Landscape connectivity and spatial prioritization in an urbanising world: A network analysis approach for a threatened amphibian.

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Abstract

Habitat fragmentation affects amphibian populations worldwide. Urban expansion and associated infrastructure (e.g., roads) are the main cause of degradation and loss of landscape-scale habitat connectivity. Mitigation measures such as barriers and underpasses the construction of corridors are frequently implemented to reduce the impacts of development on protected species. However, despite the obvious potential for consequences for outcomes at multiple scales, such efforts generally focus on local outcomes rather than envisioning how the mitigation may contribute to habitat connectivity and populations persistence at a landscape scale. We used a graph-theoretical approach to model structural and functional connectivity (corridors) for a widespread but declining endangered pond-breeding amphibian, the great crested newt (*Triturus cristatus*), by assessing movement among breeding ponds associated with at different processes scales (dispersal, migration and colonization) in. The newts occupied a landscape with different levels of urban and rural development and linear barriers (e.g., roads of different sizes and railwaywith different permeabilities to amphibian movements). This analysis provides critical information to understand the potential capacity for larger scale impacts of mitigation measures (e.g. corridors). We used recent regional pond survey data from great crested newts combined with published data on movement and habitat use to to develop a framework to explore calculate connectivity at the landscape scale-level using estimated annual home-range patches around breeding ponds as terrestrial and wetland habitat units. We identified calculated potential areas of area for terrestrial movement corridors and assessed how landscape connectivity was investigated linkages between patches (potential movement corridors), and then analysed how these linkages were affected by landscape characteristics, such as habitat quality and quantity, and scale of movement and varied between two scenarios representing different degrees of road permeability. The different permeability of linear features (e.g., roads) that cross dispersal corridors influence the effectiveness of the corridor by affecting newt movement. Our results indicate that assessing linear barriers to movement and accounting for differences in their permeabilities is critical to understanding their impact on both shorter term migratory and longer-term dispersal aspect of planning corridors for successful movements in great crested newts. Animal movement is important at various scales, to the individual, the population, and the persistence of species across a landscape. The application of corridors as a mitigation for roads is a workable conservation action but is markedly improved by i Incorporating landscape-scale connectivity modelling which includes to identify the impact of barriers such as roads would substantially improve population-level outcomes from mitigation schemes. We suggest that an understanding of the far-reaching consequences of “road mitigation” (e.g. on, colonization of sites) as well as immediate, local effects (e.g., individual survival), combined with our method of assessing road impacts/permeability could transform future mitigation efforts by directing action to places that not only improve individual survival but that also maximise connectivity at the landscape scale.

Keywords: connectivity, dispersal, graph theory; great crested newt, home-range patches; migration; pond network; road mitigation

Introduction

Pond-breeding amphibians are heavily dependent on landscape connectivity: most migrate between breeding ponds, terrestrial feeding habitat and hibernation sites on an annual basis. Since ponds are essentially ephemeral systems, long-term persistence of pond-breeding amphibian populations is also dependent on the capacity of the landscape to support long-distance dispersal (Pittman et al., 2014). However, human activity, including urbanisation and the construction of linear infrastructure such as roads, causes habitat loss and fragmentation which reduces the capacity for long-distance movements and threatens their populations (Hamer and McDonnell, 2008; Petrovan and Schmidt, 2016). In Europe, and especially in the UK, amphibian populations are frequently the focus of ecological mitigation against the impacts of development (Edgar et al., 2005), and interventions such as road tunnels or underpasses are implemented in an attempt to maintain connectivity (Matos et al. 2017). However, because of the piecemeal nature of development, mitigation or conservation measures are typically implemented at the local, site scale without properly taking into account the need for amphibians to move around a landscape and the consequent implications for connectivity within the landscape context (Denöel and Ficetola, 2007).

The great crested newt (*Triturus cristatus*) is a European protected species which has declined substantially in Europe over recent decades (Langton et al. 2001; Jehle et al. 2011) mainly due to the destruction and degradation of pond habitats. The species remains locally common in parts of the UK, including in semi-urbanised areas, and is often the subject of road mitigation projects. *T. cristatus* is a good candidate to use as a model to understand patterns of movement for pond-breeding amphibians, as individuals show a strong homing tendency with clearly defined seasonal movements between habitat patches (e.g. Jehle, 2000), which enables patterns of movement to be clearly defined spatially and temporally. At the broadest scale, movements of pond- breeding amphibians like *T. cristatus* can be categorised as either ‘migratory’: temporary intra-population movements which occur within a core area between aquatic and terrestrial habitats, or and ‘dispersal’: permanent inter-population movements (Semlitsch, 2008).

At the broadest scale, movements of pond- breeding amphibians can be categorised as either ‘migratory’: temporary intra-population movements which occur within a core area between aquatic and terrestrial habitats, or ‘dispersal’: permanent inter-population movements (Semlitsch, 2008). For pond-breeding amphibians, migratory movements can themselves be separated into two elements: primary and secondary movements. Primary movements are performed by adults from terrestrial habitats to breeding ponds. Secondary movements include those between foraging sites and between hibernation and estivation refugia (Semlitsch, 2008). Semlitsch (2008) classified these movements as intra-population, which means that movements are undertaken by individuals between two or a cluster of several reproduction sites. For the purposes of this study, we define the area covered by these movements as annual home-range (AHR) patches. Migratory movements are important for exploration of the local habitat, maintaining the capacity for recolonization of unoccupied patches and ensuring the maintenance of gene flow within the population (Sinsch, 2014).

In contrast to migratory migration movements, pond-breeding amphibian dispersal is defined as being a permanent shift. Long-distance, longer-term dispersal between habitat patches is essential to maintain metapopulation dynamics and genetic exchange between populations (Halley et al., 1996; Griffiths and Williams, 2001; Griffiths et al., 2010; Semlitsch, 2008; Sinsch, 2014). As far as breeding ponds are concerned, dispersal involves permanent movements between ponds, normally differentiated as natal ponds (birth sites) and breeding ponds (reproduction sites) and for juveniles can occur over greater distances than for adults (Semlitsch, 2008). Terrestrial habitat use during dispersal events is greater than that on spring migration from the hibernation sites (Jehle, 2000).

Therefore, investigating movement corridors for amphibians such as *T. cristatus* requires an understanding that the area of corridor habitat will vary dependent on the type of movement being considered.

Functional connectivity at landscape scales cannot be properly assessed without an understanding of the landscape's potential to support both temporary intra-population migration and permanent inter-population dispersal (Denöel & Ficetola, 2007; Ficetola et al., 2008). Mitigation measures which do not consider the landscape context are therefore likely to fail in the long term.

The great crested newt (*Triturus cristatus*) is a European protected species which has declined substantially in Europe over recent decades (Langton et al. 2001; Jehle et al. 2011) mainly due to the destruction and degradation of pond habitats. The species remains locally common in parts of the UK, including in semi-urbanised areas, and is often the subject of road mitigation projects. However, in common with mitigation for amphibians generally, measures applied for *T. cristatus* are almost universally designed while only accounting for the local context (e.g. Matos, 2018). Consequently, it is unclear whether current mitigation practices contribute to the long-term conservation of the species (Ward et al., 2015).

