

# From dispersal constraints to landscape connectivity: lessons from species distribution modeling

Divya Vasudev, Robert J. Fletcher Jr, Varun R. Goswami and Meghna Krishnadas

*D. Vasudev (vasudev.divya@gmail.com), R. J. Fletcher and V. R. Goswami, Dept of Wildlife Ecology and Conservation, Univ. of Florida, Gainesville, FL 32611, USA. DV also at: Wildlife Trust of India, Noida 201301, Uttar Pradesh, India. RJF and VRG also at: School of Natural Resources and Environment, Univ. of Florida, Gainesville, FL 32611, USA. DV and VRG also at: Wildlife Conservation Society, India Program, Bangalore, India. – M. Krishnadas, School of Forestry and Environmental Studies, Yale Univ., New Haven, CT 06511, USA.*

Connectivity plays a crucial role in determining the spread, viability, and persistence of populations across space. Dispersal across landscapes, or the movement of individuals or genes among resource patches, is critical for functional connectivity. Yet current connectivity modelling typically uses information on species location or habitat preference rather than movement, which unfortunately may not capture key dispersal limitations. We argue that recent developments in species distribution modelling provide insightful lessons for addressing this gap and advancing our understanding of connectivity. We suggest shifting the focus of connectivity modelling from locating where animals potentially disperse to a process-based approach directed towards understanding and mapping factors that limit successful dispersal. To do so, we propose defining species dispersal requirements through identifying spatial, environmental and intrinsic constraints to successful dispersal, analogous to identifying environmental dimensions that define niches. We discuss the benefits of this constraint-based framework for understanding the distribution of species, predicting species responses to climate change, and connectivity conservation practice. We illustrate how the framework can aid in identifying potential detrimental effects of human activities on connectivity and species persistence, and can spur the implementation of innovative conservation strategies. The proposed framework clarifies the validity and contextual utility of objectives and measures in existing connectivity models, and identifies gaps that may impede our understanding of connectivity and its integration into successful conservation strategies. We expect that this framework will facilitate a mechanistic approach to understanding and conserving connectivity, which will aid in effectively predicting and mitigating effects of ongoing environmental change.

Connectivity emerges from dispersal across landscapes, or the movement of individuals and genes among resource patches (see Table 1 for definition of key terms; Taylor et al. 1993, Lindenmayer and Fischer 2007, Clobert et al. 2012). These linkages influence population dynamics through a variety of mechanisms, including demographic rescue, inbreeding avoidance, colonization of unoccupied habitat, and the spread of diseases (Clobert et al. 2012). Consequently, knowledge of connectivity can enhance our understanding of species current and potential distribution patterns, population demography, genetic variability, evolutionary processes, and overall viability of species in heterogeneous landscapes, as well as provide insights into the dynamics of metacommunities. Connectivity is also increasingly relevant for conservation aimed at ameliorating negative impacts of ongoing habitat fragmentation and climate change on long-term species persistence (Taylor et al. 1993, Lindenmayer et al. 2008, Doerr et al. 2011).

Connectivity is a function of the response of individual dispersers to landscape structure (Taylor et al. 1993). Therefore, effective understanding of connectivity

necessitates knowledge of species requirements for dispersal. Yet, current connectivity modelling and management often implicitly assume that dispersal requirements of species are approximated by characteristics of their occupied habitat (Zeller et al. 2012). This set of environments constitutes the species occupied niche (sensu Peterson et al. 2011; Table 1). This assumption (i.e. that species' occupied habitat or niche approximates conditions suitable for successful dispersal) emerges from the frequent use of connectivity metrics that treat non-habitat regions of the landscape (i.e. the matrix) as homogeneously impermeable to movement (Calabrese and Fagan 2004, Smolik et al. 2010, Sawyer et al. 2011). Even when matrix heterogeneity is considered, relative matrix resistances to movement are typically assessed based on the similarity of matrix types to habitat of species (Epps et al. 2007, Eycott et al. 2012). As a direct consequence, connectivity modelling can have poor predictive power (Fletcher et al. 2011) and interventions for connectivity conservation are largely habitat-focused, frequently implemented through habitat consolidation or corridor demarcation (Moilanen et al. 2009, Worboys et al. 2010).

Table 1. Selected definitions and concepts.

