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Research article

Functional connectivity modelling and biodiversity Net Gain in England: Recommendations for practitioners

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1. Introduction

Unprecedented rates of habitat loss and climate change are raising concerns worldwide about the future of biodiversity (IPBES et al., 2019). This is because biodiversity has a direct impact on the functioning of ecosystems and their ability to provide society with the goods and services needed to prosper (Cardinale et al., 2012). Globally, urbanisation contributes to this problem via land-use change, habitat degradation and fragmentation, causing some of the highest local extinction rates and longer-lasting change than other types of habitat loss (Maxwell et al., 2016; McDonald et al., 2018; McKinney, 2002). This problem may be exacerbated in the future as, worldwide, human populations are becoming increasingly urban (UNPD, 2018).

To help address this challenge, England will introduce a new Biodiversity Net Gain (BNG) policy as part of the post-Brexit environmental policy (Defra, 2019; Environment Act, 2021). BNG is a tool to balance the objectives of nature recovery with meeting housing and infrastructure targets, requiring the provision of gains in biological diversity for the concession of planning permission to developers (Defra, 2019). BNG is still subject to the mitigation hierarchy principles (mandated by the European policy Environmental Impact Assessment (EIA) Directive (Directive, 2011/92/EU)). But, on top of that, BNG includes a standardised assessment process known as Defra's Biodiversity Metric, which yields the biodiversity *units* a site is worth depending on habitat types, extent, and quality (Crosher et al., 2019). A percentage of gain (a minimum of 10%) is applied, and the resulting units must be delivered through habitat creation or enhancement either on or offsite.

Impact assessment methods, such as BNG and EIA, have generally been accused of not considering the effects of development at the landscape scale, or not adequately taking into consideration the scales of biodiversity functioning (Bergsten and Zetterberg, 2013; Bigard et al., 2017); in response, academic literature has proposed methods to integrate habitat connectivity in the mitigation hierarchy, a main element within the EIA (Bergès et al., 2020; Ng et al., 2013; Tarabon et al., 2019, 2020). This is because increasing habitat loss and fragmentation, and the potential need for species range-shifts under novel climates, are major concerns for conservation scientists (Crooks and Sanjayan, 2006). However, the newly created BNG still fails to consider how biodiversity losses and gains, as a consequence of urban development, can affect ecological networks at landscape levels. Earlier versions of the Defra Biodiversity Metric included an Ecological Connectivity multiplier, which was removed in the latest versions (at the time of writing, version 3.0) (Natural England, 2020).

This emphasizes the need for a methodology for guiding the delivery of ecological gains at the landscape or regional scales. However, while the vision of connected landscapes may be compelling, the practice of conserving connectivity is not a simple matter (Bergsten and Zetterberg, 2013; Crooks and Sanjayan, 2006), and the spatial connectivity of ecosystems is often neglected (Bergsten and Zetterberg, 2013; Opdam et al., 2006). This indicates a knowledge gap between the academic methods for the assessment of ecological connectivity and applications in real-life projects by environmental practitioners and planners.

This paper aims to bridge these gaps by using the connectivity algorithm Omniscape (Hall et al., 2021; McRae et al., 2016a, 2016b) to model connectivity to inform mitigation avoidance and BNG allocation in a case study using the example of the Blackwell Farm development (Guildford, Surrey, UK). This paper has two objectives. First, it investigates the challenges that practitioners working in non-academic planning and environmental fields must face to perform this analysis and suggest how such challenges may be overcome. Second, Omniscape is applied experimentally to investigate how different methodological decisions affect model outputs. Four species were selected for assessment on the basis that they (1) have significance in the conservation objectives for the study area, (2) account for a wide range of dispersal

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behaviour, and (3) represent all the principal community types within the study area: the European hedgehog (*Erinaceus europaeus*), Hazel dormouse (*Muscardinus avellanarius*), Adder (*Vipera berus*), and Water vole (Arvicola amphibius). The outputs have been used to discuss the possibilities for this kind of algorithm to be widely used in the planning sector, and suggest how this could be integrated into the Defra metric.

2. Methods

2.1. Functional connectivity and circuit theory

Academic literature usually distinguishes between two types of connectivity: *structural connectivity*, which is centred around landscape mosaics (*e.g.* land cover) and their correlation with species occurrence, versus *functional connectivity,* which is centred around individual species, recognising the specific food, shelter, territory and abiotic conditions requirements (Fischer and Lindenmayer, 2007). Because a landscape can be functionally connected for some species but not for others, functional connectivity is more meaningful as it recognises that connectivity is essentially a species-based attribute that is based on the habitat requirements and dispersal ability of particular species (Keeley et al., 2021; Watts and Handley, 2010).

Functional connectivity can be quantified by various methods, each having a unique set of assumptions and best practices and producing slightly different types of maps (Wade et al., 2015). One such method is electric circuit theory, one of the most recent, yet extensively used, connectivity approaches (Dickson et al., 2019; Hall et al., 2021). It treats the landscape as a surface of resistors (a resistance grid), where the current flows from source nodes to ground nodes (core areas of suitable habitat); it quantifies the spatial patterns of current flow and accumulation, as higher resistance areas shift the flow into pathways with lower resistance (Hall et al., 2021; McRae et al., 2008a). Circuitscape was the first open software that allowed users to apply the logic and mathematics of electrical circuit theory to questions of how genes, animals, or processes flow across heterogeneous landscapes (Hall et al., 2021; McRae et al., 2008a; McRae et al., 2016a, 2016b). The underlying theoretical background of electric theory has been confirmed as suited to predict ecological connectivity and to identify important movement routes (Dickson et al., 2019; McRae et al., 2016a, 2016b), making them *realistic* models in ecological terms (McRae et al., 2008b).

Circuitscape has commonly been used in a pairwise mode, meaning that current flow is calculated between pairs of user-defined *habitat cores* (Landau et al., 2021). This is appropriate for studies with defined source and destination points (*e.g.*, joining pre-defined natural reserves) (Phillips et al., 2021). However, when cores are not defined, for example when they are not known or when the species are not isolated to discrete patches, *omnidirectional* approaches are useful for producing regional-scale maps of connectivity (Phillips et al., 2021). The Omniscape (Landau et al., 2021) algorithm builds on and expands Circuitscape applications; one of Omniscape's novelties is that it produces maps of omni-directional connectivity, which provide a representation of connectivity between *every* pair of start and endpoints in the landscape (Landau et al., 2021). This allows understanding and predicting how the likelihood that an ecological process (*e.g.*, animal movement) manifests itself in geographic space.

2.2. Steps for modelling connectivity and methodological choices

In summary, the process of modelling connectivity follows these general steps:

(1) Firstly, the focal species for which connectivity will be modelled must be selected. Then, its dispersal capabilities need to be determined. In Omniscape, this value is used to indicate the *moving window radius (mwr),* which represents the search distance for suitable habitat (Landau et al., 2021) calculated from the home range area of the species as per equation (1) below (Shirk and McRae, 2013):

$$mwr = \sqrt{(home\ range\ area)/\pi}\Big) \tag{1}$$

(2) Next, spatial data must be gathered and each environmental feature (*e.g.,* habitats, roads, *etc.*) contained in the spatial data must be assigned a resistance value, which defines the traversal cost for every environmental feature in the landscape. The combination of such data (spatial data and associated resistance values) allows the production of the *resistance raster* that represents the landscape as a resistance surface. In this step, the scale of the analysis needs to be defined, which includes deciding on the spatial extent and the cell or pixel size.

(3) Finally, the sources and destinations of movement need to be identified; this means that the areas of suitable habitat that need to be connected must be specified. In Circuitscape this requires defining the habitat cores to be connected. In Omniscape, this is done through the *source strength* raster, which, for every pixel, defines the relative amount of current to be injected into that pixel.

There are many methodological choices that a practitioner must make to create these data inputs: the focal species, the scale of the analysis, and the best way to indicate sources and destinations of movement. These decisions are not straightforward and can have a large impact on the results of the connectivity analysis. Because this research was an experimental implementation of the approach aimed at providing recommendations for model functional connectivity in the context of BNG, a series of experiments modelling the effects of different methodological choices was undertaken, as described below.