T. cristatus is a good candidate to use as a general model for understanding patterns of movement of pond-breeding amphibians, as individuals show a strong homing tendency with clearly defined seasonal movements between habitat patches (e.g. Jehle, 2000), which enables patterns of movement to be separated spatially and temporally.

However, in common with mitigation for amphibians generally, measures applied for *T. cristatus* are almost universally designed while with only accounting for the local context accounted for (e.g. Matos, 2018). Consequently, it is unclear questionable whether current mitigation practices contribute to the long-term conservation of the species (Ward et al., 2015).

In this study, we modelled *T. cristatus* movement incorporating two life stages (adults and juveniles) and multiple movement types patterns (migratory and dispersal movements, including potential colonization) across a landscape fragmented by roads of different permeability. We used a graph theoretical approach to explore how structural and functional connectivity change when prioritizing pond-breeding amphibian movement corridors at different migration and dispersal scales in a region with a variety of stages of urban and rural development and where linear infrastructures act as barriers to amphibian movement. Graph theory or network analysis has been used previously to understand and prioritize conservation efforts for amphibian habitat networks (Ribeiro et al., 2011; Decout et al., 2012; Clauzel et al., 2014). The approach allows habitat patch dynamics, distribution and habitat suitability to be combined within a landscape-scale analysis. We applied aimed to apply this approach to a landscape impacted by major and minor roads to both model and test landscape connectivity on the basis of different assumptions about roads as barriers and as a way of identifying key locationspoints for targeting mitigation measures , specifically with respect to the permeability of roads.

Methods

Study area

The study was conducted in an approximately 100 km^2 area of mixed use lowland in central England (Fig. 1). The precise location is omitted because of the sensitive nature of the records for the species in question. Similar to many other such landscapes in England, the study area has a long history of industrial use combined with more recent urban expansion. The landscape is crossed by a network of several important linear transportation infrastructure elements, largely oriented north-south, including motorways, dual carriageway roads and minor roads, as well as an active rail track. There are large zones where ponds have been created in areas of former extractive industries. These have been colonized by a range of amphibians and other freshwater species.

Field surveys and topographic data

Survey sites within the study area encompassed all known populations of *T. cristatus* obtained from the local Biodiversity Recording and Monitoring Centre and a recent large-scale pond survey project (Natura International, 2015). In total 149 ponds were surveyed in 2013 and 2014 in an effort to improve the species' regional conservation status (Fig. 1). In 2013, the effort focused on egg searches and a standard habitat assessment known as Habitat Suitability Index (HSI) to identify extant populations and opportunities for habitat restoration (Oldham et al., 2000). For selected ponds, where habitat restoration work was planned, further night-time surveys were undertaken using torches to confirm species presence or absence. Each pond was visited at least twice each breeding season of 2013 and 2014.

Data on land use and locations of key features were obtained from a variety of sources (Table 1). Information on roads and railways was obtained from digitized data provided by the UK Department for Transport, 17 land cover variables were extracted from Ordnance Survey (2012) (Meridian™ 2 v1.2 Release 2) in raster format at 10 m resolution, and pond spatial information was obtained from the local Biological Records Centre (Table 1). This set of variables was used to calculate potential annual home-range patches (AHR) and as potential predictors of presence/absence of *T. cristatus* in species distribution models (SDM, see below).

Data analysis

We modelled (1) migration movements using annual home-range patches (AHR); (2) high-quality habitat (HQH) areas, defined as those areas suitable for the species' presence; (3) dispersal movements between AHR patches and HQH areas for two road permeability scenarios and (4) functional connectivity for prioritizing both migration and dispersal movements for *T. cristatus* (Fig. 1).

Newt movement data

Quantitative information on *T. cristatus* movement at landscape scales is limited and varies substantially between studies from different geographic regions (Hartel et al., 2010; Gustafson et al., 2011; Jehle et al., 2011). For the purpose of this study, input values to model migratory and dispersal movements were based on mean interval estimates from published radio-tracking and translocation studies (Sinsch, 2014). Average movement distances ranged from 50m - 400m for migratory movements (Oldham et al., 2000; Gustafson, 2011) and from 250m - 1000m for dispersal movements (Kupfer and Kneitz 2000; Jarvis, 2012).

Annual home-range patches (AHR)

The area of a habitat patch used by *T. cristatus* expands with time due to the seasonality of their space use. To account for this we adopted the 'metapatches' concept proposed by Zetterberg et al. (2010) which includes consideration of the lifecycle of the species in question. We therefore defined annual home-range (AHR) patches as areas that contain all the resources required by *T. cristatus* throughout the year (e.g. breeding, foraging and hibernation habitat), including migratory movements distances (Zetterberg et al., 2010).

Positions of all known ponds in the study area, irrespective of whether they had been surveyed or not, were used to generate potential AHR patches. Patches were generated on the basis of migratory movement maximum distance recorded in the literature – 400 m (Kupfer and Kneitz

2000; Oldham et al., 2000; Gustafson, 2011; Jarvis, 2012). The extent of each patch was defined using least-cost distance analysis radiating out from the centroid of each pond polygon based on a 10m resolution friction surface generated by assigning different costs of movement (‘resistance’) to different habitats (Table S1). We assumed that maximum annual distances covered by newts as reported in the literature would be through optimum habitat for movement. We therefore set the maximum possible movement distance through optimum (i.e. resistance = 1) habitat at 400m with resistance to movement through other habitats scaled according to their suitability. Roads were assumed to act as physical barriers to movement and were given resistance values of 4000, rendering them impermeable. While this approach may have been conservative, it nevertheless allowed us to model the worst-case scenario with respect to landscape permeability. Analysis was carried out using ArcGIS 10.1 Spatial Analyst (ESRI Inc. USA, 2008).

Identifying high quality habitat

High quality habitat (HQH) was defined as aquatic and terrestrial habitats known to be highly suitable for the species’ presence. This included terrestrial areas suitable for migratory and dispersal movements corridors, and areas potentially suitable for colonization. These areas were identified using species distribution models for two scenarios outlined below.

Habitat cost scores were assigned to each variable in a raster land cover map (10m resolution) and later transformed into probabilities of habitat selection as a surrogate for habitat suitability (Table 4.1). Thus, suitability/cost scores within the SDMs were based on the relative preference/cost associated with species movements and life history traits in different habitat types (Oldham et al., 2000; Rohweder et al., 2012). For each factor a weight was assigned in order to define the degree of importance on the basis of *T. cristatus* habitat use and occupancy extracted from the literature (Kupfer and Kneitz 2000; Jehle, 2000; Oldham et al., 2000; Malmgren 2002; Gustafson, 2011; Jarvis, 2012).

High suitability values were given to woodland, scrubland and grassland areas near other forests and wetlands (which in our study area were exclusively ponds) (Oldham et al., 2000; Jarvis, 2012). Low suitability values were given to urbanized areas, agricultural areas and linear infrastructures. Two separate scenarios were investigated: scenario SI used low suitability scores for all the linear infrastructure (all road classes and railways) while for scenario SII only major roads and railways were given low suitability scores, leaving minor roads with higher suitability values representing some permeability for newts (Oldham et al., 2000; Jarvis, 2012) (Table S1 and S2).

