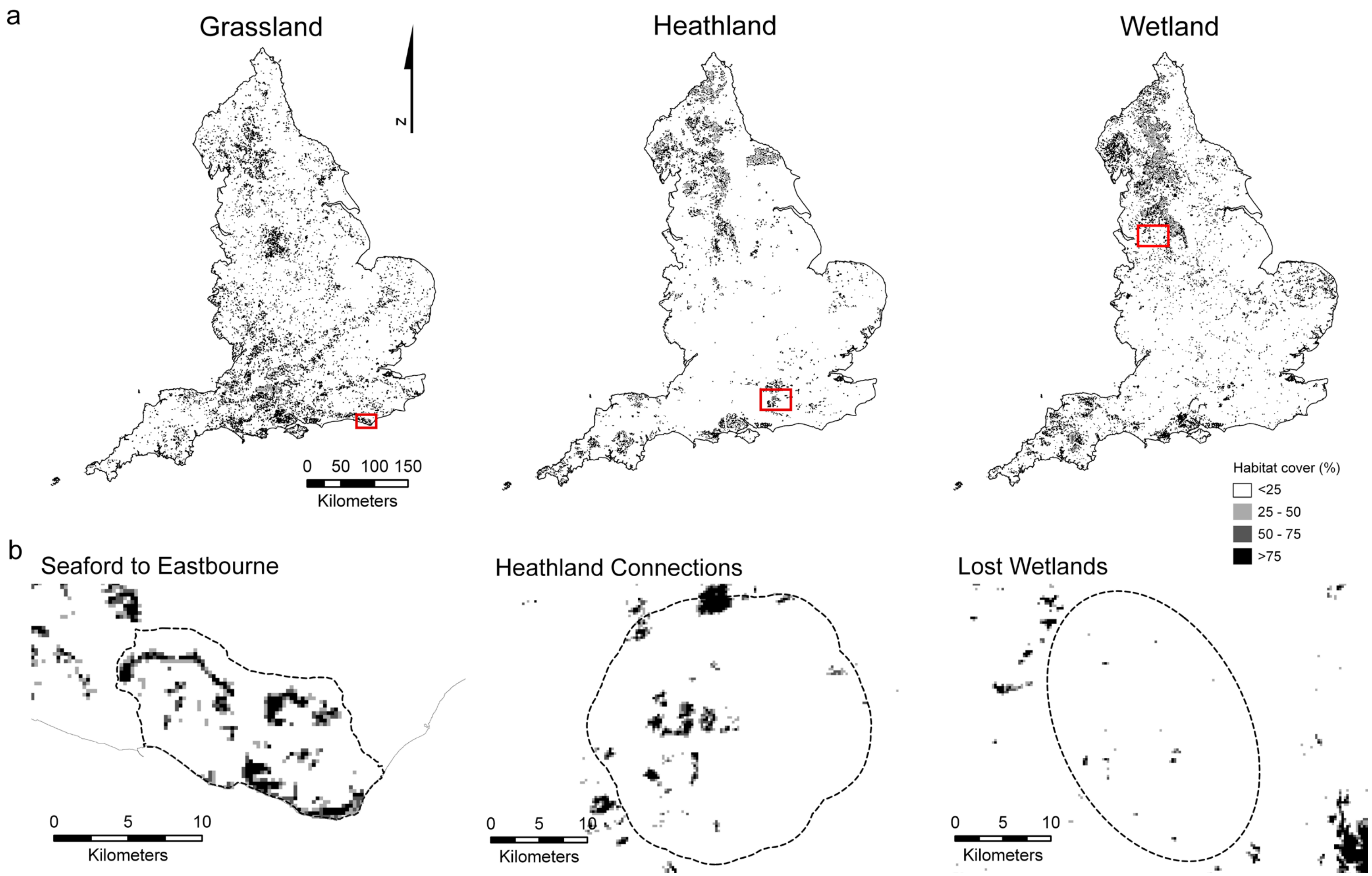

Figure 1. Broad habitats. We assessed the occurrence of connectivity bottlenecks in three broad habitats: grasslands, heathlands and wetlands at (a) the national and (b) local scales, from the latest Natural England Priority Habitats Inventory dataset (Natural England, 2022). Red boxes indicate the location of the Nature Recovery Projects for each broad habitat. Image produced by the authors with publicly available habitat data (Natural England, 2022) and local project polygons provided by Nature Recovery Project teams.

Table 1. Habitat classes of the Priority Habitats Inventory (PHI) dataset (Natural England, 2022) which formed three broad habitats used in this study. If a polygon included one of the named Priority Habitats (no matter whether other habitats were present), it was included in Condatis habitat networks (see section Habitat maps).

Broad habitat	Priority Habitat Labels
Grassland	Calaminarian grassland Lowland meadows Lowland calcareous grassland Lowland dry acid grassland Upland calcareous grassland Upland hay meadow
Heathland	Lowland heathland Upland heathland
Wetland	Blanket bog Lowland raised bog Lowland fens Reedbeds Upland flushes fens and swamps Purple moor grass and rush pastures

Nature Recovery Projects

Our local scale analyses were delimited by the area of interest of an NRP project focused on one of the broad habitats (Figure 1b). Thus, we compared the occurrence of national bottlenecks to local bottlenecks in the projects 'Seaford to Eastbourne NRP' (Sussex-Kent), Heathland Connections (Surrey) and 'Lost Wetlands NRP' (Cheshire).

Seaford to Eastbourne

Seaford to Eastbourne Nature Recovery Project takes in the landscape and seascape of the South Downs National Park, Sussex Heritage Coast and hinterland, across two chalk aquifers terminating in the Seven Sisters chalk cliffs, including the Cuckmere River. It aims to reinforce nature and natural processes as the key provider of clean and plentiful water, local food, and positive nature connections for people in the growing towns of Seaford and Eastbourne, and for the many visitors that come to the area each year.

It aims to enhance existing partnerships across 12,000 hectares, working with South-East Water, local councils and community groups, conservation organisations and landowners, farmers, and fishers, as well as public bodies. This partnership will deliver important outcomes for both people and nature by developing nature-based solutions for clean water and climate change mitigation – including flood management; focussing on species recovery; joining up visitor experiences that offer sustainable travel and providing support for mental health initiatives in the area. In terms of creating and restoring habitat, littoral habitats, intertidal/saltmarsh, chalk grass and heath will be targeted, to create a mosaic within arable, woods and vineyards. These outcomes will be supported through new initiatives, such as biodiversity net gain and green infrastructure while trying to further develop private investment in nature recovery. The project will also lead an ambitious plan to develop a super-NNR in the heart of the area, to protect and enhance nature recovery across the area for generations to come.

Heathland Connections

Heathland Connections is a partnership of landowners, foresters, and farmers across over 8,000 ha of the westernmost section of the Surrey Hills Area of Outstanding Natural Beauty. The project aims to enhance, restore, and create wildlife-rich heathland habitat across the landscape, with large areas already designated as Thursley, Hankley and Frensham Commons Special Protection Area.

Collectively, the project will find innovative solutions to management challenges such as habitat degradation, disturbance to ground-nesting birds, and the emerging threat of more frequent and more devastating wildfires. The project will also produce and deliver a sustainable recreation plan to encourage active travel, improve access and encourage responsible behaviour whilst connecting people to nature.

Funded by Natural England and led by the Heathland Connections partnership, the project aims to restore natural processes and make the landscape more resilient. These habitats are hotspots for important and rare species of birds, dragonflies and flora and provide an attractive landscape for the local community to enjoy. The project will empower local communities, generating long-term sustainable funding opportunities while providing sustainable recreation that improves people’s health and well-being as well as their understanding and appreciation of this landscape.