2.3. Experiment design

The following subsections explain the experiments with methodological choices in detail. In these experiments one variable is changed while leaving others fixed, to allow for comparison of the effects of such variable. For example, we run one model per species while maintaining other parameters fixed, such as cell size and buffer size; this produces four maps (accounting for the four focal species) allowing to compare the connectivity of the landscape attending only to the species' behaviour. The next subsections explain each of these experiments in detail, and an overview of all experiments is given in Table 1.

2.3.1. The effect of the focal species

The first step in building functional ecological network models is selecting the *focal species* for which the network is going to function since species differ in their sensitivity to changes in the landscape matrix (Bierwagen, 2007).

In this experiment, we tested how the connectivity results differ across species depending on their habitat requirements and dispersal capabilities. For this, a suite of species representative of the region's habitat types, but with very different ecological needs, dispersal distances and home ranges was selected. Comparison analysis was run for all the species at the same spatial scales and source strength inputs to determine how the outputs varied due to the different species' ecological requirements.

2.3.2. The effect of source strength inputs

This experiment was a comparative analysis of the effect of different methods for producing the source strength inputs, which specify the sources and destinations of the individuals moving through the landscape. Despite one of the main advantages of Omniscape being that there is no need to pre-define habitat cores, the question of what the best approach is for defining the sources and destinations of individuals

Table 1
Summary of modelling experiments and parameters, inputs and settings used for each model.

Experiment	Model	Fixed parameters[b]	Inputs and Settings summary
Effect of the focal species	Adder	• base-case	• Resistance raster file for Adder • Source strength input: *core-based* approach • mwr[a] = 41 m
	Dormouse	• base-case	• Resistance raster file Dormouse • Source strength input: *core-based* approach • mwr = 40 m
	Hedgehog	• base-case	• Resistance raster file Hedgehog • Source strength input: *core-based* approach • mwr = 262 m
	Water vole	• base-case	• Resistance raster file Water vole • Source strength input: *core-based* approach • mwr = 69 m
Effect of source strength inputs	*Coreless-IRV*: current source strength is the inverse of resistance values	• All species • base-case	• Resistance raster layer • mwr • Source layer is calculated as the inverse of the resistance layer; resistance cut-off = 60 • mwr
	Coreless-HV: current source strength is habitat values	•All species • base-case	• Resistance raster file • Source layer is the habitat raster; only habitats above 0.6 value are included as source • mwr
	Core-based: only habitat cores are sources	•All species •base-case	• Resistance raster file • Cores raster file, where cores = 10 and surrounding pixels = 0. • mwr
Effect of scale	Cell size 3 m Buffer 1 km	Hedgehog	• Resistance raster file • Source strength input: *core-based* approach • mwr
	Cell size 9 m Buffer 5 km (base-case)	Hedgehog	• Resistance raster file • Source strength input: *core-based* approach • mwr
	Cell size 18 m Buffer 10 km	Hedgehog	• Resistance raster file • Source strength input: *core-based* approach • mwr
Differences between Omniscape and Circuitscape	• Omniscape: *core-based* approach • Circuitscape: pairwise mode	• Adder and hedgehog • Base-case	• Resistance raster file • Core raster file • mwr

[a] mrw = moving window radius; the obtention of these values is specified in the Supplementary Materials.
[b] base-case = 5 km buffer, 9 m × 9 m cell size.

remains. Three approaches for producing the source strength input in Omniscape were examined:

(1) Coreless, where, for every pixel of the landscape, the source strength is calculated as the inverse of the resistance values (IRV). This option was introduced by Omniscape developers to reduce the data requirements as there is no need to create a second raster file with the sources of strength; this approach is referred to as *coreless-IRV*.
(2) Coreless, where, for every pixel of the landscape, the source of strength is derived from the habitat values (HV). In this scenario, the source strength is equivalent to the suitability of a habitat to support a population. This approach requires the development of both a resistance raster and another raster of habitat values; this approach is referred to as *coreless-HV*.
(3) Core-based approach, where the current is injected only in pre-defined core areas, representing the origin of individuals moving across the resistance surface. This approach requires the development of both a resistance raster and another raster for defining the habitat cores; this approach is referred to as *core-based.*

2.3.3. *The effect of scale*

The scale of the analysis includes both the size of the cells of the raster maps and the spatial extent (area coverage) included in the analysis (McRae et al., 2008b). Defining the scale of the analysis is a challenge because larger spatial scales and finer map resolutions can be computationally prohibitive (Koen et al., 2019), coarser resolutions can cause small patches or barriers to be lost, and spatial extents that are too small may result in the exclusion of connectivity paths. Consequently, these decisions can alter the connectivity patterns of the landscape. In addition, because ecological processes and elements of biological diversity occur at a variety of scales, a comprehensive strategy to conserve these processes and elements must also encompass a diversity of scales.

Despite its relevance, little guidance is available in the literature to help address how differences in scale can affect Omniscape's results. Therefore, simulations were created with a range of cell sizes (3mx3m, 9mx9m and 18mx18 m) and spatial extents (buffer areas of 1 km, 5 km, and 10 km around the development site) to explore this issue for one of the focal species. These cell sizes and buffers are meaningful for BNG land managers to implement site-specific conservation measures, yet different enough to affect connectivity patterns (*e.g.*, 18 m will inevitably lose smaller habitat patches compared to the 3 m cell).

2.3.4. *Differences between Omniscape and Circuitscape*

This experiment compared the outputs between Omniscape and the traditional Circuitscape algorithm in a pairwise mode. This was done to examine how these approaches differ, and to assess which might be more suitable depending on the study context. To our knowledge, no published literature has shown a comparison between these two modelling approaches. For this experiment, we run both algorithms for two focal species using the same input files.

2.4. *Study site*

These experiments were run on the case study of Blackwell Park (Fig. 1), a potential housing development situated on what is currently known as Blackwell Farm, an area of previous Green Belt land on the western outskirts of the town of Guildford (Surrey, UK). About 200 ha of the current Blackwell Farm are proposed to be converted to the residential-led, mixed-use, Blackwell Park development of about 1800 homes. The current Blackwell Farm comprises 269 ha of farmland with