Overall suitability scores were expressed as the geometric mean for each land use type using Corridor Design for ArcGIS 10.1 (Jenness et al., 2007). These were combined into a single model for each scenario using ArcGIS 10.1 Spatial Analyst. Habitat suitability was rescaled from 0 to 100 (lowest to highest suitability). High-quality habitat areas (HQH) were then defined as those areas that had a habitat suitability score of ≥90. Both analyses were performed using *Normalize existing HSM from 0 to 100* and *Reclassify features in HSM* functions from Corridor Design for ArcGIS 10.1 (Jenness et al., 2007).

Least-cost surface modelling for terrestrial dispersal corridors

We modelled the potential for the landscape to support annual dispersal (and, by implication, colonization) by calculating least-cost terrestrial corridors between (1) AHR patches where *T. cristatus* presence was confirmed by field surveys and the HQH patches derived from SDMs and (2) AHR patches with *T. cristatus* present and those with absence or presence not confirmed (not surveyed) to identify potential new pond colonization corridors. We assumed that un-surveyed ponds had no breeding newts in order to model the worst-case scenario.

We used the same cost surface as in previous analyses applied to AHR and HQH patches from both SDM scenarios to generate two sets of outputs. The cost-distance surface was reclassified into a permeability grid and the least-cost path was calculated using the *Create corridor model* tool from the Corridor Designer Toolbox in ArcGIS 10.1 (Jenness et al., 2007; Rohweder et al., 2012). Areas with the lowest 10% of cost-distance values were identified as potential movement corridors as these represent areas with high permeability of movement (Rohweder et al., 2012).

The resulting corridors were overlain on AHR patches and HQH areas to create contiguous habitat patches that we refer to as ‘core areas’. To identify the location of the maximum number of AHR per HQH areas in a least resistance barrier scenario (SII), ‘core areas” were grouped in cluster of corridors. To calculate the differences in the patterns of corridors between the two barrier scenarios we then sought to determine: (1) the number of HQH areas and AHR patches associated with each corridor (2) the size of ‘core areas’ and (3) the area of potential colonization corridors for each barrier scenario.

Connectivity analysis

We carried out a connectivity analysis of the landscape using a graph theoretical approach. A graph is composed of a set of patches and links; nodes are the individual components within the network and links represent connectivity between nodes (Minor and Urban, 2008). In our study, the landscape network was represented by AHR patches (nodes) connected by suitable dispersal habitat (generated in the SDMs). We used the Integral Index of Connectivity (IIC) to assess landscape connectivity and identify priority habitat patches (Pascual-Hortal and Saura, 2006). This index is based on individual patch attributes and weighted links (in our study, the least-cost path distance). Eliminating each patch sequentially and assessing IIC gives a score (dIIC) of relative importance for landscape connectivity of each individual patch in a landscape.

We calculated dIIC for two barrier scenarios using the landscape permeability surface. Two scales were used as minimum and maximum thresholds for newt movements in spring and autumn (400m and 1000m). Individual AHR patches were given a habitat suitability score equal to the mean habitat suitability of all cells in that patch. Inter-patch links were analysed for individual patches using least-cost path distance. Calculations were made from the centre of the AHR patch. If a priority AHR patch was identified within a cluster of AHR patches the loss of that patch would have a stronger effect on the overall connectivity of the patch network (Minor and Urban, 2008). Following this pattern, patches of medium and low priority and their connections can be tested to evaluate landscape connectivity (Minor and Urban, 2008, Decout et al., 2012). This analysis was performed using Conefor 26 (Saura and Torné, 2009) and MatrixGreen 1.7 (Bodin and Zetterberg, 2012).

Results

A total of 302 ponds were identified in the study area. Of these, 173 were surveyed. Presence of breeding newts was confirmed in 148 of these; no evidence of newts was found in 25 ponds and 129 ponds were not surveyed.

Annual home-range (AHR) patches

A total of 176 AHR patches around ponds were calculated. Because many ponds were within our estimated movement distance of each other, the number of distinct patches generated was smaller than the number of ponds. Overall, 80 distinct AHR patches where newt presence had been confirmed were generated with a further 96 not surveyed or where surveys had not recorded newts (Fig. S1).

High-quality habitat areas (HQH)

The distribution of HQH was patchy across the landscape (Fig. S2). For scenario I (SI, where all linear infrastructure was classified as a barrier) 69 patches were generated and for scenario II (SII, where minor roads were classified as permeable) 151 patches were generated (Fig. S2; Table 2).

Terrestrial dispersal and colonization corridors

From least-cost surface analysis between HQH areas and AHR patches with *T. cristatus* presence, we identified nine terrestrial corridor clusters (Fig. 2). These are groupings of AHR, HQH and corridors. In SI, of 80 AHR patches, 46 were connected to 69 HQH areas resulting in 25 core areas while 13 AHR patches were unconnected to any HQH areas. Clusters with the highest number of AHR patches were C and F, which included 16 and 11 AHR patches, respectively (Table 2). Landscape connectivity was substantially greater under SII: of 80 AHR patches, 72 were connected to 151 HQH areas resulting in 19 core areas with no unconnected AHR patches. Terrestrial corridor clusters with the highest number of core areas were C and F, each one covering 20 and 16 AHR patches, respectively (Table 2). When comparing both scenarios (SI and SII) the main structural connectivity variable, core area varied significantly (ANOVA F= 3.804, df=1, p=0.05) (Fig. 2; Fig. S3).

Large colonization corridors were defined by areas of higher densities of absence/not surveyed AHR patches in the proximity of AHR patches with newt presence (Fig. 2). Area for colonization corridors significantly different when comparing both (SI and SII) barrier scenarios (ANOVA F= 6.198, df=1, p=0.02) (Fig. 2; Fig. S3).

Connectivity index and the importance of AHR patches

The highest cumulative dIIC values resulted from dispersal corridors where: (1) there were higher numbers of AHR patches, (2) distances between patches were shorter and (3) when minor roads were permeable (Fig. 3; Table 3).

For both 400 and 1000m scale analyses, clusters C, F and H presented the highest cumulative connectivity (sum of the dIIC values for each AHR patch in the cluster), suggesting that the relative importance of these three clusters for overall connectivity was maintained between scales (Fig. 3). Isolated clusters D and G showed the lowest values of dIIC at both scales, including cluster I at 1000 m. Link analysis registered a high number of links for clusters C and H for both scales and cluster I for 1000m (Fig. 3; Table 3).

Overall dIIC index mean for SI was 1.81 and 2.08 and SII was 1.65 and 1.95 for 400 and 1000 m, respectively. Within scenarios, mean dIIC was higher at the larger (1000 m) scale for SI. Similarly, there was an increase in the sum of dIIC values when minor roads were permeable (SII) (Table 3). The highest sum of dIIC was 141 for SII at 1000 m, improving overall network connectivity by 70% when compared to SI at 400m (Table 3).

Discussion

By integrating recent survey information on *T. cristatus* pond occupancy at the landscape scale and knowledge of seasonal movement patterns we identified potential terrestrial dispersal corridors between suitable habitat patches under two scenarios of varying landscape permeability. We also evaluated annual home-range patches (AHR) and a connectivity index to identify and prioritise areas for improving permeability.

Through the use of AHR patches as units for least-cost modelling, both terrestrial and aquatic habitats were combined in the analysis to identify permeable land around the breeding ponds, which could facilitate seasonal movements. The size of core areas varied between barrier scenarios. As expected, HQH patch areas were larger when minor roads were permeable for movement (SI). The connectivity index (dIIC) proved a useful tool for discriminating between dispersal corridors with respect to their potential for maintaining landscape connectivity, which could be used for mitigation planning at the scale of an individual AHR patch.

