RESEARCH ARTICLE

A mechanistic approach to weighting edge-effects in landscape connectivity assessments

M. Dennis · J. J. Huck · C. D. Holt · E. McHenry

Abstract

Context Understanding landscape functional connectivity is critical for nature conservation in fragmented landscapes. Spatially explicit graph-theoretical approaches to assessing landscape connectivity have provided a promising framework for capturing functional components driving connectivity at the landscape scale. However, existing weighting schemes used to parameterise functional connectivity in graph theory-based methods are limited with respect to their ability to capture patch-level characteristics relevant to habitat use such as edge-effects.

Objectives We set out to develop a new approach to weighting habitat connectivity as a function of edge-effects exerted by non-habitat patches through better delineation of edge-interior habitat transitions at the patch-level and parameterization of intra-patch movement cost at the landscape scale.

Methods We leverage the use of raster surfaces and area-weighted exponential kernels to operationalize a mechanistic approach to computing spatially explicit edge surfaces. We integrate map algebra, graph theory and landscape resistance methods to capture connectivity for a range of species specialisms on the edge-interior spectrum. We implement our method through a set of functions in the R statistical environment.

Result Through a real-world case study, we demonstrate that our approach, drawing on these behaviours, outperforms competing metrics when evaluating potential functional connectivity in a typically fragmented agricultural landscape. We highlight options for the optimal parameterization of graph-theoretical models.

Conclusion Our method offers increased flexibility, being tuneable for interior-edge habitat transitions. This therefore represents a key opportunity that can help to re-align the fields of landscape ecology and conservation biology by reconciling patch-versus-landscape methodological stances.

M. Dennis (✉) · J. J. Huck
Department of Geography, MCGIS, University of Manchester, Room G37 Arthur Lewis Building, Oxford Road, Manchester M13 9PL, UK
e-mail: matthew.dennis@manchester.ac.uk

C. D. Holt
Department of Science, Natural Resources & Outdoor Studies, University of Cumbria, Rydal Rd, Ambleside, UK

E. McHenry
Woodland Trust, Grantham, Lincolnshire, UK

Introduction

Landscape connectivity is a crucial process contributing to the conservation of biodiversity in fragmented landscapes (Grander et al. 2020). Significant gains have been made in the efficacy of connectivity analysis following the seminal work by Hanski (1994), which outlined the potential for spatially explicit modelling approaches based on the 'incidence function'. Since then, the importance of patch size and isolation has continued to influence expectations around the likelihood that a particular species population can persist in any given landscape (Ovaskainen and Hanski 2001; Chandler et al. 2015; Bonte and Bafort 2019). Within this framework, the size of available habitat patches and the degree to which they are functionally connected are considered key determinants of meta-population capacity (Hanski et al. 2017). Since Hanski's (1994) presentation of the incidence function, much work has been done to improve the ways in which functional connections between habitat patches are operationalized (Saura and Pascual-Hortal 2007; McRae et al. 2008; Foltête et al. 2008; Saerens et al. 2009; Etherington 2016). This has largely focused on estimating functional distances between patches such as through least cost paths, random walks and topographic-based measurements. Less attention, however, has been given to describing the influence of habitat patches themselves and patch-level processes that affect connectivity. Hanski and Ovaskainen's (2000) description of metapopulation capacity in fragmented landscapes was predicated on habitat patch size as a surrogate for quality, drawing on the well-established observation that extinction rates correlate inversely with habitat area (Goodman 1987; Lande 1993). This paved the way for subsequent area-weighted graph theoretical approaches that exhibit some appealing characteristics, including intuitive outputs such as probabilities or total connected area, and improved computational efficiency (Galpern et al. 2011).

Notwithstanding their appealing attributes, limitations relating to patch-level processes such as assumptions around habitat suitability, homogeneity and the relevance of patch size remain unaddressed in area-weighted methods. One process that can influence habitat availability at the patch-level is that of edge effects incurred by neighbouring non-habitat patches. Edge effects moderate the effective patch size

for both interior and edge specialist species (Zurita et al. 2012), thereby influencing metapopulation capacity. As such, they should be reflected in area-weighted functional connectivity methods. There is clear merit, therefore, in understanding how edge effects occur as a process in the landscape and how this process influences landscape connectivity. Specifically, careful delineation of edge from interior habitat is directly relevant to area-weighted metrics given that patch area is a key component of the numerator in the calculation of landscape connectivity in the Hanski lineage, such as in the Probability of Connectivity (PC; Saura and Pascual-Hortal 2007; Eq. 1):

$$PC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}A_iA_jP_{ij}^*}{A_L^2} \qquad (1)$$

where A_i and A_j are the areas of habitat patches i and j, and A_L is the total landscape (i.e. study extent) area and dispersal probability between patches i and j is defined as the maximum probability of movement (where P_{ij}^* is the maximum product probability of all the possible paths between patches i and j) based on shortest paths in a patch-based graph (Keeley et al. 2021).

In the PC metric (Eq. 1), patch area is used as an indicator for habitat availability and quality, in the absence of any other attributes. This, however, assumes patch homogeneity, which is only ecologically meaningful for generalist species and, given that such species tend to be of least conservation concern (Miller et al. 2015), the need to capture patch-based processes to better account for a range of species is an obvious priority for conservation modelling. This assumption is not only relevant to graph-based metrics but applies equally to any method where habitat patch size is thought to influence landscape connectivity. This applies to both structural (Keeley et al. 2021) and functional (e.g. Carvalho et al. 2016) connectivity, and links to other key debates in ecology. For example, the ongoing SLOSS (Single Large Or Several Small) debate centres around the relevant importance of patch-scale (e.g., size, quality, extinction rates) and landscape-scale (e.g., dispersal, predation, permeability) processes (Fletcher et al. 2018; Fahrig et al. 2019). An additional advantage of developing a mechanistic understanding of edge effects in

connectivity assessments is the ability to model for a range species as a function of their position on the spectrum of edge-interior specialisms, for example in a traits-based approach to connectivity (Ramos et al. 2020).

Previous attempts to consider the role of edge effects have been conceptually limited, taking a binary view of edge versus non-edge (An et al. 2021), treating edge effects simply as a geometric property (e.g., Griffin and Haddad 2021) or considering edge as representing non-habitat (i.e. removing it from the habitat area, which guarantees lower connectivity estimates in area-weighted approaches; e.g., Watts and Handley 2010). A binary delineation of edge versus non-edge and an a priori assumption that edge habitat is always undesirable from a species conservation perspective prevents the modelling of edge-interior transitions specific to different land-use contexts. Such transitions may vary in their severity and length as a function of non-habitat patch hostility and size. Accounting for the variety of such transitions, we argue, would facilitate a more functional approach to delineating edge effects. To this end, Eycott et al. (2011) carried out a Delphi review on the different expected edge effects exerted by 20 different land-uses in the UK on a range of focal species, with high variance between individual land-uses. In their Probability of Functional Connectivity (PFC) metric Watts and Handley (2010) employ these parameters to delineate edge effects. However, by assuming edge effects are constant at all distances given by Eycott et al. (2011) from non-habitat patches, and disregarding non-habitat patch size, the PFC metric does not reflect a mechanistic view of how edge-interior transitions occur in space.