Lost Wetlands

Cheshire and Greater Manchester were once dominated by wetlands and rivers, but land use changes have modified rivers and drained wetlands, leading to a fragmented wetland network throughout these regions. The Lost Wetlands aims to reclaim, restore, and rewet a mosaic of wetland habitats across North Cheshire and South Greater Manchester, supporting nature recovery and wider natural capital benefits from wetlands for people and nature.

Working in partnership with key partners and stakeholders provides an opportunity to maximize joint resources and unlock new funding opportunities to develop a long-term programme of landscape restoration and community engagement. The use of nature-based solutions to establish an interconnected network of wetland habitats will not only improve species connectivity across the landscape but increase climate resilience, improve water quality, enhance carbon sequestration, and flood mitigation. Re-establishing wetland habitats will also provide access and wider benefits for local communities within and surrounding this landscape and improve people's understanding of the benefits these spaces bring.

Condatis

Condatis models populations' distribution shifts through a fragmented landscape analogously to an electrical circuit (Hodgson et al., 2012; Hodgson et al., 2016). A circuit board consists of several wires joining up resistors in combinations. When voltage is applied to the board at one end, the current will pass through the board to the other end but the amount of current passing through each wire will vary according to the resistance it meets through each pathway. Condatis considers a source population of species equivalent to the voltage, the links between habitat useable by these species equivalent to the resistors, and the flow of individuals colonising the available habitat across those links equivalent to the current (Hodgson et al., 2022).

Condatis assumes that each habitat patch is linked with every other habitat patch in a landscape. The strength of each of these links is dependent on the relative time it would take for the population of one patch to send colonists to populate the other patch. Thus, a set of habitat patches in a landscape is referred to as a 'network' in Condatis, regardless of its degree of connectedness, i.e. it can have very weak connectivity and still be considered a network. For the avoidance of doubt, we use the term 'Condatis network' to differentiate this concept from the Nature Recovery Network commitment (see Introduction) and the Network Enhancement and Expansion zones (see Potential restoration zones) of the Natural England Habitat Network Maps (Edwards and others, 2020), where 'network' refers to well-connected habitats only. The definition of this and other relevant Condatis concepts can be found in the Glossary.

Condatis requires four pieces of information to model population movement in a fragmented landscape:

1) a map of suitable habitat patches made up of cells, i.e. rasters;

2) a map defining the direction of movement that includes the source habitat patch(es) and target patch(es);

3) a mean dispersal distance in kilometres; and

4) a reproductive rate. This information can be species-specific or generic to represent populations with similar habitat requirements, dispersal abilities and reproductive rates[1]. Here, we used a generic approach to model the connectivity in three major habitat groups.

We performed the Condatis and subsequent spatial analyses in R (RCoreTeam, 2023). The Condatis tool is also available as an open-source web application[2] to facilitate its use by conservation practitioners.

Habitat maps

We obtained the habitat maps required by Condatis of the three broad habitats (grassland, heathland and wetland) using the Priority Habitats Inventory dataset (Natural England, 2022). First, we extracted the polygons of the classes forming a group (Table 1). Then we converted these polygons to a raster with a resolution of 250m. Each of the 250m-cells inherited the value of the proportion of area covered by the polygons, to the nearest 1%.

Spatial analyses, like those performed by Condatis, generally face a trade-off between the extent (i.e., landscape area) and the resolution (i.e., cell size) to which these can be performed due to limitations of processing power, time and data storage. Usually, a high-resolution analysis is performed at small geographical scales (e.g., plot or local scale), while a national or global study has a reduced resolution in comparison. Thus, for the Condatis analyses at the local scale, we used the 250m-resolution habitat maps. We then aggregated these maps to a 1 km resolution to conduct analyses at the national scale and calculated the respective proportion of habitat coverage in the 1 km cells.

We performed these and the following spatial and arithmetic operations using the *raster* (Hijmans, 2023), *sf* (Pebesma, 2018), *stats* (RCoreTeam, 2023) and *tidyverse* (Wickham et al., 2019) R packages.

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[1] The average number of individuals produced per generation per km^2 of habitat for the species of interest. Here, we use a generic reproductive rate of 1000 individuals for all analyses.

[2] Condatis v1.2 is is avilable at http://condatis.org.uk/, including full documentation, tutorials and study cases.

Dispersal distances

Condatis assumes a uniform dispersal process, where every disperser has an equal chance of colonising a new patch if they land in it, and their probability of landing in it is given by a negative exponential dispersal kernel (Hodgson et al., 2016). To model dispersal, Condatis requires the average distance one individual can travel in their lifetime (in km). This can be derived from ground data or expert knowledge.

We selected two generic dispersal distances to represent UK species with moderate-low and moderate-high dispersal abilities. Based on species-specific dispersal distances reported in the literature (Travers, 2022) for 85 animal species (58 birds, 15 mammals, five reptiles, four amphibians and three insects), we defined the moderate-low dispersal distance as the first tertile of the distance distribution, i.e. 1 km, and the higher dispersal distance as the second, i.e. 3.4 km.

We were able to conduct the connectivity analyses at the local scale using these two generic dispersal distances. At the national scale, due to inherent computational limitations, we performed analyses using only the 3.4 km dispersal distance.

Directions of movement

Condatis models species' movement from an initial habitat patch or patches in the landscape, the source, to a final patch or patches, the target. To consider a wide range of possible courses of movement through the landscape, we modelled connectivity using four directions of movement: north to south (NS), east to west (EW), northeast to southwest (NESW) and northwest to southeast (NWSE). We set sources and targets accordingly for each direction, as strips of cells just outside the boundary of the study area (i.e. national border or project polygon). The outputs produced are equal for inverted targets and sources for each direction (e.g. north-to-south equals south-to-north outputs).

To define the sources and targets, we first drew a buffer around the study area based on the resolution of habitat maps used, 1 km for the national scale and 250 m for the local scale, and then we rasterized the buffered boundary to the same resolution. We then divided these outer boundary cells into eight strips in approximately the eight compass directions. The most southerly point of the boundary becomes the centre of the southern strip. Distance around the boundary from this point then sets the position of the other strips (see Appendix 1).

Bottlenecks

Condatis assumes that each habitat cell is linked with every other habitat cell. The resistance of each of these links depends on the time it would take for the population in one of the cells to send colonists to populate the other cell. In Condatis, a bottleneck in the landscape is an area that has high resistance and yet forms part of one of the best available routes through the landscape, in circuit terms, it has high power. If habitat were added on or around the lines representing these bottleneck links, then the whole route would have a significantly higher flow (Hodgson et al., 2016).

Bottleneck scores and categories

To identify bottlenecks, we developed a scoring system that allows comparison among different landscapes and spatial scales. First, we calculated the percentage of power attributed to each of the links in our landscapes based on their power relative to the total power in the Condatis network. Then to account for the size differences in landscapes, the score was calculated as

$$\textbf{power\%} \times \textbf{number of patches}/\textbf{100},$$

where **power%** is the percentage of the power of the link within the Condatis network and the **number of patches** is the count of habitat cells in the landscape.

We consider a bottleneck to be all those links that had a score above one, i.e. had a higher power than expected if the flow was evenly distributed in all links. To provide a practical indicator of the relevance of the bottlenecks in the landscape we decided to categorise them as:

- Minor bottleneck: links with a score above 1 and less than or equal to 5
- Major bottleneck: links with a score above 5 and less than or equal to 50
- Severe bottleneck: links with a score above 50

We adopted this categorisation a posteriori to include all possible scores greater than 1 obtained for the three broad habitats at the national and NRP scale for all directions of movements (see Appendix 2 for details).

Priority areas

For each of the major and severe bottlenecks, we obtained the midpoint of the link and created a buffer of half its length, resulting in a circular polygon with a diameter of the bottleneck length. Next, we merged all overlapping polygons, independently for major and severe bottlenecks, to form ‘units’ representing areas with potential for improvement. Thus, we obtained ‘major’ priority areas and ‘severe’ priority areas (Figure 2). These areas were produced by combining bottlenecks of the four directions of movement.