AHR patches

Terrestrial habitats adjacent to wetland areas are critical for pond-breeding amphibian life cycles (Semlitsch, 1998). The analysis of AHR patches for *T. cristatus* indicated the presence of around 80 terrestrial patches containing both breeding ponds and terrestrial habitat with high landscape permeability at the study site. Patch size varied across the study area landscape, with bigger patches located within woodland areas and near (within 400m) of areas with higher numbers of ponds. The bBuffer size of AHR’s can vary depending on the quality of the habitat within which the breeding pond is located (Semlitsch, 1998; Crawford and Semlitsch, 2007), making terrestrial habitat availability and quality significant components of landscape permeability for amphibians (Crawford and Semlitsch, 2007).

We also identified distinct clusters of AHRs where there was high potential habitat suitability. A similar approach has enabled the identification of areas containing multiple breeding sites that sustain metapopulations (Ray et al., 2002; Joly et al., 2003; Safner et al., 2010), hence facilitating identification of priority areas for protection. Even when present in relative isolation, AHR patches can be considered as conservation priorities given that they serve as “stepping stones” between suitable habitat patches throughout the wider landscape (Decout et al., 2012).

Road barrier scenarios

Within the UK, the identification of high-quality habitat to support *T. cristatus* in the UK has been limited to local assessments of ponds, with little attention paid to terrestrial linkscorridors between ponds (Wilkinson and Arnell, 2012; Arnell and Wilkinson, 2013). Pond density is typically used as a basic measure of connectivity at the landscape scale, without taking into account seasonal migration over land by *T. cristatus* (Arnell and Wilkinson, 2013). However, emigration of pond-breeding amphibians from ponds is frequently in the direction of high-quality terrestrial patches including woodland and scrubland (Denöel and Lehmann, 2006). Nevertheless, the importance of nearby ponds for *T. cristatus* is consistent with maintaining sufficient connectivity with other breeding ponds already connected by terrestrial habitat (Harper et al., 2008). Model simulations indicated the most important areas for the species when migrating to and from hibernation sites or when dispersing to high-quality habitat areas. We calculated the landscape-based structural and functional connectivity by incorporating both landscape metrics and species-specific behaviour (Kindlmann and Burel, 2008; Decout et al., 2012).

Testing two scenarios with roads acting as complete barriers to *T. cristatus* movement or having some permeability revealed the importance of roads and their permeability for landscape connectivity for this species. Core areas were substantially larger when minor roads were permeable, suggesting the potential for greater dispersal distances if high quality terrestrial corridors are maintained or created via mitigation at the landscape scale.

The probability of regional population persistence is enhanced by opportunities for recolonization of vacant patches by individuals (Harper et al., 2008). In heterogeneous environments the dispersal probability is highly dependent on the position and distance between AHR's, where populations that are closer will receive more individuals annually than populations that are further away (Zetterberg et al., 2010; Baguette et al., 2012). Consequently, the identification of multiple dispersal corridors and potential new colonization sites could facilitate efficient and effective planning for road mitigation and *T. cristatus* conservation.

Newt populations isolated from the surrounding habitat patches can represent significant challenges for regional planning and conservation. However, occupied isolated patches may benefit from improvement of connectivity between ponds or even the addition of new ponds to existing patches (the "rescue effect", Karlsson et al., 2007). At the landscape scale, a high density of ponds combined with sufficient, suitable terrestrial habitat for dispersal will offer the best conditions for the persistence of pond-breeding amphibian populations (Denöel & Lehmann, 2006).

Among the road permeability scenarios SI (low road permeability) simulations predicted that 50% of AHR patches were connected to HQH areas while, and 90% were connected for the SII scenario (higher road permeability). We specifically tested the impact of minor roads on landscape connectivity for *T. cristatus* intra-population movements. In these traffic-calmed areas, home-range patch permeability was increased, which should be beneficial for *T. cristatus* populations. However, of all road types, minor roads often impose the highest rates of mortality for amphibians and can significantly impact local population dynamics and viability (Sillero, 2008; Matos et al., 2012). While our approach can inform decisions about landscape management to improve permeability, mitigation planning should also include consideration of road mortality and identify more sustainable solutions such as tunnel and fence systems (Matos et al. 2017; 2018; Jarvis et al. 2019).

Resistance within the landscape matrix is one main factors affecting movement behaviour of this species (Kindlmann and Burel, 2008). Our results highlight the potential for mitigation efforts to be planned to create new corridors between habitat patches and increase connectivity at the landscape scale. From a planning perspective, creating high-quality habitat in areas where newts are present can secure and maintain local populations (Baguette et al., 2012). However, new habitat in colonization corridors where the species is not detected or is absent will likely benefit the long-distance dispersal of individuals into unoccupied areas by providing stepping-stone habitats (Baguette et al., 2012).

Patch prioritization as a tool for conservation

The dIIC index identified important patches by measuring the topology (number of links) within the network as a structural attribute and taking habitat suitability into account as a functional attribute (Pascual-Hortal and Saura, 2006; Pereira et al., 2011). This allowed the identification of priority terrestrial corridors for long-term dispersal.

We identified differences in spatial ranking for AHR patches at two scales under two barrier scenarios. This approached showed which dispersal corridors would maintain the most valuable patches for inter-population movements within the network at two dispersal scales (400 and 1000 m). High quality AHR patches located near each other in areas with low degree of fragmentation are ranked higher within the terrestrial corridors.

AHR patches importance changed with both scale and barrier scenarios showing the high variability of management options when considering a regional-scale pond network. SII with dispersal at 1000m is the considered optimal design for *T. cristatus* at regional scale – where corridors are prioritized when minor roads are more highly permeable. These results showed that by changing dispersal distances and adding permeable roads would improve the overall (connectivity of the network for *T. cristatus* would improve. However, the network connectivity and gene flow between sub-populations is dependent on the stability of local conditions for dispersal to take place (Schön et al., 2011). Permeability at the regional scale is dependent on the local home-range habitat conditions and the possibility of individuals' choice to search for new areas and initiate the dispersal process (Doerr and Doerr, 2005). Information on local patches that would benefit from implementing minor road mitigation was valuable for predictions of this species' movement over the long-term.

However, ecological uncertainties at the population level and local environment are inherent to the modelling process and need to be considered: (1) stochastic effects and temporal scales were not included in our models, (2) changes in land use after our data were collected may modify the overall network and hence the conclusions regarding the relative importance of habitat patches; and (3) terrestrial corridors and the connectivity index were specifically calculated for the patch network at our study site. If new ponds are added or removed the pond network will change with consequent change to the relative importance of patches and corridors. Due to these uncertainties it is not appropriate to conclude that that the worst connected or least important habitat patches at the study site could or should be lost. All patches likely incorporate some benefits for *T. cristatus* at the landscape scale.

Graph-theory analysis was a useful tool for understanding the effects of roads for management of *T. cristatus* dispersal corridors. It enables the analysis of best and most important locations where potential movements can be restored and maintained. At the same time it incorporates both structural and functional connectivity into a network structure approach by using information on life cycle traits and real landscape features. This is translated into an optimal spatial representation of a complex model that can be metapopulation dynamics at regional-level in heterogeneous landscapes (Fortuna et al., 2006).

