Landscape Ecol (2020) 35:41–58
https://doi.org/10.1007/s10980-019-00935-3

REVIEW ARTICLE

Landscape connectivity modeling from the perspective of animal dispersal

Milena F. Diniz · Samuel A. Cushman · Ricardo B. Machado · Paulo De Marco Júnior

Received: 11 October 2018 / Accepted: 12 November 2019 / Published online: 19 November 2019

Abstract
Context Dispersal plays a key role in linking populations, habitat (re)-colonization, and species range expansion. As fragmentation and habitat loss are ubiquitous threats and can disrupt dispersal, landscape connectivity modeling has become a valuable tool in conservation planning.
Objectives We provide an overview of how current connectivity modeling has incorporated the different aspects of animal dispersal. We describe the most popular connectivity models and highlight their main assumptions related to dispersal, suggesting a series of questions that could clarify the advantages and disadvantages of using a particular approach.
Methods We review the structure of the connectivity models based on least-cost analysis, circuit theory, and the individual-based dispersal models. We use some studies as case examples to discuss how important elements of animal dispersal were considered through models to predict movement routes.
Results Ongoing developments in connectivity modeling have made it possible to represent animal dispersal in a more realistic way by implementing key elements such as dispersal behaviors, mortality, and inter-individual variability. However, the potential to consider such elements and how this is done in connectivity modeling depends on the selected approach, since each model represents animal dispersal through a different perspective.
Conclusions We recommend that the choice of a connectivity model should be made after considering the study objectives, the species dispersal mechanism, and the prior knowledge available about it. By understanding and incorporating dispersal behavior into connectivity modeling, we can improve our capacity to generate useful information aimed to construct more effective conservation strategies.

Keywords Circuit theory · Dispersal movement · Least-cost path analysis · Individual-based models · Resistance surface · Resistant kernels

M. F. Diniz (✉) · P. De Marco Júnior
The MetaLand: Theory, Metacommunity and Landscape Ecology Lab, Ecology Department, Federal University of Goiás, Goiânia, GO 74001-970, Brazil
e-mail: mifiuzadiniz@gmail.com

R. B. Machado
Zoology Department, University of Brasilia, Brasilia, DF 70910-900, Brazil

S. A. Cushman
USDA Forest Service, Rocky Mountain Research Station, 2500 S Pine Knoll Dr., Flagstaff, AZ 86001, USA

Introduction

In a world with increasingly fragmented natural habitats, landscape connectivity has become a global

priority for long-term biodiversity conservation (Rudnick et al. 2012). Connectivity is the "degree to which the landscape facilitates or impedes movements among resource patches" (Taylor et al. 1993). This landscape property can be analyzed under the view of its structure, i.e., considering the raster or vector representation of the position, size, and architecture of its elements (e.g., patches and corridors), or under its functionality, when considering how a particular organism perceives such structure (Tischendorf and Fahrig 2000).

The study of the effects of connectivity on species is of great scientific interest, since understanding the factors that maintain or affect the local dynamics of organisms is fundamental for the management and conservation of sustainable landscapes (Rudnick et al. 2012). Under the functional perspective, a well-connected landscape emerges from the successful dispersal of individuals, a life-history trait primordial for reproduction and survival of many species (Baguette et al. 2013). Albeit with great variation, dispersal is often seen as a three-stage process (emigration, transfer, and immigration) in which individuals move from their natal locations to the site of first reproduction or move between successive reproductive sites (Clobert et al. 2012). Beyond individual consequences, dispersal is one of the key processes in shaping population and metapopulation dynamics, community assembly, and species' global range dynamics, whose direct assessment, tracking the movement of organisms, can allow significant advances in ecology, evolution, and biogeography (Jønsson et al. 2016).

Understanding how species disperse and what are the requirements and constraints to dispersal can ensure that this process is properly modeled and used to report successful connectivity conservation strategies (Vasudev et al. 2015). In the last decade and a half, connectivity modeling has shifted from an oversimplified representation of dispersal to process-driven approaches, from which movement routes are modeled considering the response of organisms to different landscape elements (Etherington 2016; Dickson et al. 2018). These approaches have been particularly prominent in the conservation context since it is possible to map structures capable of facilitating (e.g., corridors and stepping stones) or preventing (e.g., barriers) animal movement across the landscape (Rudnick et al. 2012). Even though they represent a breakthrough compared to purely structural approaches, some of these connectivity models were initially developed in other disciplines (e.g., least-cost analysis and circuit theory) and then adapted to predict animal movements (McRae et al. 2008; Etherington 2016). As a consequence of the different conceptual and analytical backgrounds, the applications of the models are followed by specific assumptions about animal dispersal and distinct opportunities to integrate certain aspects of this ecological process.

Here we provide an overview of how elements of dispersal ecology have been incorporated into connectivity modeling through the most commonly used approaches: the least-cost (LC) models, including least-cost path and resistant kernel analyses, the circuit theory-based model (CT), and individual-based dispersal models (IBDMs). We did not perform a systematic review, but rather an analysis of the models' structure using some studies as examples of cases to discuss the ability of each approach to represent some aspects of dispersal. Additionally, we suggest a research agenda to clarify the appropriate use of the different methods and to guide their improvement. Although the reviewed models are currently used to assess connectivity at different scales, from within-territory movements to migrations, this review focuses on their application to identify important areas for animal dispersal in terrestrial systems.

Resistance surfaces: the foundation of current connectivity models

All connectivity models described here, except some IBDMs, are based on a landscape raster representation commonly known as resistance surface. The values of this layer indicate the resistance or difficulty imposed by environmental components on movement of individuals (Fig. 1a; Spear et al. 2010; Zeller et al. 2012; Etherington 2016). Resistance or cost values are assigned to each landscape cell to represent the organism's differential propensity to use a particular habitat type during its movement. This propensity may reflect the physiological costs and/or mortality imposed by the different landscape elements represented in the cells (Spear et al. 2010; Zeller et al. 2012). The use of resistance surfaces allowed the transition from connectivity models based on

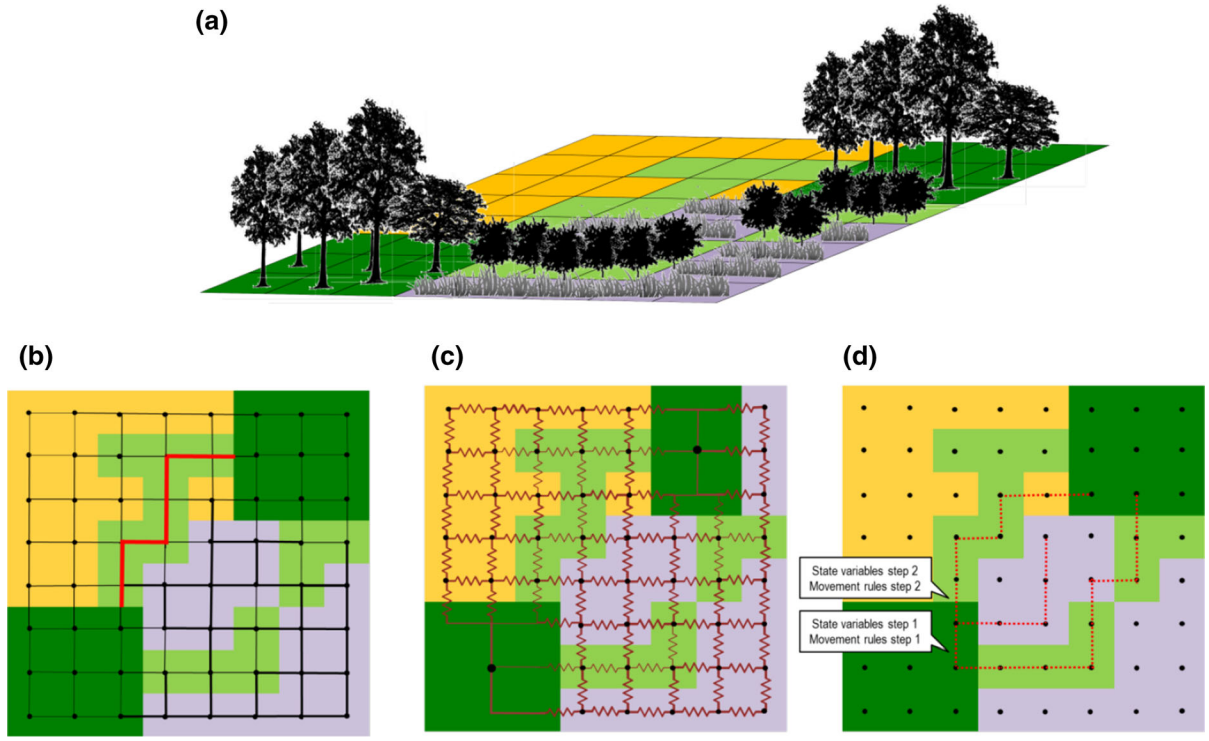

Fig. 1 Landscape resistance to animal movement and the framework of connectivity models. A resistance surface represents the differential propensity of an organism to use a particular habitat type (**a**). Least-cost models convert the resistance surface into a weighted-graph network in which nodes (cells' centroids) are connected by weighted edges according to the Euclidean distance and resistance values from the neighboring cells (**b**). In the circuit theory-based model, the edges are replaced by resistors (**c**). Using an IBDM, it is possible to incorporate behavioral elements that drive individuals' movement (**d**)

homogeneous landscapes to those capable of incorporating the effect of different landscape characteristics on the species dispersal and gene flow (Spear et al. 2010; Zeller et al. 2012).