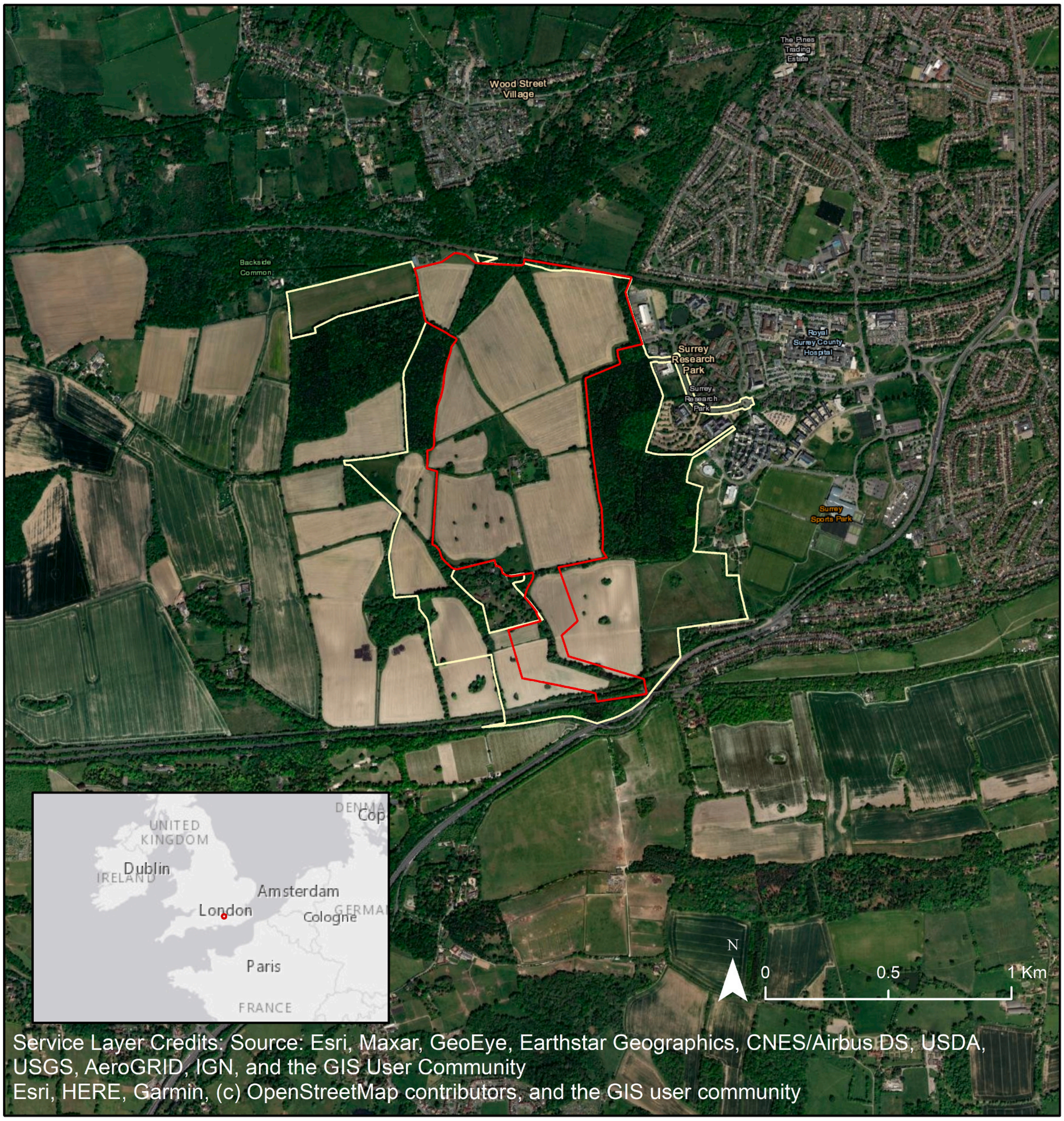

Fig. 1. Blackwell Park development (red outline) will be located on what is currently known as Blackwell Farm (yellow outline), an extension of land, owned by the University of Surrey, on the outskirts of Guildford primarily composed of agricultural and woodland areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mature hedgerows and is bounded by the ancient Blackwell Woodland (70 ha) to the Northeast.

2.5. Gathering data and running the models

A summary of the methodology followed for running the models is presented here; an extended version is included as Supplementary Material.

The focal species for this study were selected on the basis that they have significance in the conservation objectives for the study area and account for a wide range of dispersal behaviour: (1) European hedgehog (*Erinaceus europaeus*); (2) Hazel dormouse (*Muscardinus avellanarius*); (3) Adder (*Vipera berus*); (4) Water vole (*Arvicola amphibius*). Their dispersal values (*mwr*) were derived from a review of academic literature (see Supplementary Material).

The spatial inputs (GIS data) were gathered through online searches of official databases, as well as through data kindly provided by Blackwell Farm Ltd and the Surrey Wildlife Trust. A detailed list of the GIS data used is supplied as Supplementary Material. For obtaining *habitat and the resistance values* associated with each GIS feature for each species, we used expert elicitation; this expert knowledge was gathered via an online survey. Next, the *resistance*, *habitat* and *core* habitat layers were created using ArcGIS Desktop 10.5 software (Redlands, 2011) and the Gnarly Landscape Utilities toolbox (McRae et al., 2014; Shirk and McRae, 2013).

Finally, to run Omniscape, an INI file per model was prepared to contain the model specifications. This file specifies file paths for raster inputs and user-specified options, such as the *mwr* values. Circuitscape was run in pairwise mode. For all models, raw cumulative current maps were produced. In addition, histograms displaying the distribution of the image pixels were created with the current flow values of the pixels on the x-axis, and the pixel counts on the y-axis.

3. Results

The output maps represent the *cumulative current flow*, which is the current flow of all Omniscape moving window iterations (or pairwise comparisons in Circuitscape) summed together. This creates a continuous connectivity surface with a single current value for every pixel on the mapped landscape. These maps depict the likelihood for a given focal species to move through the landscape, with higher flow/conductance representing a greater likelihood of movement. This flow is represented by a graded colour scale ranging from cool (blue) to warm (red) to show low to high electric conductance.

3.1. Evaluating the differences between Omniscape and Circuitscape

Fig. 2 compares the outputs of Omniscape and Circuitscape when using the same inputs (resistance and core raster) for the adder and the hedgehog.

For the adder, it is apparent that Circuitscape displays connectivity pathways that are absent in the Omniscape map. However, this seemingly higher connectivity depicted by Circuitscape may be an artefact of the visualization technique. This is because map visualization techniques or styles improve the appearance of the data by spreading the pixel values along a histogram, emphasising differences in values despite them being very small. In this example, when *histogram equalize stretch* visualization is used, it spreads out the most frequent intensity values, allowing areas of lower contrast to gain a higher contrast without affecting the global contrast. When *equal intervals* visualization is used, the range of connectivity values is divided into equal-sized subranges; this resulted in cumulative current being highly concentrated in the cores, and with values near zero for the surrounding landscape. The latter technique better conveys the idea that the suitable habitat for the adder is extremely fragmented, but it gives no useful information to land managers or planners as to where are the most effective locations for improving connectivity between adder populations (which *histogram equalize stretch* provides).

Finally, it should be noted how the hedgehog presents similar connectivity patterns between Omniscape and Circuitscape models. This is because, due to its more generalist habitat needs and better dispersal capabilities, this species is far less restricted to specific areas compared with the adder. The hedgehog's core areas are more numerous and are closer together, facilitating the movement of individuals in the landscape matrix, and therefore Omniscape and Circuitscape outputs present similar connectivity patterns.

3.2. Evaluating the effect of Omniscape inputs

Fig. 3 presents the results of the three procedures for preparing source strength inputs: *coreless-IRV, coreless-HV*, and *core-based.* Overall, all Omniscape approaches model the same primary movement corridors on the landscape, with the pattern of movement being largely dependent on the differences between species rather than the modelling technique.

Regarding the accompanying histograms (Fig. 4), they give information on the level of the species isolation as follows. For the adder and the water vole (both are habitat specialists, and their areas of suitable habitat are very far apart), most of the current values are zero or very close to zero, indicating high habitat isolation. In contrast, connectivity