Habitat management and conclusions

The integrative approach used here showed how corridor assessment techniques areis helpful to the evaluation of structural and functional connectivity analysis at the landscape scale when joined together with species presence records, behaviour and ecology. We were able to produce spatial representations which indicated the potential terrestrial corridors where long-term dispersal and consequently long-term connectivity would be beneficial.

Despite the coarse resolution of input data (presence/absence and not-surveyed pond locations) we derived projection scenarios for the visualization of connected and isolated habitat patches for *T. cristatus*. Results clearly indicated a variety of corridors that can be regarded as planning and design priorities for road mitigation efforts. Especially directed to local patches where ecological conservation projects are needed and are carefully considered.

This study has highlighted the importance of including information on spatial and temporal patterns and scales of connectivity in newt movements for planning and designing road mitigation at the landscape scale. The aim of these projects must be to maintain conservation status by maintaining metapopulation dynamics. This may be achieved by maintaining/improving landscape connectivity to facilitate dispersal and migration. It is not feasible for all road projects to measure population dynamics as long-term measurement of population flux at landscapes scales (including before-after comparisons), such as newt tracking, mark-recapture or detailed, genetic studies are time and cost prohibitive, and hence potential connectivity analysis may offer a proxy prior to mitigation implementation.

Connectivity analysis can be used to define the aim of a road project and to set a value standard against which scale effectiveness can be assessed (Schmidt and Zumbach, 2008; Lesbarères and Fahrig, 2012; Hamer et al., 2015). Our results do not confirm that mitigation effectiveness is maintained over the long-term only by calculating potential connectivity at a regional or scale level. However, we demonstrated how potential connectivity can be calculated to prioritize areas where roads may have an important impact on population dynamics and identify major newt terrestrial corridors.

Potential connectivity of a landscape is therefore a tool hence to assess structural connectivity in combination with data on a species' presence and movement patterns in relation to landscape structures (Ernst, 2014). In this way, spatial and temporal connectivity patterns are estimated to help define the most appropriate scale to maintain connectivity for a certain region or population. Within these spatial scales, road mitigation planning has to account for the possible variability in movement and climatic factors that influence newt responses (Matos, 2018).

Finally, we suggest the incorporation of this protocol as a preliminary assessment of the conservation status and connectivity degree at regional-level for the species (Neel et al., 2014). Once population abundances and movement patterns are not accessible to complement further analysis, the quantitative aspect of this method ensures a well-established aim and measurable standard when data are limited.

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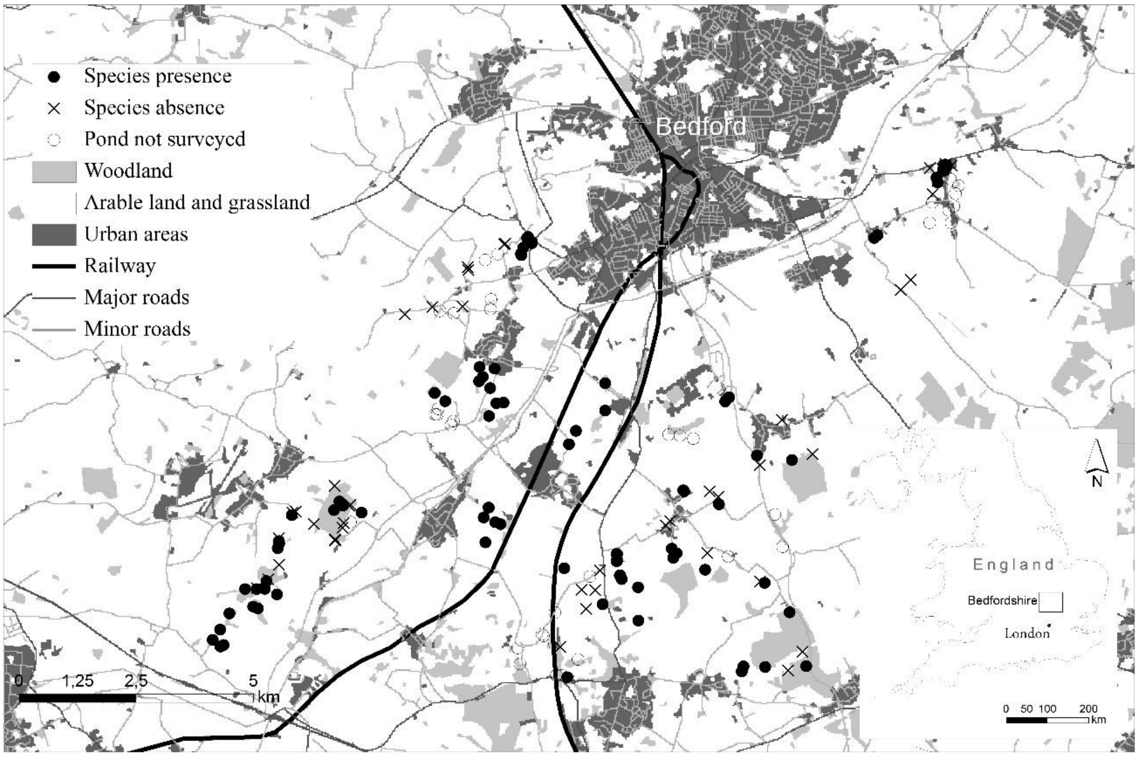

Fig. 1 – Map of the study area showing the main land-use features, linear infrastructure and location of surveyed and unsurveyed ponds with and without *T. cristatus* detected.

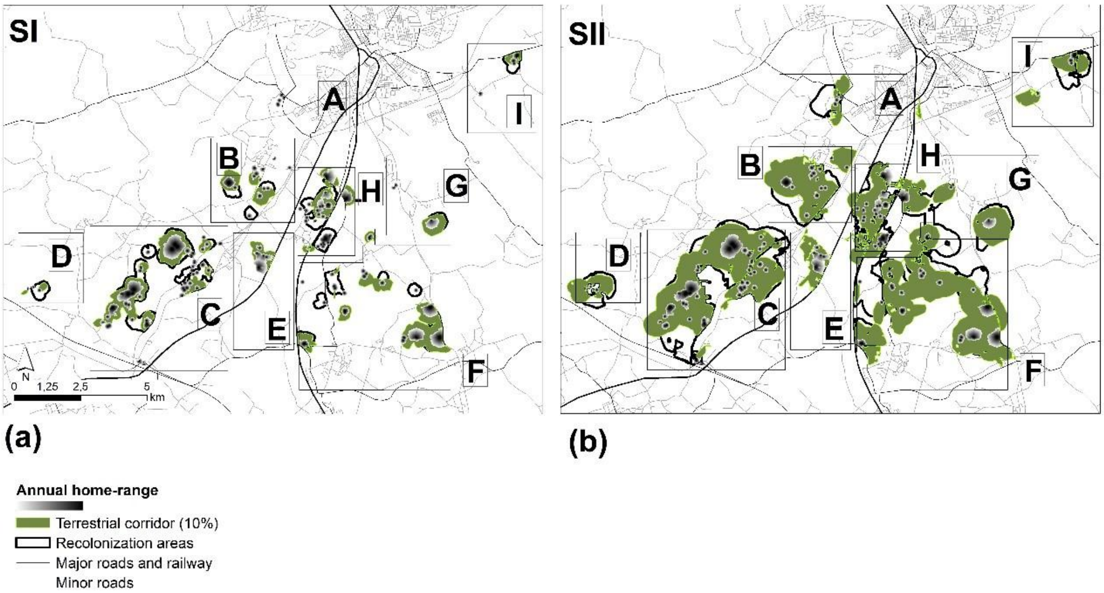

Fig. 2 - Terrestrial dispersal corridors (10th percentile of the least-cost path modelling) calculated from (a) SI (all linear infrastructures as barriers) and (b) SII (minor roads permeable for movement) for *T. cristatus*. Potential colonization corridors between AHR patches (presence) and AHR patches (absence/not surveyed) are represented by the black line areas.