Although many different methods have been used to create resistance surfaces (Zeller et al. 2012), in general the modeling process usually consists of: (1) selection of known or assumed environmental variables to affect the species movement; (2) selection of biological data (most commonly detection data, relocation data, pathway data, and/or genetic data); (3) application of an analytical approach to associate the biological movement data (2) with environmental factors (1). In recent years, resource selection functions have become very popular analytical approaches to estimating landscape resistance (Chetkiewicz and Boyce 2009; Zeller et al. 2012, 2018; Abrahms et al. 2017). From this approach, habitat suitability values are obtained by comparing "used" habitat (captured through biological data, with the exception of genetic data) to "available" habitat, and translated into resistance estimates through transformation functions such as negative linear or exponential functions (e.g., Keeley et al. 2016). Depending on the analytical approach selected, many competing surfaces can be created and confronted with independent biological data sets, and after the application of some model selection procedure, the best candidate is identified (e.g., Cushman et al. 2006; Zeller et al. 2012, 2018).

How do connectivity models work?

Many different approaches have been used to assess landscape connectivity and the choice of the most appropriate methodology will depend essentially on the purpose of the study (Kool et al. 2013). For example, some studies aim to evaluate the importance of discrete landscape elements for connectivity (e.g., habitat patches), while others focus on identifying

potential movement routes. In the first case, connectivity indices, such as the popular habitat availability indices, are commonly used (e.g., Diniz et al. 2018a); in the second one, approaches based on movement path modeling can be applied (e.g., McClure et al. 2017; Osipova et al. 2019).The first two models we described here, the least-cost path and the circuit models, are based on the structure of graphs (Adriaensen et al. 2003; McRae et al. 2008). Since the principles of graph theory were applied to an ecological context (Urban and Keitt 2001), this framework has gained popularity among landscape ecology and conservation studies (Correa Ayram et al. 2016). Using graph theory, habitat patches are represented as nodes that can be linked by edges that represent the functional connectivity (i.e., the way that an organism perceives the landscape structure), forming a network of graphs (Urban and Keitt 2001). A link can be expressed as a probability of connection or certain limiting distance, being both related to the organism under consideration (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007). Thus, some nodes can form clusters of connected elements, while others can be isolated or disconnected. Graph models include those based on a lattice or grid of cells (least-cost path and circuit models) and "land class" or patch based models.

The factorial least-cost path analysis and other improvements

Least-cost (LC) modeling was first developed in the geographic transport context and consists of identifying the path with the lowest cost distance among all possible paths linking predefined sources and destinations (SD) (Etherington 2016). The data required for this analysis is a resistance surface and the SD coordinates. Most LC methods convert the resistance surface into a weighted lattice graph (Fig. 1b), structure where raster cells are represented by their centroids (nodes) connected by weighted edges, which are in turn determined as functions of both Euclidean distance and cost or resistance units (Etherington 2016). Then an algorithm (being the graph theory shortest-path the most commonly used; Dijkstra 1959) is applied to find the combination of edges with the lowest accumulated cost-distance linking a pair of SD sites. In the end, the calculated LC distance will be the sum of the edge weights along the LC path (i.e., its accumulated cost; Etherington 2016).

Ecologists have extensively used LC analysis since its formal introduction by Adriaensen et al. (2003). Currently, LC models have been the most applied methods to analyze landscape functional connectivity (Correa Ayram et al. 2016). Many variations from the classic LC path analysis have been developed in an attempt to overcome some limitations of the original framework when applied to animal movement (e.g., Compton et al. 2007; Pinto and Keitt 2009; Landguth et al. 2012; Etherington 2016). The classic LC path approach seems to poorly match animal dispersal due to three main reasons (Rudnick et al. 2012; Etherington 2016; Ribeiro et al. 2017). First, the specified pairs of SD among which the individual will disperse are rarely known. Moreover, predicting population connectivity, here referred as the degree of connections among populations in a landscape or "the outcome of dependencies between populations or individuals" (Kool et al. 2013), may require modeling over hundreds or thousands of sites. Second, the model assumes that all individuals will follow the LC path (i.e., they have a clear destination as a goal, and a complete knowledge of the landscape routes to that destination, and always travel by the 'cheapest' one). This omniscience is not biologically realistic, making the results quite questionable. Finally, the LC path has a 1-pixel width, which is dependent on the resistance surface resolution, and proposing these narrow paths as corridors may not be suitable for many species.

To work around these problems, some authors have modified and implemented additional steps inside the classic LC path routine. A factorial application, for instance, computes the LC paths for all pairwise combinations among the SD, thereby providing a broader perspective of species population connectivity (Rudnick et al. 2012). Considering multiple additional suboptimal routes or smoothing the LC paths using a probability density function have been used to deal with the unrealistic assumption of a single optimal path with a 1-pixel width (Pinto and Keitt 2009; Landguth et al. 2012; Ribeiro et al. 2017). For example, Cushman et al. (2013) implemented factorial least-cost corridor analysis which couples computation of all pair-wise paths in a system of nodes with resistant kernel buffering to provide a spatially synoptic and biologically realistic model of connectivity across a continuously distributed population in a

heterogeneous landscape. In addition, the factorial least-cost path approach as implemented in the software UNICOR (Landguth et al. 2012) includes incorporation of dispersal thresholds that limit the calculation of paths between nodes to a specified threshold representing the dispersal ability of the organism in question. A swath of cells surrounding the LC path forming an LC corridor (Pinto and Keitt 2009; Rudnick et al. 2012; Etherington 2016) avoids the unrealistic view of one very narrow permanent route. For LC connectivity models that generate multiple paths, the resulting routes can be overlapped to generate a density map indicating the number of paths passing through each landscape pixel (e.g., Pinto and Keitt 2009; Ribeiro et al. 2017).

Circuit theory

The application of a circuit theory-based model (CT) to understand evolutionary and ecological processes was only possible thanks to the previously established theoretical relationship between electric circuits and random walk on analogous graphs (McRae et al. 2008; Dickson et al. 2018). A random walk is a modeled movement of an organism where one step is taken independently of the previous one, making the displacement process absolutely stochastic in a landscape (see Codling et al. 2008 for a review). Circuit theory can be used to model connectivity in both evolutionary and ecological contexts (McRae 2006; McRae et al. 2008) and has become one of the most popular methods to model gene flow and dispersal routes since its introduction (Dickson et al. 2018). In ecology (which will be our focus hereafter), electrical nodes in a circuit are used to represent landscape matrix cells and habitat fragments, and the resistors that connect them indicate functional connections such as dispersal (McRae et al. 2008). The resistance value offered to the current in the resistors represents the difficulty imposed by a landscape element (e.g., land cover) or a set of them to animal movement (Fig. 1c; McRae et al. 2008).

Using CT as a movement model requires a raster representation of the landscape, where cells with finite resistance will be transformed into electrical nodes while cells with infinite resistance are dropped and used to represent complete barriers to movement (see McRae et al. 2008 for a detailed description). Cells belonging to habitat patches that are sources and destinations of individuals' movement have zero resistance and are converted into single nodes (Fig. 1c; McRae et al. 2008). Resistors are placed between each node and its four or eight neighboring nodes, with resistance values generally defined as the mean of the cells' resistance being connected (McRae et al. 2008). After the landscape has been converted into a large electrical circuit, to analyze the current flow between two habitat patches, one node is usually connected to a current source (source patch) and the other is connected to ground (destination patch). The Ohm's and Kirchhoff's laws are applied through the nodal analysis method to determine voltages at each node, and then the currents passing through individual resistors or nodes are calculated (McRae et al. 2008). As circuit theory is linked to animal movement via random walk, the current value flowing through a resistor is equal to the expected net number of times that individuals moving randomly starting at a source location or patch will cross that branch before reach a destination patch (McRae et al. 2008).

From the mapping of current density along the landscape, it is possible to visualize and identify movement patterns and, consequently, the most important routes for connectivity throughout the study area (e.g., McClure et al. 2017; Osipova et al. 2019). The higher the current value in a landscape cell, the greater the net passage probability for individuals moving randomly from a source to a destination (McRae et al. 2008). The current values also allow the identification of pinch points, generally narrow areas that have a high current value because they condense many potential paths (McRae et al. 2008; Pelletier et al. 2014).