These areas are associated with an overall score calculated as the sum of the scores of the bottlenecks included in a given area. Thus, major or severe bottleneck areas can also be prioritised according to their overall score.

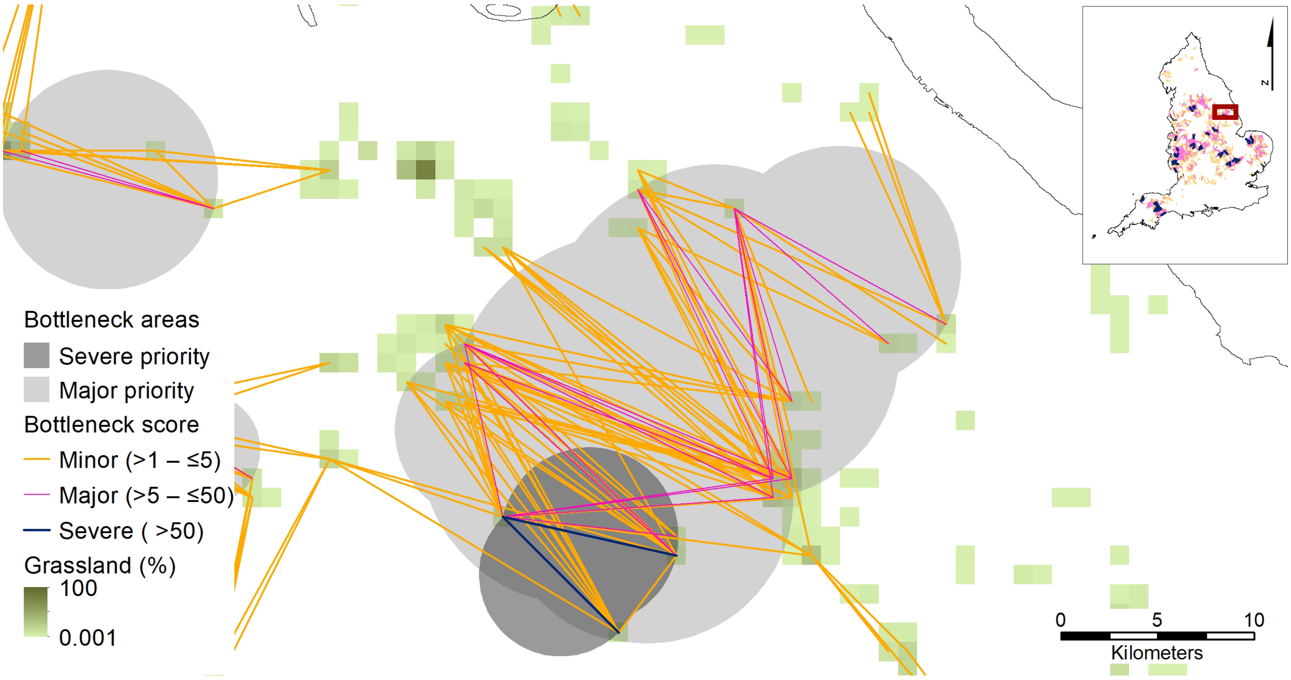

Figure 2. An example to illustrate the conversion of bottleneck lines with scores to bottleneck area polygons. Condatis network links are classified as bottlenecks if their power score is above one and are divided into minor (score >1 - ≤5), major (score>5 - ≤50) or severe (score >50). Bottleneck areas correspond to overlapping features of major and severe bottleneck buffers, the diameter corresponds to the bottleneck length. Image produced by the authors with publicly available habitat data (Natural England, 2022) and the outcomes (bottleneck score and areas) of the analyses performed with the decision support tool Condatis (Hodgson et al., 2022).

Potential restoration zones

In liaison with local NRP teams, we used appropriate habitat-specific data to shed light on restoration opportunities. First, for the Heathland Connections project, we combined three of the Enhancement and Expansion zones identified by Edwards et al. (2020) for heathland creation. These zones are 1) Network Enhancement Zone 1, suitable land for heathland creation based on their proximity to existing habitat, land use (urban/rural), soil type, slope and proximity to coast; 2) Fragmentation Action Zone, land within Enhancement Zone 1 that connects existing habitat patches which are currently highly fragmented; and 3) Network Expansion Zone, land with potential for expanding, linking/joining networks across the landscape. We estimated the overlap of these zones with the identified bottleneck areas.

Similarly, for the Lost Wetlands project, we estimated the bottleneck area overlap with the Wetland Creation Zones previously identified by the local team with the 'Nature Recovery Network for Wetlands and Woodlands' project in the Cheshire to Lancashire Area as part of the EU-LIFE funded programme, Natural Course. This creation zone corresponds to sites where wetland connectivity is most restricted due to fragmentation and full-scale wetland creation is not viable, but other small-scale restoration actions could take place (e.g. lined ponds) to provide natural capital benefits (Drake & Smart, 2022).

The Seaford to Eastbourne NRP team chose to compare their bottlenecks to underlying landcover and other priority habitats in the area.

Results

The three broad habitats cover approximately 8% of the national territory (Table 2. National). The heathland predominates with 4.5%, with the highest coverage distributed in the north, followed by wetlands (2.3%) mainly concentrated in the northwest. Grassland has the lowest coverage (0.9%) sparsely distributed across the country, with major cover in the southwest (Figure 1a).

Table 2. Broad habitats' area and percentage at the national and local scales (England area, 130,834.1 km²).

Habitat	National		Local			
	km²	%	Nature Recovery Project	Project km²	Habitat km²	%
Grassland	1,214.5	0.9	Seaford to Eastbourne	134.9	20.0	14.8
Heathland	5,872.4	4.5	Heathland Connections	620.7	46.7	7.5
Wetland	2,956.9	2.3	Lost Wetlands	462.4	2.0	0.4

The NRPs Heathland Connections and Seaford to Eastbourne have more of their focal habitat type in their areas than the national average (Figure 1b, Table 2. Local), whereas the habitat in the Lost Wetlands project is below the national average.

Overview of bottlenecks

Nationally, the bottleneck areas of the three broad habitats are mainly concentrated in the midlands (Figure 3). Additionally, the grassland Condatis network shows some severe bottlenecks in the southwest (Figure 3a) affecting the northeast-southwest movement. Equally, the east-west movement of the heathland Condatis network is affected by severe bottlenecks in the south.

Figure 3. National bottleneck areas. Priority areas for nature recovery were identified for three broad habitats' Condatis networks: a) grassland, b) heathland and c) wetland, based on the length of major and severe bottlenecks (see Priority areas) estimated for dispersers with an average dispersal ability of 3.4 km moving in four possible directions (see Directions of movement). Image produced by the authors with the outcomes (bottleneck areas) of the analyses performed with the decision support tool Condatis (Hodgson et al., 2022).

Severe priority areas, formed by severe bottlenecks (score >50), cover 7.3% of the land, while major priority areas (score >5 - ≤50) cover 30.5% (Table 3), with some overlap of the different habitat areas. The grassland Condatis network shows the largest proportion of major priority areas (16.3%) and has the largest km^2 ratio of major to severe priority areas (7:1), compared to wetland (4.5:1) and heathland (3:1). The wetland Condatis network shows the largest proportion of severe priority areas (3.2%, Figure 3c), mainly distributed in the western and central midlands.

Table 3. Land cover area of major and severe bottlenecks in the three broad habitats and respective percentage of national coverage (England area, 130,834.1 km^2). There is an overlap between the different habitat areas.