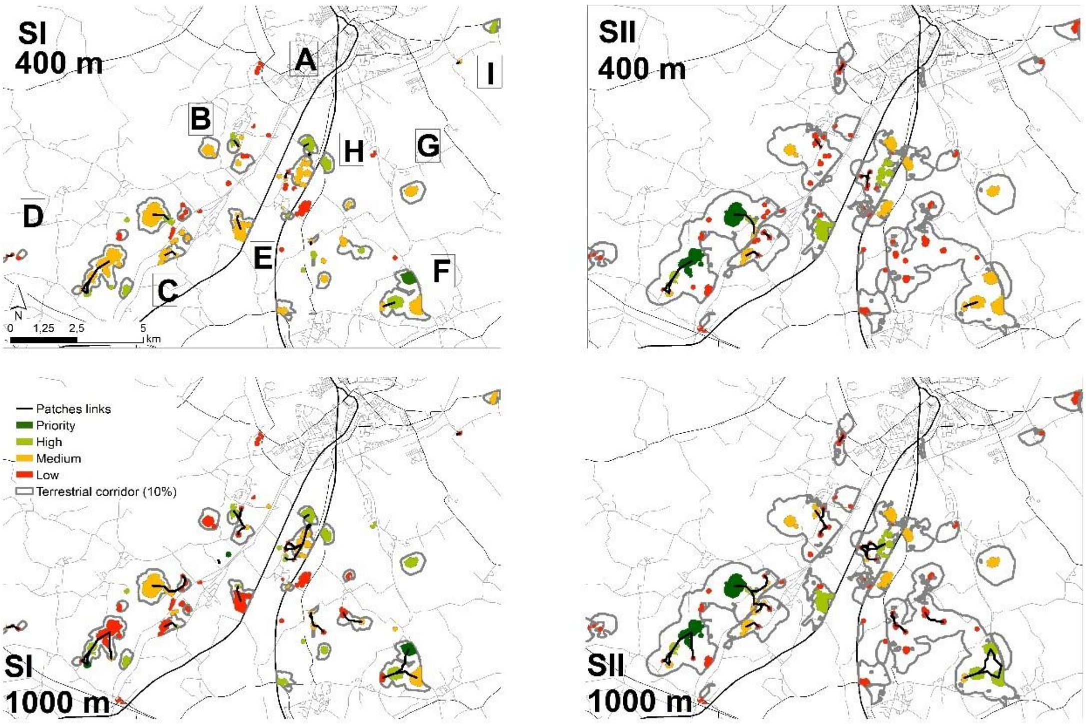

Fig. 3 – Graph connectivity analysis results from SI and SII with ranked dIIC at 400m and 1000 m dispersal distance thresholds. Terrestrial dispersal corridors are represented with light grey areas for both scenarios.

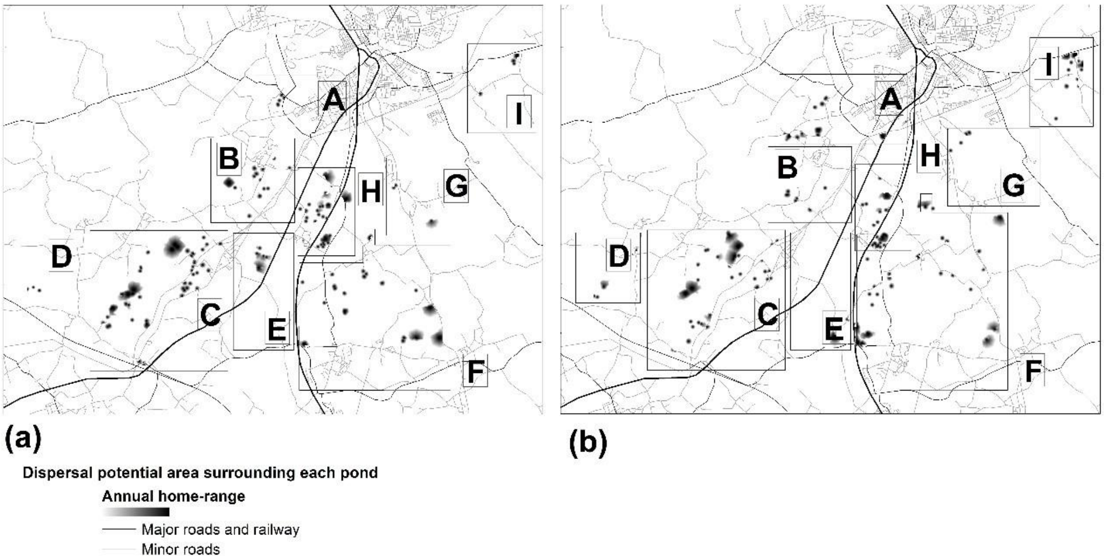

Fig. S1 - Location of annual home-range (AHR) patches for *T. cristatus* records with (a) presence and (b) absence and ponds not surveyed in the study area. Main artificial linear infrastructures are also represented.