Term	Definition
Concepts relevant to connectivity	
Connectivity	Functional linkages between resource patches for a given species
Connectivity conservation	All research and action taken to conserve such linkages. To date, the predominant strategy for connectivity conservation has been the demarcation of corridors
Corridors	Linear sections of habitat that facilitate dispersal between fragments
Dispersal	Movement leading to spatial gene flow. Here, we specifically refer to movement in heterogeneous landscapes, wherein dispersal represents a behavioural complex that includes emigration from a local habitat fragment, movement across a non-habitat matrix, immigration and settlement into a new habitat fragment. While we largely restrict our discussion to animal, and largely active, dispersal, concepts expanded upon are also relevant, albeit with slight modifications, to dispersal of sessile organisms (e.g. plants)
Matrix	All non-habitat regions of the landscape
Matrix resistance	The permeability of a matrix type to the movement of individuals
Concepts relevant to species niche	
Geographic space	A two-dimensional space representing the physical location of landscape elements. It has been contrasted in niche modelling to the environmental space, or a multi-dimensional space of environmental variables represented in the study domain. We contrast the geographic space to the multi-dimensional niche hyperspace that encompasses aspects of physical location, as well as environmental and intrinsic dimensions relevant for the focal species (see below)
Species occupied (or actual) niche	The set of environments that a species actually inhabits. In geographic space, this constitutes the occupied habitat of the species
SEI framework	The spatial-environment-intrinsic (SEI) framework is a heuristic representation of the spatial, environmental and intrinsic constraints to successful dispersal

Source: Lindenmayer and Fischer (2007), Worboys et al. (2010), Peterson et al. (2011) and Clobert et al. (2012).

Dispersal is predominantly undertaken in the non-habitat matrix (Clobert et al. 2012). As a corollary, habitat of species, or the occupied niche, often may not fully encompass requirements for successful dispersal (Kupfer 2006, Revilla and Wiegand 2008). Recent empirical evidence suggests that while certain species may, on average, prefer matrix types that are similar to their habitat, this preference is highly variable across species (Eycott et al. 2012). In fact, habitat and microhabitat selection exhibited by individuals while dispersing may vastly differ from those exhibited while residing within their occupied niche (Bowne et al. 1999, Selonen and Hanski 2006). Identifying the limits or constraints to successful dispersal across landscapes thus remains a largely unanswered, albeit crucial, issue for the understanding of connectivity patterns across landscapes. This knowledge gap exists despite recent methodological advances that allow for understanding species dispersal requirements (Cagnacci et al. 2010, Knowlton and Graham 2010). We suggest that a framework emphasizing a process- and threat-based approach to assessing connectivity, which facilitates the systematic incorporation of knowledge on species dispersal requirements, can effectively address this gap in current approaches to understanding, modelling and conserving connectivity.

There are strong parallels between viewing connectivity from the perspective of limiting factors and recent advances in species distribution modelling which describe species distribution through abiotic, biotic and movement-related limiting factors (Soberón and Peterson 2005, Peterson et al. 2011). Isolating these limiting factors aided in distinguishing the occupied, realized and potential niche spaces and it enabled assessments of the validity and contextual utility of research models related to species distribution for conservation problems (Soberón and Nakamura 2009, Barve et al.

2011, Peterson et al. 2011, Guisan et al. 2013). These developments relating the species niche to distribution modelling may therefore provide key lessons for the development of an analogous framework within which we can validate current connectivity models, identify key gaps in implementation, and align research models with conservation objectives.

We develop a framework, adapted from recent concepts relating the species niche to distribution modelling, to aid in the identification and assessment of limiting factors to successful dispersal relevant for connectivity modelling and conservation. While niche theory has advanced considerably in recent years (Chase and Leibold 2003, Holt 2009), here we refer specifically to developments that link species niches to their geographic distribution (Peterson et al. 2011) and the relevance of these developments to problems in connectivity science. We show how mapping dispersal constraints in space can facilitate identification of potential and actual dispersal routes of species. This framework clarifies the scope of existing approaches to understanding connectivity and provides insights for the evaluation of their utility. Furthermore, it can identify species for which connectivity may be limiting, but where current practices would suggest otherwise. As a consequence, we argue for the need to extend the focus of connectivity from locating potential dispersal routes to identifying species dispersal constraints across landscapes, and illustrate the implications of applying this framework for modelling and connectivity conservation planning. We largely focus our discussion on animal dispersal. Nevertheless, the framework we describe can have utility in understanding and modelling dispersal of plants and other sessile organisms as well. Plant dispersal abilities may vary across species, populations and individuals, in addition to landscape