Habitat	Major		Severe	
	Area(km^2)	%	Area(km^2)	%
Grassland	21,348.9	16.3	2,881.9	2.2
Heathland	8,428.4	6.4	2,897.8	2.2
Wetland	18,218.0	13.9	4,161.3	3.2
All broad habitats	39,894.5	30.5	9,589.9	7.3

Locally, bottlenecks tend to be less severe than national ones. No severe bottlenecks were identified when considering either a 1 km or a 3.4 km dispersal distance. For a 1 km dispersal distance, there are minor bottlenecks (score >1 - ≤5) in all three project areas but there are no major bottleneck areas (score >5- ≤50) in the Seaford to Eastbourne grasslands (Figure 4a). For a 3.4 km dispersal distance, only minor bottlenecks were identified for the local heathland (Figure 4b) and wetland Condatis networks (Figure 4c).

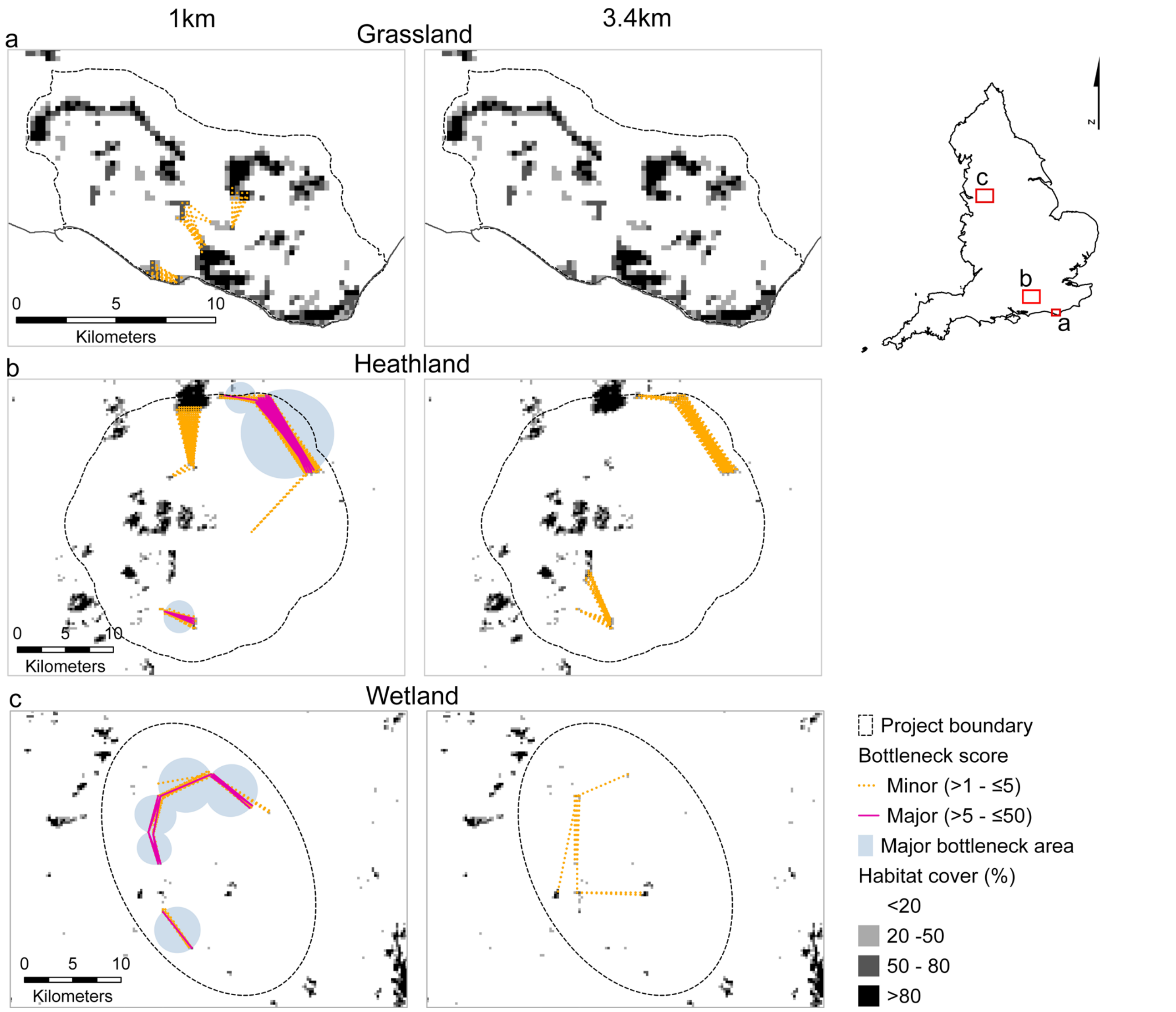

Figure 4. Bottlenecks at the local scale (all directions). Minor bottlenecks (yellow dashed lines) estimated with a 1 km-dispersal distance (left) were identified in the three project areas, and major bottlenecks (pink solid lines) were found in the b) Heathland Connections and c) Lost Wetlands NRPs, major bottleneck areas in grey. For a 3.4 km-dispersal distance (right), there were no bottlenecks in a) the Seaford to Eastbourne NRP grasslands and only minor bottlenecks were identified in the heathland and wetland projects. No severe bottlenecks were identified at the local scale. Image produced by the authors with publicly available habitat data (Natural England, 2022), local project polygons provided by the Nature Recovery Project teams and the outcomes (bottleneck score and areas) of the analyses performed with the decision support tool Condatis (Hodgson et al., 2022).

Comparing bottlenecks to restoration possibilities

The local teams saw the potential to compare bottlenecks to local knowledge about restoration possibilities – whether these were mapped or not.

Taking the Network Enhancement and Expansion zones (Edwards et al., 2020) as a reference for possible restoration areas in the Heathland Connections project, there is a 16 km^2 area overlap with major bottleneck areas at the northeast and south of the project area (Figure 5a), covering 8.6% of the suggested expansion zones in the area (185.6km^2).

The south and southwest borders of the Heathland Connections project adjoin a nationally significant major east-to-west bottleneck area. This major bottleneck area overlaps with 116.1 km^2 of the network expansion zones, while the nested severe bottleneck area overlaps by 35.1 km2 (Figure 5b).

Regarding the area-specific wetland creation zones identified by the Lost Wetlands teams, there is a 4.5 km^2 overlap with major bottleneck areas (Figure 5c), which represents 19% of the suggested creation zone area (24.2 km^2).