In addition, the assumption that edge comprises non-habitat, prompting its subsequent removal from the PFC numerator (e.g. Watts and Handley 2010), may not always be warranted. In highly fragmented anthropogenic landscapes, a high proportion of the species pool consists of non-interior specialists. As such, many woodland edge-exploiting species are of current conservation value, appearing in local and regional biodiversity action plans in the United Kingdom (e.g., Kirklees Council 2023). Where agricultural landscapes dominate, narrow but vital riparian corridors can provide connectivity between fragmented patches of interior semi-natural habitat as well as vital habitat for edge exploiting species

(Hale et al. 2012). In this context, there is a clear requirement for connectivity metrics that are better fit to the reality of habitat provision in modern landscapes. Though edge effects in fragmented landscapes can undoubtedly have negative outcomes for some species (Dixo and Martin 2008), we argue that edge-exploiting species (especially those of conservation value) are unnecessarily under-considered. Therefore, the effective delineation of edge from interior habitat presents an advantage where functional connectivity can be modelled on the same network of patches but for a range of species, as opposed to only generalists, towards which simple area-weighted approaches exemplified in Eq. 1 may be biased.

We note that attempts to improve on area-weighted approaches through additional assessments of patch quality have been developed, for example through site surveys (Hodgson et al. 2009) or habitat suitability models (HSMs) using secondary environmental data (Jaquiéry et al. 2008). However, field surveys may not be feasible for large-scale studies and while there has been much interest in using HSMs to delineate habitat availability or quality in lieu of existing habitat maps (Jaquiéry et al. 2008; Hunter-Ayad and Hassall 2020; Godet and Clauzel 2021), the efficacy of HSMs for the delineation of habitat patches is limited. This is because any modelled response to non-habitat patches will be highly species-and landscape-specific in well-performing HSMs. This detracts from the generalizability of edge-related processes for the sake of wider habitat management goals (e.g. planning habitat connectivity for a range of woodland specialists in landscape restoration or rewilding scenarios). For these reasons, we believe there is merit in developing a method of interior-edge habitat delineation that can reflect responses by focal species that are generalizable across connectivity scenarios. For example, Watts et al. (2010) developed the use of the Generic Focal Species (GFS) to model outcomes for groups of species with similar habitat requirements under different landscape change scenarios. An advantage of a GFS approach is the ability to determine landscape parameters (e.g. landscape resistance, sensitivity to edge-effects) that can act as indicators to inform connectivity outcomes. GFS indicators parameterized, for example, through expert consultation (Eycott et al. 2011), could be readily incorporated into graph theory connectivity

models providing that methods to effectively delineate edge-effects in a mechanistic way are available.

In this paper we propose such a method that captures the transition gradient between edge-interior environments as a function of neighbouring non-habitat patch land-use and size. This facilitates the option of modelling for a full range of specialisms along the interior-edge spectrum and provides a logical means to parameterize within-patch movement when calculating effective distances. These new developments make use of raster surfaces and area-weighted spatial kernels to estimate edge effects and allow for a re-characterization of the role of edge habitat. Our approach focusses on habitat patches and the size and spatial distribution of neighbouring non-habitat patches which, as well as providing the basis of graph-based modelling, are also relevant to individual-based connectivity approaches (e.g. Landguth et al. 2012). The method is highly transferable and can be incorporated into any existing graph-based approach where outcomes are weighed by habitat patch size and where information on the size of non-habitat patches and estimates of edge effects are available.

Methods

Our methodological approach was to incorporate recent landscape-ecological knowledge into connectivity modelling and, specifically, to provide practical solutions to problems stemming from the biases outlined above. As with the development of other recent functional connectivity indices, we take the basic form of Hanski's Incidence Function (1994) as a motivation and build on more recent derivations of this, such as the Probability of Connectivity (PC: Saura and Pascual-Hortal 2007, Eq. 1).

Edge-weighted habitat for connectivity

We propose a new metric: the Edge-weighted Habitat Index (EHI), in which the numerator varies depending on the focal habitat type: interior *(Int)*, generalist *(Gen)* or Edge *(Edg)*. To build this metric, we first generate an edge surface for each cell in a raster representation of the landscape. This is achieved by summing, for each cell, all edge effects exerted by neighbouring non-habitat patches ($edgeSum_i$: Eq. 2).

Here, for each location (raster cell), a non-habitat patch i will exert an edge effect as a function of its Euclidean distance from the cell. The strength of the edge effect is set according to an exponential kernel determined by non-habitat patch i's *edgeMax* value (the maximum distance at which a non-habitat patch can exert an edge effect) and the size of non-habitat patch i (Eq. 4 and "Justification of area-weighted edge effects" section). Therefore, the influence (the edge effect) decreases exponentially with distance as a function of the type and size of non-habitat patch i. Note that, similar to landscape resistance values for least-cost path analysis, *edgeMax* must be decided a priori through, for example, recourse to the literature or expert consultation (Godet and Clauzel 2021).

$$edgeSum_i = \sum_{i=1}^{n} edge_i \tag{2}$$

where $edge_i$ is the edge effect exerted by neighbouring non-habitat patch i on habitat cell i and is defined as:

$$edge_i = (e^{-\alpha D_i}) \tag{3}$$

where e is the natural exponent, D_i is the distance from the neighbouring non-habitat patch and α is a constant that determines the strength of effect at distance D_i and is defined as:

$$a = \frac{-\log(d)}{edgeMax} \tag{4}$$

where d is a distance decay parameter ranging between 0 and 1 calculated from a sigmoidal function applied to the non-habitat patch area (see "Justification of area-weighted edge effects" section) and *edgeMax* is the maximum possible distance at which a particular non-habitat patch (as a function of its land-use) can exert an edge effect (this value must be determined a priori e.g. through a literature search or, as in the application in "Case study application" section, reference to expert consultation).

The edge-weighted habitat of each cell is then determined as a function of whether interior or edge habitat is to be modelled. If interior, then the edge-weighted habitat value of each cell within the habitat patch is defined as.

$$intC_i = 1 - edgeSum_i, edgeSum_i \in [0, 1] \tag{5}$$

where $intC_i$ has a maximum value of 1 (i.e. $edgeSum_i$ = 0 and the entire cell is interior habitat) and a minimum of 0 (i.e. $edgeSum_i$ = 1 and the entire cell is edge habitat) and where $edgeSum_i$ must be set to a maximum of 1 to avoid negative values in subsequent graph-based calculations. Note that, in practice, a multiplier of range 0–1 can also be applied to $edgeSum_i$ (for example reflecting a species sensitivity to edge or an additional measure of quality). Once the edge-weighted habitat of each cell in a habitat patch is determined, the edge-weighted habitat of the entire habitat patch is then the sum of all cell values within the habitat patch multiplied by the cell area (i.e. the resolution of the raster surface squared). In the case of edge-weighted interior habitat this is given by:

$$EH_{Int} = \left(\sum_{i=1}^{n} intC_i \right) Ac \tag{6}$$

where Ac is the area of a cell in the habitat patch.