Other graph-based approaches

Several connectivity measures can be derived from a graph representation to indicate the degree of connectivity in a landscape according to characteristics of the organism under analysis (Pascual-Hortal and Saura 2006; Saura and Torné 2009). From the approaches that the graph topology is given by nodes representing habitat patches, the relative position of a node, the node attributes (e.g., its size), the role of forming clusters (i.e., a peripherical or central node), and the number of connections are used to calculate several connectivity indices (Rayfield et al. 2011). Graph-based connectivity indices can express the overall

aspect of a landscape (e.g., Integral Index of Connectivity, Probability of Connectivity Index, number of components, total number of links), or node-level properties (e.g., clustering coefficient, closeness centrality), all available in software such as Conefor (Saura and Torné 2009) or Graphab (Foltête et al. 2012). Among the graph-based measures, habitat availability indices have gained prominence in connectivity studies as they have shown high sensitivity to various types of landscape changes (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Correa Ayram et al. 2016). These indices can be used to rank landscape elements according to their potential to maintain connectivity, allowing the prioritization of habitat patches and corridors for conservation (e.g., Diniz et al. 2018a).

Resistant kernels

While all model variations shown above are focused on the identification of discrete structures such as corridors or linkage zones, in some situations a continuous and more synoptic view of connectivity may be required (Cushman and Landguth 2012). This can be achieved through the approach known as resistant kernel, which arose from the union of two well-known methods, the dispersal kernel estimator and the LC path modeling (Compton et al. 2007). To apply the resistant kernel analysis is necessary to have (1) a resistance surface depicting the cost imposed on the species movement by landscape elements; (2) the source locations representing the origin points of dispersers; (3) a dispersal function by which the cumulative cost from sources will be converted into expected densities of dispersing individuals; and (4) a dispersal threshold representing an intrinsic condition of the species that limits its movement (Compton et al. 2007; Cushman and Landguth 2012; Rudnick et al. 2012).

The resistant kernel modeling works as follows (Compton et al. 2007; Cushman and Landguth 2012). First, the LC path starting at a source cell and ending at each cell surrounding it is identified using the resistance surface. Then, the accumulated cost of each path is stored in the respective cell creating a map of movement cost. The model computes the optimal path only for cells adjacent to the source cell where the accumulate cost is less than the cost distance dispersal threshold. Next, the accumulated-cost value maintained in each cell is converted into an estimate of relative density using the defined dispersal function. The expected density of dispersing individuals at the source is the highest and it is down-weighted for the neighboring cells by the cumulative cost up to the dispersal threshold. The way in which the reduction of the density occurs as the cumulative cost increases (e.g., linearly, exponentially or following a normal curve) is determined by the dispersal function. All the LC dispersal kernels are made individually for each source cell and summed to yield a synoptic, all-directional dispersal map (i.e., a surface with the total expected density of dispersers or the expected movement rates at each pixel of the landscape, which is the most effective algorithmic way of representing the spatial incidence function of dispersal).

The integration of resistant kernel modeling with factorial LC path analysis allows mapping and assessing broad scale population connectivity considering the configuration of different elements. Generally, core area, fracture zone (locations where connectivity is potentially reduced by barriers or cumulative dispersal cost) and/or barriers are identified by the resistant kernel analysis, and dispersal corridors are designed using the factorial LC paths (e.g., Moqanaki and Cushman 2017; Khosravi et al. 2018). The relative importance of those elements for landscape connectivity can be assessed through connectivity metrics such as habitat availability indices (e.g., Albert et al. 2017; Khosravi et al. 2018).

Individual-based dispersal models

An individual-based dispersal model (IBDM) explicitly simulates how animal movement occurs at individual scale by incorporating species-specific dispersal traits (e.g., Gardner and Gustafson 2004; Revilla et al. 2004; Kanagaraj et al. 2013; Hauenstein et al. 2019). Generally, IBDMs have a common structure in which virtual dispersers are released from predefined locations and their movement paths are progressively formed step by step (e.g., Kanagaraj et al. 2013; Allen et al. 2016). The displacement of an individual occurs according to the interplay between a set of state variables or attributes characterizing the individual, movement rules (used to simulate its behavior) and the landscape structure (Fig. 1d). Information processing and decision-making (represented by the movement rules) by

individuals can be defined using a statistical model (e.g., non-linear regression models or finite mixture models) that in turn has been selected and parameterized from field data (e.g., Tracey 2006); or according to a weighted random walk which may or not consider autocorrelation in movement (e.g., Kanagaraj et al. 2013; Allen et al. 2016). Movement rules incorporate elements that are chosen based on species' dispersal traits such as perceptual range (i.e., the radius of perception in which the movement decision can be affected by the landscape elements), homing behavior, memory size, and bias of movement away from the natal patch (e.g., Péer and Kramer-Schadt 2008; Aben et al. 2014; Coulon et al. 2015; Hauenstein et al. 2019). Each simulated animal is allowed only perform a maximum number of steps, which may be a fixed parameter (e.g., Tracey 2006; Coulon et al. 2015) or defined based on a probability distribution (e.g., Kramer-Schadt et al. 2004; Kanagaraj et al. 2013).

A variety of connectivity measures can be produced from an IBDM's output. Most commonly, inter-patch connectivity is described as a function of the relative numbers of successful dispersers (e.g., Tracey 2006; Kanagaraj et al. 2013; Coulon et al. 2015). The spatial identification of corridors can be performed overlapping of the individuals' movement paths across the simulations (Allen et al. 2016; Hauenstein et al. 2019). The spatial incidence function can be computed by summing the total locations visited by all individuals in all time steps, and is conceptually equivalent and highly correlated to the predictions of the cumulative resistant kernel, when the IBDM is based on cost-weighted random walks.

The calibration, selection or redefinition of IBDMs can be accomplished using strategies such as the pattern-oriented modeling, through which the model complexity can be optimized based on multiple patterns observed in real systems, and the realism added to their structures may make them less sensitive to parameters' uncertainty (Grimm et al. 2005). Despite the flexibility and the ability to deal with the behavioral aspects of individual dispersal, feature that makes IBMDs seem more advantageous over other connectivity models, they have some potential drawbacks. Most important is its dependence on a large number of parameters that require high-resolution dispersal data, which are normally difficult to acquire in the field (e.g., Watkins et al. 2015; Hauenstein et al. 2019). Being more complex in relation to the number of parameters also turns IBDMs more sensitive to the variation and interaction of those parameters. This may be an advantage to understand the functioning of complex systems (e.g., the population dynamics within a community), but it will be a problem in generating prediction in a pattern-oriented approach such as to identify corridors. In addition, one of the most striking features of IBDMs, the favoring of realism, can be at the same time one of its major advantages and disadvantages, since greater realism and precision are accompanied by the loss of generality (Levins 1966). Finally, another hindrance for further applications of some IBDMs is the statistical complexity (Hauenstein et al. 2019), which can also make analysis computationally demanding, especially for large spatial and/or temporal scales.

How do connectivity models incorporate dispersal?

Like any other scientific model, connectivity models are designed to represent key characteristics of real systems (landscape resistance and movement behavior) in order to understand certain processes and patterns (dispersal and landscape connectivity) (Rudnick et al. 2012; Baguette et al. 2013). Because they are attempts to represent one aspect of reality, they are essentially inaccurate and there is no way to choose the best model that applies to all cases due to two main reasons. First, trying to choose and apply a single model to describe the movement patterns of all species would be a misleading and naive way of describing an ecological process as variable as animal dispersal (Clobert et al. 2012; McClure et al. 2016). Second, there are still few studies comparing the predictive performance of connectivity models using independent dispersal data (McClure et al. 2016; Zeller et al. 2018).

Because different connectivity models express different hypotheses about animal movement and do so using a greater or lesser degree of complexity (e.g., McRae et al. 2008; Ribeiro et al. 2017; Hauenstein et al. 2019), we argue that the models described above may be useful depending on the weighting between three main factors: (1) the study objectives, (2) the particularity of the study system, and (3) the prior knowledge available about it (Rudnick et al. 2012; McClure et al. 2016). In this section, we selected some fundamental aspects to understand how the bridge

between dispersal and connectivity has been constructed and presented the pros and cons of using the modeling approaches in light of the three main factors mentioned above (Table 1). We use some studies as examples to illustrate when it is indispensable to consider each dispersal ecology element in the connectivity modeling and how this will guide the choice of the most appropriate model.