features and their spatial configuration (Nathan and Muller-Landau 2000, Carlo and Morales 2008). Insights into the relevance of these factors for plant dispersal can improve our understanding and predictions of plant distribution patterns, impacts of ongoing climate change and forest dynamics (Hanson et al. 1990, Dullinger et al. 2004, Svenning and Skov 2007).

## Species dispersal requirements, the species niche and distribution modelling

Species dispersal limitations have been incorporated within species distribution modelling as a delineator of niche space (Pulliam 2000, Kneitel and Chase 2004, Soberón and Peterson 2005). Movement constraints of species serve to distinguish regions that fall within the occupied niche from that of the potential niche (areas that are amenable to species persistence, but inaccessible to the species; Soberón and Peterson 2005). Within this framework, dispersal has been included in species distribution models as an important predictor of where colonization can occur (Engler and Guisan 2009), and to clarify focal regions of study and inference (Barve et al. 2011). Therefore, understanding species dispersal requirements can be beneficial not just in the field of connectivity, but can additionally improve predictions of current and future habitat of species within traditional ecological niche modelling (Engler and Guisan 2009, Smolik et al. 2010).

Current connectivity modelling focuses predominantly on identifying actual or potential dispersal routes of focal species (Sanderson et al. 2002, Rabinowitz and Zeller 2010, Lawler et al. 2013), or on areas accessible to animals (Smolik et al. 2010). These approaches amount to viewing connectivity primarily in geographic space. Ecological niche modelling translates species distribution patterns in geographic space to a heuristic hyperspace depicted by limiting factors. In operational terms, such a hyperspace can be defined as one where the probability of occurrence, or of long-term persistence of populations, is above a set threshold (Elith et al. 2006, Smolik et al. 2010). In a similar vein, we envision a translation of dispersal patterns in geographic space to a heuristic hyperspace defined by factors relevant to successful dispersal, including, but not limited to, spatial location. Here, we envision delimiting a hyperspace wherein the probability of successful dispersal, conditional on an animal taking a decision to disperse, is above a set threshold. This perspective of dispersal moves beyond the traditional representation of movement responses as spatial locations (Adriaensen et al. 2003, Nathan et al. 2008), while retaining space as an important influencing factor for individual movement and connectivity patterns.

Niche concepts distinguish the geographic space, or locations of species presence (and absence), from the environmental space, representing factors influencing species distribution (Peterson et al. 2011). Similarly, we envision an environmental space comprised of factors that constrain successful dispersal. Yet the environmental space currently defined to delimit species' niche is insufficient for developing a framework for dispersal limitations relevant to connectivity for at least three reasons. First, niche require-

ments primarily include habitat and resources relevant to the survival and reproduction of species (Chase and Leibold 2003, Soberón 2007), whereas dispersal largely occurs in non-habitat matrix. Second, successful dispersal requires entire routes in geographic space. Therefore, interpreting the cumulative configuration of landscape elements in space (or the arrangement of landscape elements along entire dispersal routes) is necessary for identifying species dispersal requirements (Revilla and Wiegand 2008). Third, recent approaches to movement ecology emphasize the role of intrinsic attributes of the individual disperser in determining movement patterns (Nathan et al. 2008, Clobert et al. 2009), whereas individual variation plays a minimal role in conventional species distribution modelling or conceptualization of species niches (Peterson et al. 2011). Furthermore, the incorporation of movement into species distribution and ecological niche modelling has been largely focussed on delimiting areas that are accessible to species on an evolutionary time-scale (Soberón and Peterson 2005); on the other hand, connectivity modelling is typically focussed on identifying locations in the landscape that are crucial for movement of species between habitats and populations on ecological time scales (Lowe and Allendorf 2010). Notwithstanding these divergences from ecological niche modelling, successful dispersal routes are delineated by the manifestation of identified dispersal constraints in geographic space, akin to the relationship between the species niche and geographic distribution.