In the case of edge-weighted edge habitat, $edgC_i = edgeSum_i$ and:

$$EH_{Edg} = \left(\sum_{i=1}^{n} edgC_i \right) Ac \tag{7}$$

In the case where the entire cell consists of edge-weighted habitat (i.e. when modelling for true generalists) $genC_i = 1$ and:

$$EH_{Gen} = \left(\sum_{i=1}^{n} genC_i \right) Ac \tag{8}$$

Integrating EH into landscape connectivity assessments is then simply a case of replacing habitat area with edge-weighted habitat which, in the case of the PC metric, means replacing A_iA_j with EH_iEH_j (where i and j represent patches of habitat cells). This Edge-weighted Habitat Index (EHI) is then a general form of the PC metric that delineates focal habitat by accounting for edge-effects. Note that PC is then a special case modelling for true generalists (i.e. the entire patch is focal habitat) and PFC is simply EHI with parameter d set to 1. We suggest one more modification to the original PC formula in which the square root of the numerator, which is also described as the Equivalent Connected Area (ECA; Saura et al. 2011), is divided by the total landscape area as opposed to the numerator being divided by the total landscape-squared, such that EHI is given as:

$$EHI = \frac{\sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} EH_iEH_jP_{ij}^*}}{A_L} \tag{9}$$

where EH_i and EH_j are edge-weighted habitat values ($EH_{Int}, EH_{Edg}, EH_{Gen}$) for patches i and j, A_L is the total landscape (i.e. study extent) area and dispersal probability between patches i and j is defined as the maximum probability of movement (where P_{ij}^* is the maximum product probability of all the possible paths between patches i and j) based on shortest paths in a patch-based graph (Keeley et al. 2021). Note that in our application, we model distance between patch centroids to test the influence of setting intra-patch movement as $edgeSum_i$ but distances could also be modelled as edge-to-edge if required (for example by setting resistance values of cells within patches to zero (McRae et al. 2008)).
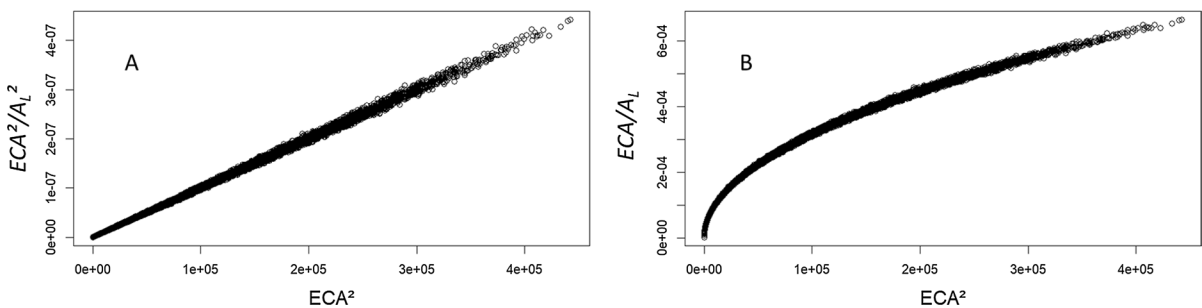

Fig. 1 Relationship between the numerator *(ECA²)* and PC (on the Y axis) when alternatively normalized by **A** *ECA²/A_L²* or by **B** *ECA/A_L*

We propose this change for two reasons. Firstly, the results of executing Eq. 1 (PC) on real data often yield very small numbers that can appear counter-intuitive or even meaningless to practitioners, as reported by Neel (2008) and the authors of the PC metric (Saura et al. 2011). Secondly, the behaviour of the original PC metric (ECA^2/A_L^2) results in the relationship between connectivity (PC) and the numerator (ECA^2) being linearized (Fig. 1a). However, we could not find support in the literature for the supposition that this relationship should be linear. Rather, the relationship reflected in Fig. 1b, where increases in ECA^2 at lower value ranges on the x axis (which therefore reflect a larger percentage increase in ECA^2) results in the greatest increase in connectivity (on the y axis). In other words, the non-linear trend in Fig. 1b reflects the logical assumption that an increase in the numerator should have a bigger impact on the metric at low levels of connectivity relative to the same increase at already high levels of connectivity. Conveniently, the connectivity values on the y-axis in 1(b) can be rendered as a percentage of the landscape area by multiplying by one hundred. In order to illustrate the benefits of our method, we have tested both approaches against real data to compare performance ("Case study application" section). We implemented EHI using the R statistical environment (R Core Team 2022).

Parameterizing edge effects

To operationalize EHI we use a surface of area-weighted edge intensity values in order to capture: (1) Edge effects from adjacent and non-adjacent land cover: considering only immediately adjacent land cover patches (e.g., Watts and Handley 2010), can provide misleading results in situations where the adjacent land-use is small and/or has minimal edge impact but is itself adjoined by a much larger and/or much more deleterious land-use patch. (2) Varying edge effects dependant on neighbouring non-habitat patch area: we argue that assuming non-habitat patches have equal edge impacts regardless of their size is unrealistic. (3) Varying edge effects with distance from non-habitat patches: the assumption of equal edge effect at all distances (red line, Fig. 2), causes problems in previous applications (e.g., Watts and Handley 2010) where all edge is removed from the habitat patch (conflicting with a mechanistic view
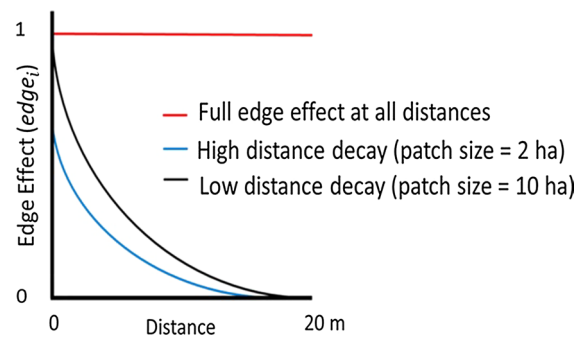
Fig. 2 Distance decay of edge effects from neighbouring non-habitat patches as a function of non-habitat patch size

of edge effects). We address these three issues by applying an area-weighted kernel to operationalize edge effects from neighbouring non-habitat patches, with a distance decay (black and blue lines in Fig. 2).

### Justification of area-weighted edge effects

We propose that edge effects should decay with distance from non-habitat patches, which we operationalize using a negative exponential function in the model (Eq. 3). We acknowledge that edge effects should also be a function of the size of neighbouring non-habitat patches. This, for example, ensures that very small non-habitat patches in the matrix do not have unrealistically large edge impacts. Likewise, we do not assume that edge effects scale to infinity. Our solution is to set the edge-effect distance decay parameter (d in Eq. 4) according to values calculated from a sigmoidal function (Fig. 3) that is related to neighbouring non-habitat patch size. The function ranges from 0 where $x = 0$, and 1 where $x >= $ fullEdgeEffectArea (which is a parameter describing the patch size after which the full edge effect is realized).