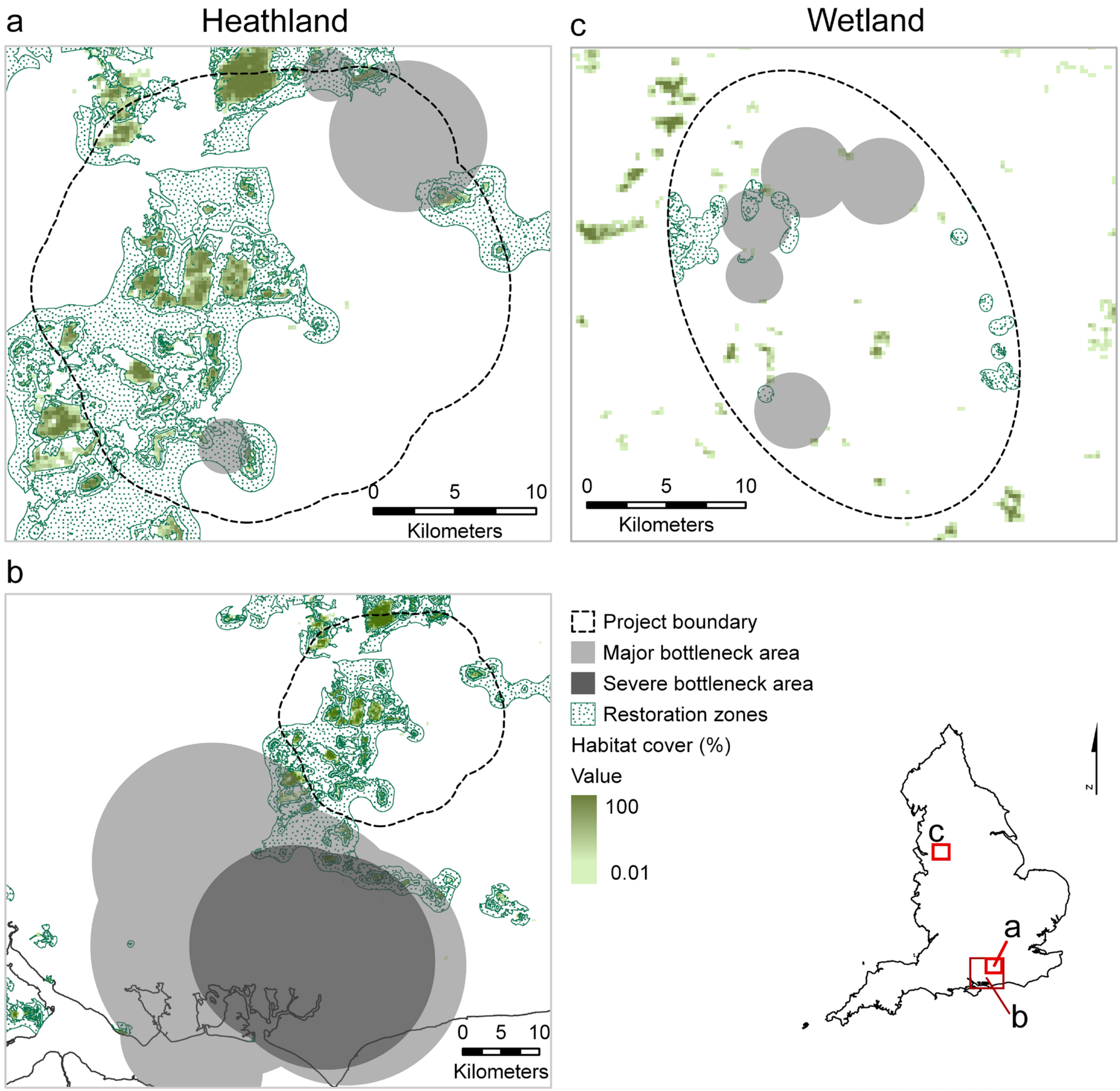

Figure 5. Restoration possibilities in bottleneck areas. a) Overlap areas (16 km^2) of the identified local major bottleneck within the Heathland Connections project area with the Network Enhancement and Expansion zones (Edwards et al., 2020); while b) the national east-west major and severe bottleneck areas adjacent to the Surrey project cover 116.1 km^2 and 35.1 km^2 of the zones respectively. c) The area-specific habitat creation zones of the Lost Wetlands project (Drake & Smart, 2022) overlap by 4.5 km^2 with the identified local major bottleneck areas. Image produced by the authors with publicly available habitat data (Natural England, 2022) and restoration zones (Edwards et al., 2020); and outcomes (bottleneck areas) of the analyses performed with the decision support tool Condatis (Hodgson et al., 2022).

Given the extent of habitat available (Table 2. Local) and particular habitat configuration (Figure 4a), the Seaford to Eastbourne NRP grasslands landscape presents only minor bottlenecks for moderate-low dispersers (1km), and it is seemingly well connected for moderate-high dispersers (3.4 km). Nevertheless, the team has found the outputs informative (see Box 1).

Box 1. Seaford to Eastbourne Nature Recovery Project and grassland bottlenecks.

As part of the Condatis bottlenecks' assessment with local nature recovery projects (NRPs), the Sussex and Kent project 'Seaford to Eastbourne Nature Recovery Project' was chosen as one of the pilot projects. Located between Eastbourne and Seaford in East Sussex, the NRP stretches from the South Downs to the Marine Conservation Zone, covering over 15,413 ha (land and sea). Composed predominantly of calcareous grassland due to its position above two large chalk aquifers, the chosen priority habitat was grassland.

The Condatis study estimated that grassland covered approximately 15% of the project area. Condatis' overall speed (see Glossary) was relatively high in the area **(>>1 for all directions, Hodgson et al., 2016)**, bottlenecks were limited, and on average only 1.6 km in length. We can therefore be confident the grassland habitat for this site is accommodating of species movement.

To assess the limits imposed on the bottlenecks, we have overlayed the Priority Habitat Inventory to identify the level of mobility allowed by the habitats surrounding the grassland habitats. As Figure 6 highlights, bottleneck area 1 is mostly a result of the deciduous woodland (Friston Forest), and bottleneck area 2 is a result of the coastal floodplain and grazing marsh surrounding the Cuckmere River. Given the natural condition of these habitats, a certain permeability of some species associated with the grassland habitats can be expected. However, further work is required to assess the need and extent of conservation intervention in these areas. Bottleneck area 3 appears to be a result of a gap in the grassland habitat. Cross-checking with the UK Centre for Ecology and Hydrology landcover map **(Morton et al., 2022)** and satellite imagery, this gap is classified as 'improved grassland', and therefore is unlikely to be a bottleneck of concern.