## A framework for revealing species dispersal constraints across landscapes

To facilitate identification of species dispersal constraints, we adopt an approach similar to distribution modelling (as used in Peterson et al. 2011) in that we consider factors that have been shown, theoretically or empirically, to limit dispersal. We classify these limiting factors into three general categories: a) spatial constraints pertaining to the location of landscape elements, b) external environmental factors, and c) intrinsic factors, or internal constraints of dispersers. Together, these factors constitute the spatial-environment-intrinsic (SEI) framework. By demarcating regions of a heuristic hyperspace unconstrained by each of these categories, one can characterize requirements for successful dispersal of species (Fig. 1A).

Dispersal encompasses three stages: emigration, a transient search or transfer stage, and immigration or establishment (Clobert et al. 2012). Spatial, environmental and intrinsic factors may differentially influence each of these stages through two mechanisms: first, alteration of demographic parameters (such as mortality or energetic costs that can impact fitness), and second, modification of movement behaviours. These factors can operate alone or in synergistic ways to limit successful dispersal across landscapes.

### Spatial constraints

Spatial constraints arise from limiting effects of the arrangement of landscape elements in space (e.g. landscape configuration), including the relative location of

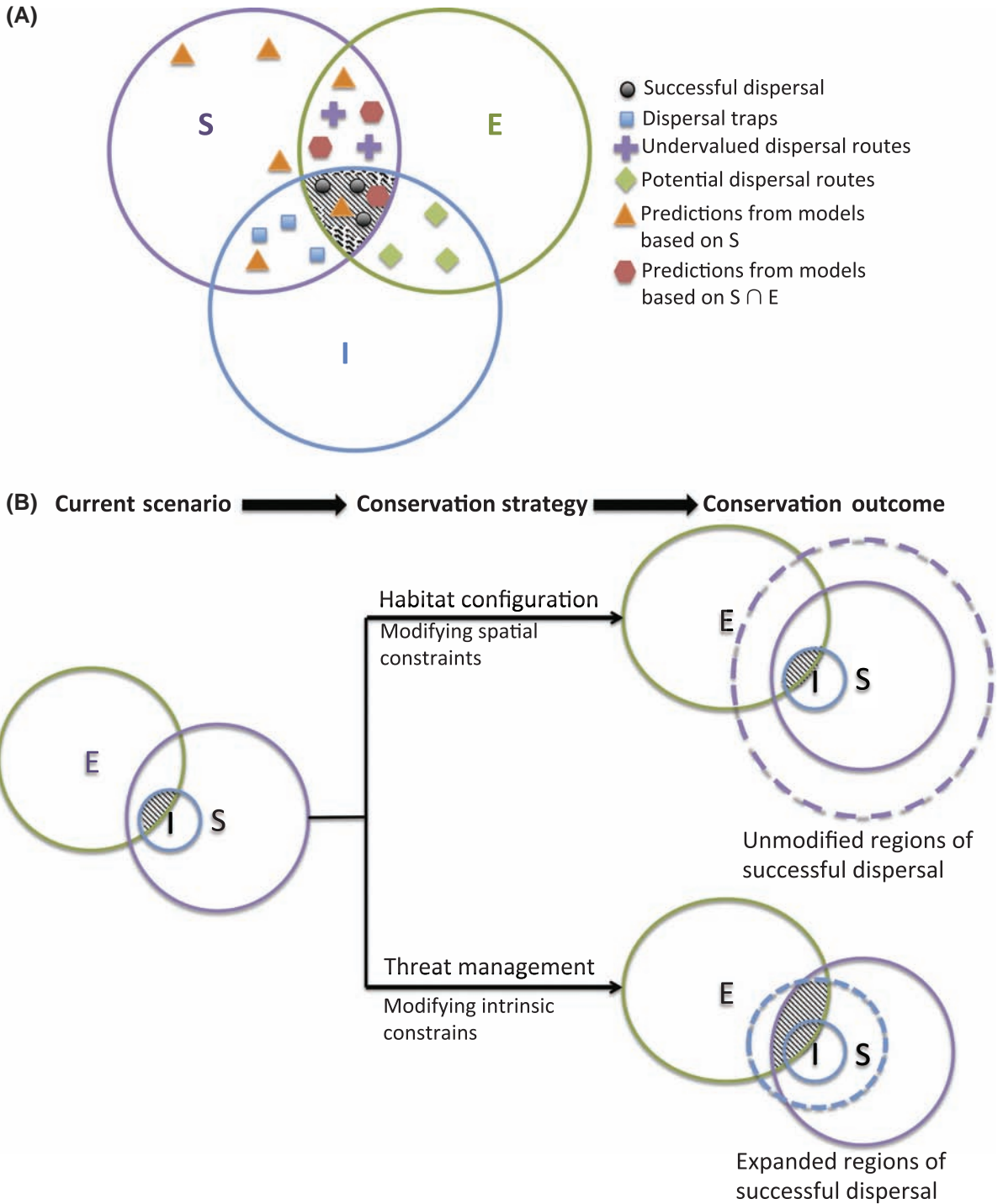


Figure 1. (A) The spatial-environmental-intrinsic (SEI) framework facilitates identification of conditions that allow for successful dispersal (diagonally shaded), through spatial (S), environmental (E) and intrinsic (I) constraints to successful dispersal. We contrast locations of successful dispersal with dispersal traps, undervalued dispersal routes, and potential dispersal routes. We additionally illustrate that dispersal models based on spatial constraints, or cost- or resistance-distance ( $S \cap E$ ), may over-predict regions of successful dispersal. (B) We illustrate the efficacy of threat-based conservation in facilitating connectivity in a hypothetical formulation of the SEI framework. We assume a situation where intrinsic constraints maximally limit successful dispersal. Results of conservation interventions are represented as dashed circles. Conservation interventions that focus on the most limiting factor to successful dispersal (I) may result in facilitating dispersal, while those focused on non-limiting factors (e.g. S) may not facilitate dispersal.

both habitat and matrix elements. Constraints imposed upon dispersal by the location of habitat undoubtedly constitute the most studied aspect of connectivity and form the theoretical foundation for many concepts in the science of connectivity (MacArthur and Wilson 1967, Adriaenssen et al. 2003). Their consideration in connectivity can perhaps be traced back to the description of spatial patterns of dispersal that arise out of random diffusion processes (Skellam 1951) and the