Figure 4 visualizes the process of calculating edge-weighted interior habitat for a group of habitat patches (Fig. 4A) through the area-weighted kernel approach where edge effects decrease exponentially with distance at a rate reflecting the size of neighbouring non-habitat patches (parameter d in Eq. 4; Fig. 3). Figure 4B gives values for *edgeMax* in Eq. 4, which is the maximum possible distance at which a non-habitat patch can exert an edge effect. Alpha (a in Eqs. 3 and 4) is then derived for each non-habitat patch from *edgeMax* and d according to Eq. 4. All

Fig. 3 Logistic function for setting edge effect distance decay as a function of patch size with the maximum edge intensity (lowest distance decay: fullEdgeEffectArea) set to 10 Ha
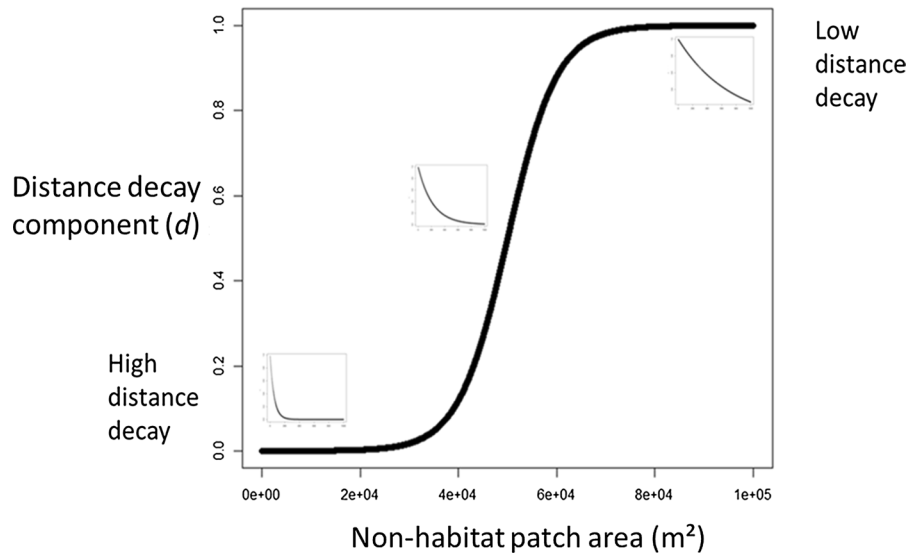
Fig. 4 Worked example of edge-weighted habitat delineation. **A** habitat patches, **B** *edgeMax* for neighbouring non-habitat patches, **C** edge effect surface with patch boundaries shown, **D** interior edge-weighted habitat values with patch boundaries shown
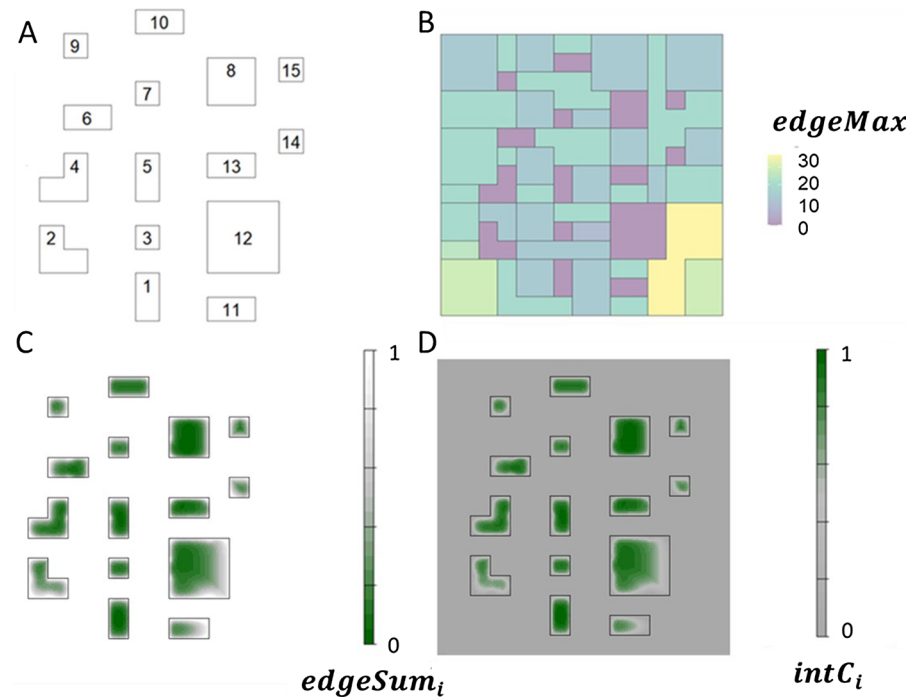
cells in the landscape then receive an edge effect value from each neighbouring non-habitat patch (*edge$_i$* in Eq. 3) as a function of distance from that patch and parameter *a* (which is specific to that patch; Eq. 3). Taking the sum of all received edge values for each cell results in Fig. 4C with edge effect values ranging from 0 (no edge) to 1 (completely edge), representing *edgeSum$_i$* in Eq. 2. In a subsequent step, the edge effect values in Fig. 4C are subtracted from a habitat raster (a rasterized version of Fig. 4A where 1 = habitat and 0 = matrix), resulting in the scenario for interior edge-weighted habitat in Fig. 4D (Eq. 5). Calculating edge-weighted habitat is then a simply a matter of summing all cell values within habitat patches and multiplying this number by the area of the raster cells (Eq. 6; Table 1). R code for reproducing this worked

Table 1 Patch attributes for interior specialist edge-weighted habitat scenario in Fig. 4

Patch	Patch area (m²)	No. of cells (N)	Sum of cells (sN)	Edge-weighted habitat (m² = sN x cell area)
1	3405.90	578	412.40	2430.06
2	5108.85	867	373.39	2200.24
3	1702.95	289	173.24	1020.83
4	5108.85	867	531.90	3134.25
5	3405.90	578	391.97	2309.68
6	3405.90	578	337.75	1990.22
7	1702.95	289	159.33	938.86
8	6811.80	1156	863.18	5086.34
9	1702.95	289	131.54	775.08
10	3405.90	578	367.59	2166.06
11	3405.90	578	223.74	1318.38
12	15326.54	2601	1537.67	9060.78
13	3405.90	578	388.92	2291.73
14	1702.95	289	120.16	708.03
15	1702.95	289	140.50	827.89

example can be found at: https://gitlab.com/anonymous4review/rhi.

Figure 5 gives a real-world example of the process described in Fig. 4A–D. Here the edge surface is created for a patch of woodland in the application study area (details in "Case study application" section). Cell values in Fig. 5B show the maximum distance at which each land-cover can exert an edge effect (*edgeMax*, taken from Eycott et al. 2011). Cell values in Fig. 5C represent the local cumulative edge effect (*edgeSum_i*, Eq. 2). Figure 5D shows the resulting interior edge-weighted habitat value per cell (*intC_i*). The greater effect of the industrial estate to the north of the habitat patch can clearly be seen in comparison with the lesser effect of the agricultural fields to the south (see figure caption for details).

Details of the EHI function

The EHI function (as implemented in R, available in the repository listed above) takes six parameters. The user must provide the patches of habitat and non-habitat (as vector GIS data with *maxEdge* values as an attribute), and can select to tune (1) the focal habitat (interior, edge or generalist), (2) the maximum species dispersal distance, (3) the dispersal rate (reflecting dispersal probability at the distance specified in 2) and (4) the area (size) of a non-habitat patch at which

the parameter d is set to 1. The role of each parameter is described in Table 2.

