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Review and Synthesis

Defining and quantifying effective connectivity of landscapes for species' movements

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Ecosystem functioning depends on multiple successful interactions, many supported by individual movements. The degree to which the landscape allows these interactions to take place has been referred to as 'effective connectivity' (EC). Many of the cumulative impacts of anthropogenic activities on ecosystem functioning arise from changes in EC. Therefore, a coherent framework to quantify EC is urgently needed. Recent theoretical developments propose that studying EC requires the simultaneous consideration of spatial, environmental and species intrinsic characteristics (SEI framework).

In this paper we further expand the SEI framework by integrating advances in geographic information science, ecological niche modelling, movement ecology, island biogeography and network sciences to develop a comprehensive three-step methodological approach for quantifying EC. First, using niche modelling and movement ecology, we quantify the species movement probabilities with respect to local environmental conditions. Second, we quantify ecological distances between non-adjacent locations by integrating species movement responses to the local environment with the spatial configuration of the landscape using the expected cost obtained from the randomized shortest paths (RSP) framework. This expected cost generalizes the two most frequently used ecological distance metrics, i.e. least-cost distance and resistance distance. Moreover the 'absorbing random walk' properties of RSP allow the integration of new developments in connectivity research, i.e. spatial absorbing Markov chains, to account for movement-related mortality. Third, drawing from island biogeography and metapopulation ecology, we scale ecological distances by relevant species- and area-specific parameters to estimate EC for the ecological process of interest, e.g. migration, dispersal or gene flow.

The integrative and highly interdisciplinary approach we propose can lead to increasingly more realistic measures of EC at different organizational levels. Moreover efficient computation allows its application to large-scale high-resolution landscapes for theoretical studies, conservation planning and sustainable management of real landscapes.

Keywords: Circuitscape, movement cost, landscape resistance, least-cost distance, randomized shortest paths, resistance distance, SAMC, step selection function, survival

Introduction

The majority of the earth's surface is profoundly affected by human developments (Barnosky et al. 2012, Díaz et al. 2019). The resulting loss of natural habitats and connectivity – following a global reduction in species' mobility (Tucker et al. 2018) – are the main drivers of the current ongoing loss of biodiversity (Foley et al. 2005). Connectivity conservation and restoration have been suggested as key strategies for protection of biodiversity under climate change (Heller and Zavaleta 2009). Therefore the quantification of landscape connectivity and the extent to which human activities affect it is central to landscape ecology (Correa Ayram et al. 2016). Despite the large and growing scientific literature on landscape connectivity, the adequacy of current approaches for successful hands-on connectivity conservation interventions has been repeatedly questioned (reviewed by Sawyer et al. 2011, Zeller et al. 2012). This criticism reflects the challenges scientists are currently facing in the arduous process of developing a comprehensive framework for studying connectivity and consequently improving its relevance for applied studies.

Landscape connectivity can be defined as 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor et al. 1993). The movement of individuals alone may, however, be insufficient to infer connectivity for specific ecological processes, such as genetic connectivity among patches (Robertson et al. 2018). Therefore Robertson et al. (2018) coined the term 'effective connectivity' (EC) to indicate landscape connectivity that is followed by the successful reproduction of immigrants. The ecological dynamics affecting the movement process and those affecting reproduction success are generally not the same (Vasudev and Fletcher Jr. 2016, Robertson et al. 2018). We generalize the EC concept's focus on the outcome of movement, in addition to successful movement itself, to other landscape ecological processes involving individual movement, and define EC as 'the degree to which the landscape facilitates or impedes movements that contribute to the focal ecological process'. The factors contributing to the successful outcome of connectivity depend on the ecological process of interest. Following Fletcher et al. (2016), we consider the effectiveness of connectivity for different ecological processes at three organizational levels: individual, population and community (Table 1). For instance, EC for seasonal migration requires connectivity for an individual between suitable seasonal ranges, whereas EC for gene flow requires successful reproduction upon arrival of immigrants (Webster et al. 2002, Lowe and Allendorf 2010, Robertson et al. 2018).

The quantification of connectivity – and even more so of EC – is challenging, as it requires the integration of multiple processes in geographic space (longitude, latitude and altitude) and environmental space (i.e. the multidimensional hyperspace of environmental conditions; Hutchinson 1957). Most connectivity studies have focused on some of these aspects, while simplifying or omitting others. Recent theoretical developments, however, propose quantifying successful dispersal by focusing simultaneously on three aspects: a) spatial constraints due to the configuration of landscape features, b) environmental characteristics and c) species' intrinsic limitations (the SEI framework; Vasudev et al. 2015).

In this paper we further elaborate the theoretical SEI framework (Fig. 1) and present a comprehensive analytical approach for quantifying EC using concepts and cutting-edge tools from geographic information systems (GIS), ecological niche modelling, movement modelling, island biogeography (including metapopulation theory) and network sciences. Our approach consists of three steps, each referring to a pair of the three SEI components (Fig. 2): 1) intrinsic–environment (IE), 2) environment–space (ES) and 3) space–intrinsic (SI). The IE step estimates habitat permeability for a species, from which the ES step computes the ecological distance, from which in turn EC is derived by including other key factors affecting the outcome of connectivity. Below we briefly introduce these three steps, which we further expand in the following sections.

We address first the link between the species' intrinsic movement capabilities and its environment (IE – Fig. 2) by drawing from advances in movement ecology and niche

Table 1. Data requirements for the EC workflow.

Ecological outcome		Data required		
Level of organization	Ecological process	Movement probability S_{ij}	Movement cost c_{ij}	Pre/post-arrival effectiveness ζ_s and ζ_t
Individual	Home range	Tracking	Energy	Resource availability, resource needs
	Seasonal migration	Tracking	Energy and mortality	Seasonal range quality
Population	Distribution	Tracking, CMR	Mortality	Number of immigrants, reproduction, habitat quality
	Gene flow	Landscape genetics	Mortality	Reproduction, genetic distance
Community	Species interactions	Tracking, CMR	Mortality	Habitat suitability, presence of recipient species
	Biodiversity	Tracking, CMR	Mortality	Habitat suitability, competitive exclusion