Landscape resistance to dispersal

Corridors designed to promote or improve the movement of individuals between populations are probably more reliable when developed directly from dispersal movement data (Elliot et al. 2014; Zeller et al. 2018) or from genetic data, which captures the multi-generational effect of dispersal across a resistant landscape (e.g., Cushman et al. 2006; Shirk et al. 2010). However, because dispersal can be difficult to detect, especially in the case of long-distance dispersal

Table 1 The importance of some aspects of animal dispersal and how they have been incorporated into connectivity modeling

Dispersal aspect	Importance	Possible approach	Examples
Resistance to dispersal	It must reflect the pattern of habitat use during dispersal	It can be captured using direct dispersal data to produce the resistance surface. Proxies such as home-range movement data can be used for some species	Abrahms et al. (2017) and Zeller et al. (2018)
Seasonality	Systems with pronounced seasonal spatial variation in forage and water availability or when the species exhibits differences in habitat preferences between seasons	Produce seasonal resistance surfaces	Benz et al. (2016) and Osipova et al. (2019)
Animal perception	How an organism perceives the landscape around it and makes its decisions will have strong effect on its movement pattern	Different perceptions can be represented by different connectivity models. Exploratory movements and other dispersal behaviors may help define the most appropriate model. Complex behavior can be better modeled using an IBDM	Kramer-Schadt et al. (2004) and McClure et al. (2016)
Perceptual range	It is important to consider in connectivity analyses made in high resolution and where the cell's size does not match with the radius of target species' perception	Some LC models and IBDMs are able to explicitly incorporate this feature. A multi-scale model of landscape resistance can consider the specific scale with which environmental variables can affect movement	Péer and Kramer-Schadt (2008), Palmer et al. (2011), Krishnamurthy et al. (2016), and Ribeiro et al. (2017)
Mortality during dispersal	Neglecting mortality may overestimate successful dispersal and compromise the effectiveness of corridors	It can be inserted indirectly via resistance surface or modeled through IBDMs and CT (although in a not very trivial way in the latter)	Kramer-Schadt et al. (2004), McRae et al. (2008)
Individual variability	Heterogeneity in dispersal among individuals may arise as a consequence of differences between sex, physiological condition, and personalities	It is possible to incorporate via resistance surface and modifying some models' parameters such as dispersal distance	Elliot et al. (2014), Palmer et al. (2014), Maiorano et al. (2017), and Osipova et al. (2019)
Time	Patch connectivity may depend on time	Only IBDMs can incorporate a time framework for connectivity	Kramer-Schadt et al. (2004) and Hauenstein et al. (2019)

movements (e.g., Abrahms et al. 2017), accessing the trajectories of dispersers along different landscape elements often becomes very laborious. Due to the difficulty of obtaining adequate samples of dispersers, landscape resistance values are commonly estimated using proxies such as the habitat suitability based on home-range movement or, less preferably, from expert opinion (Zeller et al. 2012; Keeley et al. 2016).

The use of habitat suitability derived from non-dispersal data to estimate dispersal movements may be appropriate for some species. For example, Fattebert et al. (2015) demonstrated that dispersing leopards (*Panthera pardus*) use habitats in accordance to resident adults. Similarly, Keeley et al. (2016) showed that habitat suitability estimated from desert bighorn sheep (*Ovis canadensis nelsoni*) home-range movements can predict habitat use during long-distance, prospecting movements, which frequently precede dispersal. However, some species have different patterns of habitat selection depending on the movement purpose. For example, Elliot et al. (2014) parameterized demographic-specific resistance surfaces using telemetry data from African lions (*Panthera leo*) and showed that path selection and, consequently, the connectivity pattern varied widely among male natal dispersers, adult males, and adult females. Using data from various types of kinkajous' (*Potos flavus*) movements, another study concluded that the landscape matrix imposes less resistance to the movement of dispersers than for individuals performing home range movements (Keeley et al. 2017). Similarly, Gastón et al. (2016) showed that Iberian lynx (*Lynx pardinus*) is more tolerable to roads and steep terrain when dispersing than when establishing home ranges. The apparent idiosyncrasy in resource selection during different behavioral states (e.g., foraging, dispersing) prevents habitat suitability derived from any type of biological data from being a comprehensive proxy for landscape resistance to dispersal. Despite this, it is possible to apply some analytical approaches to clean data based on indirect detection in order to isolate dispersal-related movement behavior and subsequently build resistance surfaces (Abrahms et al. 2017).

As important as being aware of the correspondence between ecological processes (i.e., habitat selection during home range and dispersal movements) is the choice of the transformation function to convert habitat suitability values into resistance. Findings from recent studies indicate that a negative exponential relationship between habitat suitability and resistance is more appropriate than a negative linear function, which is frequently used as the default assumption (Beier et al. 2008; Trainor et al. 2013; Keeley et al. 2016, 2017; Zeller et al. 2018). The choice of the transformation function has important implications. Applying a negative exponential relationship, we are assuming that dispersers might readily cross habitat of moderate to low suitability. Using this function, only areas with very low suitability values may offer significant resistance to dispersal movements (Keeley et al. 2016, 2017). On the other hand, a negative linear transformation implies that resistance decreases at a constant rate as suitability increases and, therefore, only areas of high suitability offer low resistance to movement (Keeley et al. 2016, 2017).

Although using expert opinion to estimate landscape resistance is recommended only when empirical approaches are not available (e.g., Shirk et al. 2010; Zeller et al. 2012), in some cases, this more subjective approach has shown to be reliable and even preferable to other methods until more appropriate data is collected (e.g., Keeley et al. 2016; Reed et al. 2017; Liu et al. 2018). As experts are probably more familiar with habitat selection within home range of target species than with their preferences during dispersal, the use of this strategy to define resistance also has the same implications discussed earlier (Zeller et al. 2012).

Because the utility and effectiveness of all connectivity models discussed here depend first and foremost on the ability of resistance estimates to reflect habitat selection during dispersal, we recommend that studies should state clearly: (1) the definition of resistance according to the biological data used, the environmental variables considered, and the connectivity model applied; (2) the assumptions and implications of the definition and methodology adopted to operationalize resistance; and (3) what inferences are allowed from the presented definition and analytical background. These last two recommendations should be indispensable, especially for studies that use proxies to estimate dispersal movements.

Source and destination locations

Ideally the source locations used in the connectivity models should accurately represent the sources of

dispersers (i.e., potential populations). Specifically, the flow of individuals between populations and, therefore, connectivity is a function of three things: (1) the density and distribution of the source population (unless dispersal is density-independent), (2) the resistance patterns in the landscape, and (3) the dispersal ability and behavior of the dispersing organisms (Clobert et al. 2012).Therefore, when there is no knowledge about the capacity of protected areas or other sites to sustain populations of target species, there are several strong disadvantages in using the strategy of predefined sources and destinations (Koen et al. 2014; Pelletier et al. 2014). Most notably, the size and location of patches are often a very poor proxy for the actual population distribution and abundance (Cushman et al. 2008). Another disadvantage is a possible mismatch between movement scales (Mimet et al. 2016). One could assess the connectivity between habitat patches belonging to the home range of one or more individuals linked by daily movements and mistakenly assume to be assessing population connectivity via dispersal (Mimet et al. 2016). Furthermore, the location and amount of source/destination nodes within the study area can strongly influence the connectivity results (Koen et al. 2014; Pelletier et al. 2014). Thus, when there is no good reason to place nodes in specific sites or when it is intended to have an overview of connectivity throughout the study region, the use of synoptic connectivity modeling may be more appropriate (e.g., Carroll et al. 2012; McClure et al. 2017; Fabrizio et al. 2019). The use of techniques that avoid arbitrary placement of nodes can also be valuable for assessing the connectivity of species for which habitat is not arranged in discrete patches (e.g., Dilts et al. 2016).

From the application of CT in its original format and factorial LC path analysis, connectivity is assessed in a pairwise fashion (e.g., Khosravi et al. 2018; Osipova et al. 2019). Using this strategy, we are assuming that emigration and immigration occur from predefined SD. Consequently, all possible links between focal sites are assumed before the connectivity analysis is performed and the models are applied to inform the most likely dispersal paths between those locations. This strategy is often adopted by studies that aim to identify potential corridors linking large protected areas (PAs), which are assumed to have relatively stable populations and thus constitute sources/destinations for individuals. For instance, accounting for seasonality and inter-individual variability, Osipova et al. (2019) used GPS movement data to elephants to predict movement corridors, through CT and LC path analysis, connecting the largest PAs in a region between Kenya and Tanzania.

Resistant kernels and IBDMs do not require a priori identification of destinations (e.g., Cushman and Landguth 2012; Allen et al. 2016). The most important conceptual difference between the LC path and resistant kernel approach is that in the path model individuals have a priori destinations and the model finds optimal routes between them while in the resistant kernel approach organisms disperse optimally based on cost away from source points but without a priori destinations, with probability of final location a function of cumulative cost from the source point (Compton et al. 2007; Etherington 2016). Specifically, the resistant kernel approach simulates least-cost dispersal from source points, reflecting the density and distribution of the population, to all locations in the landscape accessible to those individuals, based on the resistance of the surrounding landscape and the dispersal ability of the species (Compton et al. 2007; Cushman and Landguth 2012). As noted above, this creates a biologically realistic estimate of the spatial incidence function of dispersal, in terms of the probability or density of movements through each and every location in the landscape (Compton et al. 2007; Cushman and Landguth 2012). Summing the locations of all individuals in all time steps in cost-weighted random walks, IBDMs create an equivalent measure of the spatial incidence function of dispersal. In these methods point-to-point or patch-to-patch connectivity is a property that emerges from dispersal assessment considering only starting points. An omnidirectional assessment of connectivity can also be achieved through relatively simple adaptations of CT (Koen et al. 2014; Pelletier et al. 2014) and LC path analysis (Carroll et al. 2012).