Case study application

We tested our method in a real landscape to evaluate how the approach performs relative to other metrics. Specifically, we compared connectivity estimates from the Probability of Connectivity (PC; Saura and Pascual-Hortal 2007), Probability of Functional Connectivity (PFC, Watts and Handley 2010) and our Edge-weighted Habitat Index (EHI) for broadleaf woodland patches ($>=$1 ha) and all non-habitat patches ($>=2 \times 2$ 10 m pixels) in an agricultural landscape where the majority of remaining tree cover is within the riparian zone (and hence largely consists of edge habitat). These were delineated from the UK Land Cover Map 2020 (10 m resolution; Morton et al. 2021). Priority species lists for the study area contain representative woodland edge users (e.g., *Mustelidae, Chiroptera, Talpidae, Cricetidae*). We consider this case study to be typical of the large parts of rural UK where riparian corridors not in agricultural or forestry production represent a refuge for native broadleaf woodland (see Fig. 6).

To parameterize this evaluation, we used land-cover resistance and *edgeMax* values for a woodland focal generic species (WFGS) taken from Eycott et al. (2011) for a UK context. These values were obtained
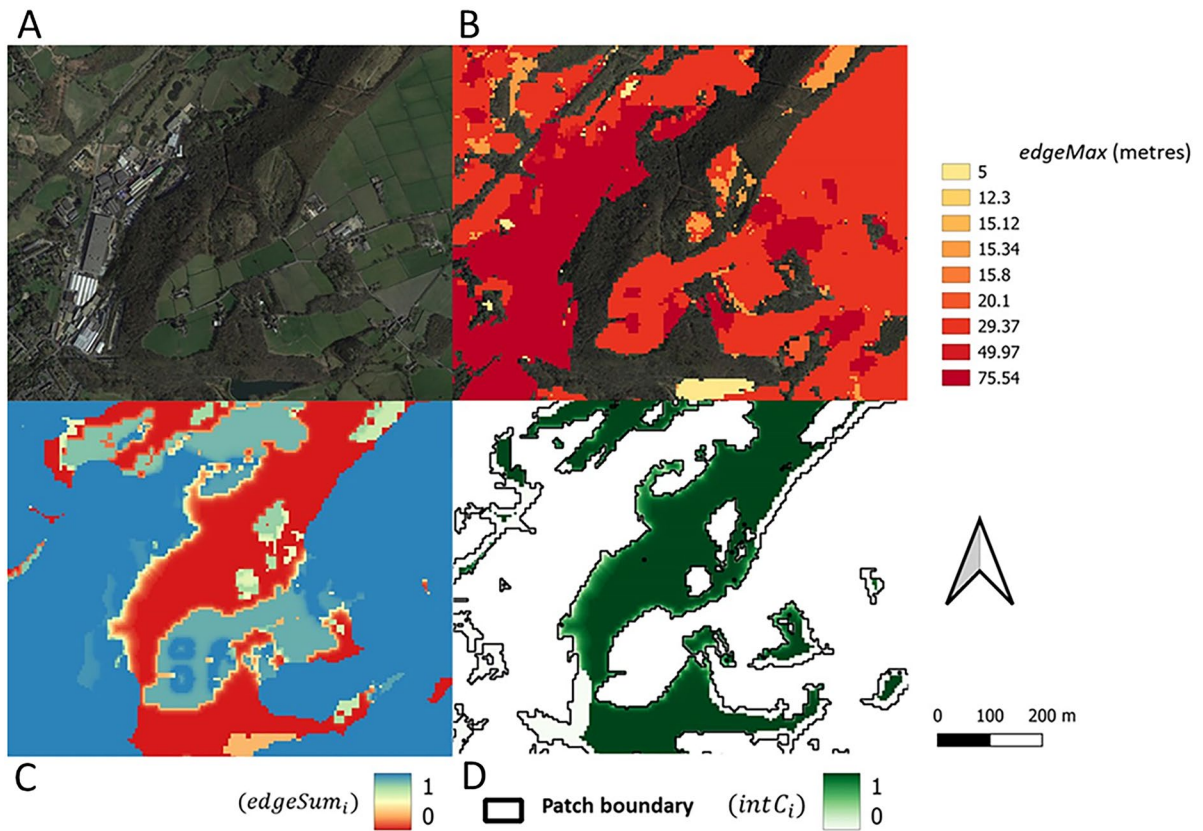
Fig. 5 A satellite image of an area of woodland in the case study area (Google Maps, 2023). **B** *maxEdge* values for non-habitat patches in the UK Land Cover Map (Morton et al. 2021) according to a Delphi review by Eycott et al. (2011). **C** Resulting edge raster surface delineating areas of high (red) and low (blue) edge effects in the same landscape. **D** Edge-weighted (Interior) Habitat ($intC_i$) with patch boundaries shown

via a Delphi review by Eycott et al. (*Ibid*) based on land-covers in the UK Land Cover Map and we apply these values to the same classification in a recent update of the UK Land Cover Map (Morton et al. 2021). Resistance values and *edgeMax* values (as distances in metres) are presented in Supplementary

Materials (Table S1). Functional distances between habitat patches were calculated as the least-cost path based on the Eycott et al. (2011) resistance values using the *gdistance* package in R. We alternatively set intra-patch movement cost to 1, 0 and edge effect ($edgeSum_i$) values for comparison. We assumed that

Table 2 Description of the role and required format of model arguments

Parameter	Description
Patches	Polygons (e.g. shapefile) delimiting habitat patches
Matrix	Polygons of non-habitat patches with cost (if least-cost based effective distances are to be used) and *maxEdge* attributes
Habitat	One of "edge", "interior" or "generalist"
maxDist	The assumed maximum dispersal distance of the focal species
dispersalRate	Value reflecting the probability of dispersal to patches at a distance from the focal patch equal to maxDist
fullEdgeEffectArea	Area (size) at which d is set to 1
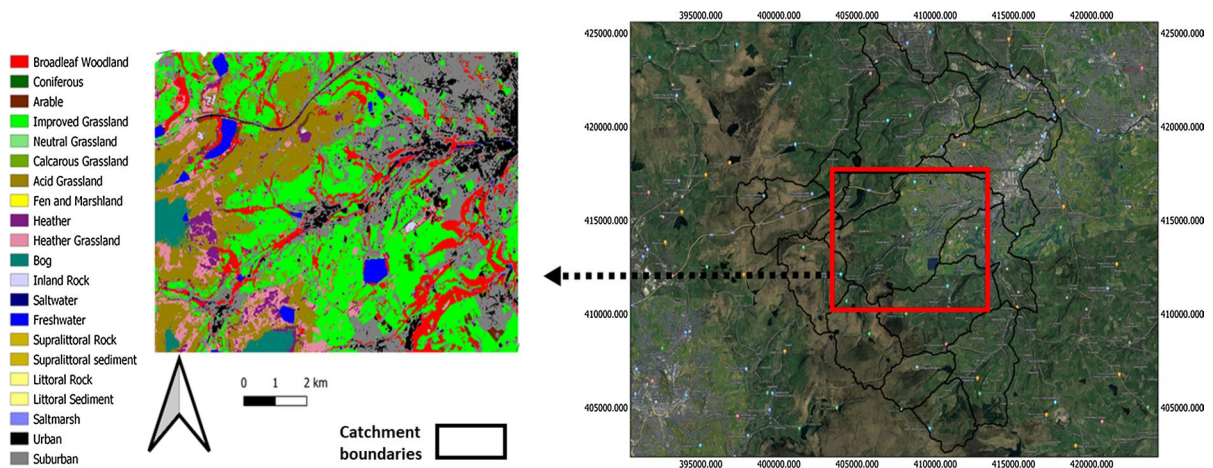
Fig. 6 Application study area. Case-study extent with catchment boundaries (right) (Environment Agency, 2023) and detail on land-covers present (left) (Morton et al. 2021)