Overview of data required to measure effective connectivity (EC) for different ecological outcomes. Following Fletcher et al. (2016), we describe the data requirement to evaluate outcomes at three levels of organization: individual, population and community. To estimate EC using the three-step approach, spatially-explicit information is required for three parameters: probability (S_{ij}) and cost (c_{ij}) of movement (in step 2, Fig. 2), and other ecological factors contributing to the outcome of connectivity (ζ_s and ζ_t in step 3, Fig. 2). In step 1, we extrapolate S_{ij} and c_{ij} in geographic space from environmental space, which requires in addition to environmental explanatory variables (e.g. from remote sensing) data about the probability (e.g. tracking, capture–mark–recapture/CMR or genetic data) and cost (e.g. energy expenditure or mortality) of movement. In addition, in step 3 other ecological factors (ζ) are required to assess the effectiveness of connectivity for the outcome of the focal ecological process. See main text for further details.
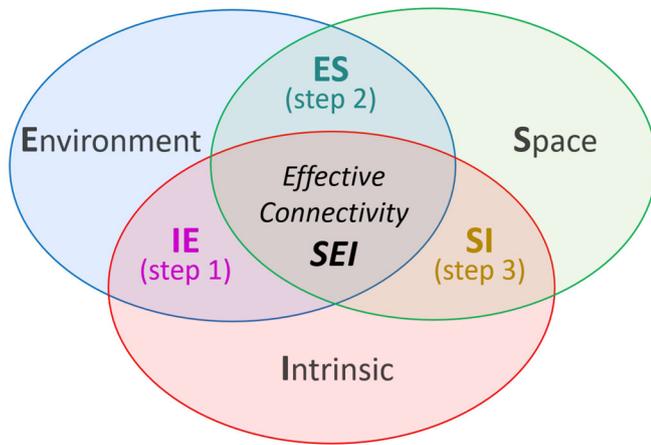
Figure 1. Space–environment–intrinsic (SEI) conceptual framework, adapted after Vasudev et al. (2015). The estimation of effective connectivity (EC) requires the integration of the following three components: environment (E), i.e. the environmental characteristics of the landscape (e.g. vegetation type, altitude, anthropogenic infastructures), space (S), i.e. the spatial configuration of the landscape (e.g. the position of landscape features), intrinsic (I), i.e. the species and process intrinsic characteristics, (e.g. dispersal abilities, trophic requirements, life-history, local population size). Broadly speaking, pairwise combinations of these three aspects represent the study objects of different disciplines. Niche modelling traditionally focuses on environmental factors affecting species occurrence (EI). Applications of network sciences in geographic information systems typically investigate the spatial configuration of environmental features (SE), while frequently overlooking the species' intrinsic characteristics (I). Finally, island biogeography and metapopulation theory traditionally focus on the link between metapopulations and the spatial configuration of habitat patches (SI), while ignoring the environmental (E) characteristics of the matrix and thus oversimplifying the species movement patterns. The assessment of EC requires that all these components (SEI) be integrated, as we propose in the three-step methodological framework shown in Fig. 2.

modelling. Occurrence or movement data are commonly used to estimate the suitability of environmental features with respect to the species' intrinsic requirements or movement preferences in environmental space (Zeller et al. 2012), using methods such as environmental niche models (Guisan and Thuiller 2005) and resource or step selection functions (Manly et al. 2007, Thurfjell et al. 2014). The results of these models are typically used for predictions in geographic space to produce maps indicating the suitability of local environmental conditions for the presence of a species ('preference maps' or 'species distribution maps'; Guisan and Thuiller 2005, Thuiller et al. 2009) or its movements ('friction maps', 'resistance surfaces' or 'cost surfaces'; Zeller et al. 2012). As models in environmental space their treatment of the spatial configuration of the landscape is limited to for instance habitat contiguity and grain size (Boyce 2006, Laforge et al. 2015, Panzacchi et al. 2015). Hence efforts to integrate connectivity in geographic space are of paramount importance (for instance Engler and Guisan 2009, Franklin 2010).

Second, we focus on the link between environmental features and geographic space (ES – Fig. 2), i.e. the manner in which the spatial configuration of environmental features affects the ecological distance, or paths, between a source s and a target t location. Although Euclidean distances are commonly used to represent spatial relationships (but see Fletcher et al. 2016), they are often poor approximations of the actual ecological distance as experienced by an organism (Sutherland et al. 2015), as barriers in the matrix affect movement paths and associated ecological distances. Applications of network theory in GIS science and geomatics are focused on the emergence of landscape connectivity from spatial connections among adjacent landscape features which allows researchers to assess the 'functional connectivity' between pairs of locations by linking the physical structure of the landscape with the organism's response (Taylor et al. 2006). Two movement models are frequently used in ecology to upscale the permeability of local environmental conditions to entire paths between source and target locations (Zeller et al. 2012): optimal movement along the least-cost path (Adriaensen et al. 2003) and random movement using circuit theory (McRae and Beier 2007), which were recently integrated and generalized using the randomized shortest paths (RSP) framework (Saerens et al. 2009, Van Etten and Hijmans 2010, Panzacchi et al. 2016). These network-based methods allow the assessment of ecological distances through the geographic space of the landscape.

Third, we need to assess the effectiveness of connectivity with respect to the outcome of the focal ecological process, which requires two components to be successful: 1) reaching the target, and 2) achieving the strategic objective of the movement. Approaches that build on the theory of island biogeography (MacArthur and Wilson 1967), e.g. large-scale ecological networks (Urban and Keitt 2001), meta-population theory (Hanski and Ovaskainen 2000) or meta-communities (Leibold et al. 2004), rely on the effective demographic connectivity for population persistence between 'islands' of habitat embedded in a non-habitat 'matrix' given a species' movement capabilities. In metapopulation theory the two components of effective connectivity between two patches are represented by: 1) the proximity between the patches, and 2) the number of dispersers from the source and the likelihood of settlement in the target patch (Table 1). The size of the source and target patch have been used as a proxy for respectively number of dispersing individuals and likelihood of settlement (Hanski and Ovaskainen 2000). The proximity between patches is commonly approximated as an exponential function of the Euclidean distance between patches scaled by the species' dispersal abilities (Hanski and Ovaskainen 2000, Urban and Keitt 2001), while environmental characteristics of the matrix are frequently ignored. Unfortunately, Euclidean distance is often a poor approximation of the ecological distance (Sutherland et al. 2015). Therefore the estimation of EC requires the foundation of the aforementioned steps 1 and 2 to obtain ecological distances, rather than relying on mere Euclidean distance. Thus, in this final step to quantify EC, we need to combine the
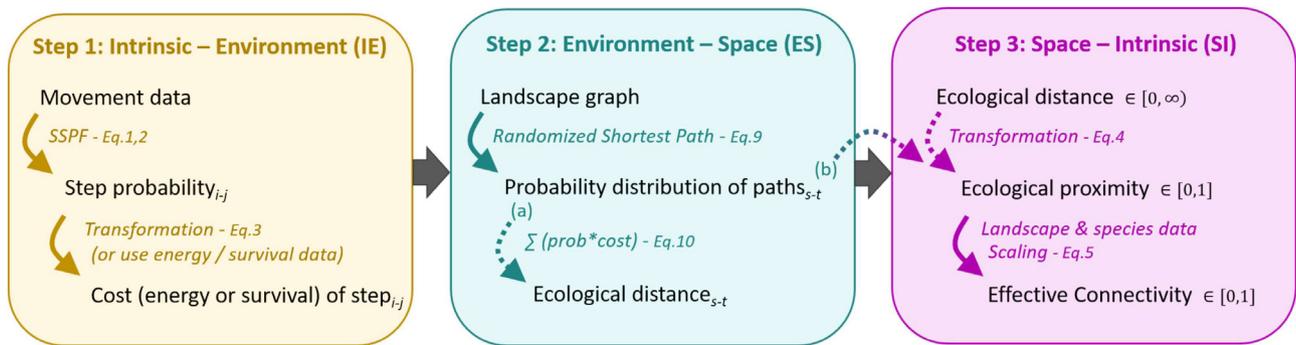
Figure 2. Three-step workflow for the quantification of effective connectivity (EC) based on Fig. 1. First, the intrinsic–environment step estimates the species-specific likelihood of moving between adjacent locations i and j based upon local environmental characteristics. It also infers or estimates (if data on the costs of performing each step are available) the cost associated to each step in terms of energetics and/or mortality risk. Second, the environment–space step scales up this pixel-specific information to the entire landscape, represented as a network of nodes and links. This is achieved first by employing frameworks and algorithms developed in network science (e.g. randomized shortest paths) to obtain the probability distribution of all paths in the landscape. For EC based on energetic costs of movements (a), or a proxy thereof, the ecological distance between a source s and target location t is computed from the landscape graph, which in step 3 is converted into an ecological proximity by including species and process intrinsic movement capabilities. Whereas, for EC based on mortality costs (b), the survival probability is computed, which serves directly as the ecological proximity between s and t. Finally, the space–intrinsic step focuses on the ecological outcome (connectivity for what?). This is achieved using approaches from island biogeography and metapopulation theory to scale ecological proximity with the intrinsic characteristics of the focal species and the ecological process, thus producing estimates of EC.