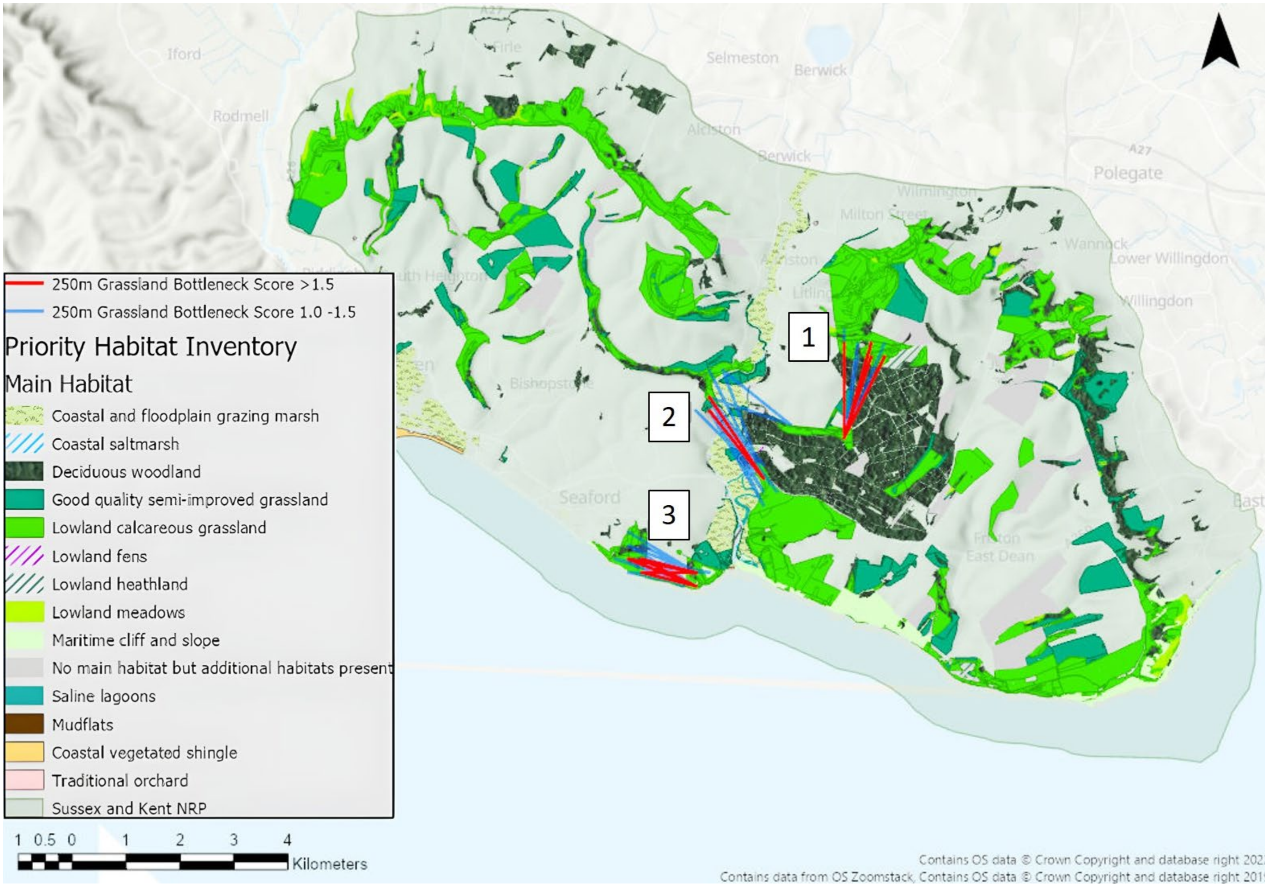

Figure 6. Three areas of minor bottlenecks were identified in the Seaford to Eastbourne Nature Recovery Project area at 1) the Friston Forest, 2) the floodplain and grazing marsh surrounding the Cuckmere River and 3) improved grassland sites south of Seaford. Red lines indicate bottleneck links with a score above 1.5 and below five and blue lines bottlenecks with scores between one and 1.5.

The next steps from this pilot could involve working with projects that also have a chalk grassland focus e.g., Big Chalk, to collaborate on data and learn how to best support species migration across the habitat. A closer inspection to analyse what species cannot use these neighbouring habitats to migrate will also be useful to help inform what actions we could take to ensure there are passable routes. Additionally, the NRP can compare this assessment to the species used to inform this analysis, and whether the dispersal rates are representative of all species of interest for the grassland habitats.

Discussion

National bottlenecks

In this study, we have provided national maps of the most significant bottlenecks in England for three broad habitats. These are ready for use by practitioners as 'search areas' when they are planning the restoration of semi-natural habitats. We anticipate the

GIS layers will be made available on Natural England's geodata portal. These could be useful tools to help inform the design and delivery of Local Nature Recovery Strategies and the Environmental Land Management Scheme, as well as Biodiversity Net Gain – all key Government policies as described in the Environmental Improvement Plan (Defra, 2023).

It is of utmost importance for practitioners to understand what the bottleneck areas mean and how to combine them with other important information. First, bottlenecks occur in areas where there is a lack of habitat, where a colonising species would have to take a bigger-than-usual step in their journey across the country. But not every large gap is a bottleneck: only those that restrict long-distance routes that have better connectivity upstream and downstream. This feature means that alleviating a bottleneck would have a disproportionate effect on the total source-target journey time. Practitioners can be confident that restoration action in these areas would deliver efficiently and effectively if it was feasible.

Second, it is important to consider the outlined bottleneck areas as 'search areas' rather than prescriptions, largely because they are drawn irrespective of the reasons behind habitat gaps. In some cases, the creation of the target habitat in the bottleneck area could be physically impossible, or socio-economically unfeasible. Thus, we recommend the use of bottleneck maps together with other relevant spatial information (e.g. topographic, infrastructure, or land use maps), to identify sites where restoration is feasible.

How to plan restoration in light of bottleneck maps

If possible, give priority to addressing severe areas before major areas, and in turn, major before minor areas. This is based on the theory that the resistance of the entire Condatis network is most sensitive to the resistance of the high-power links. If you address a minor bottleneck, but a severe bottleneck still exists elsewhere on the same route that species have to traverse, the speed improvement might not be very noticeable. Additionally, the overall score, as developed in this project, of major or severe bottleneck areas can help to prioritise areas within the same category.

When searching and planning inside bottleneck areas, try to provide stepping stones of habitat such that the maximum step distance (i.e. maximum distance between two habitat patches) is reduced. Geometrically, there are many ways to reduce the maximum step distance, and this offers useful flexibility to take into account restoration options, local conditions and preferences.

Even in cases where restoration is not possible, awareness of a bottleneck could still be useful. For instance, it can bring into consideration plans for the translocation of certain species or to look for longer ways around that could still allow the species' movement.

The concentration of bottlenecks in the Midlands

The Condatis network maps derived from the Priority Habitats Inventory (PHI, Figure1a) show that habitat is relatively sparse and fragmented in the areas identified as major and severe bottlenecks. These are predominantly in the lowlands where major urban and intensive farming areas are distributed. These results should be a prompt to consider whether enough nature recovery effort is being invested in these areas relative to others and are consistent with the conclusions of other studies that have shown the unequal distribution of protected areas (e.g. Shwartz et al., 2017). However, considering the current land use of the region, restoration plans can be difficult and expensive, there may be trade-offs involved, and other factors need to be considered in an integrated planning process. Also, habitat creation in an area of low connectivity could attract less biodiversity in the short term, despite having a potentially large long-term impact.

An additional reason for bottlenecks being in the midlands could be their centrality *per se*. The shortest national-scale paths in all four directions will tend to converge somewhere in the middle. However, the importance of the midlands is not a mere statistical artefact: the paths of real species could converge just as the paths of the modelled species do. The clear differences between the heathland, grassland and wetland outputs indicate that habitat distribution matters more than centrality in the country.

Particular caution should be taken to consider bottlenecks in the West Midlands area. As a result of analysing England's priority habitats, suitable wetlands habitats close to the England-Wales border were not considered. The inclusion of additional information would be required to assess whether national bottleneck areas are affected by the inclusion of Welsh habitats (see Caveats).

Comparison of national and local scale analyses

There were fewer and mostly minor bottlenecks in project areas, which can be expected for several reasons. Firstly, these areas are receiving funding for enhancing existing habitat networks. According to our estimates, the grassland and heathland NRPs have higher habitat availability than the national average. A better-connected start-off state was thus anticipated, especially for moderate-high dispersers, as is the case for the Sussex-Kent grassland project. Additionally, the project areas are relatively small in a national context (0.1%-0.5% of England's land area), so their chance of overlapping a major or severe bottleneck, if they had been randomly selected, was low.

It is important to mention that NRPs were not chosen with a specific remit to address nationally significant habitat gaps. For instance, the Lost Wetlands NRP area was selected given its historical relevance for wetland habitats, the evidence of high potential for restoration obtained through a different modelling approach (i.e. Drake & Smart, 2022), the well-established partnership to carry out restoration plans in the region and the strong influence of these habitats in the local people's identity. All these components will enhance the project's success.

In general, there are some advantages and disadvantages of running Condatis analyses at a local vs national scale. Local analyses can be run at finer spatial resolution and use shorter dispersal distances, avoiding computational limitations. They can inform on the functioning of the local Condatis network as if it were in isolation from everything else, which is potentially useful to a local team who can only influence the local conditions (see further discussion in Using bottleneck areas locally). National analyses, however, set an important context which can inform every local area. They are better for showing the options that species have for using alternative routes through the Condatis network.

The NRP scale is relatively small, spanning only a few generations-worth of average dispersal for the moderate-high disperser we modelled. For the future, we would recommend modelling at an intermediate scale such as region, county, or several 'landscape character areas', to get an overview of multi-generation movement potential, and to set local priorities in that context. Initiatives such as the Local Nature Recovery Strategies focused on mapping key areas for restoration at county-level scales could find this approach highly informative.

Using bottleneck areas locally

When the suggested bottleneck areas were overlaid with previous exercises that had identified areas that are feasible and/or desirable for habitat creation locally, possible target sites were strongly narrowed down (Figure 5). The combined use of the Network Enhancement and Expansion zones in conjunction with the bottleneck map in the Heathland Connections exemplifies how recovery strategies can be optimised by identifying feasible zones for habitat creation or restoration that could have a considerable positive impact on long-distance habitat connectivity.