theory of island biogeography (MacArthur and Wilson 1967). As dispersal distances increase, individuals incur cumulative time and energy costs (Bonte et al. 2012), which suggests increased overall dispersal costs for more geographically isolated habitat fragments (Adriaenssen et al. 2003). The configuration of habitat fragments also limits the distribution and occupied niche of species, thus relating this category to species 'movement limitations' identified in species distribution modelling (Barve et al. 2011). Habitat fragments can occasionally serve as stepping-stones, such that dispersal between two habitat fragments can be facilitated by a third (Fletcher et al. 2014).

Beyond distance effects, other spatial effects of configuration of habitats can alter movements. For instance, Fletcher et al. (2014) experimentally altered the configuration of stepping-stone habitat of the cactus bug *Chelinidea vittiger*, while keeping the overall area of stepping-stones and distances to target patches constant, finding that colonization probability increased when stepping-stones were configured such that they had a funnelling effect on emigrants. Spatial constraints can also emerge from the location of matrix elements (Fig. 2). For example, Uezu et al. (2005) found that emigration propensity for some forest birds was suppressed when open habitat was located adjacent to forest fragments.

## Environmental constraints

Environmental constraints to successful dispersal arise from factors extrinsic to the dispersing organism. These constraints relate to 1) the biotic community (Orrock et al. 2008, Bowler and Benton 2009) and 2) abiotic factors including structural attributes of the matrix (Prevedello et al. 2011), climatic factors (Vasconcelos and Calhoun 2004), and landform or terrain (Cushman et al. 2009). These constraints can alter environmental quality for dispersers. These can be considered analogous to the factors limiting the biotic and abiotic niche of species, respectively.

Biotic factors include predators, competitors, facilitators, and resources. The presence of predators in the matrix can constrain successful dispersal through heightened mortality costs or through anti-predator behaviour (Orrock et al. 2008). Competition in the matrix, in particular with humans, can suppress the movement of individuals across landscapes and be a significant contributor to mortality (Cushman et al. 2010). On the other hand, the presence and utilization of resources in the matrix can facilitate dispersal by offsetting energetic costs (Manning et al. 2006, Bowler and Benton 2009). Resources in the matrix could also facilitate dispersal across multiple generations, such that emigration is followed by reproduction in sink or stepping-stone habitat; descendants of the emigrating animal may then complete the dispersal process by locating and immigrating into a suitable habitat fragment (Apte et al. 2000). These demographic events in the matrix, while not contributing substantially to population recruitment, may play an important role in increasing the long-term probability of successful dispersal among habitats.