ecological distances on the landscape with intrinsic characteristics of the focal ecological process and species, such as dispersal distance, home range size, mortality risk, reproductive behaviour, local population size and inter-specific interactions (SI – Fig. 2).

Each of the disciplines mentioned above contributes an important piece of the 'puzzle' of EC estimation. In the following sections we describe advances in each of these disciplines and present a comprehensive three-step approach for integrating them within the SEI framework (Vasudev et al. 2015) to quantify EC (Fig. 2). First, the IE step quantifies the species-specific landscape permeability. Second, the ES step measures the ecological distance between locations using network science approaches to account for the spatial configuration of the species-specific landscape permeability (from the IE step). Third, the SI step converts the ecological distance between locations (from the ES step) into EC, by integrating species- and process-specific characteristics that influence the effectiveness of connectivity for a given ecological process.

Step 1. Estimation of habitat permeability: environment–intrinsic step

The first step in estimating EC (Fig. 2) is to quantify the permeability of landscape features to a moving organism, that is the degree to which they facilitate or hinder its steps or movements. Different terms have been employed in landscape ecology to describe permeability (reviewed in Zeller et al. 2012), the most common of which are movement cost, used for least-cost modelling (Adriaensen et al. 2003) and resistance/conductance in circuit theory (McRae and Beier

2007). In network theory the ease of moving between neighbouring nodes is described using weights, which are labelled differently according to the application, e.g. as 'affinities' in social networks or as 'capacities' in transport networks.

In general two elements contribute to the permeability of a landscape element (Fletcher Jr. et al. 2019): the probability of the agent traversing it and the cost of doing so. The cost of movement is the negative effect of movement on an individual's expected fitness due to both energetic losses and mortality risk. An adapted agent (through natural selection) would show a negative relationship between the probability and the cost of a movement. Individuals can, however, behave maladaptively, especially in human-dominated landscapes, and their movements may lead them to attractive sinks or dispersal traps; for instance Delibes et al. (2001) and Vasudev et al. (2015). Fletcher Jr. et al. (2019) used 'spatial absorbing Markov chains' to model dispersal movements of individuals, where the likelihood and mortality of movement can be treated independently.

Ideally, researchers would have access to independent data informing on these two elements of permeability (Table 1). However, in practice, this is often not the case and researchers may have to assume that movement choices are an adaptive response to environmental characteristics and therefore derive movement costs from estimations of movement probabilities. In the following we first present a synthesis of the most relevant approaches for estimating the probability to move between adjacent cells, i–j, and then discuss a mathematical transformation to obtain movement costs from their likelihood. We discuss in more depth independent probability and cost of movement for the 'absorbing random walk' in 'Spatial absorbing random walk' section.

Estimation of step probabilities

Zeller et al. (2012) reviewed approaches for estimating landscape permeability, from methods based on expert-opinion to resource selection analysis and movement analysis. Different data sources have been used to infer landscape permeability, from observations of individuals to genetic samples and movement data, e.g. GPS tracking data (Table 1). When only occurrence data are available, estimates of habitat suitability or preference are frequently used as proxies for movement probability. This practice may, however, lead to biased estimates, as a species' habitat preference may not adequately reflect the manner in which the environment influences its locomotion. Zeller et al. (2012) concluded that the analysis of high-resolution tracking data provides the strongest empirical basis for inferring landscape permeability, a conclusion also supported by a virtual ecology approach using agent-based models (Simpkins 2017). Note however that also capture–mark–recapture or genetic data can be used to evaluate the probability of movement (Table 1, Sutherland et al. 2015, Remon et al. 2018, Robertson et al. 2018, Peterman et al. 2019).

Step selection functions (SSF) are one of the approaches most widely used to quantify step probabilities that utilize movement data and produce close-up representations of landscape permeability (Fortin et al. 2005, Thurfjell et al. 2014). In movement ecology, the movement between subsequent observations is commonly referred to as a 'step' (Turchin 1998, Calenge et al. 2009), a term which we use more generally to denote transitions between any pair of consecutive locations, e.g. two neighboring pixels. The SSF approach compares environmental attributes recorded along the observed step, such as proportion of a land cover type, maximum traversed slope or road crossings, with those recorded along a set of available random steps that the individual could have takenfrom the same starting point. The predicted SSF is proportional to the probability of an individual crossing a given environmental feature, not equal to it. Lele and Keim (2006) further extended this method to quantify the actual probability that a step will be taken or 'used' given that it is encountered (Lele et al. 2013), which can be used to estimate step selection probability functions (SSPFs). In the SSPF approach also the probability of not moving is estimated; hence the entire distribution of movement is quantified, which allows for the prediction of actual step selection probabilities. SSPFs represent arguably the most theoretically sound analytical framework to quantify organism-intrinsic landscape permeability (Zeller et al. 2012; for a review of alternative methods).