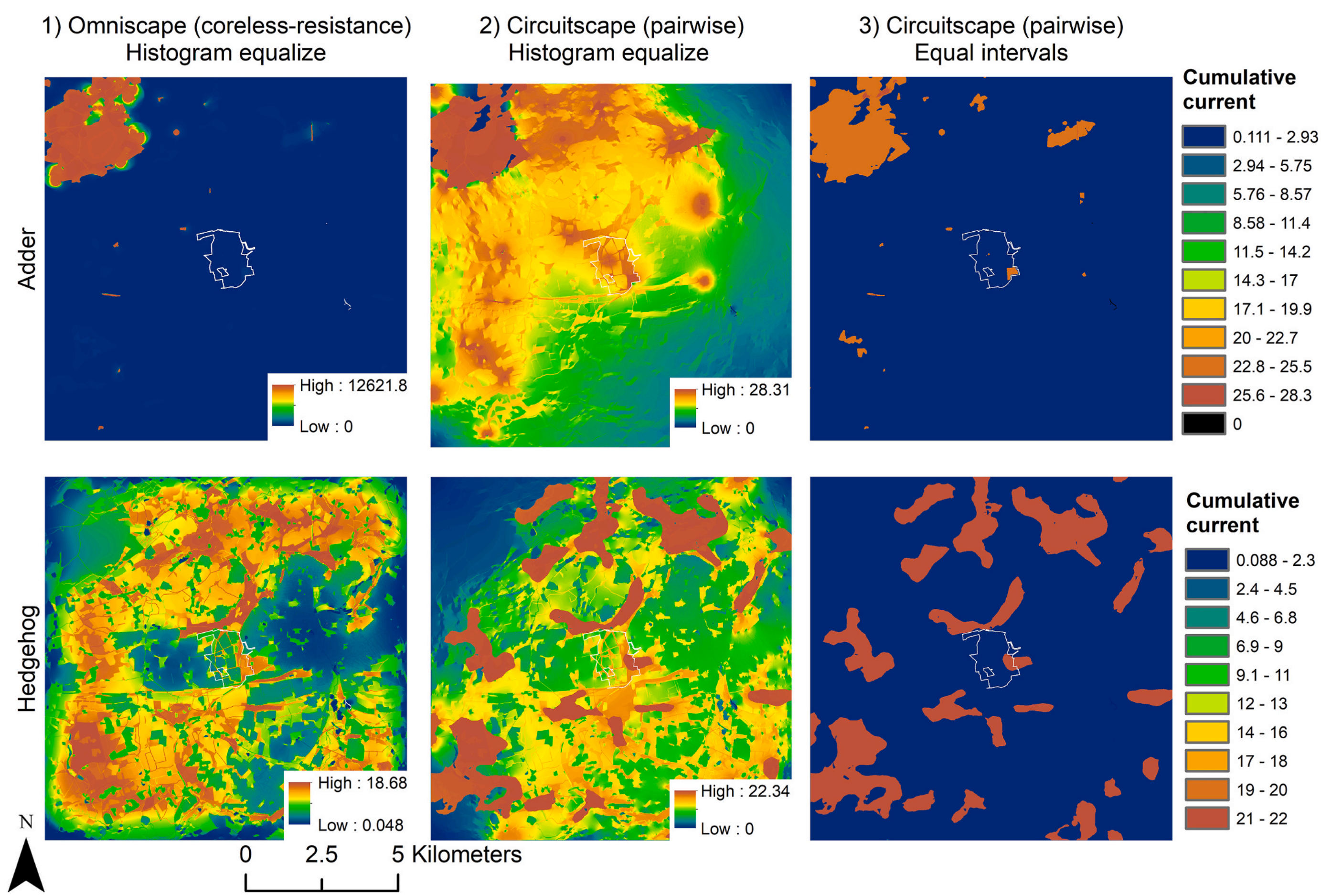

Fig. 2. Comparison of results between (1) Omniscape (coreless-IRV) and (2) and (3) Circuitscape (pairwise) for the adder and the hedgehog. (2) and (3) depict the same Circuitscape outputs but using two different visualization techniques (histogram equalization and equal intervals respectively). The grey outline represents the boundary of the Blackwell Farm potential development site.

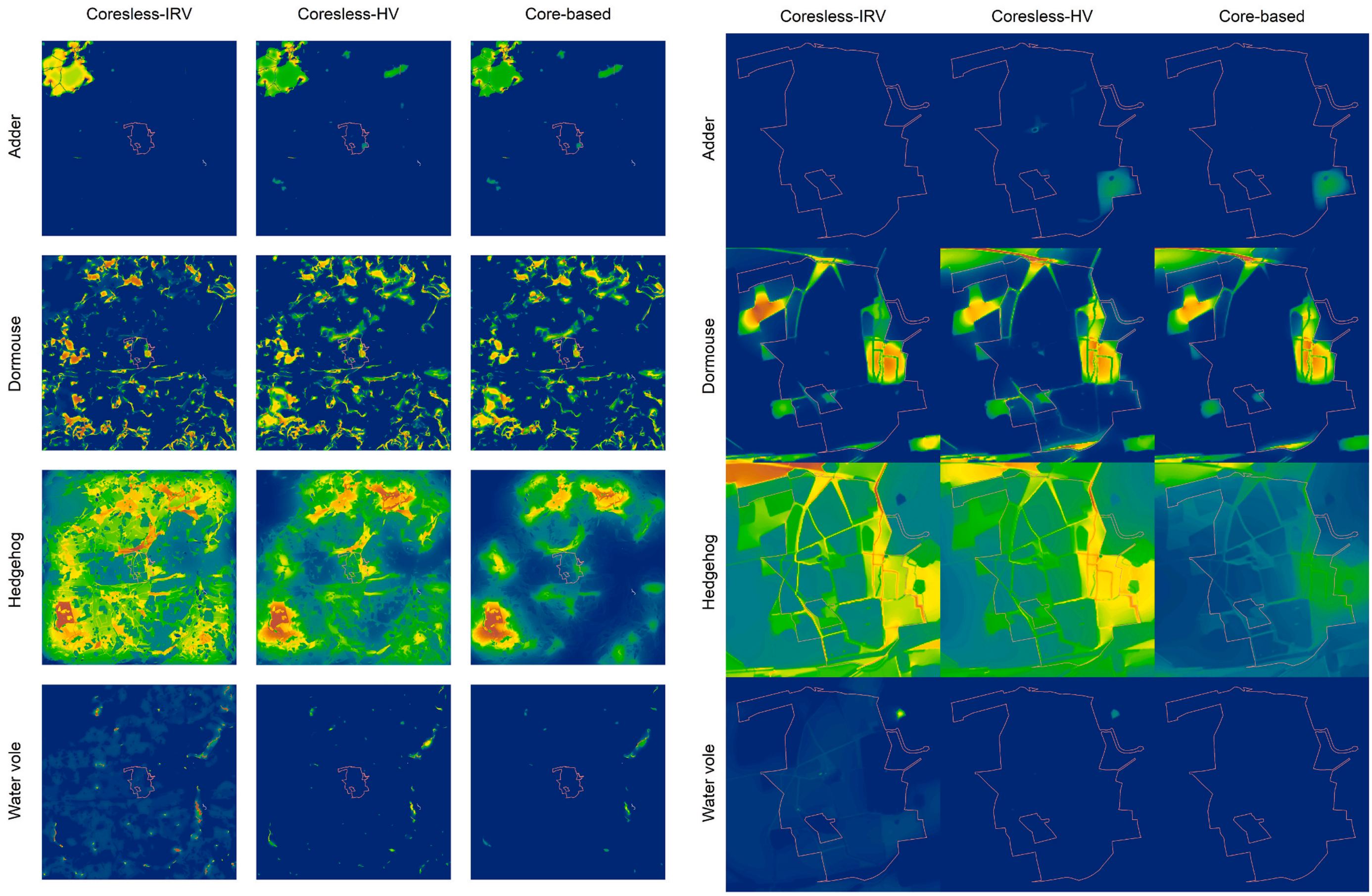

Fig. 3. Comparison of cumulative current maps across four species (the adder, Hazel dormouse, hedgehog, and water vole) and three types of Omniscape inputs: coreless-IRV (Inverse Resistance Values) coreless-HV (Habitat Value) and core-based. On the left, the whole spatial extent of the analysis is shown; the red outline represents the boundary of the Blackwell Farm potential development site. The right-hand graphs are zoomed in to show primarily the Blackwell Farm site extent. Maps are displayed using percentage clip visualization. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

for the dormouse is still highly concentrated within its patches (it is a forest-specialist species), but there is more abundance of suitable habitat in the landscape matrix. This is reflected in the histogram having many values close to zero but a larger standard deviation. Finally, the higher mobility of, and the more general habitat suitability for the hedgehog is well represented in the histogram's much larger relative mean and standard deviation. Note that pixel count has been log-transformed to improve visualization, due to the extreme accumulation of close-to-zero values for highly isolated species.

3.3. Evaluating the effect of spatial scales

Fig. 5 shows the results of the analysis scale comparison; determining the appropriate scale is important because larger sizes allow for reduced software processing times, which may be critical for assessing larger landscape scales. In this study, running the analysis at a 1 km buffer and a 3 × 3m cell size took longer than running the same scenario with a 5 km buffer and a 9 × 9 cell size (12 h 12 min vs 10 h 35 min). In the extreme, running a 10 km buffer with a 3 × 3m cell size was estimated to take 50 days on the same laptop device. In addition, concerning running times, the size of the *mwr* was the factor that seemed to have the greatest effect on the run times. For example, running the analysis at base-case scale for the *core-based* approach, took 8 min for adder (*mwr* = 41 m), 10 min for dormouse (*mwr* = 40 m), 2 min for water vole (*mwr* = 69 m) and 10 h 35 min for hedgehog (*mwr* = 262 m). No differences were found in the connectivity patterns based on buffer extent or cell size. However, at larger spatial scales, the maximum cumulative connectivity was lower, and the current was more diffused since it is not dominated by smaller high-conductivity areas. This allowed for better differentiation of connectivity features such as hedgerows.

3.4. Evaluating differences between species

Bearing in mind the effect of the methodological choices and visualization techniques above the effect of the species ecology as represented through these techniques can be addressed (Fig. 6). The different habitat needs and dispersal abilities of each of the focal species resulted in vastly different connectivity patterns illustrating how the same landscape can be highly connected for some species (*e.g.*, hedgehog) and disconnected for others (*e.g.*, adders and water voles).