Dispersal phases

Dispersal is often described as a three-phase process composed sequentially of emigration, transfer, and immigration whose concepts vary according to the organism, the dispersal mode, and the scale considered (Clobert et al. 2012). In general, emigration consists of the act of leaving natal territory, where the individual already has some familiarity with the environment.

The subsequent transfer phase, in which movement per se occurs, refers to the crossing of a completely or partially unknown habitat matrix (or non-habitat matrix in the case of human altered landscapes) with the aim of searching for new locations. Finally, immigration occurs when the dispersing organism establishes itself in a new reproductive site (Clobert et al. 2012).

Typically, connectivity approaches, including flexible and complex IBDMs, only model the transfer phase of dispersal while neglecting other demographic processes (e.g., Kanagaraj et al. 2013; Allen et al. 2016; Hauenstein et al. 2019). Models that evaluate connectivity in paired fashion generally represent the transfer phase as a single event (i.e., individuals move directly between the areas from which emigration and immigration are known or assumed). However, in some species, dispersers perform a complex sequence of movements concatenated over time, which can be derived by different environmental factors, to reach new areas from the natal sites (Clobert et al. 2012). This composite transfer phase occurs, for example, during the dispersal of de young male elk (*Cervus elaphus*) tracked between winter ranges (Killeen et al. 2014; Benz et al. 2016). To capture that dispersal feature, Benz et al. (2016) combined a sequence of migratory and dispersal movements to model connectivity via least-cost corridors approach between winter ranges (i.e., core areas). Incorporating fine-scale information of habitat selection of male elks dispersers (Killeen et al. 2014), this study applied step selection functions to estimate habitat selection during spring and autumn movements to create two different resistance surfaces to predict seasonal movement corridors connecting winter with summer areas (spring resistance map) and, in sequence, corridors connecting summer with winter areas (autumn resistance map). Similarly, Osipova et al. (2019) used different seasonal resistance surfaces to demonstrate the importance of incorporating seasonal changes in connectivity modeling for African elephant (*Loxodonta africana*). This study showed that not accounting for that variability source can overestimates and underestimates landscape connectivity for the dry and wet season, respectively.

One of the main applications of connectivity models is the identification of areas or elements that may offer greater chances of success for individuals' movement among core areas (Rudnick et al. 2012; Kool et al. 2013). Despite the importance of ensuring the transfer phase, if we ignore the other dispersal phases, the proposed connector structures may have questionable functionality. After all, there is no point in having well-connected areas and not making sure that they are able to provide dispersers and/or ensure their establishment. Therefore, we recommend that whenever it is feasible, a more realistic representation of dispersal, explicitly considering its three stages should be implemented. This more complete view of the process can produce more reliable predictions about the pattern of species dispersal and, consequently, inform more efficiently the management strategies capable of restoring or ensuring its continuity (Travis et al. 2012). For example, one model that can represent all three phases of dispersal is CDPOP (Landguth and Cushman 2010), which models individual-based dispersal, mating, mortality, and gene flow across a costs and mortality risk surface. This model simulates the transfer phase as a cost-weighted dispersal process, and also simulates dispersal cost and mortality risk of the locations where dispersing individuals settle. By enabling simulation of dispersal, selection, mating, and mortality across large populations and long time periods in complex landscapes, this model provides realistic dispersal dynamics within a comprehensive individual-based population and genetics model.

Animal perception of the landscape

As mentioned before, many improvements have been implemented in LC analysis in recent years, mainly aiming to overcome the unrealistic assumption that all individuals will always follow the optimal path between two locations (Pinto and Keitt 2009; Landguth et al. 2012; Ribeiro et al. 2017). Studies using the classic single LC paths (factorial or not) assume that animals have perfect knowledge of the landscape, have specific destinations, and always make their decisions in order to optimize the movement to those destinations (i.e., reduce the cost-weighted distance). Both resistant kernel and the other LC approaches presented here break the assumption of omniscience in different ways. In the resistant kernel model, movement is not goal orientated and, consequently, the dispersal is treated diffusely since all paths around the source with an accumulated cost lower than the species dispersal threshold are possible (Compton

et al. 2007; Cushman and Landguth 2012). Kernel-smoothed LC paths represent possible deviations from the optimal route due to stochastic behavioral choices of individuals and/or an incomplete knowledge about the adjacent environment (Cushman et al. 2013). Although this approach considers that individuals will imperfectly follow LC paths, a greater probability will still be attributed to the optimal paths, and the possible deviations will still be centralized in their vicinity (i.e., individuals are assumed to have near-perfect knowledge of the landscape). The use of multiple low-cost paths created from stochastic variations assumes that individuals can disperse via different routes, some of which may deviate considerably from the LC paths. As far as we know, LC models rarely explicitly incorporate the perceptual range of species (but see Ribeiro et al. 2017).

Using CT, we are assuming that the studied species follows a resistance weighted random walk from specified source to a priori destination location (McRae et al. 2008). Although all paths from a source to a destination are possible, those with low resistance (i.e., higher current values) are more likely to be taken since they have higher net passages probabilities to the walkers (McRae et al. 2008). The movement decisions are taken probabilistically according to the resistance values imposed by the surrounding habitat and no local directional bias is considered (McRae et al. 2008). Because these decisions are only influenced by the resistance in the four or eight neighboring cells, the model assumes that the perceptual range is invariably equivalent to 1-cell size.

Similarly, in IBDMs, cell-to-cell movements are usually the result of a cost-weighted random choice based on the adjacent cells' movement probabilities, which are attributed according to the habitat characteristics of those cells. Although dispersal is modeled as a probabilistic event driven by animal's habitat type preferences, as in circuit theory and resistant kernels, IBDMs can still make the shift from one cell to another dependent on the degree of autocorrelation in the movement, mortality, food availability, conspecific interactions, perceptual range, and other parameters (e.g., Gardner and Gustafson 2004; Kramer-Schadt et al. 2004; Kanagaraj et al. 2013; Watkins et al. 2015). While there is no algorithmic or theoretical limitation to extending perceptual range in IBDMs to a larger range (e.g., Péer and Kramer-Schadt 2008; Landguth and Cushman 2010; Palmer et al. 2011), many of them consider that an individual will move to a cell according to its perception of the environment in the eight cells surrounding its current location, also assuming a 1-cell size perceptual range (e.g., Gardner and Gustafson 2004; Revilla and Wiegand 2008; Kanagaraj et al. 2013; Allen et al. 2016; but see Hauenstein et al. 2019).

The different assumptions about the animal perception of the landscape and the dynamics of movement incorporated by each model make them more or less appropriate to model dispersal routes according to the particularity of the target species. For example, the assumption of no knowledge beyond dispersers immediate surroundings seems to make CT suitable to model dispersal movements of species for which exploratory movements outside of the natal sites were uncommon (e.g., Harrison et al. 1991). On the contrary, for species in which juveniles frequently performed movements before dispersal, the assumption of near-perfect knowledge of LC models might be more appropriate (e.g., Debeffe et al. 2013). In some cases, the use of a hybrid approach may represent better species dispersal. The use both CT and LC model may be justified to model connectivity for species such as eagle owl (*Bubo bubo*), in which the dispersers follow routes that are intermediate solutions between the optimized and the random ones (Penteriani et al. 2010).

Although the ability of animals to perceive and respond to different landscape features (e.g., forests, water bodies, and cities) can change connectivity quantitatively and qualitatively (Péer and Kramer-Schadt 2008), the necessity of accounting for species-specific perceptual range and other fine-scale movement behavior into connectivity modeling will depend on the purpose and scale of the study. For example, applying resistant kernel analysis to a landscape resistance surface of 5 km pixel size, Riordan et al. (2016) evaluated connectivity across snow leopard (*Panthera uncia*) global range, providing an opportunity to direct future connectivity research and conservation actions for the species. Given that the main objective is to provide a big picture of species connectivity, it is acceptable to ignore certain dispersal details, such as perceptual range, in assessing movement among populations from this coarse view of space due to the large extension of the study area. When it is important to incorporate perceptual range into connectivity modeling, it is possible to do so in

different ways. For example, animal's perceptual range can be incorporated directly into IBDMs as a component of decision-making during movement (e.g., Palmer et al. 2011; Hauenstein et al. 2019), or indirectly through the development of a multi-scale model of landscape resistance (Krishnamurthy et al. 2016). From this last approach, resistance values are derived using environmental variables individually adjusted at specific scales in which they affect the movement of individuals (Krishnamurthy et al. 2016).