The decision-making response to the overlaid information can be three-fold. First, accelerate efforts in the areas of overlap, since there are multiple reasons for investing in these areas. Second, continue to consider remaining bottleneck areas as 'search areas' in case more information comes to light, potentially looking for the reasons that restoration is judged unfeasible there. Third, to look outside the bottleneck areas in case a 'detour' route can be created.

In the specific case of the Network Enhancement and Expansion zones, there was an upper limit of distance from the existing priority habitat of approximately 500m, based on a valid rationale of strengthening metapopulations (Edwards et al., 2020). However, Condatis analyses can recommend that stepping stones beyond that distance might be useful in the long term. Understanding the reasons for differing recommendations (non-overlap) will help local teams to make evidence-based decisions not only for the immediate future but also for their long-term visions.

Generally, we believe there is no substitute for a human brain in deciding what information to bring to bear locally, and how to combine it. Condatis is a decision-support tool, not a decision-making tool. Therefore, bottleneck modelling helps to narrow down potential sites but judgment and additional local information will still be required to inform the best areas to target.

Connectivity metrics

There is a vast diversity of connectivity metrics aimed to inform conservation planning and monitoring, each of them with particular data requirements and useful to different conservation goals (see Keeley et al., 2021; Kindlmann & Burel, 2008). Thus, the selection of a connectivity metric must be consistent with the conservation objective.

Condatis assesses connectivity and identifies bottlenecks in terms of the capacity of a fragmented landscape to allow a long-distance multigenerational movement, i.e. range shifting. It is important to mention that it does not take into account several aspects of population dynamics. Condatis ignores the possibility of extinction of the population and does not assess whether the patches are capable to sustain a viable population. If this is of interest, other metrics should be considered (see section 3.1 (ii) in Keeley et al., 2021). The use of other approaches to assess connectivity — in terms other than the facilitation of range shifting — can produce recommendations different to the ones we present here.

Caveats

In this study, we were able to explore the applicability and utility of Condatis' bottleneck analyses for identifying key areas for habitat connectivity at national and local scales. However, there are some factors related to our data source and parametrisation of the model to take into account when interpreting these results.

First, we decided to use the Priority Habitats Inventory (PHI) dataset as it was the most updated and standardised mapping exercise of habitats of major importance for conservation in England. However, it is important to consider that this is a multisource dataset, in which primary data sources vary in the temporality of data acquisition, spatial scale and habitat specificity. While validation has been carried out to resolve conflicts among the multiple datasets, there is a possibility of inaccuracies involving recorded habitat that no longer exists or excluding habitat present but unrecorded in the current version of the PHI.

The bottleneck areas were identified based on the landscape configuration produced by our broad habitat categorisation. A different grouping, a more specific habitat selection, or a different data source could provide different results. In this sense, an important trade-off of choosing the PHI dataset over other UK-wide or global habitat datasets to analyse the most relevant habitats for England involves the exclusion of possible continuous habitats in Wales and Scotland. Thus, bottlenecks identified in bordering areas could change if additional information is included in future assessments.

Also, to provide a standardised approximation to model several directions of movement across all areas of interest, we set sources and targets around study area boundaries where there may be no recorded habitat. This has the potential to generate a flow of dispersers that would not occur in reality. More informative source and target patches can be selected in a landscape-specific approach.

Finally, related to our generic approach of dispersal distances selection, even though our estimates are based on a data sample that includes a varied set of species (with diverse sizes and dispersal mechanisms), it is important to consider that our outputs offer a limited representation of dispersal ability. Although it often happens that the top-ranked bottlenecks in a Condatis network are in the same location for low and high dispersal distances, there can be differences (e.g. Figure 4b and 4c).

Recommendations for further work

Next steps to enhance the potential for decision support arising from this work could take several forms and could be undertaken by the Condatis team in continuing partnership with practitioners.

Applied work

Teams that are running NRPs or LNRSs in the areas that are identified as national bottlenecks could immediately be interested in the results we have presented. Further engagement and support could allow them to use the outputs, explore reasons for bottlenecks and look for restoration opportunities. Once some specific restoration has been planned, it could be possible to reassess the landscape connectivity by incorporating the potential restoration areas into the habitat maps and quantify the impact that this addition will have on the overall flow in the network.

Further analyses would be needed to test how consistent the bottleneck areas identified at the national scale are when assessed at the regional scale. Areas with robust outcomes at both regional and national scales can be considered a top priority. Equally, the analyses applied to the three major habitat networks can be extended to other networks, and sensible scale-dispersal distance combinations can be assessed.

In this study, the value of the patches (i.e. cells) of the Condatis network corresponded to the proportion of habitat in the patch, i.e. the effective area (see Habitat maps). However, if there is a concern that habitats are of varying quality, this can be incorporated into the Condatis model by modifying the effective area values (Travers, 2022). For instance, by weighting these values based on the condition of priority habitats (e.g. favourable, unfavourable-recovering, unfavourable or unfavourable-declining; Natural England, 2021) or based on the habitat type that forms a broad habitat class (e.g. grassland types).

Currently, the bottleneck output of the Condatis web app is limited to linear features and is restricted to a single direction of movement. The Condatis team will look for opportunities to update the web app and/or release an R library to incorporate the methodological improvements developed in this study. These include setting sources and targets in four directions around a boundary, bottleneck scoring, bottleneck categorisation and producing bottleneck area polygons.

Further work with a wider variety of landscapes would be needed to assess whether the categorisation adopted here (see Bottleneck scores and categories) is consistently helpful for other study areas and scales.

Fundamental work

Some questions have arisen related to the methodological approach developed in this study. First, more work would be needed to assess how the overall score of a bottleneck area relates to the marginal impact of habitat creation there. Also, does addressing a minor bottleneck, while leaving a severe one, have a proportionate impact? How this could vary with spatial scale, is there a bigger impact at a smaller spatial scale?

Finally, related to the computational limitation, further exploration of a possible workaround for analysing short-distance dispersers at a national scale would be beneficial for many future projects.

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Glossary

Bottleneck. In Condatis, a gap between habitat patches in the landscape that has high resistance and yet forms part of one of the best available routes through the landscape. In circuit terms, it has high power. Adding new habitat in these gaps will improve the flow along the associated route, improving the overall flow between the source and target.

Condatis network. A set of habitat patches where each habitat patch is linked with every other habitat patch in a fragmented landscape. The strength of each of these links is dependent on the relative time it would take for the population of one patch to send colonists to populate the other patch. The connectivity of a Condatis network can vary from extremely weak to extremely strong.

Flow. Measure assigned to each habitat cell, which indicates the relative number of individuals moving through that cell that will go on to colonise the target. The larger the flow value of a habitat cell, the more important that cell is for connectivity between the source and the target.

Speed. This is a measure of overall or total flow, i.e. successful movement of a species/taxonomic group from the source to the target. The faster the speed, the shorter the time taken to reach the target, measured in units analogous to generations of individuals.

Source. The desired start-point of population movement for the modelled species moving towards a target.

Target. The desired end-point of population movement for the modelled species moving from the source.