Adder. Heathlands are rare, fragmented, priority habitats at risk due to the recent decline in their extent (Natural England, 2011). Due to the adder's low dispersal capabilities and fragmented habitat, the landscape matrix is almost impenetrable resulting in high isolation for the species. Due to this, analysis in Omniscape reflects almost zero connectivity values between habitat patches (Fig. 3). In contrast, Circuitscape was better able to show possible dispersal paths between potential habitat cores (Fig. 2a). However, it should be remembered that, although the paths reflected in Fig. 2 a suggest a degree of connectivity between habitat patches, such connectivity is still extremely low.

Water vole. Similarly to the adder, the landscape resistance for the water vole is very high due to their specialization in water courses. In addition, most of the watercourses in the study area cross urban areas, therefore interrupting the potential connectivity that water features

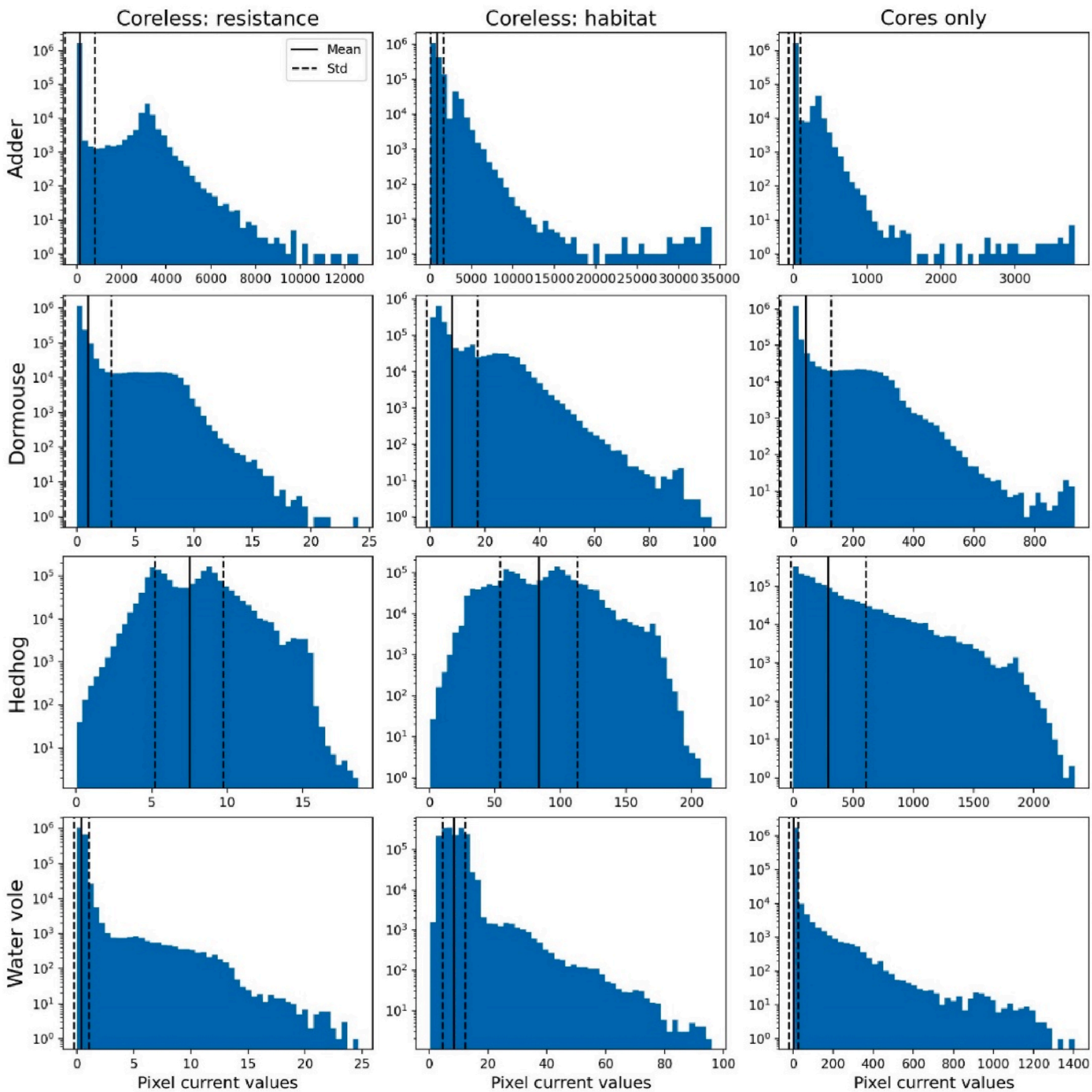

Fig. 4. Histogram representing the pixel count in logarithmic scale (y-axis), against the intensity of cumulative current in each pixel (x-axis), for the models presented in Fig. 3. The continuous line represents the mean of current values; the striped line represents the standard deviation.

provide to water voles.

Dormouse. Although the dormice are still isolated within their habitat patches, their potential habitat is more widespread and connected than the adder's, resulting in a more permeable landscape matrix. Fig. 3 also shows that, similarly to the water vole, urban areas act as an impenetrable barrier for the dormouse. The analysis shows the importance of hedges for the dispersal of this species, since areas with higher hedge density appear more connected, which is fully consistent with the literature (Büchner, 2008).

Hedgehog. The hedgehog is the most generalist of these focal species, resulting in a landscape matrix that displays as far more permeable than any of the other three species, even within urban areas (Figs. 3 and 6). The highest connectivity values for hedgehogs were found at the southwest and northeast of the study area, as well as on the northern edge of Blackwell Farm, corresponding with areas of broadleaved woodland. This is consistent with the literature as hedgehogs forage in pastures (which are abundant in earthworms) but mainly rest in wooded areas (Driezen et al., 2007).

The models indicate how ground-dwelling mammals and forest specialists, which rely on arboreal and bushy features to thrive and disperse, can be encouraged through careful design of the development and associated green infrastructure (including BNG sites), whereas the site lacks connectivity significance for the other two species, the adder and the water vole. The next section describes the significance of these