the parameters used to define habitat requirements for the WFGS can be used as a baseline to make assumptions about edge-dependent species. In other words, the preferences of an edge-dependent focal generic species should be inversely related to those of the WFGS. Therefore, we define edge habitat as that which is unfavourable for the WFGS and, reciprocally, that which is favourable for an edge specialist.

To model the relationship between landscape connectivity and species density we used all available

Table 3 Description of each of the model runs conducted as part of the evaluation (all models were run with intra-patch cost set alternately to 0, 1 and $edgeSum_i$)

Model name	Connectivity model description
EHI_edge	EHI with focal habitat set to "edge" (EH_{Edg}). d is set manually for all non-habitat patches*
EHI_int	EHI with focal habitat set to "interior" (EH_{Int}). d is set manually for all non-habitat patches*
EHI_edge_Eq	EHI with focal habitat set to "edge" (EH_{Edg}). d is set manually for all non-habitat patches* *maxEdge* is equal for all non-habitat patches calculated as the area-weighted mean of the Eycott et al. (2011) values based on the total area of each land-cover in the study area
EHI_int_Eq	EHI with focal habitat set to "edge" (EH_{Edg}). d set manually for all non-habitat patches* *maxEdge* is equal for all non-habitat patches calculated as the area-weighted mean of the Eycott et al. (2011) values based on the total area of each land-cover in the study area
EHI_Edge_areaWeighted	EHI with focal habitat set to "edge" (EH_{Edg}). d set as a function of non-habitat patch size
EHI_Int_areaWeighted	EHI with focal habitat set to "interior" (EH_{Int}). d set as a function of non-habitat patch size
EHI_Edge_areaWeighted_Eq	EHI with focal habitat set to "edge" (EH_{Edg}). d set as a function of non-habitat patch size. *maxEdge* is equal for all non-habitat patches calculated as the area-weighted mean of the Eycott et al. (2011) values based on the total area of each land-cover in the study area
EHI_Int_areaWeighted_Eq	EHI with focal habitat set to "interior" (EH_{Int}). d set as a function of non-habitat patch size. *maxEdge* is equal for all non-habitat patches calculated as the area-weighted mean of the Eycott et al. (2011) values based on the total area of each land-cover in the study area
PC	Probability of Connectivity metric (Saura and Pascual-Hortal, 2007) Equivalent to EHI set to "generalist" (EH_{Gen})
PFC	Probability of Functional Connectivity (Watts and Handley 2010). Equivalent to EHI set to "interior"; and d set to 1
Percent woodland	No connectivity assessment. Predictor variable = percentage cover by woodland in each catchment
MPA	No connectivity assessment. Predictor variable = mean area of woodland patches in each catchment

*Values of 0.05, 0.25, 0.5, 0.75 and 0.95 were all tested with the value leading to best model performance retained

Table 4 Results of regression models (all models are polynomial second order, which gave the best fit)

Model	R-squared	Sig	Adjusted R-squared
EHI_edge_10km	0.78	0.0001	0.75
EHI_edge_Eq_10km	0.77	0.0002	0.73
EHI_edge_1km	0.68	0.001	0.63
EHI_edge_Eq_1km	0.66	0.002	0.60
EHI_int_10km	0.67	0.001	0.62
EHI_int_Eq_10km	0.68	0.001	0.63
EHI_int_1km	0.63	0.002	0.57
EHI_int_Eq_1km	0.62	0.001	0.56
PC	0.61	0.003	0.55
EHI_int_areaWeighted 10km_100ha	0.54	0.009	0.47
EHI_int_areaWeighted_Eq_10km_100ha	0.61	0.003	0.55
EHI_edge_areaWeighted_10km _100ha	0.85	<0.0001	0.83
EHI_edge_areaWeighted_Eq_10km_100ha	0.88	<0.0001	0.86
EHI_edge_areaWeighted_10km_100ha_AL^2	0.84	<0.0001	0.81
EHI_edge _areaWeighted_Eq_10km_100ha_AL^2	0.86	<0.0001	0.84
Percent Woodland	0.73	0.0004	0.68
MPA	0.54	0.002	0.46

Values of 1 km and 10 km denote the dispersal distance used for the maxDist parameter and, for models in which the parameter *d* was derived from non-habitat patch size, model names are suffixed by the value for fullEdgeEffectArea that was used. Best performing models were those with dispersalRate set to 0.05 (reflecting a 5% dispersal probability at a distance equal to maxDist) and, for non-area-based estimates of *d*, a value of 0.05 produced best model performance. Therefore, only the results of these models are shown

data on mammal occurrences in the National Biodiversity Network (NBN) atlas (https://nbnatlas.org/) for the case-study. Almost all available mammal records were species with an association with woodland, but none were interior specialists. The exceptions to this were species of the *Lepus* genus, and *Arvicola amphibius* which were excluded as open and aquatic habitat specialists, respectively. We combined occurrence data for all woodland species and converted them to a point pattern then a Kernel Smoothed Intensity map using a bandwidth selected with the method proposed by Cronie and van Lieshout (2018); implemented using the *Spatstat* library in R. Values were then aggregated (as mean occurrence density) at the catchment level.

We compared the ability of the PC, PFC and EHI connectivity metrics to predict mammal density within each catchment. This was straightforward because of the relationship between the metrics: PC is simply EHI with the model parameters set to *Gen* (generalist, no edge effect); and PFC is simply EHI with the edge distance decay component (*d*) set to 1 (edge effect is maximal for all distances given in Table S1). As described in "Edge-weighted habitat for connectivity" section, Saura et al. (2011) proposed the square root of the numerator of the PC equation as the ECA metric, which represents the size of a single patch that, if maximally connected, would provide the same probability of connectivity as the habitat pattern under investigation. In our case-study assessment we compared results for the original form of the PC metric (Eq. 1) and, alternatively, ECA/A_L.