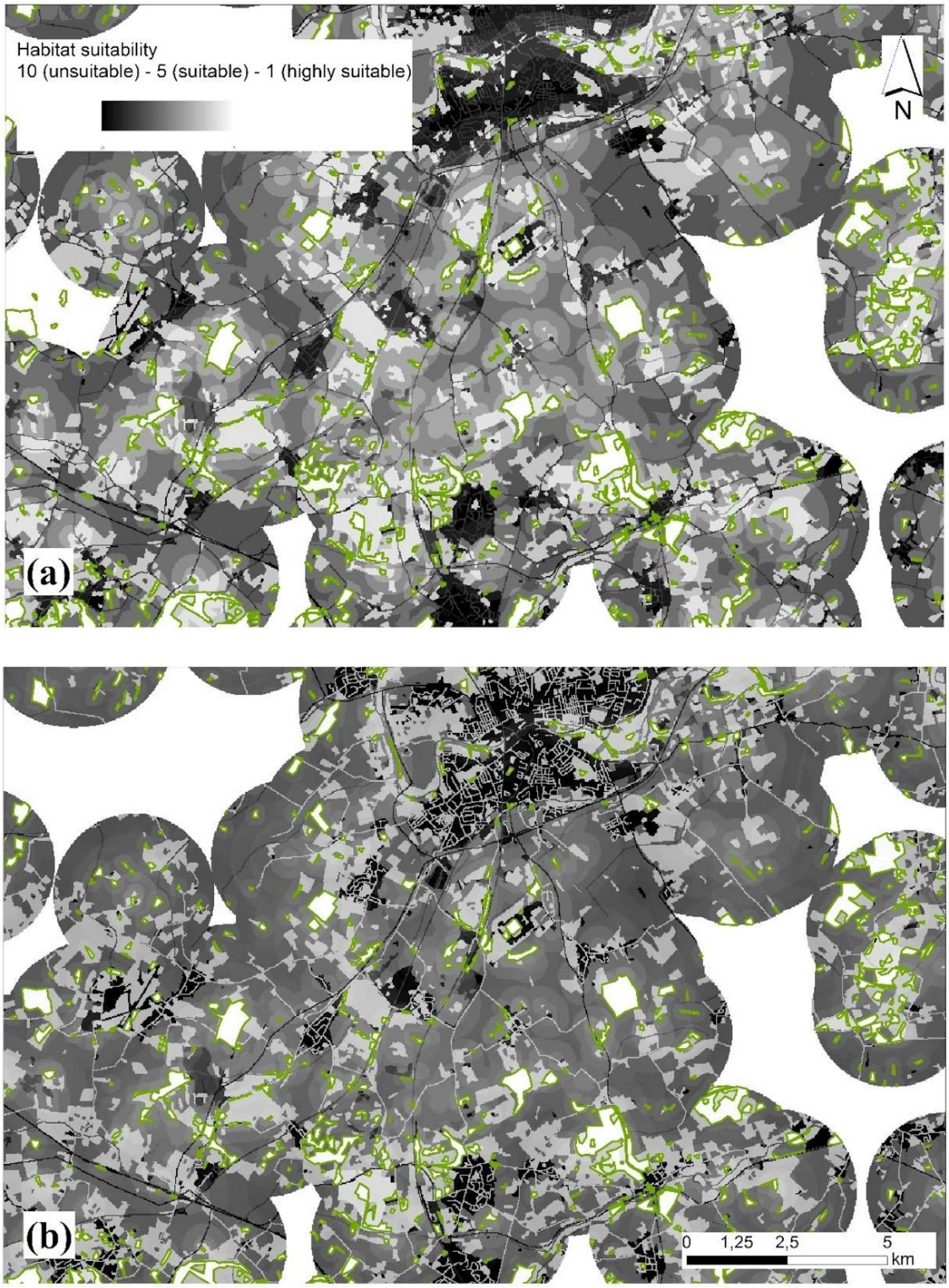

Fig. S2 - Species distribution models (SDM) results for (a) SI (all linear infrastructures as barriers) and (b) SII (minor roads permeable for movement) cost surfaces for *T. cristatus*. Location of high-quality habitat (HQH) patches in green. Habitat suitability ranges between 10 (unsuitable areas for movement) and 1 (highly suitable areas for movement).

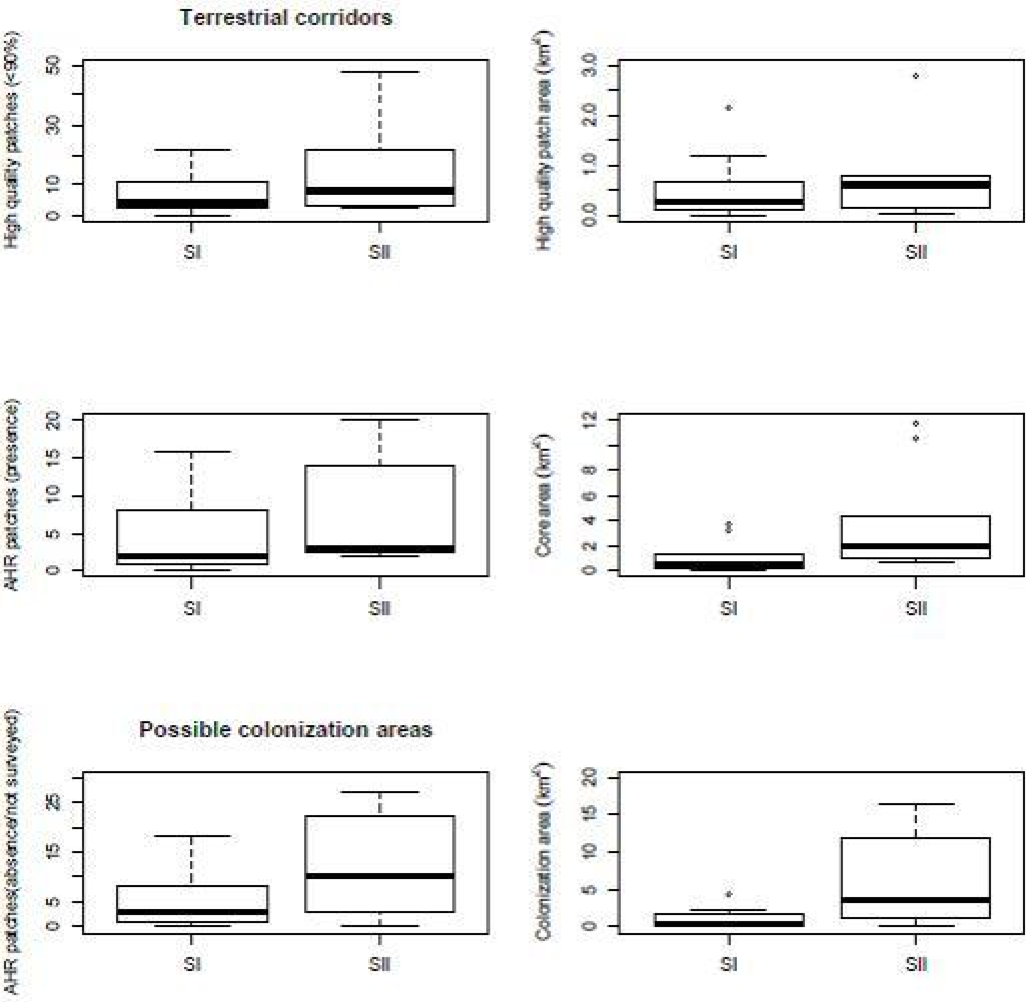

Fig. S3 - Differences between the two barrier scenarios (SI and SII) for corridor clusters (n=9). We compared the results of SI and SII for: HQH areas and AHR patch numbers; HQH area and core area extent (km^2); number of AHR patches and colonization corridor extent (km^2); and connectivity index (dIIC) comparison for two dispersal (400m and 1000m) scales.

Table 1 - Description and respective code, format, unit and source of variables used to develop the habitat suitability with correspondent cost values for the AHR (annual home-range) patch analysis (cost-surface models).