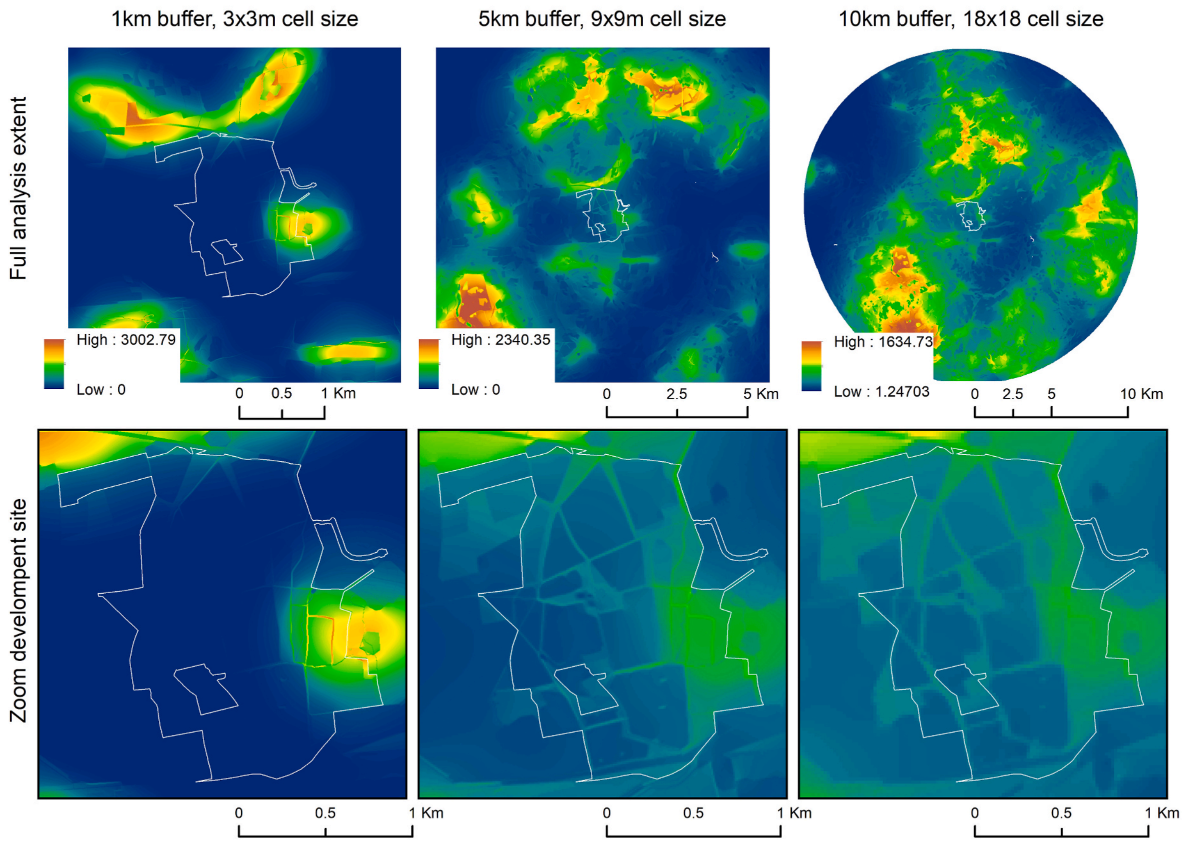

Fig. 5. Cumulative current map for the hedgehog comparing the effects of buffer and cell size, using the core-based approach. Larger cell sizes result in better visualization of intermediate connectivity areas, as the plots are not dominated by very high-connectivity areas. The upper maps display the total spatial extent of the analysis, the lower ones are zoomed in to show primarily the Blackwell Farm site extent (grey outline).

results for Blackwell Farm and discusses the significance of these experiments for the BNG context.

4. Discussion

4.1. Main challenges for applying this connectivity modelling in a BNG context?

One of the objectives of this study was to investigate the challenges that practitioners working in non-academic planning and environmental fields can be expected to face in performing this analysis, and to suggest ways these may be overcome. Similar to the results found by Bergsten and Zetterberg (2013), this study faced similar difficulties when implementing connectivity analysis techniques, and also defined new challenges. Each of these challenges is key for the successful application of connectivity analysis techniques in practice.

4.1.1. Focal species

This challenge refers to the selection of a relevant suite of species for the connectivity analysis. This step is critical because the selection of species will affect the prioritization outcomes (Meurant et al., 2018). Based on the literature and the results of this study, the following guidelines and observations are proposed as a starting point for focal species selection. The chosen focal species for a given scenario should:

- Have significance in the conservation objectives for the study area, such as specialised, rare and/or endangered species (Ehlers Smith et al., 2019). For example, the creation of an ecological network for an endangered species will likely be advantageous for local biodiversity goals in the study area.
- Account for a wide range of dispersal behaviour (Kintsch et al., 2005). This is important because using high-mobility species exclusively will fundamentally fail to represent the vast numbers of less mobile species, for which connectivity may be a far more important factor in their conservation. However, using low-mobility species exclusively may miss large-scale landscape connections.
- Achieve a balance of keystone, foundation, indicator, flagship and umbrella species that represent all the principal community types within the study area (Miller, 2003). In addition, particularly for BNG delivered close to urban areas, the inclusion of flagship species may grant public support for biodiversity conservation. It is important to highlight that a single species may fall under more than one category, which emphasizes the need to define the purpose of each species carefully.
- Regarding the number of species to be selected, Meurant et al. (2018) found that the use of a higher number of species resulted in more effective, comprehensive and congruent prioritization schemes. In their study, 5 to 7 species per (priority) habitat type, with diverse habitat needs and movement abilities was found to be optimal.
- A workshop of regional experts, as described by (Kintsch et al., 2005), could be the best approach for selecting a such suite of species.

All in all, a careful assessment of the relevant focal species for inclusion in the connectivity analysis is the first step for any practitioner performing this analysis. The selection of a suite of species that represent a range of behaviours, dispersal mechanisms and habitat requirements is the best approach for ensuring that the modelling outputs reflect the overall needs of the species in the landscape.

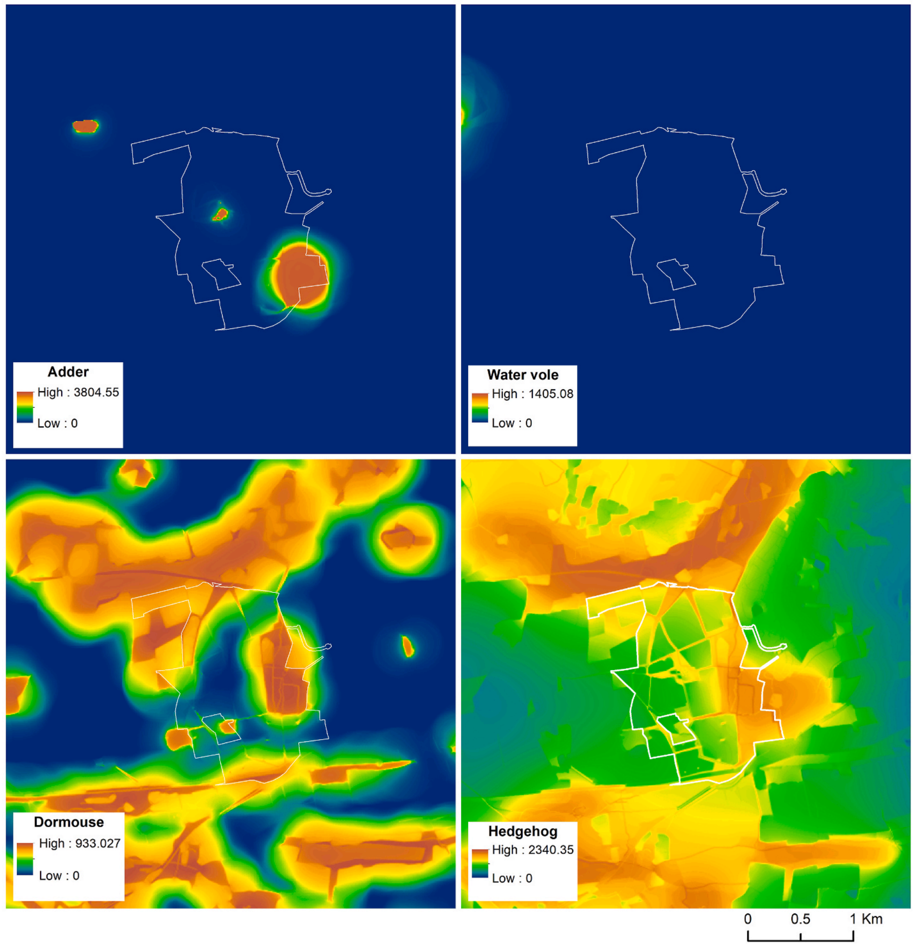

Fig. 6. *Species connectivity within, and immediately around, the development site, using the core-based approach and the* histogram equalize *visualization. The grey outline represents the boundary of the Blackwell Farm potential development site.*

4.1.2. Model requirements for landscape data (maps) and model parameters (habitat and resistance values)

The lack of biological data is a well-known limiting factor for calculating functional connectivity metrics (Keeley et al., 2021). The main input to Omniscape and Circuitscape is a comprehensive and detailed habitat map of the area for analysis. This includes a land cover map, but also other environmental features that can be strong barriers or corridors for the species, such as rivers or roads. Some environmental features that could be meaningful for the species dispersal are not, however, well represented in the analysis due to the lack of available data. For example, there is no database of Sustainable Urban Drainage systems, which may be important for predicting water vole presence in urban areas (Leivesley et al., 2021). Similarly, the data layer for hedges only includes those present in Biodiversity Opportunity Areas identified by the Surrey Wildlife Trust. In addition, to represent greenspaces in urban areas, we could only obtain ORVal Parks database, which does not include private gardens that are suitable habitats for hedgehogs and other urban species (Baker and Harris, 2007).

The lack of model parameters for the selected species is another data availability challenge. Practitioners performing this type of analysis will need to produce or obtain habitat and resistance values for each habitat and environmental feature included in the GIS data layers, which in this study was done via expert elicitation. A lack of such data for the model parameters was experienced for one of the focal species considered initially for the analysis (the butterfly Adonis Blue, *Polyommatus bellargus*, a focal species for calcareous grasslands), and this species consequently had to be left out of the focal species set due to no expert survey responses. Therefore, as it stands presently, the strategic significance of the site for this chalk grassland species connectivity is not accounted for.