For EHI estimates, we ran models with *d* set according to non-habitat patch size as described in "Parameterizing edge effects"-"Justification of area-weighted edge effects" section. As there is no established method to estimate the precise relationship between patch size and the distance at which edge effects are exerted, we set the fullEdgeEffectArea parameter alternatively to 10 ha, 100 ha and 1000 ha. This reflected the 99th percentile of patch sizes in the study area matrix and an order of magnitude lower and higher for comparison. We ran non-area-weighted models,

setting d to sequentially to 0.05, 0.25, 0.5, 0.75 and 0.95. We also tested the effectiveness of modelling edge as a factor independent of land-use (according to the values in Table S1) by running alternative models with *maxEdge* parameterized as a single value for all non-habitat patches. For this we used the area-weighted mean of the Eycott et al. (2011) values based on the total area of each land-cover in the study area. Given that the response variable consisted of aggregated species data, we tested a range of dispersal distances (1 km, 5 km and 10 km) for the maxDist value. Model performance was compared via first and second order regression models with density of mammal occurrence points from the NBN dataset as the response variable (see Table 3 for model variable names and description). Regression models were compared based on the coefficient of determination (R^2 value) of the regression model.

Where relevant, model names are suffixed with a dispersal distance (e.g., "_10km") and with a value representing fullEdgeEffectArea (e.g., "_10ha", "_100ha") in the table of results (Table 4). Where the original form of the PC metric is used (ECA^2/A_L^2), the model name is suffixed by "$\_A_L^2$".

Results

This assessment demonstrated that EHI models differed in expected ways relative to the PC and PFC metrics. Overall, our method produced smaller estimates than the PC metric ("generalist" in our EHI approach) and PFC produced a zero result for all catchments (because PFC removed all habitat according to the values in Table S1). The area-weighted edge approach, parameterized for edge specialists (model EHI_edge_areaWeighted_ Eq_10km_100ha), best explained the variation in the response variable (Table 4). Setting intra-patch movement cost to $edgeSum_i$ values did not result in better model R-squared values compared to setting cost to 0 or 1 for EHI models. Notably, area-weighted models based on the use of a fixed-distance edge raster performed better than those based on the variable edge extent values (Table 4). For non-area-weighted edge models, setting d to 0.05 produced the best performance (model R-squared; models taking other values are not shown) whereas for models where edge effects were weighted by non-habitat patch area, setting the fullEdgeEffectArea

parameter to 100 ha resulted in best performance. The best performing area-weighted edge configured model (EHI_edge_areaWeighted_Eq_10km_100ha) explained considerably more variance in mammal density than a simple measure of percentage woodland cover or mean patch size and > 55% better than the PC metric.

Discussion

The evaluation based on data (Colne Valley, Table 4) demonstrated the greater explanatory power of models properly configured for edge species groups than for those configured for interior specialists or by PC and PFC metrics. Weighting d by area presented a considerable improvement on non-weight approaches, exhibiting a > 55% improvement on the PC metric ("generalist" in the EHI) and edge-configured models demonstrated up to 37% higher adjusted R-squared values than the best interior-configured model. This is a promising step forward towards more functionally relevant connectivity assessments and a key development in aligning patch and landscape-level functional properties. The area-weighted model with fixed edge effects (EHI_edge_areaWeighted_ Eq_10km_100ha, Table 4) performed better than models parameterized by variable edge-effects. This implies that the gains achieved by our approach result from capturing the spatially-dependant influence of non-habitat patches rather than from qualitative assessments of edge effects as a function of land-use. This is promising for two reasons. Firstly, the impact of non-habitat on edge-weighted habitat may be more closely mediated by processes related to spatial characteristics, which are objective and easily measured, than land use characteristics, which are more subjective. Secondly, if fixed edge extents prove to be sufficient for successfully estimating EHI, then the process of estimating edge extents could be greatly simplified. That is to say, fewer values would need to be estimated (the fixed edge distance and fullEdgeEffectArea), avoiding the need for lengthy deliberation over the impact of multiple land-uses. There may, therefore, be considerable merit in conducting further research into how this relationship unfolds in other real-world landscapes. Our approach presents a potential route to testing related hypotheses against data.

Setting within-patch movement cost to $edgeSum_i$ only marginally improved model performance.

Though models were not significantly improved, this implementation of intra-patch movement is more ecologically justified than setting intra-patch cost to 1 or some other small arbitrary value (e.g., Williams 2008; Hunter-Ayad and Hassall 2020; Godet and Clauzel 2021). We note that, even if such numbers are well justified (e.g., when derived from expert review) the assumption that such cost is equal throughout habitat patches still does not reflect the mechanistic understanding of change in habitat quality as a function of proximity to the matrix (i.e., edge effects). Given the size of the study area, the dispersal distance considered and the aggregated nature of the response data, it is possible that any potential improvement derived from this solution was diminished in the case-study application. Exactly how this parameter performs as a function of landscape context (e.g., level of fragmentation, patch size distribution, focal species) would be worthy of further investigation. Our analysis also suggests that ECA/A_L performed better than ECA^2/A_L^2 at capturing variance in edge species density as a function of connectivity gains at high levels of fragmentation and is another update worthy of further testing in real-world landscapes.

In terms of facilitating future research, our approach offers an opportunity to better integrate connectivity modelling into practical conservation management and research by accounting for edge and landscape permeability in a more functional way. An important implication of this is that models can be parameterized to explore optimum values when applied to data, thus helping researchers to isolate parameters that explain differences in species persistence in landscape comparisons. In multi-species studies, our method should be able to delineate the contribution of connectivity to species richness, thus making a valuable (and hitherto absent) contribution to key research agendas (such as the SLOSS debate). That EHI explained > 25% more variance in mammal density than models based on either percentage cover or mean patch size suggests that connectivity metrics such as EHI have much to offer future assessments of species richness as a function of landscape configuration. However, such work requires the careful parameterization of landscape permeability and sensitivity to edge. For example, a limitation of our application was the use of identical cost and edge effect parameters for both interior and edge habitat models. Though our models showed promising behaviour and good agreement to data, more functional estimates differentiating edge and interior species requirements

would be desirable. In this respect, the use of focal generic species (e.g., for interior, edge and generalist groups) may prove useful (Watts et al. 2010). Similarly, the current method assumes that the same land-use will have a comparable edge effect in different locations in the landscape. This may in fact vary, for example as a function of management or the sensitivity of individual species. It may therefore be desirable to incorporate such factors through spatially-varying values of *edgeMax*. Developing techniques to incorporate such variation would be a promising future direction for this research.

Conclusions

Existing area-weighted approaches to landscape connectivity offer much promise but tend to be biased towards generalists or interior specialists without adequately accounting for the ecology of either, nor other species along the interior-edge spectrum, with respect to landscape configuration. The method described here presents an opportunity for better capturing edge-weighted habitat as a function of edge-interior transitions and non-habitat edge effect dynamics in the landscape. Our approach offers an example of the benefits of more explicitly addressing both patch and landscape-scale processes in overall assessments of connectivity. As such, there is an opportunity for landscape ecology practice and research such that by harnessing the power of spatial-ecological theory and techniques we might move towards a more complete theory of landscape functional connectivity, one that can contribute to key persistent debates in ecology.

project, which is funded by NERC award number NE/V021117/1.