Variable	Unit	Source	Resistance cost value
Linear Instrastrutures (including railways)*			
Motorway	Presence/absence and distance from	Department for Transport (2012)	4000
Primary	Presence/absence and distance from		4000
A road	Presence/absence and distance from		4000
B road	Presence/absence and distance from		4000
Railway	Presence/absence and distance from		20
Land cover			
Major river	Presence/absence and distance from	Ordnance Survey. (2012). Meridian™ 2 v1.2 Release 2	10
Minor river	Presence/absence and distance from		4
Canal	Presence/absence		10
Unclassified	Presence/absence		4000
Broadleaved, mixed and yew woodland	Presence/absence and distance from		1
Coniferous woodland	Presence/absence		1
Arable and horticulture	Presence/absence		4
Improved grassland	Presence/absence		3
Rough grassland	Presence/absence		3
Neutral grassland	Presence/absence		3
Calcareous grassland	Presence/absence		3
Acid grassland	Presence/absence		3
Heather grassland	Presence/absence		3
Inland rock	Presence/absence		5
Freshwater	Presence/absence		1
Urban	Presence/absence and distance from		4000
Suburban	Presence/absence and distance from		4000
Ponds	Presence/absence and distance from	Bedfordshire and Luton BRMC	1

***Great Britain road numbering scheme.** Motorway, primary and A road: major roads, separate carriageways for the two directions of traffic, separated from each other, either by a dividing strip not intended for traffic, or exceptionally by other means; B roads: minor roads, dual carriageways to single track roads with passing places.Table 2 –Landscape metrics for AHR patches with GCN presence obtained from the least-cost modelling. For clusters in SI and SII, number of high-quality patches and respective area (km*2*), results for each core area between high-quality patches area and AHR.

SI - All roads and railway as barriers								
Cluster	**High-quality patches (>90%)**				**Core area (Cluster)**			
	Patches	**%**	**HQ_{area} (km^2)**	**%**	**AHR (GCN presence)**	**Corridors**	**C_{area} (km^2)**	**%**
A	0	0	0	0	0	0	0	0
B	6	8.7	0.59	11.41	5	3	1.05	9.7
C	22	31.88	1.2	23.21	16	7	3.73	34.44
D	2	2.9	0.15	2.9	2	2	0.1	0.92
E	4	5.8	0.11	2.13	2	1	0.59	5.45
F	21	30.43	2.14	41.39	11	6	3.22	29.73
G	1	1.45	0.68	13.15	1	1	0.55	5.08
H	11	15.94	0.26	5.03	8	4	1.39	12.83
I	2	2.9	0.04	0.77	1	1	0.2	1.85
Total	69	100	5.17	100	46	25	10.83	100
SII - Permeable minor roads								
A	3	1.99	0.04	0.34	3	1	0.69	1.87
B	12	7.95	0.66	5.63	9	2	4.4	11.91
C	48	31.79	6.5	55.46	20	3	10.59	28.67
D	3	1.99	0.06	0.51	3	1	1.07	2.9
E	8	5.3	0.16	1.37	2	1	1.04	2.82
F	48	31.79	2.78	23.72	16	3	11.77	31.86
G	2	1.32	0.79	6.74	2	1	2.06	5.58
H	22	14.57	0.6	5.12	14	5	4.21	11.4
I	5	3.31	0.13	1.11	3	2	1.11	3
Total	151	100	11.72	100	72	19	36.94	100

Table 3 – Connectivity index results for patches in SI and SII corridors at two scales (400m and 1000 m) - number of patches, links, priority patches, sum and mean of dIIC index for each cluster.

	Connectivity index - SI corridors									
	dIIC (400 m)					dIIC (1000 m)				
	Patches	Links	Priority	Sum	Mean	Nodes	Links	Priority	Sum	Mean
A	0	0	0	0	0	0	0	0	0	0
B	5	1	0	7.31	1.46	5	4	1	9.91	1.98
C	16	6	0	28.23	1.76	16	9	1	32.11	2
D	2	1	0	1.17	0.58	2	2	0	1.85	0.92
E	2	1	0	1.17	1.23	2	1	0	5.27	2.63
F	11	1	1	26.22	2.38	11	4	1	20.76	2.65
G	1	0	0	1.91	1.91	1	0	0	3.58	3.58
H	8	5	0	14.88	1.86	8	10	0	20.76	2.59
I	1	0	0	2.54	2.54	1	0	0	1.79	1.79
Total	46	15	1	83.43	13.72	46	30	3	96.03	18.14
	Connectivity index - SII corridors									
A	3	1	0	0.5	0.16	3	1	0	0.42	0.14
B	9	1	0	3.33	0.37	9	4	0	4.86	0.54
C	20	8	2	73.5	3.67	20	13	2	79	3.95
D	3	0	0	0.07	0.02	3	0	0	0.06	0.02
E	2	0	0	9.01	4.5	2	0	0	4.18	2.09
F	16	1	0	15.05	0.94	16	8	0	33.28	2.08
G	2	0	0	1.56	0.78	2	0	0	1.26	0.63
H	14	3	0	15.34	1.09	14	8	0	17.22	1.23
I	3	0	0	0.62	0.21	3	0	0	0.72	0.24
Total	72	14	2	118.98	11.74	72	34	2	141	10.92

Table S1 - Habitat-suitability scores attributed to land cover included into building the habitat-suitability model. In scoring land cover, costs values were ranked by 1-3: strongly preferred (1 being best); 4-5: usable but suboptimal habitat; 6-7: not breeding habitat, but perhaps occasionally used; 8-10: strongly avoided (with 10 being worst) (Jenness et al., 2007).

Land cover	**Value**	**Cost**	**Suitability**
Unclassified	0	10	0
Broadleaved, mixed and yew wodland	1	1	9
Coniferous woodland	2	2	8
Arable and horticulture	3	6	4
Improved grassland	4	3	7
Rough grassland	5	3	
Neutral grassland	6	3	7
Calcareous grassland	7	4	6
Acid grasssland	8	4	6
Heather grassland	11	4	6
Inland rock	14	8	2
Freshwater	16	3	7
Urban	22	10	0
Suburban	23	10	0
Railway	24	8	2
Motorway	25	10	0
Primary road	26	10	0
A road	27	10	0
B road	28	10	0
Minor road	29	8	2
Canal	30	7	3
Main river	31	7	3
Minor river	32	7	3

Table S2 - Habitat-suitability scores attributed to distances from woodland, ponds and urban areas introduced to build the habitat-suitability model. All variables comprise distances from 0 to 2000 meters. Scoring distances from 0-200; 200-500; 500-1000 and 1500-2000: 1-3: strongly preferred (1 being best); 4-5: usable but suboptimal habitat; 6-7: not breeding habitat, but perhaps occasionally used; 8-10: strongly avoided (with 10 being worst) (Jenness et al., 2007).

	Lower	**Upper**	**Use value**
Distance from forests (meters)	0	200	3
	200	500	3
	500	1000	4
	1000	1500	4
	1500	2000	6
Distance from lakes (meters)	0	200	1
	200	500	2
	500	1000	4
	1000	1500	6
	1500	2000	8
Distance from urban areas (meters)	0	200	10
	200	500	9
	500	1000	7
	1000	1500	5
	1500	2000	3

Table S3 – Results for the patches connectivity index analysis. dIIC value rank calculated for both scenarios (SI and SII) at two thresholds for species dispersal (400 and 1000 m).

		dIIC intervals	
Scenario	**Category**	**400 m**	**1000m**
SI	Priority	6.9 - 4.3	10.93 - 5.3
	High	4.31 - 2.0	5.31 - 2.9
	Medium	2.01 - 1.0	2.91 - 1.3
	Low	1.01 - 0.18	1.31 - 0.13
SII	Priority	25.06 - 9.9	21.56 - 10.7
	High	9.91 - 4.7	10.71 - 4.3
	Medium	4.71 - 0.9	4.3 - 1.0
	Low	0.91 - 0.001	1.01 - 0.001