In the approach presented in this paper, we chose to quantify step probabilities using SSPFs. To parameterize an SSPF, the following log-likelihood needs to be maximized (Lele and Keim 2006, Lele 2009; for details):

$$\mathcal{L}(\beta; \mathbf{x}_1, \mathbf{x}_2, \ldots, \mathbf{x}_n) = \sum_{k=1}^{n} \left(\log \pi(\mathbf{x}_k; \beta) - \log P_k(\beta) \right) \quad (1)$$

where $\mathbf{x}_k$ is the vector of L covariates associated to the kth sample from n observed steps in the data set, π is the probability of selection, and $P_k(\beta) = \int \pi(\mathbf{x}; \beta) f_k(\mathbf{x}; s_k) d\mathbf{x}$, where $f_k(\mathbf{x}; s_k)$ denotes the distribution of resources available for step s_k. The available resources for step s_k are sampled with random steps from the same starting point as s_k, having random length and direction (Forester et al. 2009). This likelihood optimization is implemented in the `ResourceSelection` library (Lele et al. 2017) for R (<www.r-project.org>); see demonstration in Supporting information. The probability of a step from i to j is then computed from the SSPF coefficients (for a logit link function):

$$S_{ij} = \frac{\exp(\beta_{SSPF} \times \mathbf{x})}{1 + \exp(\beta_{SSPF} \times \mathbf{x})} \quad (2)$$

where β_{SSPF} and $\mathbf{x}$ are vectors with L elements corresponding respectively to the coefficients from the SSPF and the environmental characteristics of the step (the first element, the intercept, equals 1). Thus, S_{ij} is the estimated probability of the individual selecting step i-to-j, instead of staying at location i, based on the vector of covariates characterizing this step. These step probabilities provide a strong theoretical basis for quantifying organism-intrinsic landscape permeability (Zeller et al. 2012, 2016).

Estimation of movement costs

As discussed above, the landscape permeability depends on two components: movement probability and cost of movement (Fletcher Jr. et al. 2019). The cost of movement can be further divided into energetic and mortality costs. Although, both affect an individual's expected fitness, their integration over a path is not the same. Intuitively, the energetic costs of a path is the sum over all steps, whereas the survival probability for a path is the product of the survival probability at each step. The energetic landscape is commonly estimated using measurements of overall dynamic body acceleration with miniature acceleration dataloggers attached to individuals in tracking studies (Halsey et al. 2009, Gleiss et al. 2011, Pagano et al. 2020), these can be calibrated using physiological measures of energy expenditure from individuals in captivity (Mosser et al. 2014, Pagano and Williams 2019). The spatial distribution of mortality risk can be estimated using habitat-dependent mortality risk, which can be obtained from field experiments (Nowakowski et al. 2015, Fletcher Jr. et al. 2019), habitat-dependent survival analysis (Low et al. 2010, Basille et al. 2013, Plante et al. 2020) or mortality data, such as roadkill data (Zeller et al. 2018, Lin et al. 2019). Whether costs in terms of energy, mortality or both are most important for EC will depend upon the species and scope of the study (Table 1): energetic costs are likely to dominate connectivity at smaller scales (such as within an individual's home range), whereas connectivity at larger scales (such as dispersal between areas) are probably more affected by mortality costs.

Although much progress has been made in the quantification of costs associated to movement using additional data sources, such data remain rare in most empirical studies. It is therefore common practice to derive the movement costs from their assumed negative relationship with the likelihood of movement (but see: Fletcher Jr. et al. 2019). Whereas step probabilities (S_{ij}) are constrained between 0 (impossible) and 1 (certain to be selected, if available), the cost of movement (c_{ij}) is often less clearly defined and may lack an upper bound (although, mortality probability $P_{Mort} \in [0,1]$). As the function used to transform step probabilities into costs defines the cost scale, the choice of transformation affects crucially the ecological distance between two points and therefore the overall estimates of EC. Many mathematical forms could be used to describe this negative relationship between movement probability and cost (for instance Chetkiewicz and Boyce 2009, Poor et al. 2012, Panzacchi et al. 2016). The logarithmic transformation has a theoretical advantage over other transformations when cumulative costs along a path ($\wp$) are considered, as the sum of logarithms is the logarithm of the product. The use of a logarithmic transformation to link step probabilities and cost (Poor et al. 2012) is known in information theory as the 'surprisal' or 'self-information' of the step, i.e. steps with a low probability will have a high surprisal or self-information:

$$c_{ij} = -\log S_{ij} \tag{3}$$

Thus the exponential transformation of cumulative 'surprisal' costs equals the product of step probabilities, which is the likelihood of the path (for further details: Hock and Mumby 2015). Note that this transformation requires that $S_{ij} \in [0,1]$, because, if $S_{ij} > 1$, costs become negative.

In conclusion, as a first step (Fig. 2), we estimated the permeability of each landscape feature by fitting an SSPF to movement data (demonstration in Supporting information) and transforming the resulting step probabilities into movement costs using the logarithmic transformation; as a transformation is an assumed relationship between both permeability components, they should only be used when no independent estimates of movement cost (i.e. energy and mortality) are available. Both step probability and cost surfaces can then be obtained by predicting the step probability and costs on map

Step 2. Quantification of ecological distances: environment–space step

From steps to movement paths

The second step in estimating EC consists of upscaling the local pixel-based information on movement permeability, i.e. step probability and/or cost, to movement paths at the landscape scale. That is, it uses information on steps between adjacent cells i and j to identify entire paths between non-adjacent source s and target t locations. Methods developed in network science are frequently used to assess how the spatial configuration of the landscape affects the ecological distance between s and t (Fig. 2; Dale 2017). Network science, in general, studies phenomena that can be represented as graphs, i.e. mathematical abstractions consisting of nodes connected by edges, each of which can have attributes. The computation of the ecological distance between locations is achieved by representing a landscape as a graph, where the connection between two neighbouring cells is represented by the step probability (S_{ij}) and/or cost (c_{ij}). Different choices exist for modelling paths between non-adjacent source and target cells s and t along steps between adjacent cells i and j. The two most frequently used are optimal or least-cost paths (LCPs; Adriaensen et al. 2003), and random paths based on circuit theory (McRae and Beier 2007, McRae et al. 2008).

The LCP is the path between s and t with the smallest accumulated cost (the 'least-cost distance'). It relies on the assumption that individuals have perfect knowledge of the global landscape and make optimal movement choices. Thus the LCP approach usually identifies a single, one-pixel-wide path, while ignoring all other alternative paths, which leads to heavily biased estimates of connectivity in real landscapes. In a somewhat 'ad hoc' attempt to diminish the severity of this problem, researchers have buffered LCPs to incorporate adjacent areas (LaRue and Nielsen 2008) or summed a number of LCPs (Beier et al. 2008). Unfortunately, these solutions have limited theoretical support.

McRae and Beier (2007) and McRae et al. (2008) pioneered the use of random walks based on circuit theory, one of the oldest branches of electrical engineering, for landscape connectivity studies. Circuit theory describes the movements of electricity on a network, which is analogous to the movement of random walkers on undirected graphs (Doyle and Snell 1984). The random walk relies on an assumption that is opposite to that of the LCP, i.e. that individuals have no knowledge of the landscape and respond only to their immediate surrounding of adjacent cells. Another more implicit assumption in the random walk model is the immortality of the walker. However, Fletcher Jr. et al. (2019) recently used 'spatial absorbing Markov chains' or 'absorbing random walks' to explicitly include mortality into random walk movements. The random walk approach uses resistance distance (and related metrics: commute time and commute cost distances; Chandra et al. 1989, Klein and Randic 1993, Kivimäki et al. 2014) to quantify the distance between s and t, which explicitly takes into account the number of alternative paths between the two locations, in contrast to the LCP approach. Circuit theory, and its associated popular software for ecological applications Circuitscape (McRae and Shah 2009, Anantharaman et al. 2020), have rapidly gained popularity for connectivity studies (Marrotte and Bowman 2017, Dickson et al. 2019). Unfortunately, as the number of possible paths increases, as in the case of large or high-resolution landscapes, the chance of a random walker finding its target becomes increasingly dependent on the number of local connections leading to this

target, rather than on the global properties of the entire paths, such as path costs. This phenomenon is known as the 'lost in space' or 'global information loss' problem (Von Luxburg et al. 2010a, b, Nguyen and Mamitsuka 2016, Odor 2017).