In addition, some caution is needed with the process of expert elicitation due to possible biases in this process (O'Hagan, 2019). In future applications, it is recommended that the order of the habitats included in the questionnaire is randomized, and the dispersal for the average habitat/resistance values should be evaluated and tested to reflect the very high levels of heterogeneity among expert opinions. If such heterogeneity occurs, a more participative approach that looks for consensus judgement may be more appropriate (O'Hagan, 2019). In addition, empirical approaches to obtaining these values can be considered as another option; they are the least subjective, yet they are extremely time and resource-intensive (see (Braaker et al., 2014), (Driezen et al., 2007)).

4.1.3. Spatial scale

A challenge faced by practitioners when mapping resistance-based connectivity across large areas is the computational power required to run these models, which can limit the number of cells or the extent of the study area that can be analysed (Koen et al., 2019). Solutions to overcome this problem include the use of supercomputers (unlikely to be available for many practitioners) and/or using parallel processing (an option that is available both in Circuitscape and Omniscape, but which requires a suitable computer). To overcome these computational problems, practitioners can lower the spatial extent of the analysis and/or increase cell size. However, small patches or barriers may be *lost* when selecting a coarser pixel size, and a smaller spatial extent may result in the exclusion of cores or connectivity paths that alter the connectivity patterns of the landscape. It is well known that numerical landscape connectivity indices are affected by the scale (extent and pixel size) of the source spatial data (Pascual-Hortal and Saura, 2007) and that the patterns displayed in connectivity maps when using Circuitscape in the traditional pairwise mode vary depending on the scale (Koen et al., 2019).

In the BNG context, large-extent connectivity maps can be useful for the creation of Nature Recovery Networks that may guide gains at regional scales. Additionally, long-term conservation planning should cover the species conservation requirements at broad spatial scales, allowing connectivity to be planned for broader time horizons. At the same time, small pixel sizes will be useful at development scales to aid developers in fine-grain decisions such as regarding how to minimize impacts on connectivity and how to maximize the connectivity onsite through the best distribution of the BNG units (Rudnick et al., 2012).

There is little guidance available in the academic literature on these considerations. Consequently, a clear 'best-practice' framework is lacking for practitioners to decide on study area extent or cell size. Among the existing literature, McRae et al. (2016a, 2016b) recommend running the models at various scales and comparing the results with local permeability analysis. In the present study, we investigated how different spatial scales and cell sizes affected Omniscape's outputs for the hedgehog. No changes in connectivity patterns were found based on the spatial extent (1, 5 and 10 km buffers around the development site) nor cell size (3, 9, and 18 m cell size). At larger spatial scales, the maximum cumulative connectivity was lower, and the current appeared more diffused, since it is not dominated by smaller superconductive areas, allowing for better differentiation of connectivity features such as hedges.

This is contrary to the findings of Pascual-Hortal and Saura (2007) who, using Circuitscape in pairwise mode, found that the analysis of connectivity at smaller map scales impeded the detection of larger-scaled patterns of connectivity. This contradiction can perhaps be attributed to the differences in modelling approaches between Omniscape and Circuitscape. In pairwise mode, Circuitscape finds the best pathways between pairs of cores and adds up the resulting current maps for all pairs of cores; therefore, the inclusion of cores due to the use of larger spatial extents of smaller pixel sizes would affect such patterns. On the other hand, Omniscape produces *omni-directional* connectivity using a moving window to develop an overall connectivity surface. Hence, we consider that Omniscape is more robust than Circuitscape for mapping larger spatial extents and the tiling approach of Pascual-Hortal and Saura (2007)—which allows producing connectivity maps at large spatial scales whilst maintaining small cell sizes—may be better suited for use with Omniscape than Circuitscape for constructing high resolution, large scale connectivity maps.

Based on this and our experience in the case study, we recommend that future research should investigate the effect of map tiling with Omniscape's models. The ecological requirements of the target species clearly must also be considered when choosing the spatial scale. For example, for species with long dispersal distances, the spatial extent must be larger to capture the connectivity of cores further away. Similarly, the spatial resolution can be lowered for species with large home ranges, since losing small patches of suitable habitat will not affect the overall connectivity of the landscape for such species.

4.1.4. Source strength

Because this analysis is an early application of Omniscape, insufficient literature could be found on the effects of using different Omniscape inputs for the source strength layer. Therefore, three approaches, requiring increasing data and/or effort from practitioners were assessed.

The *core-based* approach consisted of pre-identifying the habitat cores and using the pixels within the cores as the only current source. This is the most data-hungry option, as it requires a resistance raster surface, a habitat value raster surface, and dispersal distances and home range values to calculate core areas, in addition to increased computing effort since more tools (*e.g.*, Gnarly Core Mapper) are needed to produce a cores layer. However, this approach is arguably the most ecologically grounded since the identification of habitat cores drives explicit consideration of the minimum home range size, which is necessary for the conservation of the species population. This means that suitable habitat patches that are smaller than the minimum requirements for the species are *not* included in the analysis, as they are not considered core sites.

The *coreless-HV* approach uses habitat value as the source strength. It does not require pre-identification of cores but does require the creation of a habitat value raster layer. The output maps were very similar to the *core-based* approach.

The *coreless-IRV* approach was produced by Omniscape's developers to reduce data needs as the resistance layer can be used as the source layer. This method requires obtaining a single resistance value for each class item in each data layer, as opposed to obtaining both resistance and habitat value. It assumes that pixels with low resistance are equivalent to a high habitat value, which is true in many cases. For example, for a forest species, a pixel of a forest habitat will have a low resistance as well as a high habitat value. However, this is not the case in several other instances (*e.g.*, a gravel path will have a low resistance value for a mammal, but it does not imply that it has a high habitat value). In other words, habitat value will not be directly equivalent to the inverse of resistance value in many cases. Despite this, the connectivity patterns resulting from this approach closely resembled those of the other methods.

Because no substantial differences were observed in this research between the three connectivity modelling methods, future assessments may opt to employ only the *coreless-IRV* approach, reducing analytical time and data needs. From an ecological point of view, this approach is something of a pragmatic compromise because the identification of habitat cores beforehand is highly appropriate as it includes more species parameters (for example, the size of cores that match the species' home range needs).

4.1.5. Dispersal distances and home ranges

In the connectivity modelling, the species' ability to disperse is reflected in the *mwr* value, which reflects the capacity of an individual to search for suitable habitats (Landau et al., 2021). Different studies have selected *mwr* values using different criteria ((de Rivera et al., 2022), (Thorne et al., 2020), (Jennings et al., 2020)) and such values can be obtained from the existing literature (such as in this study), movement data and/or expert judgement. This process was also found to be challenging in the present study, since different studies report significantly different values for the same species (*e.g.*, hedgehog), some species being understudied (*e.g.*, adder) *etc*. It can be recommended that the chosen *mwr* for a given scenario should satisfy the following:

- For species with several values reported in the literature, results of studies undertaken close to the study area should be preferred to better reflect the particular behaviours of local populations.
- It is worth distinguishing between migration distance, home range values and daily movements. It makes ecological sense that, for species with a clear dispersal phase in their life history, this value is used (*e.g.*, the adder). However, for species that do not have a clear dispersal phase, the radius for the home ranges or daily movements is a good indicator of their ability to search for new habitats. For species that show great variability in home ranges (*e.g.*, the hedgehog), the largest value should be preferred because it will better reflect the minimum core size that is required for the species' survival.
- According to the existing literature (Schloss et al., 2022), the use of larger *mwr* (*e.g.*, 50 km) allows accommodation of dispersal over longer periods, while still being representative of the short distances that characterize less mobile species. However, we did not find an ecological explanation for this assertion, and recommend using this approach of large *mwr* to model connectivity across large spatial

scales (*e.g.* at the county level) *only* if the results are complemented with smaller spatial scales where ecologically comprehensible *mwr* (*e.g.*, home range and dispersal distances) is used (McRae et al., 2016a, 2016b).

All in all, the best approach to selecting *mwr* depends on the ecology of the species assessed. There are many options to choose from, and a careful justification based on the best evidence needs to be made.