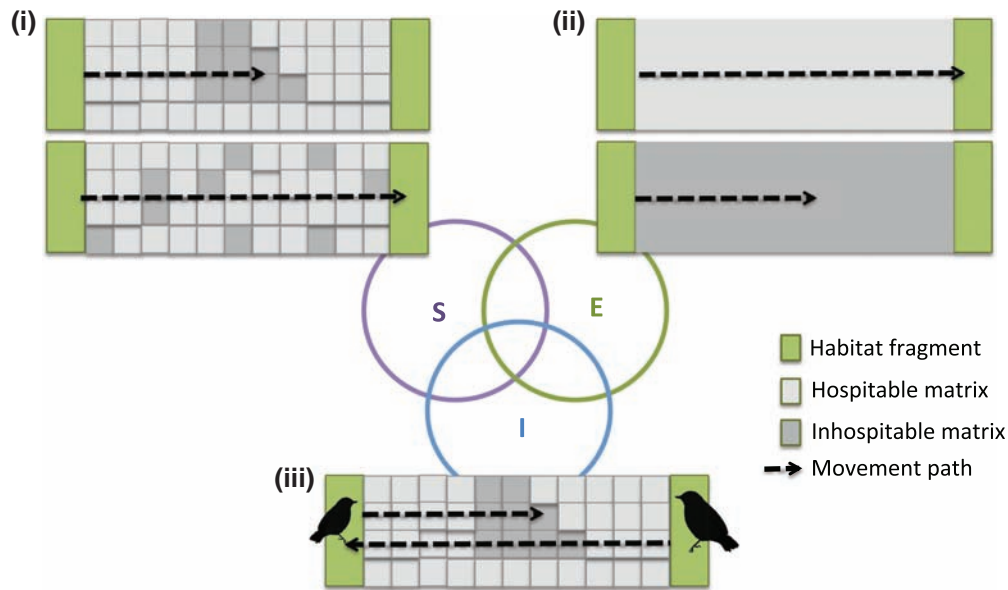


Figure 2. Illustration of the effects of constraining factors on dispersal mortality when two fragments are separated by a matrix. Inhospitable matrix types are shown as dark grey. In each case, a potential movement path is illustrated, and mortality occurs when a movement path ends in the matrix. (i) Similar matrices when configured in different manners can vary in their mortality effects, illustrating how spatial constraints (S) can impact dispersal. (ii) Increased inhospitability of the matrix can constrain successful dispersal, illustrating environmental constraints (E) from heightened mortality risk. (iii) Effects may vary across populations, in this example, based on body size (an intrinsic constraint, I).

Vegetation structure in the matrix can pose physical obstructions to the movement of animals. The structure of the matrix can provide cover against perceived predation (Bowne et al. 1999). It can obstruct the perception of habitat (Prevedello et al. 2011) and hence depress immigration into habitat fragments. Certain matrix elements, such as roads, are associated with significant mortality risk and can be particularly influential on dispersal mortality and observed movement paths (Frair et al. 2008). These influences of environmental constraints to movement are often collectively incorporated into connectivity assessments in the form of matrix resistances (Zeller et al. 2012). Climatic conditions, such as temperature and precipitation (Vasconcelos and Calhoun 2004), as well as landform, such as terrain (Johnson et al. 2002, Cushman et al. 2009), also modify movement paths of dispersing animals, influence energetic costs, and ultimately can limit successful dispersal (Bonte et al. 2012).