Thus, whereas optimality approaches, e.g. LCP, focus solely on the cost of a single path and ignore the multitude of paths, random walk approaches suffer the opposite problem. This can be readily observed in a simple simulated landscape. Figure 3 (top row) shows that widening a corridor, i.e. increasing the number of paths, affects least-cost distances very little. Conversely, expected-cost distances for the random walk (bottom row in Fig. 3) are relatively uniform (especially with a wide corridor) with an edge effect (i.e. the increased expected cost of reaching edges and especially corners). This edge effect is caused by the dependency of the distance on the local characteristics of the cells, i.e. the number of neighbours, rather than their global characteristics. The distances have become also relatively uniform within each patch, as the global properties of the entire path have been lost, e.g.

its length, probably corresponding to the 'lost in space' phenomenon. However, in these small landscapes, not all global information has disappeared from the random walk distance in the presence of a very strong bottleneck (lower left panel in Fig. 3), and the difference between the two patches becomes smaller as the corridor becomes wider.

Randomized shortest paths framework

Because individuals are unlikely to move either perfectly optimally (and be omniscient) or eternally at random, landscape connectivity depends on both the number of paths and their overall cost. Advances in computer science inspired by work in transportation science (Akamatsu 1996) recently led to the development of the randomized shortest paths framework (RSP; Saerens et al. 2009), which defines a probability distribution over all paths between a source and target using a 'randomness' parameter. This 'inverse temperature' parameter θ controls the degree of randomness in the movements (Saerens et al. 2009, Kivimäki et al. 2014). When $\theta = 0$, the
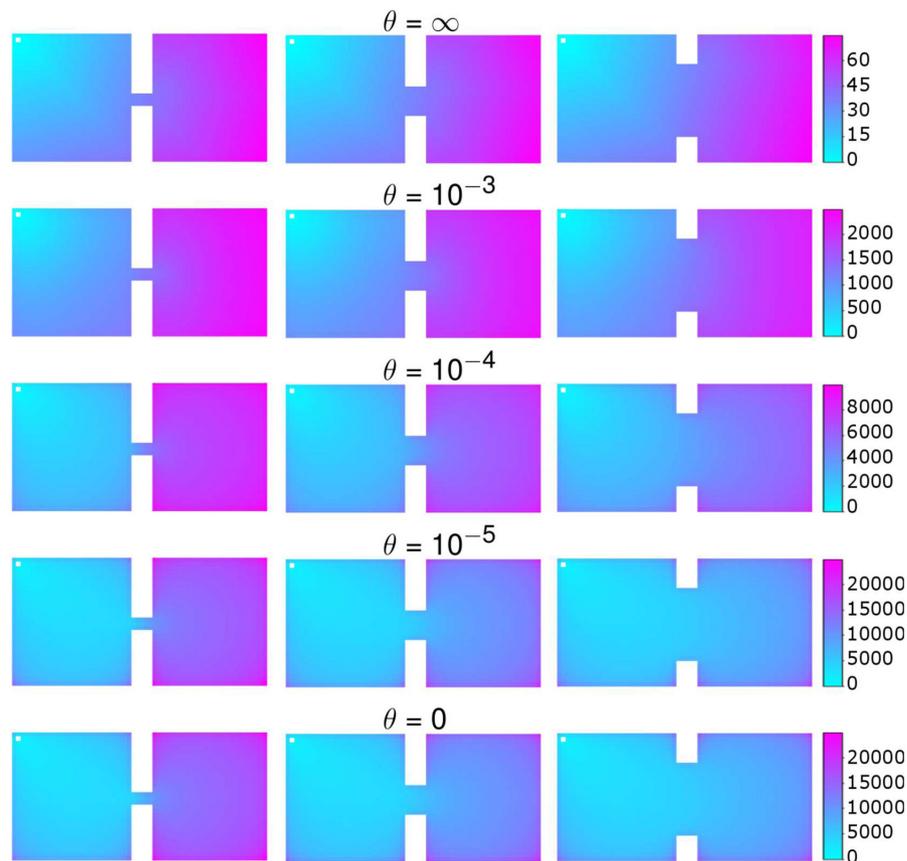
Figure 3. Effect of the randomness parameter in the randomized shortest paths framework on expected cost distances in three simulated landscapes. The expected cost from the white pixel in the upper left corner of the landscape to all other pixels is shown. The columns depict from left to right an increase in the corridor width, whereas the rows show a decrease in the randomness parameter θ from the least-cost path in the top row ($\theta = \infty$) to random paths in the bottom row ($\theta = 0$). The top row shows that the least-cost distances are sensitive for the Euclidean distance from the source, whereas increasing the number of paths by widening a corridor affects them only little. In contrast, the expected-cost distances for the random walk on the bottom row are less affected by the Euclidean distance from the source and therefore relatively uniform (especially with a wide corridor), moreover they show an edge effect (i.e. the increased expected cost of reaching edges and especially corners). See main text for further explanation and discussion.

RSP distribution equals a pure random walk probability distribution over all paths between s and t; as θ increases, the RSP distribution increasingly emphasizes paths of lower cost, until it finally focuses exclusively on the LCP (as $\theta \rightarrow \infty$). Hence the RSP distribution bridges the gap between the extreme assumptions associated to both random walks, i.e. random movements without knowledge of the landscape, and the LCP approach, i.e. optimal movements based upon perfect knowledge of the landscape. That is, θ influences the degree to which movements are determined exclusively by the transition probabilities (or 'choice probabilities' sensu Lele et al. 2013) between adjacent locations or by the cost of the entire path between non-adjacent source and target locations, respectively. Figure 2 (2nd and 3rd row) demonstrates the sensitivity of RSP to both the cost and the number of paths for intermediate values of θ, as the ecological distances to the source are affected by both the widening of the corridor (number of paths) and an increasing Euclidean distance (path costs). The θ parameter thus controls the relative importance of the cost of paths and the number of possible alternative paths, which renders the RSP framework especially attractive for connectivity studies in ecology. We demonstrate the use of RSP using the `gdistance` (van Etten 2017) and `samc` (Marx et al. 2020) libraries in R (<www.r-project.org>; Supporting information).