Mortality during dispersal

Because dispersal is costly and often involves relatively high risk of mortality (Bonte et al. 2012), neglecting this factor may overestimate dispersers success and, consequently, landscape connectivity. In addition to mortality risk driven by certain matrix elements (incorporated via resistance surface), in some cases, it is important to identify and include factors that impose additional mortality. For example, even including baseline mortality, most of the patches were connected for Eurasian lynx (*Lynx lynx*) according to the IBDM developed by Kramer-Schadt et al. (2004), but adding realistic levels of road mortality produced an opposite scenario. This study reinforces the idea that in some landscapes, especially those intensely disturbed by human actions, connectivity may not only depend on the distribution of dispersal habitat (structural connectivity) or animal's vagility (potential connectivity), but essentially on elements that allow access functional connectivity (Crooks and Sanjayan 2006). Additional mortality caused by roads may be particularly important for species that exhibit weaker avoidance of roads during dispersal (Gastón et al. 2016). It is worth noting that landscape connectivity might be a main factor in determining roadkill risk especially for habitat-generalist species (Fabrizio et al. 2019).

None of the LC models reviewed is capable of directly incorporating mortality during dispersal. In contrast to LC paths, which are "reflective" models (e.g., paths are reflected around obstacles to their a priori destination), resistant kernels are "absorptive" (e.g., resistant kernel value decreases cumulatively with accumulated cost from the dispersal source), which in some systems and for some species can reflect mortality losses during dispersal, while in others it can simply reflect the relative probability of final destination of dispersal. The difference between the two approaches would be reflected in whether the total kernel volume is constant or is down weighted by cumulative cost, the latter reflecting losses (mortality) during dispersal, and the former reflecting purely the dispersal phase without any modeled mortality.

Although it is conceptually possible to model mortality in CT, it does not seem to be a very trivial task (McRae et al. 2008). The main concern is related to the definition of probability of mortality so that the model does not overestimate death events (McRae et al. 2008). To simulate the probability of a random walker dying along the way, grounded resistors can be added on each node with resistance reflecting the probability of death as individuals pass through them (McRae et al. 2008). However, even if the probability of mortality is high in a given node, individuals can still visit it several times since they are moving randomly, inflating the mortality rates. This is because individuals are not allowed to have memory or long-distance perception and, consequently, they are incapable of avoiding these high-risk points (McRae et al. 2008). When incorporated in this way, mortality is assumed to be constant and independent of any individual condition (e.g., age or sex).

Stochastic mortality depending on habitat quality defined based on human disturbances (Kanagaraj et al. 2013) or due to starvation and predation (Gardner and Gustafson 2004) can be associated with each movement step or time step within IBDMs and may be age-dependent (Watkins et al. 2015). This arguably is one of the main strengths and advantages of IBDMs, as incorporating both the effect of the landscape on dispersal (e.g., resistance) and mortality (e.g., risk) is essential to reliable predictions of the population-level implications of any landscape condition or change.

Inter-individual variability

Animal dispersal is driven by multiple factors, being often both condition- and phenotype-dependent (i.e., some phenotypic differences are related to different dispersal propensity and individuals may adjust their dispersal tactics based on external factors such as habitat quality; Clobert et al. 2009). Because individual variability in dispersal behaviors has been widely documented for many species (e.g., Bowler and Benton 2005; Clobert et al. 2009; Penteriani et al. 2010) and can substantially impact landscape

connectivity (Palmer et al. 2014; Vasudev et al. 2015; Osipova et al. 2019), it is important to capture this source of variation in the wildlife corridor design (Baguette et al. 2013). The heterogeneity in dispersal decisions among individuals may arise as a consequence of differences between sex, physiological condition, as well as previous experiences and ability to use external cues (e.g., Penteriani et al. 2010).

All connectivity models that consider stochastic variation to produce multiple alternative routes implicitly incorporate some inter-individual variability. However, stochastic variation does not enable separation of effects of particular organism characteristics on movement or connectivity. It is possible to use two main strategies to explicitly consider individual variability into connectivity modeling: varying specific model parameters or producing different resistance surfaces. Instead of considering only average individuals when describing the species dispersal ability in LC models and IBDMs, it would be interesting to use a range of values also allowing for the occurrence of less frequently observed long-distance dispersal events. For example, Cushman et al. (2016) evaluated how a range of dispersal distances affect predictions of connectivity for African lions. The same strategy can also be applied to species exhibiting inter-sexual differences in dispersal distances (Penteriani et al. 2010). For LC path and resistant kernel analyses, the maximum dispersal distance can be specified based on the Euclidean distance or converted to a maximum cumulative cost value (Compton et al. 2007; Cushman and Landguth 2012; Landguth et al. 2012). IBDMs may additionally incorporate variability in the parameters used to define dispersal behavior such as directional persistence (Palmer et al. 2014) and perceptual range (Olden et al. 2004), making them variable among individuals and/or dependent on landscape context. To account for inter-individual variability in the way little owls (*Athene noctua*) respond to their environments during dispersal, Hauenstein et al. (2019) built an IBDM and implemented a habitat-specialization-level parameter, defining for each individual the importance of habitat suitability during its movement.

All connectivity models considered here may incorporate inter-individual variability through resistance values to reflect different dispersal strategies such as that presented by bolder individuals, which may take greater risks during dispersal (Palmer et al. 2014). Sex-specific resistance surface can also be used to incorporate differences in patterns of habitat use during movement of males and females (Elliot et al. 2014; Maiorano et al. 2017). To take into account the variability across individuals in connectivity predictions for African elephant, Osipova et al. (2019) suggested a weighted overlay framework, in which the final resistance surface used to model connectivity was constructed by adding resistance values weighted by the distance to the home-range center obtained for each individual. They demosntrated that the weighted overlay method significantly improves the movement predictions.

Time

Only IBDMs are able to explicitly consider time during dispersal modeling. A movement threshold in IBDMs can be set in terms of maximum number of movement steps or cumulative cost that may represent the entire dispersal process (e.g., Palmer et al. 2011; Allen et al. 2016) or a fraction of it, and in this last case the threshold is renewed following a temporal mark (e.g., days) until it reaches a certain period of time such as a year (e.g., Kramer-Schadt et al. 2004; Kanagaraj et al. 2013). Since patch connectivity may be dependent on the simulated time period, the time window during which the dispersal process is modeled may be important, especially for those models operating on an intraday time scale (Kramer-Schadt et al. 2004; Hauenstein et al. 2019).

Conclusions

The effectiveness of conservation efforts to mitigate the impacts of rapid global changes on biodiversity is strongly linked to our ability to adequately understand and represent the ecological processes underlying population dynamics. Hence the success of conservation measures focused on improving connectivity among populations will depend on how well data and modeling approaches can capture the actual process of species dispersal. Dispersal is a multifaceted process that results from complex interactions between intrinsic attributes of dispersers and external environmental factors (Clobert et al. 2012; Vasudev et al. 2015). Therefore, to ensure dispersal success, it is necessary

to understand the dispersal process itself (Vasudev et al. 2015).

The current connectivity modeling has allowed the incorporation of several important aspects to represent and evaluate animal dispersal. Many aspects of dispersal (e.g., individual heterogeneity, perceptual range, and mortality) can be considered through the resistance surface, the backbone of the most commonly used connectivity models. We emphasize the need to ensure that resistance surfaces capture and represent the real costs imposed on animal dispersal. When directly using dispersal data is not possible, we recommend that the study make clear what implications and inferences are allowed from the proxy used to measure resistance. Other particularities of the dispersal ecology of the target species in line with the data nature and availability, as well as the study and conservation objectives, will dictate the most appropriate choice among the available connectivity approaches.

Because the connectivity models reviewed here represent different assumptions about animal dispersal, we recommend that the choice of them should not be based solely on its popularity, but rather on the three factors mentioned above. We suggest that, whenever possible, researchers should opt for approaches that can represent movement behavior more realistically, in addition to incorporating factors known to influence the species' dispersal success. When the use of such models is impracticable and/or the information on dispersal behavior is very limited or not available, we indicate to estimate connectivity from different models and confronting their results with independent empirical dispersal data. This practice will bring substantial gain to the ability of the models to represent the studied system and other similar systems. In this scenario, perform sensitivity analyses or incorporate uncertainty into the parameter estimates is also essential for evaluating the results robustness.