Appendices

Appendix 1

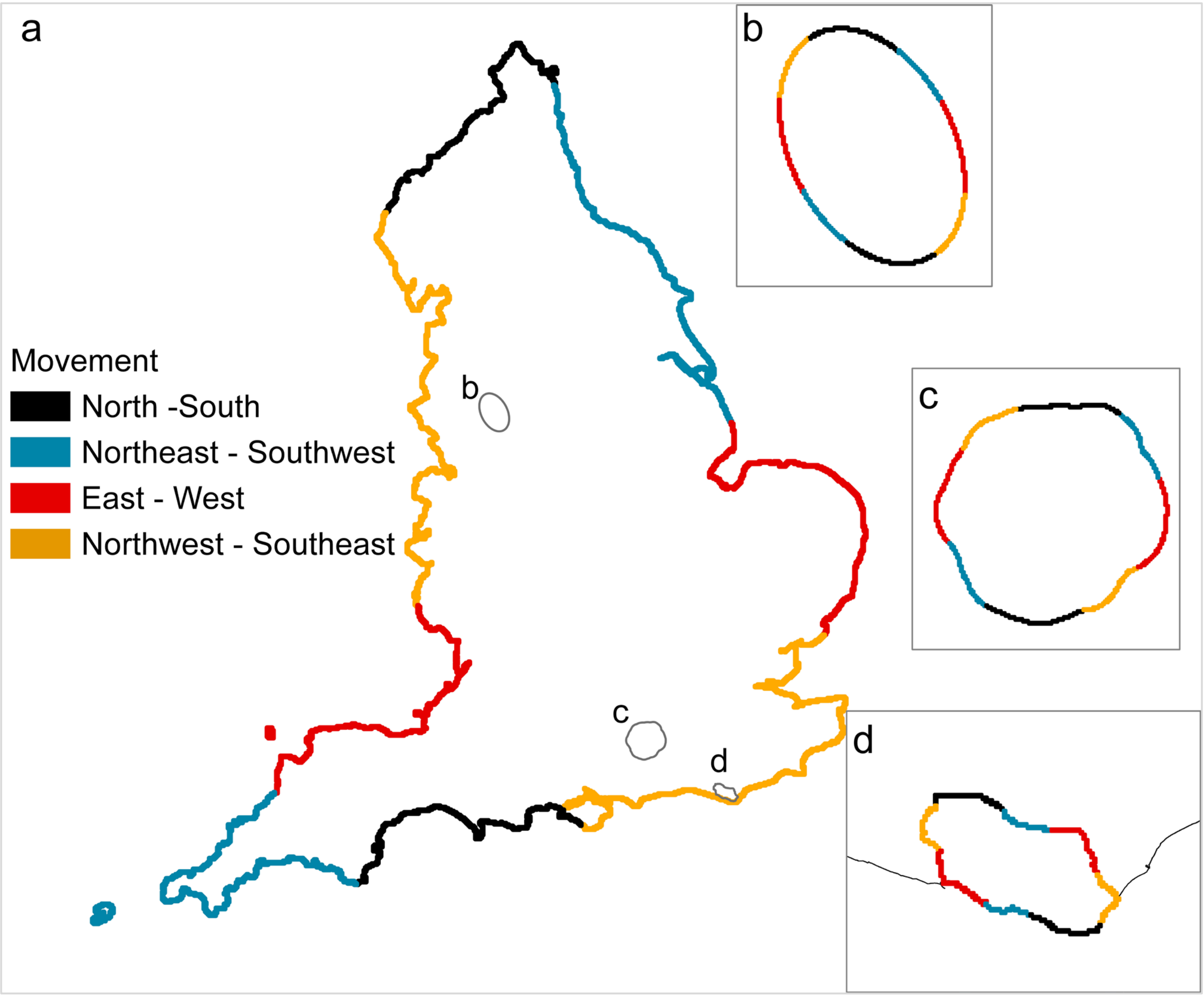

Figure A1. Boundary segments used as sources and targets in Condatis analyses to represent four different directions of movement. Boundaries are plotted at a) national scale and at the local scale for the Nature Recovery Projects b) Lost Wetlands, c) Heathland Connections and d) Seaford to Eastbourne (grassland).

Appendix 2

To facilitate the use of bottleneck scores in the three broad habitat landscapes at the national and local scale, we categorised bottlenecks with scores above one (above the yellow line in Figure A2) as minor (score >1 - ≤5, in between yellow and purple lines), major (score>5 - ≤50, in between purple and pink line) or severe (score >50, above the pink line).

As shown in Figure A2, there is no clear steep change in scores that can define a threshold for different categories for all scenarios (i.e. three landscapes, four directions of movement and two dispersal distances), but an overall continuous decrease in score values. Therefore, we decided on a categorisation that elucidated the differences between the national and local scales (Table A1). Further work with a wider variety of landscapes would be useful to assess whether this categorisation is consistently helpful.

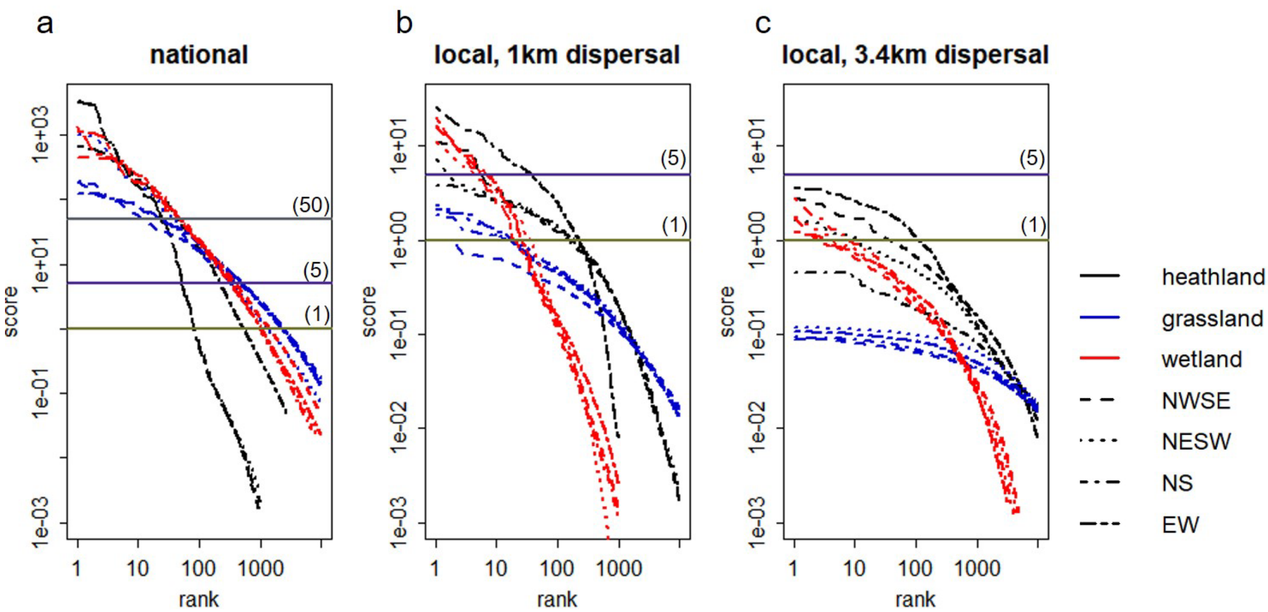

Figure A2. Trajectories of bottleneck scores sorted from highest to lowest for every Condatis network analysed at a) the national scale (3.4 km dispersal distance), b) the local scale for a moderate low disperser, and c) the local scale for a moderate high disperser. Each line connects the ranked points for one analysis. Line style denotes the direction of movement and colour denotes the broad habitat: heathland (black), grassland (red) and wetland (blue). Note that both axes are in log space. Horizontal lines indicate threshold score values (in brackets) at one (dark green), five (purple) and 50 (grey).

Table A1. Summary of the percentage of bottleneck scores (i.e. scores>1) by category identified in each broad habitat at national and local scales in all directions of movement. Minor (score >1 - ≤5), major (score>5 - ≤50) and severe (score >50).

	Natio-nal			**Local 1km**			**Local 3.4km**		
	Minor	Major	Severe	Minor	Major	Severe	Minor	Major	Severe
Grass-land	78.5	20.4	1.1	100	0	0	0	0	0
Heath-land	52.2	33.6	14.2	94.3	5.7	0	100	0	0
Wet-land	68.4	24.3	4.3	78.1	21.9	0	100	0	0