Following its recent introduction into movement ecology, the RSP framework has already been applied to a variety of data, such as archaeobotanical and genetic data (Van Etten and Hijmans 2010, Gruber and Adamack 2015), and GPS tracking data for reindeer (Panzacchi et al. 2016), caribou (Fullman et al. 2017, Long 2019), grizzly bears (Peck et al. 2017) and elk (Brennan et al. 2018). RSP generalizes and extends previous approaches used in movement ecology, and its flexibility allows the identification of more realistic movement corridors as compared to either the LCP or random walk approaches (Panzacchi et al. 2016). Hence we chose this framework to scale up step probabilities and costs between adjacent i and j locations to entire paths between non-adjacent source and target locations at the landscape scale. We provide a brief overview of the RSP framework in the Supporting information and refer to Kivimäki (2018) for a technical review. Note that, in addition to RSP, other interesting approaches have been developed to interpolate between LCP and random walk distances (Fouss et al. 2016), such as the logarithmic forest distance (Chebotarev 2011) and the p-presistance distance (Herbster and Lever 2009, Alamgir and Luxburg 2011). However, up to now, these alternatives seem to lack the interpretability or computational convenience of RSP (Kivimäki et al. 2014) and have not been introduced yet into ecological applications. This could be an interesting avenue left for future work.

Randomness in ecological distances

The main advantages of RSP are its flexibility and its generality, and that it allows more realistic movement corridors to be modelled as compared to either the LCP or random walk approaches. However the cost of its flexibility implies that the level of randomness, $\theta \in [0,\infty)$, must be set explicitly for the ecological process of interest. Note, however, that when adopting either the LCP or random walk approach the user implicitly also sets the level of randomness (respectively $\theta \rightarrow \infty$ and $\theta = 0$), which represent only the extremes of a continuum. As Marrotte and Bowman (2017) noted, researchers should recognize the bias they may be adding when choosing one of these extreme parameters. Moreover, intermediate values of 6 are more likely to describe adequately species movements in real landscapes than any of the two extremes themselves (Panzacchi et al. 2016).

No protocol has yet been developed for selecting the best θ-value for any given ecological process. Several authors have, however, tested a range of values and validated the choice on observed species movement data. For instance Panzacchi et al. (2016) used the GPS tracking data of migrating reindeer to estimate the randomness that minimizes the deviance between the modelled movement flow obtained from the RSP approach and the empirical one obtained from the observed trajectories collected over several years. In their study θ was thus a combination of intra-individual randomness and inter-individual plus inter-year variation. Recently, Kivimäki et al. (2020) developed a maximum likelihood method for the estimation of θ from individual movement data given a permeability and cost surface and applied it also to reindeer GPS-tracking data. In this case θ was estimated for each single trajectory, and thus the randomness was estimated for a single individual in a single year. In general the RSP framework can be interpreted in different manners, which affect the meaning of θ and guide the steps leading to its parameterization (Kivimäki 2018). We first explore the role of θ in the context of RSP as a model for movement with incomplete knowledge and then, in 'Spatial absorbing random walk' section, discuss θ further as a scaling parameter of the absorption rate in its 'absorbing random walk' interpretation.

Similar to the contribution of both movement probability and cost to the permeability of landscape features, i.e. the connectivity between adjacent locations i and j, that of the movement between two non-adjacent locations in the landscape is determined by two constraints: information (about the landscape) and cost (in terms of energy and mortality risk). The amount of information available to an individual regarding the characteristics of its environment affects its ability to navigate the landscape (Peer and Kramer-Schadt 2008). In the absence of such knowledge, only random movements would be possible, while on the contrary the ability to find the optimal path connecting distant locations requires perfect knowledge of the entire landscape. Frequently, animals possess at least some, although only partial, knowledge of the broader landscape within both their perceptual (Lima and Zollner 1996) and familiar range (reviewed in Fagan et al. 2013), which leads to non-random and yet sub-optimal movements. In other words, if an individual knows its environment reasonably well, its movements could be modelled with a higher value of θ; whereas, smaller values of θ are more

suitable for modelling connectivity with obvious knowledge constraints, such as dispersal through novel landscapes and reintroductions.

The RSP framework allows one to incorporate explicitly the amount of spatial knowledge available to individuals in ecological distance metrics, as the RSP probability distribution (P_{st}^{RSP}) minimizes the expected cost of following a path between the source and target, constrained by the information available to the individual (Eq. 8 in Supporting information). From this RSP distribution we can derive the expected cost for moving between a source s and target location t, the 'RSP expected cost' ($\overline{C}_{st}^{RSP}$, Eq. 10 in the Supporting information) subject to incomplete knowledge. As already mentioned, this RSP expected cost generalizes the two standard distance measures used in ecology (Kivimäki 2018): the least-cost distance (Adriaensen et al. 2003) and the resistance distance (McRae et al. 2008). With a low degree of randomness, the RSP expected cost converges to the least-cost distance, whereas with increasing randomness it converges towards the resistance distance (multiplied by a constant; Kivimäki et al. 2014). The RSP expected cost is particularly suited to represent the expected energy cost of move between s and t, whereas the mortality cost is better dealt with using the survival probability ('Spatial absorbing random walk' section).

Step 3. Estimation of effective connectivity: space–intrinsic step

The last step in our workflow transforms ecological distances into estimates of EC for a given ecological process. First, EC requires the ability of individuals to reach the target from a source or their proximity. The proximity of a source s to a target t is usually in the range [0,1], where 0 denotes no connection and 1 perfect connectivity. Ecological distances, $d_{st} \in [0,\infty)$, are in general not scaled to the species' intrinsic movement capabilities, because of the use of indirect proxies for the cost of movement, e.g. utilizing a transformation of movement probabilities in step 2, 'Step 1: Estimation of habitat permeability: environment–intrinsic step' section. However, when movement costs are estimated directly, for instance through the probability of mortality, then the survival probability between s and t could serve directly as a proximity measure that is scaled to species-specific movement capabilities ('Spatial absorbing random walk' section).

Second, as mere arrival at the target will seldom be enough for connectivity to be effective with respect to the focal process, non-movement related ecological characteristics will also affect EC (Table 1). Therefore, in addition to the proximity between a source and target, EC is also affected by non-movement related ecological characteristics that contribute to the outcome of connectivity, those characteristics depend on the focal ecological process. Fletcher et al. (2016) describe the outcomes of connectivity at three organization levels. For instance, at the individual level connectivity within a home range is effective in so far it provides an individual's daily resources, and migration connectivity is effective when it results in access to seasonally suitable ranges. Similarly, distribution and genetic connectivity at the population level and connectivity supporting species interactions and biodiversity at the community level are effective not only when individuals arrive at the target, but also depending on species and process specific factors (Table 1).

In this section we first introduce the 'absorbing random walk' framework, followed by the scaling of distances with a species' intrinsic movement capabilities, and then finally assess the effect of other ecological processes on the effectiveness of connectivity.