It is noteworthy that although we have described and discussed connectivity models from the perspective of a single species, in recent years, there has been a growing number of studies applying these models to design habitat networks for multiple species (e.g., Albert et al.; Brodie et al. 2015; Khosravi et al. 2018). Most commonly, multispecies connectivity scenarios can be generated through composite resistance surfaces (e.g., Brodie et al. 2015) or from the intersection of individual connectivity scenarios (e.g., Khosravi et al. 2018). Designing a conservation planning based on a multispecies perspective representing a diversity of habitat and/or movement needs is recommended, since a single surrogate species cannot represent the demands of all co-occurring species (Meurant et al. 2018; Diniz et al. 2018b). However, since no connectivity scenario is likely to be as effective as the one designed to meet the demands of a particular species, trade-offs between single- and multispecies approaches may be unavoidable (Breckheimer et al. 2014; Brodie et al. 2015). This is a recently debated topic in the literature and provides an opportunity for future development and enhancement of connectivity models.

Improvements in tracking technologies integrated with remote sensing data have enabled the start of "a golden age of animal tracking science" (Kays et al. 2015). Nevertheless, there are still relatively few studies comparing the predictive power of the models and the suitability of different data types to represent dispersal (Zeller et al. 2018). Given the immense and increasing interest in connectivity and dispersal modeling, there are few topics in landscape ecology and conservation biology more urgent than evaluating the relative performance and utility of alternative connectivity modeling methods, and under which situations and for which questions each is best suited. The comparative validation of connectivity models has great implications mainly for conservation research since they can offer different solutions to the same problem (Avon and Bergès 2016). We suggest a focused research agenda to explore the behavior, accuracy, and similarities among connectivity modeling methods (e.g., Cushman et al. 2014; Zeller et al. 2018). Specifically, we recommend studies that use simulations of animal movement based on known and specified relationships between landscape resistance, mortality risk, and other costs to generate movement paths which then can be compared to the predictions of alternative connectivity modeling approaches. This will enable robust determination of the effectiveness of alternative connectivity modeling methods and, consequently, will guide us toward a better allocation of limited conservation resources to determine functional wildlife corridor placements.

Acknowledgements We thank the two anonymous referees for their careful reading and their many helpful and insightful

comments that have greatly improved this manuscript. We also thank Daniel Brito for discussions and suggestions. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001. M. F. Diniz is supported by a graduate fellowship from CAPES. The Brazilian National Research Council (CNPq) provided a Research Grant (#306838/2016-8) to R. B. Machado.

References

Aben J, Strubbe D, Adriaensen F, Palmer SCF, Travis JMJ, Lens L, Matthysen E (2014) Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. J Appl Ecol 51:693–702

Abrahms B, Sawyer SC, Jordan NR, McNutt JW, Wilson AM, Brashares JS (2017) Does wildlife resource selection accurately inform corridor conservation? J Appl Ecol 54:412–422

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least-cost' modelling as a functional landscape model. Landsc Urban Plan 64:233–247

Albert CH, Rayfield B, Dumitru M, Gonzalez A (2017) Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change. Conserv Biol 31:1383–1396

Allen CH, Parrott L, Kyle C (2016) An individual-based modelling approach to estimate landscape connectivity for bighorn sheep (*Ovis canadensis*). PeerJ 4:e2001

Avon C, Bergès L (2016) Prioritization of habitat patches for landscape connectivity conservation differs between least-cost and resistance distances. Landsc Ecol 31:1551–1565

Baguette M, Blanchet S, Legrand D, Stevens VM, Turlure C (2013) Individual dispersal, landscape connectivity and ecological networks. Biol Rev 88:310–326

Beier P, Majka DR, Spencer WD (2008) Forks in the road: choices in procedures for designing wildland linkages. Conserv Biol 22:836–851

Benz RA, Boyce MS, Thurfjell H, Paton DG, Musiani M, Dormann CF, Ciuti S (2016) Dispersal ecology informs design of large-scale wildlife corridors. PLoS ONE 11:1–20

Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehouck V, Matthysen E, Mustin K, Saastamoinen M et al (2012) Costs of dispersal. Biol Rev 87:290–312

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev 80:205–225

Breckheimer I, Haddad NM, Morris WF, Trainor AM, Fields WR, Jobe RT, Hudgens BR, Moody A, Walters JR (2014) Defining and evaluating the umbrella species concept for conserving and restoring landscape connectivity. Conserv Biol 28:1584–1593

Brodie JF, Giordano AJ, Dickson B, Hebblewhite M, Bernard H, Mohd-Azlan J, Anderson J, Ambu L (2015) Evaluating multispecies landscape connectivity in a threatened tropical mammal community. Conserv Biol 29:122–132

Carroll C, Mcrae BH, Brookes A (2012) Use of Linkage Mapping and Centrality Analysis Across Habitat Gradients to Conserve Connectivity of Gray Wolf Populations in Western North America. Conserv Biol 26:78–87

Chetkiewicz CLB, Boyce MS (2009) Use of resource selection functions to identify conservation corridors. J Appl Ecol 46:1036–1047

Clobert J, Le Galliard JF, Cote J, Meylan S, Massot M (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol Lett 12:197–209

Clobert J, Baguette M, Benton TGBJ (2012) Dispersal ecology and evolution. Oxford University Press, Oxford

Codling EA, Plank MJ, Benhamou S (2008) Random walk models in biology. J R Soc Interface 5:813–834

Compton BW, McGarigal K, Cushman SA, Gamble LR (2007) A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conserv Biol 21:788–799

Correa Ayram CA, Mendoza ME, Etter A, Salicrup DRP (2016) Habitat connectivity in biodiversity conservation: a review of recent studies and applications. Prog Phys Geogr Earth Environ 40:7–37

Coulon A, Aben J, Palmer SCF, Stevens VM, Callens T, Strubbe D, Lens L, Matthysen E, Baguette M, Travis JMJ (2015) A stochastic movement simulator improves estimates of landscape connectivity. Ecology 96:2203–2213

Crooks KR, Sanjayan M (2006) Connectivity Conservation. Cambridge University Press, Cambridge

Cushman SA, Landguth EL (2012) Multi-taxa population connectivity in the Northern Rocky Mountains. Ecol Modell 231:101–112

Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. Am Nat 168:486–499

Cushman SA, McKelvey KS, Flather CH, McGarigal K (2008) Do forest community types provide a sufficient basis to evaluate biological diversity? Front Ecol Environ 6:13–17

Cushman SA, Lewis JS, Landguth EL (2013) Evaluating the intersection of a regional wildlife connectivity network with highways. Mov Ecol 1:1–11

Cushman SA, Lewis JS, Landguth EL (2014) Why did the bear cross the road? Comparing the performance of multiple resistance surfaces and connectivity modeling methods. Diversity 6:844–854

Cushman SA, Elliot NB, Macdonald DW, Loveridge AJ (2016) A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change. Landsc Ecol 31:1337–1353

Debeffe L, Morellet N, Cargnelutti B, Lourtet B, Coulon A, Gaillard JM, Bon R, Hewison AJM (2013) Exploration as a key component of natal dispersal: dispersers explore more than philopatric individuals in roe deer. Anim Behav 86:143–151

Dickson BG, Albano CM, Anantharaman R, Beier P, Fargione J, Graves TA, Gray ME, Hall KR, Lawler JJ, Leonard PB et al (2018) Circuit-theory applications to connectivity science and conservation. Conserv Biol 33(2):239–249

Dijkstra EW (1959) A note on two problems in connection with graphs. Numer Math 1:269–271

Dilts TE, Weisberg PJ, Leitner P, Matocq MD, Inman RD, Nussear KE, Esque TC (2016) Multiscale connectivity and