Data availability The code for carrying out all analyses presented in this article will be made available on the corresponding author's github repository. Data for reproducing the case-study can be freely obtained from the Centre for Ecology and Hydrology: https://www.data.gov.uk/dataset/042e702f-9614-48dd-a5a0-bb25a0502ae3/land-cover-map-2020-10m-classified-pixels-gb Catchment data are available at: https://www.data.gov.uk/dataset/1a494e3e-e414-456c-9c2e-ca367a2945b6/wfd-surface-water-management-catchments-cycle-2. Species occurrence data can be downloaded from the National Biodiversity Network Atlas: https://nbn.org.uk/.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

An Y, Liu S, Sun Y, Shi F, Beazley R (2021) Construction and optimization of an ecological network based on morphological spatial pattern analysis and circuit theory. Landscape Ecol 36:2059–2076

Bonte D, Bafort Q (2019) The importance and adaptive value of life-history evolution for metapopulation dynamics. J Anim Ecol 88(1):24–34

Carvalho F, Carvalho R, Mira A, Beja P (2016) Assessing landscape functional connectivity in a forest carnivore using path selection functions. Landscape Ecol 31:1021–1036

Chandler RB, Muths E, Sigafus BH, Schwalbe CR, Jarchow CJ, Hossack BR (2015) Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. J Appl Ecol 52(5):1325–1333

Cronie O, Van Lieshout MNM (2018) A non-model-based approach to bandwidth selection for kernel estimators of spatial intensity functions. Biometrika 105(2):455–462

Dixo M, Martins M (2008) Are leaf-litter frogs and lizards affected by edge effects due to forest fragmentation in Brazilian Atlantic forest? J Trop Ecol 24(5):551–554

Environment Agency (2023) WFD River Waterbody Catchments Cycle 2. Available at: https://www.data.gov.uk

Etherington TR (2016) Least-cost modelling and landscape ecology: concepts applications and opportunities current landscape. Ecol Report 1(1):40–53. https://doi.org/10.1007/s40823-016-0006-9

Eycott AE, Marzano M, Watts K (2011) Filling evidence gaps with expert opinion: the use of Delphi analysis in least-cost modelling of functional connectivity. Landsc Urban Plan 103(3–4):400–409

Fahrig L, Arroyo-Rodríguez V, Bennett JR, Boucher-Lalonde V, Cazetta E, Currie DJ, Eigenbrod F, Ford AT, Harrison SP, Jaeger JA, Koper N (2019) Is habitat fragmentation bad for biodiversity? Biol Cons 230:179–186

Fletcher RJ Jr, Didham RK, Banks-Leite C, Barlow J, Ewers RM, Rosindell J, Holt RD, Gonzalez A, Pardini R, Damschen EI, Melo FP (2018) Is habitat fragmentation good for biodiversity? Biol Cons 226:9–15

Foltête JC, Berthier K, Cosson JF (2008) Cost distance defined by a topological function of landscape. Ecol Model 210(1–2):104–114

Galpern P, Manseau M, Fall A (2011) Patch-based graphs of landscape connectivity: a guide to construction, analysis and application for conservation. Biol Cons 144(1):44–55

Godet C, Clauzel C (2021) Comparison of landscape graph modelling methods for analysing pond network connectivity. Landscape Ecol 36:735–748

Goodman D (1987) The demography of chance extinction. In: Soule ME (ed) Viable populations for conservation. Cambridge University Press, New York, pp 11–43

Grander TO, Aguiar LM, Machado RB (2020) Heating a biodiversity hotspot: connectivity is more important than remaining habitat. Landscape Ecol 35:639–657

Griffin SR, Haddad NM (2021) Connectivity and edge effects increase bee colonization in an experimentally fragmented landscape. Ecography 44(6):919–927

Hale JD, Fairbrass AJ, Matthews TJ, Sadler JP (2012) Habitat composition and connectivity predicts bat presence and activity at foraging sites in a large UK conurbation. PLoS ONE 7(3):e33300

Hanski I (1994) A practical model of metapopulation dynamics. J Anim Ecol 63:151–162

Hanski I, Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. Nature 404(6779):755–758

Hanski I, Schulz T, Wong SC, Ahola V, Ruokolainen A, Ojanen SP (2017) Ecological and genetic basis of metapopulation persistence of the Glanville fritillary butterfly in fragmented landscapes. Nat Commun 8(1):14504

Hodgson JA, Moilanen A, Thomas CD (2009) Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. Ecology 90(6):1608–1619

Hunter-Ayad J, Hassall C (2020) An empirical, cross-taxon evaluation of landscape-scale connectivity. Biodivers Conserv 29(4):1339–1359

Jaquiéry J, Guélat J, Broquet T, Berset-Brändli L, Pellegrini E, Moresi R, Hirzel AH, Perrin N (2008)

Habitat-quality effects on metapopulation dynamics in greater white-toothed shrews. Crocidura Russula Ecol 89(10):2777–2785

Keeley AT, Beier P, Jenness JS (2021) Connectivity metrics for conservation planning and monitoring. Biol Cons 255:109008

Kirklees Council (2023) Kirklees Council Biodiversity Opportunity Zones: https://www.kirklees.gov.uk/beta/delivering-services/pdf/biodiversity-opportunityZones-background.pdf

Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. Am Nat 142:911–927

Landguth EL, Hand BK, Glassy J, Cushman SA, Sawaya MA (2012) UNICOR: a species connectivity and corridor network simulator. Ecography 35(1):9–14

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89(10):2712–2724

Miller JE, Damschen EI, Harrison SP, Grace JB (2015) Landscape structure affects specialists but not generalists in naturally fragmented grasslands. Ecology 96(12):3323–3331

Morton RD, Marston CG, O'Neil AW, Rowland CS (2021) Land Cover Map 2020 (10m classified pixels, GB). NERC EDS Environmental Information Data Centre. https://doi.org/10.5285/35c7d0e5-1121-4381-9940-75f7673c98f7

Neel MC (2008) Patch connectivity and genetic diversity conservation in the federally endangered and narrowly endemnoc plant species *Astragalms albens* (*Fabaceae*). Biol Cons 141:938–955

Ovaskainen O, Hanski I (2001) Spatially structured metapopulation models: global and local assessment of metapopulation capacity. Theor Popul Biol 60(4):281–302

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramos DL, Pizo MA, Ribeiro MC, Cruz RS, Morales JM, Ovaskainen O (2020) Forest and connectivity loss drive changes in movement behavior of bird species. Ecography 43(8):1203–1214

Saerens M, Achbany Y, Fouss F, Yen L (2009) Randomized shortest-path problems: two related models. Neural Comput 21(8):2363–2404. https://doi.org/10.1162/neco.2009.11-07-643

Saura S, Pascual-Hortal L (2007) A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landsc Urban Plan 83(2–3):91–103

Saura S, Estreguil C, Mouton C, Rodríguez-Freire M (2011) Network analysis to assess landscape connectivity trends: application to European forests (1990–2000). Ecol Ind 11(2):407–416

Watts K, Handley P (2010) Developing a functional connectivity indicator to detect change in fragmented landscapes. Ecol Ind 10(2):552–557

Watts K, Eycott AE, Handley P, Ray D, Humphrey JW, Quine CP (2010) Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. Landscape Ecol 25:1305–1318

Williams S (2008) Red squirrel strongholds consultation. Forestry Commission, Edinburgh

Zurita G, Peer G, Bellocq MI, Hansbauer MM (2012) Edge effects and their influence on habitat suitability calculations: a continuous approach applied to birds of the Atlantic forest. J Appl Ecol 49(2):503–512