Spatial absorbing random walk

As discussed above, two types of costs may be associated with movement: energetic and mortality costs. Recently, Fletcher Jr. et al. (2019) introduced the 'spatial absorbing Markov chains' (SAMC) also called 'absorbing/killed random walks' (Fouss et al. 2016) into landscape ecology to account explicitly for differences in the response of animal movement probabilities and mortality to the landscape. Interestingly, as an alternative to movement with incomplete knowledge, the RSP model can also be interpreted in terms of an absorbing random walk (Fouss et al. 2016).

A standard random walk moves on a graph according to the random walk transition probabilities or normalized step probabilities ($p_{ij} = S_{ij}/\sum_j S_{ij}$); however an absorbing random walk assigns, for all edges or nodes, some of the transition probability mass to the possibility of 'absorbing' or terminating the walk in i (Fletcher Jr. et al. 2019). Any ecological process that results in the individual terminating its random walk before reaching the target would lead to the 'absorption' of the random walk, such as the death of the individual or its settlement in an intermediate location.

Formally, in the RSP model, the absorbing of the random walk is obtained by multiplying the transition probabilities with $\exp(-\theta c_{ij})$; thus the absorbing probability is nonzero for all $\theta > 0$ and $c_{ij} > 0$. The RSP model is identical to the model presented by Fletcher Jr. et al. (2019), when $\exp(-\theta c_{ij}) = (1 - r_i)$ with r_i the probability of mortality in i (Fletcher Jr. et al. 2019; for a discussion of r_i). In other words, when costs are the 'surprisal' of the survival probability (i.e. $c_{ij} = -\log(1 - r_i)$) and $\theta = 1$, the RSP model is the SAMC in Fletcher Jr. et al. (2019). Hence, the 'partition function' (Eq. 9 and 11 in the Supporting information) provides the arrival (or 'survival') probability of a random walker from a source to a target, i.e. the probability of it reaching t from s without being absorbed during the walk. This survival probability is well suited to account for the mortality costs of movement. Although the inclusion of θ in the RSP framework eneralizes the absorbing random walk model in Fletcher Jr. et al. (2019), the ecological interpretation of values differing from 1 is probably less meaningful in this context than it is in the application of the RSP model to movement with incomplete knowledge discussed above.

When the 'absorption' is related to non-lethal habitat-related mechanisms, such as the settling of a dispersing individual in a suitable intermediate location i rather than continzuing its walk towards the target t, then the c_{ij} could incorporate this habitat-settlement link (in this case, c_{ij} no longer represents only movement costs). In other words, the availability of many vacant settlement areas in between source and target would decrease the direct ('arrival') connectivity between s and t, although these settlement areas would function as sources in their own right increasing the overall connectivity of the landscape.

Scaling distances

The relationship between connectivity and ecological distances depends on both the movement capabilities of a species (Bunn et al. 2000) and the specific ecological process of interest (Fletcher et al. 2016, Fletcher and Fortin 2018). In general a negative relationship exists between the distance an individual is willing to travel and the frequency of its trips (Bowman et al. 2002, Carbone et al. 2004). For instance daily movements within the home range are typically much shorter than migratory movements between seasonal ranges (van Moorter et al. 2013). Hence, for a given species, areas that are connected for seasonal migration may not be effectively connected for daily foraging movements. In island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Hanski and Ovaskainen 2000) it has long been recognized that the manner in which the distance between two locations translates into their proximity depends on the movement abilities of the species. Therefore the proximity (k_{st}) between a source and target in these models is commonly represented using an exponential function of their (Euclidean) distance scaled based on the species' average or median dispersal distances:

$$k_{st} = \exp(-\alpha d_{st})\qquad(4)$$

where the distance (d_{st}) is multiplied by a scaling factor α characterizing a species specific movement capabilities, e.g. so that $1/\alpha$ is the average dispersal distance. The species-specific scaling factor α is typically obtained from the literature but can also be derived from other sources relevant to the study aim, e.g. the theoretical relationships between daily or dispersal distances and body mass (Sutherland et al. 2000, Carbone et al. 2004).

In the framework presented in this paper, we propose measuring ecological distances using RSP expected costs, rather than the simple Euclidean distance used in island bio-geography, and converting them to estimates of ecological proximity using the negativevexponential transformation for any given ecological process of interest. This transformation is among the most frequently used, and it is also, conveniently, the inverse function of the logarithmic transformation used in Step 1 to translate step probability into cost. Note, however,

that other transformations could be possible (for instance, Clark et al. 1999).

Ecological distances based on proxies for movement costs are not measured in standard units. Moreover published movement capabilities are typically expressed in metric units, which therefore need to be converted. The easiest approach consists of approximating ecological distance to the length of the paths in metric units, i.e. the number of transitions (in the LCP) or expected number of transitions (known as the 'commute time' of a random walk) multiplied by the pixel size. These path lengths can then be scaled using species-specific movement capabilities in metric units (Bunn et al. 2000). The main drawback of this approach is that it does not account for the cost along the path (Simpkins et al. 2018). Alternatively, ecological distances between s and t can be regressed against the corresponding Euclidean distances to obtain a conversion rate (Foltête et al. 2012), which can then be used to express ecological distances in metric units to scale with species-specific movement capabilities (demonstrated in Supporting information).

Although ecological distances can be converted into metric distances using published data, if suitable data are available, it seems preferable to estimate the movement capabilities of a species directly as ecological distances. For instance the ecological distance of observed dispersal paths of individuals provides an empirical basis for inferring movement capabilities, which can be used to transform those distances to ecological proximities (demonstrated in the Supporting information). Similarly, when movement costs are scaled to represent the 'true' cost of a step between adjacent locations, e.g. probability of mortality, then the 'absorbing random walk' or RSP framework allows the direct estimation of the proximity between non-adjacent locations s and t as the probability of survival from source to target.

Effectiveness for the outcome of connectivity

Finally, the effectiveness of connectivity between a source and a target depends not only on the ecological distance and movement abilities of the species for an ecological function, but also on other intrinsic factors (e.g. the reproductive success of immigrants; Robertson et al. 2018) and ecological characteristics (e.g. resources available in a patch) of the landscape for a species (Table 1). Again in island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Hanski and Ovaskainen 2000), the EC EC (K^{EFF}) between a source and target island or patch is a function not only of their proximity (k_{st}, Eq. 4), but also of other ecological factors (ζ) at s and t affecting the effectiveness of connectivity:

$$K_{st}^{\text{Eff}} = \zeta_s \zeta_t k_{st}\qquad(5)$$

where the area size of each patch is commonly used for ζ (Hanski and Ovaskainen 2000), the area size is used as a proxy for both the number of individuals that emigrate from the source (ζ_s) and the likelihood of immigration into the

target patch (ζ_t). The area size or quality of habitat patches is a common means of integrating other ecological characteristics relevant to the effectiveness of connectivity for processes related to population persistence (Drielsma et al. 2007, Saura and Pascual-Hortal 2007, Drielsma and Ferrier 2009, Saura and Rubio 2010). However, as with movement capabilities, the relevance of other ecological, behavioural or life-history characteristics to the effectiveness of connectivity depends on the process of interest (Fletcher et al. 2016, Fletcher and Fortin 2018). For instance, effective demographic connectivity depends on the relative contribution of the immigrants to population growth, whereas effective genetic connectivity is affected more by the absolute number of dispersers (Lowe and Allendorf 2010). These characteristics, such as the reproduction probability of immigrants, can be included in the measure of EC (for instance, Robertson et al. 2018). Table 1 for more examples, however an exhaustive treatment of all the ecological characteristics of a system that contribute to the effectiveness of connectivity is likely to fall outside the scope of many connectivity studies, which focus instead on the minimum requirements for EC.