4.1.6. Interpretation of results

Academic papers rarely indicate which visualization technique is used to display cumulative current flows. In addition, very little guidance was found on best practices for visualizing and interpreting Circuitscape or Omniscape outputs. However, visualization techniques affect the interpretation of the results. For example, Fig. 2.2 and 2.3 depicts the same results arising from the same input data but using two different visualization techniques. Whereas the landscape matrix in Fig. 2.2 may be interpreted as highly connected, Fig. 2.3 and associated species histograms in Fig. 4 indicate extremely low connectivity across areas. Fig. 2.2 should therefore be interpreted as pathways of the higher likelihood for movement of the adder, although the likelihood of using these pathways is very low. Therefore, caution must be used when interpreting Circuitscape results because its map visualization may compromise the interpretation for species that are highly isolated, such as the adder.

In addition, caution must be taken in some special cases. When interpreting the output maps, high current values typically represent high movement potential, and the pattern of the current flow describes the network of pathways with higher probabilities of movements. However, for sections of the landscape that have little variation in resistance (*e.g.*, highly intact landscapes), or where current can spread out in many different directions, current will not become highly concentrated. This can result in valuable landscapes with moderate current magnitudes incorrectly being interpreted as having low movement potential (*i.e.*, low connectivity value) if they are not subject to careful examination (Hall et al., 2021).

To avoid this, the following cautions are advised. Firstly, accompanying the connectivity maps with the histograms representing the pixel count against the intensity of cumulative current in each pixel (Fig. 4) is extremely valuable. The histograms depict the level of isolation of the species in the landscape, without accounting for the possible biases caused by the visualization techniques used in the map outputs. Secondly, careful consideration of moderate flow values is needed which, as explained above, can indicate diffuse yet effective, near-natural levels of connectivity, with multiple redundant pathways for movement rather than weak or ineffective connectivity (Hall et al., 2021). To avoid misinterpretation in these cases, Hall et al. (2021) recommend studying the resistance and source strength surfaces alongside the model outputs, to discern whether the moderate current values represent large expanses of suitable habitat.

4.1.7. Circuitscape or Omniscape?

When circuit theory is selected as the best approach to model connectivity, practitioners will be faced with a decision between Circuitscape and Omniscape. Because Circuitscape is better known and has been widely used for conservation work, practitioners may prefer to use Circuitscape as it is well accepted by the academic community, and there is more literature on its use and interpretation. However, it is important to guide the decision with an understanding of the strengths and limitations of these models to evaluate connectivity (Rudnick et al., 2012).

Each algorithm is best suited to somewhat different applications and so the choice of which to use should depend on the focal species. Circuitscape (in pairwise mode) is well suited to predicting movements between defined habitat blocks that act as obvious source and destination points (*e.g.*, adders and water voles), whereas the Omniscape approach can estimate connectivity in regions that do not have distinct habitat blocks (*e.g.,* hedgehogs and dormice). Therefore, as previously discussed, consideration of the species' ecology and behavioural features should be the first step for selecting the best connectivity approach.

4.1.8. Software requirements

Both Circuitscape and Omniscape are open-source software and do not need associated software to be run. However, creating the resistance, habitat and core layers in this study was done using an associated software Gnarly Landscape Utilities (McRae et al., 2014; Shirk and McRae, 2013) that is only available for ArcGIS 10 with the Spatial Analyst extension. ArcGIS is a licensed software and not all practitioners may have access to it. Although other approaches can be used for creating habitat and resistance raster, these tools were specifically created by Circuitscape developers to support connectivity analysis and enormously facilitate this task.

This finalises the recommendations for the challenges identified in the literature and experienced while performing these analyses. These practical recommendations are intended for real-life practitioners who need to inform important planning decisions on any landscape, development site or area. Next, how these results can guide habitat loss avoidance and creation is considered.

4.2. Development schemes and contributions to creating/maintaining ecological networks

This modelling approach allows evaluation of the effects of potential future landscape changes on habitat connectivity, which can enable the development of sustainable strategies in urban planning and the implementation of conservation measures that take into account habitat connectivity, a fundamental requirement for maintaining and enhancing urban biodiversity (Braaker et al., 2014). Electric circuit models are particularly good at highlighting *pinch points* because in locations with few options for movements, such as a green bridge over a highway, current will concentrate into a small number of pixels (Hall et al., 2021). Therefore, the pinch points signal a high risk of connectivity loss through a relatively small amount of landcover change; something of particular importance concerning avoiding severing corridors during the design of developments.

The models in Figs. 3 and 6 depict the likelihood for four focal species to move through and around the development site; the yellow to red colours represent flow that is channelled around areas of high resistance or barriers, which can be natural or manmade. At the moment, such areas are agricultural fields and urban areas. The high connectivity areas vary depending on the species evaluated. For water voles, the area has extremely low connectivity value. For the adder, there is suitable habitat corresponding to an area of neutral grassland, but this patch is highly isolated from any other. Therefore, one could argue that the development site and immediate surroundings cannot be considered ecologically relevant for habitat improvement or the creation of heathland and water-related species. For the dormouse, the connected cores are highly restricted to woodland areas that in most cases are too far apart to be properly connected in the current land configuration; existing hedges provide some degree of connectivity, but the strategic use of green infrastructure within the new housing development may be able to enhance such connectivity. For the hedgehog, current flow is more diffuse across the whole area, but still concentrated in non-agricultural areas; existing hedges appear as highly important connectors. The loss of habitat in high-connectivity areas could prove to be the most damaging to the connectivity of the urban planned environment for the species examined here.

But in addition, these models can be used *proactively* to visualize the effects of habitat creation and/or improvement, and how these could facilitate movement for two of the focal species: the dormouse and the hedgehog. This allows developers and land planners to understand that this area has high importance for ground-dwelling mammals and forest specialists, and therefore how the enhancement of those habitats could be prioritized and integrated into the development planning to enhance particular functional aspects of the overall landscape important for those species, and the associated BNG.

5. Concluding remarks

The application of Omniscape in this research emphasizes how development sites are embedded in the wider landscape, and how species connectivity modelling can form part of BNG considerations for such sites. Clearly, addressing habitat connectivity *alone* is not enough to address BNG, since the effect of habitat loss is larger than the effect of habitat fragmentation *per se* (Fahrig, 2003). This means that, although interconnected habitats are essential for maintaining biodiversity over time, connectedness is not enough if the habitat patches are not able to sustain a population or an individual's territory. Therefore, connectivity enhancement should be incorporated as a valuable co-objective of BNG strategies coupled with increasing the extent and quality of habitats, which are the current objectives of BNG.

Based on this research, it appears highly desirable and feasible to incorporate connectivity modelling into BNG policy, for example through its integration within Defra's Biodiversity Metric. One way to do this would be by creating a single, multi-species map at an appropriate scale by merging several individual species maps (such as the ones generated here). This way, each cell will have a connectivity value that reflects the importance of that parcel for the overall connectivity of the landscape. Such a value could be used as an additional multiplier within the BNG metric. This way, the connectivity value of the biodiversity units within important parcels, both within the site and in the wider landscape, could be reflected in the biodiversity units for the development and its BNG attributes. Further research is warranted to help guide the identification of the best approach(es) to creating multi-species networks for habitat connectivity within the BNG metric, as no perfect solution exists to maximize the benefit for all species (Santini et al., 2016).

Overall, Omniscape multi-model habitat connectivity modelling for wildlife species has been shown here to offer a reasonably efficient and cost-effective approach to representing this key aspect of biodiversity support in the context of development planning. This modelling provides a strong foundation and qualitative and quantitative information for planning decisions; this can be particularly useful for the crucial, but often overlooked, maintenance of habitat networks across the landscape. In addition, this work also contributes to the more general field of the assessment of the movement of species due to external pressures, as the learnings from the experiments can be used in other environmental management processes and the creation of adaptation plans for individual species.

Credit author statement

Rocio Martinez-Cillero: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Software; Visualization; Writing - original draft, review & editing. Ben Siggery: Methodology; Resources. Prof Richard Murphy: Supervision; writing – review & editing. Dr Alvaro Perez-Diaz: Formal analysis; Methodology; Resources; Writing - review & editing. Ian Christie: Supervision. Sarah Jane Chimbwandira: Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data suporting the models in this article (habitat and resistance parameters) have been shared in a public, online data repository: https://data.mendeley.com/datasets/7ry6s7fxb4/1

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