graph theory highlight critical areas for conservation under climate change. Ecol Appl 26:1223–1237
Diniz MF, Machado RB, Bispo AA, Brito D (2018a) Identifying key sites for connecting jaguar populations in the Brazilian Atlantic Forest. Anim Conserv 21:201–210
Diniz MF, Machado RB, Bispo AA, De M. Júnior P (2018b) Can we face different types of storms under the same umbrella? Efficiency and consistency of connectivity umbrellas across different patchy landscape patterns. Landsc Ecol 33:1911–1923
Elliot NB, Cushman SA, Macdonald DW, Loveridge AJ (2014) The devil is in the dispersers: predictions of landscape connectivity change with demography. J Appl Ecol 51:1169–1178
Etherington TR (2016) Least-cost modelling and landscape ecology: concepts, applications, and opportunities. Curr Landsc Ecol Rep 1(1):40–53
Fabrizio M, Di Febbraro M, D'Amico M, Frate L, Roscioni F, Loy A (2019) Habitat suitability vs landscape connectivity determining roadkill risk at a regional scale: a case study on European badger (*Meles meles*). Eur J Wildl Res 65:7
Fattebert J, Robinson HS, Balme G, Slotow R, Hunter L (2015) Structural habitat predicts functional dispersal habitat of a large carnivore: how leopards change spots. Ecol Appl 25:1911–1921
Foltête J-C, Clauzel C, Vuidel G (2012) A software tool dedicated to the modelling of landscape networks. Environ Model Softw 38:316–327
Gardner RH, Gustafson EJ (2004) Simulating dispersal of reintroduced species within heterogeneous landscapes. Ecol Modell 171:339–358
Gastón A, Blázquez-Cabrera S, Garrote G, Mateo-Sánchez MC, Beier P, Simón MA, Saura S (2016) Response to agriculture by a woodland species depends on cover type and behavioural state: insights from resident and dispersing *Iberian lynx*. J Appl Ecol 53:814–824
Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, Thulke H-H, Weiner J, Wiegand T, DeAngelis DL (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310:987–991
Harrison DJ, Harrison JA, O'Donoghue M (1991) Predispersal movements of coyote (*Canis latrans*) pups in Eastern Maine. J Mammal 72:756–763
Hauenstein S, Fattebert J, Grüebler M, Naef-Daenzer B, Peer G, Hartig F (2019) Calibrating an individual-based movement model to predict functional connectivity for little owls. Ecol Appl 0:e01873
Jønsson KA, Tøttrup AP, Borregaard MK, Keith SA, Rahbek C, Thorup K (2016) Tracking animal dispersal: from individual movement to community assembly and global range dynamics. Trends Ecol Evol 31:204–214
Kanagaraj R, Wiegand T, Kramer-Schadt S, Goyal SP (2013) Using individual-based movement models to assess inter-patch connectivity for large carnivores in fragmented landscapes. Biol Conserv 167:298–309
Kays R, Crofoot MC, Jetz W, Wikelski M (2015) Terrestrial animal tracking as an eye on life and planet. Science 80-(348):aa2478
Keeley ATH, Beier P, Gagnon JW (2016) Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc Ecol 31:2151–2162
Keeley ATH, Beier P, Keeley BW, Fagan ME (2017) Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. Landsc Urban Plan 161:90–102
Khosravi R, Hemami M-R, Cushman SA (2018) Multispecies assessment of core areas and connectivity of desert carnivores in central Iran. Divers Distrib 24:193–207
Killeen J, Thurfjell H, Ciuti S, Paton D, Musiani M, Boyce MS (2014) Habitat selection during ungulate dispersal and exploratory movement at broad and fine scale with implications for conservation management. Mov Ecol 2(1):1–13
Koen EL, Bowman J, Sadowski C, Walpole AA (2014) Landscape connectivity for wildlife: development and validation of multispecies linkage maps. Methods Ecol Evol 5:626–633
Kool JT, Moilanen A, Treml EA (2013) Population connectivity: recent advances and new perspectives. Landsc Ecol 28:165–185
Kramer-Schadt S, Revilla E, Thorsten W, Breitenmoser U (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. J Appl Ecol 41:711–723
Krishnamurthy R, Cushman SA, Sarkar MS, Malviya M, Naveen M, Johnson JA, Sen S (2016) Multi-scale prediction of landscape resistance for tiger dispersal in central India. Landsc Ecol 31:1355–1368
Landguth EL, Cushman SA (2010) CDPOP: a spatially explicit cost distance population genetics program. Mol Ecol Resour 10:156–161
Landguth EL, Hand BK, Glassy J, Cushman SA, Sawaya MA (2012) UNICOR: a species connectivity and corridor network simulator. Ecography (Cop) 35:9–14
Levins R (1966) The strategy of model building in population biology. Am Sci 54:421–431
Liu C, Newell G, White M, Bennett AF (2018) Identifying wildlife corridors for the restoration of regional habitat connectivity: a multispecies approach and comparison of resistance surfaces. PLoS ONE 13:1–14
Maiorano L, Boitani L, Chiaverini L, Ciucci P (2017) Uncertainties in the identification of potential dispersal corridors: the importance of behaviour, sex, and algorithm. Basic Appl Ecol 21:66–75
McClure ML, Hansen AJ, Inman RM (2016) Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. Landsc Ecol 31:1419–1432
McClure ML, Dickson BG, Nicholson KL (2017) Modeling connectivity to identify current and future anthropogenic barriers to movement of large carnivores: a case study in the American Southwest. Ecol Evol 7:3762–3772
McRae BH (2006) Isolation by resistance. Evolution (NY) 60:1551–1561
McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724
Meurant M, Gonzalez A, Doxa A, Albert CH (2018) Selecting surrogate species for connectivity conservation. Biol Conserv 227:326–334
Mimet A, Clauzel C, Foltête JC (2016) Locating wildlife crossings for multispecies connectivity across linear infrastructures. Landsc Ecol 31:1955–1973

Moqanaki EM, Cushman SA (2017) All roads lead to Iran: predicting landscape connectivity of the last stronghold for the critically endangered Asiatic cheetah. Anim Conserv 20:29–41

Olden JD, Schooley RL, Monroe JB, Poff NL (2004) Context-dependent perceptual ranges and their relevance to animal movements in landscapes. J Anim Ecol 73:1190–1194

Osipova L, Okello MM, Njumbi SJ, Ngene S, Western D, Hayward MW, Balkenhol N (2019) Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons. Anim Conserv 22:35–48

Palmer SCF, Coulon A, Travis JMJ (2011) Introducing a 'stochastic movement simulator' for estimating habitat connectivity. Methods Ecol Evol 2:258–268

Palmer SCF, Coulon A, Travis JMJ (2014) Inter-individual variability in dispersal behaviours impacts connectivity estimates. Oikos 123:923–932

Pascual-Hortal L, Saura S (2006) Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landsc Ecol 21:959–967

Péer G, Kramer-Schadt S (2008) Incorporating the perceptual range of animals into connectivity models. Ecol Modell 213:73–85

Pelletier D, Clark M, Anderson MG, Rayfield B, Wulder MA, Cardille JA (2014) Applying circuit theory for corridor expansion and management at regional scales: tiling, pinch points, and omnidirectional connectivity. PLoS ONE 9:1–11

Penteriani V, Revilla E, Nams VO (2010) The effect of phenotypic traits and external cues on natal dispersal movements. J Anim Ecol 79(3):620–632

Pinto N, Keitt TH (2009) Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. Landsc Ecol 24:253–266

Rayfield B, Fortin MJ, Fall A (2011) Connectivity for conservation: a framework to classify network measures. Ecology 92:847–858

Reed GC, Litvaitis JA, Callahan C, Carroll RP, Litvaitis MK, Broman DJA (2017) Modeling landscape connectivity for bobcats using expert-opinion and empirically derived models: how well do they work? Anim Conserv 20:308–320

Revilla E, Wiegand T (2008) Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. Proc Natl Acad Sci USA 105:19120–19125

Revilla E, Wiegand T, Palomares F, Ferreras P, Delibes M (2004) Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. Am Nat 164:E130–E153

Ribeiro JW, Silveira dos Santos J, Dodonov P, Martello F, Brandão Niebuhr B, Ribeiro MC (2017) LandScapeCorridors (LSCORRIDORS): a newsoftware package for modelling ecological corridors based on landscape patterns and species requirements. Methods Ecol Evol 8:1425–1432

Riordan P, Cushman SA, Mallon D, Shi K, Hughes J (2016) Predicting global population connectivity and targeting conservation action for snow leopard across its range. Ecography (Cop) 39:419–426

Rudnick D, Ryan SJ, Beier P, Dieffenbach F (2012) The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues Ecol 16:1–20

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

Saura S, Torné J (2009) Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environ Model Softw 24:135–139

Shirk AJ, Wallin DO, Cushman SA, Rice CG, Warheit KI (2010) Inferring landscape effects on gene flow: a new model selection framework. Mol Ecol 19:3603–3619

Spear SF, Balkenhol N, Fortin MJ, McRae BH, Scribner K (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Mol Ecol 19:3576–3591

Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. Oikos 68:571

Tischendorf L, Fahrig L (2000) On the usage and measurement of landscape connectivity. Oikos 90:7–19

Tracey JA (2006) Individual-based modeling as a tool for conserving connectivity. In: Crooks KR, Sanjayan M (eds) Connectivity conservation. Cambridge University Press, Cambridge, pp 343–368

Trainor AM, Walters JR, Morris WF, Sexton J, Moody A (2013) Empirical estimation of dispersal resistance surfaces: a case study with red-cockaded woodpeckers. Landsc Ecol 28:755–767

Travis JMJ, Mustin K, Bartoń KA, Benton TG, Clobert J, Delgado MM, Dytham C, Hovestadt T, Palmer SCF, Van Dyck H et al (2012) Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. Methods Ecol Evol 3:628–641

Urban D, Keitt T (2001) Landscape connectivity: a graph-theoretic perspective. Ecology 82:1205–1218

Vasudev D, Fletcher RJ, Goswami VR, Krishnadas M (2015) From dispersal constraints to landscape connectivity: lessons from species distribution modeling. Ecography (Cop) 38:967–978

Watkins A, Noble J, Foster RJ, Harmsen BJ, Doncaster CP (2015) A spatially explicit agent-based model of the interactions between jaguar populations and their habitats. Ecol Modell 306:268–277

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landsc Ecol 27:777–797

Zeller KA, Jennings MK, Vickers TW, Ernest HB, Cushman SA, Boyce WM (2018) Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. Divers Distrib 24:868–879