Discussion

Because of the rapid decline of ecological connectivity caused by human land use (Tucker et al. 2018), its quantification to assess the effects of land use changes and guide connectivity conservation is a high research priority in landscape ecology (Correa Ayram et al. 2016). Recently, Vasudev et al. (2015) developed the first conceptual basis for the study of EC, the SEI framework argues that reproductive connectivity is limited by 1) spatial constraints related to the geographic location of landscape elements, 2) external environmental factors and 3) intrinsic constraints related to the moving organism and its ecology. Although, intrinsic movement constraints can vary within or between individuals of the same species (e.g. due to varying energy reserves; Vasudev et al. 2015), and modeling approaches such as agent-based models allow for more flexible ecological dynamics (Revilla and Wiegand 2008), often at the expense of computational complexity. Instead, we focused on variation across species (although, a similar approach could be used to incorporate group variation within a single species, e.g. sex or age classes). In this paper we first generalized the definition of EC to include any movement-related ecological process of interest. We then further expanded the SEI theoretical framework with a three-step analytical approach to quantify EC (for instance Revilla and Wiegand 2008 and Robertson et al. 2018 as other examples of a similar workflow), using advances from different research disciplines.

We started our assessment of EC from arguably one of the best data sources on individual movement to quantify landscape permeability (individual tracking data in the IE step), however other data sources, such as capture–mark–recapture data, can be used (Remon et al. 2018, Robertson et al. 2018). Moreover, in some cases it may be more convenient to study permeability at a higher organizational level (Table 1). For instance it may be easier to investigate effective genetic connectivity directly at the genetic level (Spear et al. 2010) rather than indirectly through the movement of individuals, which requires the addition of other ecological dynamics to assess the effectiveness of those movements for gene flow. The field of landscape genetics has evolved rapidly over the last two decades (Storfer et al. 2010, Manel and Holderegger 2013), and tools have been developed to quantify landscape permeability using genetic data (Spear et al. 2010, Peterman et al. 2019). Interestingly, these tools rely on the same three steps we have described, although iteratively, as data are available only regarding the effective genetic connectivity. The tools optimize the weighted combination of environmental layers for the permeability surface (the IE step) that minimizes the differences between the modelled EC (the ES and SI step) and the observed genetic similarity between pairs of sample locations (Peterman 2018, Peterman et al. 2019).

The estimation of EC between a source and target is data demanding (Table 1), as data on both the probability and cost of movement are needed and data on ecological dynamics at s and t that contribute to the effectiveness of movement for the focal process (e.g. home range use, seasonal migration or colonization). However, gaps in data can be 'patched' through additional assumptions or the use of expert opinion. For instance, the assumption of individuals behaving well-adapted to their environment would allow: 1) the cost of movement to be derived from the movement probability, and 2) the abundance of resources from occupancy data (e.g. resource selection functions: Manly et al. 2007) to assess, for instance, the effectiveness of home range or migration connectivity (Table 1). Data to estimate the likelihood of movement have become increasingly available due to the development of tracking technology (Cagnacci et al. 2010), and occurrence data are readily available for many species from monitoring programs or citizen science data (Hochachka et al. 2012, Altwegg and Nichols 2019). However, even in the absence of any data on species-habitat responses, the proposed three-step framework for EC could be implemented based solely on expert knowledge (Gurrutxaga and Saura 2014, Avon and Bergés 2016).

The definition of ecological distance commonly relies on either 'least cost'- or on 'random walk'-based distances (Marrotte and Bowman 2017, Peterman 2018). Recently, however, the RSP framework (Saerens et al. 2009) was introduced into landscape ecology (Van Etten and Hijmans 2010, Panzacchi et al. 2016); the RSP model interpolates between the two extremes of a continuum from optimal to random movement. In addition to its interpretation as movement with incomplete knowledge, the RSP model can also be interpreted as an 'absorbing random walk' or 'spatial absorbing Markov chain' (Fletcher Jr. et al. 2019). We discussed two RSP-based metrics for the ES and SI steps of EC: first, the RSP expected cost interpolates between the least

cost and resistance distance, and second, the survival probability (Fletcher Jr. et al. 2019). Hence the RSP model represents a general framework for the distance and proximity metrics that are frequently employed in ecology, rendering it ideally suitable as a model for use in a general framework for quantifying EC. For the two costs of movement, i.e. energetic and mortality costs, the RSP expected cost and the survival probability respectively will be the most appropriate metrics. The simultaneous assessment of both movement costs, however, is still and interesting avenue for future research.

Software for the three-step analytical approach is readily available in open-source latforms. We presented a demonstration of this workflow in R (<www.r-project.org>, Supporting information) using SSF and SSPF for the EI step fitted with respectively the survival-library (Therneau and Grambsch 2000) and the ResourceSelection-library (Lele et al. 2017) with both the RSP framework (Saerens et al. 2009) from the gdistance-library (van Etten 2017) and the 'absorbing random walk' approach from the samc-library (Marx et al. 2020) for the ES step. We are actively developing an open-source library to improve computational efficiency for these RSP-based metrics. The computation of LCPs is available in all major GIS and computing environments, and Circuitscape is a highly popular choice among landscape ecologists for modelling random movements using circuit theory (McRae and Beier 2007, McRae et al. 2008, Dickson et al. 2019). We focused in our approach to estimate EC on its steady-state behavior; however, interestingly in the samc-library connectivity can be computed over a specific time interval (Marx et al. 2020), which would allow for future studies on the transient dynamics of EC.

The large societal demands for connectivity conservation and restoration have placed the measurement of ecological connectivity at the forefront of research in landscape ecology. We presented an integration and synthesis of research developments for the different steps involved in the estimation of the EC between areas using the SEI framework (Vasudev et al. 2015). This integrative approach will enable practitioners and researchers to quantify EC for an ecological function of a focal species and study the manner in which it is affected by land use changes. This is especially important in the context of climate change, as connectivity conservation has been identified as a major strategy for climate-change adaptation for biodiversity (Heller and Zavaleta 2009, Keeley et al. 2018).

Data availability statement

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.wpzgmsbmj> (Van Moorter et al. 2021).

Author contributions

Bram Van Moorter: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Ilkka Kivimäki**: Conceptualization (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Manuela Panzacchi**: Conceptualization (equal); Funding acquisition (lead); Project administration (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Marco Saerens**: Conceptualization (supporting); Investigation (supporting); Methodology (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

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