### Intrinsic constraints

Limitations to successful dispersal can also arise through intrinsic characteristics of individual dispersers (Belisle 2005, Baguette et al. 2013), groups of individuals (Thouless and Sakwa 1995), populations (Resasco et al. 2014), or species (Ball and Goldingay 2008). At the species level, traits such as movement modes and average body mass have been shown to influence dispersal across landscapes (Ball and Goldingay 2008). We note that while such species-level effects will be crucial for comparisons of the dispersal requirements or constraints across species, our framework is species-centred (as is the species niche; Peterson et al. 2011), such that species-level intrinsic constraints are only implicitly captured. Populations, or groups of individuals, can also show characteristic variability in movement mode and behaviour, inducing a within-species bias in dispersal patterns (Fig. 2, Resasco et al. 2014). Resasco et al. (2014) further demonstrated that intrinsic constraints, namely the movement mode of different groups of individuals of invasive fire ants *Solenopsis invicta* (polygynes versus monogynes) influenced the effectiveness of corridors in facilitating connectivity between habitat fragments. Thus, intrinsic constraints can mediate the efficacy of conservation interventions that manage for connectivity. Characteristics of habitats, such as habitat quality and environmental conditions, as well as the density of populations that reside within habitats, can influence population-specific probability of emigration, disperser ability to successfully traverse the matrix, and their immigration into destination habitat patches (Stamps 2006, Benard and McCauley 2008, Bonte and de la Peña 2009, Bitume et al. 2014).

At the individual level, the internal state of animals, such as their energy reserves or physiological stress, has theoretically been suggested to influence individual decisions (Fraser et al. 2001, Belisle 2005, Zollner and Lima 2005). Prior experience of individuals can influence dispersal ability and propensity, as well as their capacity to appropriately respond to habitat cues in fragmented landscapes (Benard and McCauley 2008). Dispersal is increasingly recognized as a process wherein individuals make behavioural decisions based on information perceived about the environment (Clobert et al. 2009). Therefore, the ability of individu-

als to perceive and respond to information can influence emigration, search and immigration decisions in fragmented landscapes (Doligez et al. 2002, Zollner and Lima 2005, Fletcher 2006, Fletcher et al. 2013). For instance, Fletcher (2006, 2009) showed that the presence of conspecifics could augment immigration rates into habitat fragments. These intrinsic constraints can provide insights into various patterns of connectivity observed in fragmented habitats (e.g. leptokurtic dispersal kernels: Fraser et al. 2001, fragment size-related target effects: Fletcher 2006).

### From dispersal constraints to landscape connectivity

By identifying constraints arising from spatial, environmental and intrinsic factors, the SEI framework sheds light on the extent to which existing connectivity models and analytical approaches adequately capture successful dispersal routes (Fig. 3). Predictive models informed solely by spatial constraints will typically over-predict regions of successful dispersal (Fig. 1A, Smolik et al. 2010). Consideration of environmental constraints in the form of movement 'costs' (e.g. matrix resistance: Zeller et al. 2012) provides an assessment of constraints arising from the quality of the extrinsic environment, while the translation of these resistances to an 'effective distance' between habitat fragments represents the intersection of environmental and spatial constraints ( $S \cap E$ ; Fig. 1A). Yet such regions might still be unsuitable for dispersal due to intrinsic constraints (Fig. 1A). Therefore, the area suitable for successful dispersal may frequently be smaller than what is commonly assumed.

Demarcating specific constraints to dispersal could also identify regions of the landscape that inflict environment-induced mortality costs on dispersers. For example, regions that are not limited through spatial or intrinsic factors, but are limited through environmental effects on mortality can result in dispersal traps (Fig. 1A; Frair et al. 2008, Stokes et al. 2010). Further, regions may exist that are amenable to dispersal, but where dispersal fails to occur due to avoidance behaviours displayed by individual dispersers (Harris and Reed 2002, Ciuti et al. 2012). These regions are analogous to suitable habitats unoccupied by species due to a disassociation of cues from habitat (Gilroy and Sutherland 2007), and can be considered as undervalued dispersal routes (Fig. 1A). Potential dispersal routes, or regions amenable to dispersal, but currently inaccessible by virtue of their location, are also revealed through this framework (Fig. 1A). Knowledge of potential dispersal routes can aid reserve design, habitat restoration, reintroduction programs and conservation in the face of climate change (Schultz and Crone 2005, Grimbacher and Catterall 2007). This framework can thus help contextualize assessments and predictions of connectivity models, validate their utility, and identify gaps in their implementation in the context of connectivity modelling in ecology.

### Methodological advances that allow for linking dispersal constraints to connectivity

Dispersal has traditionally been a difficult process to study and understand, particularly across complex landscapes. This difficulty has, in part, led to the practice of

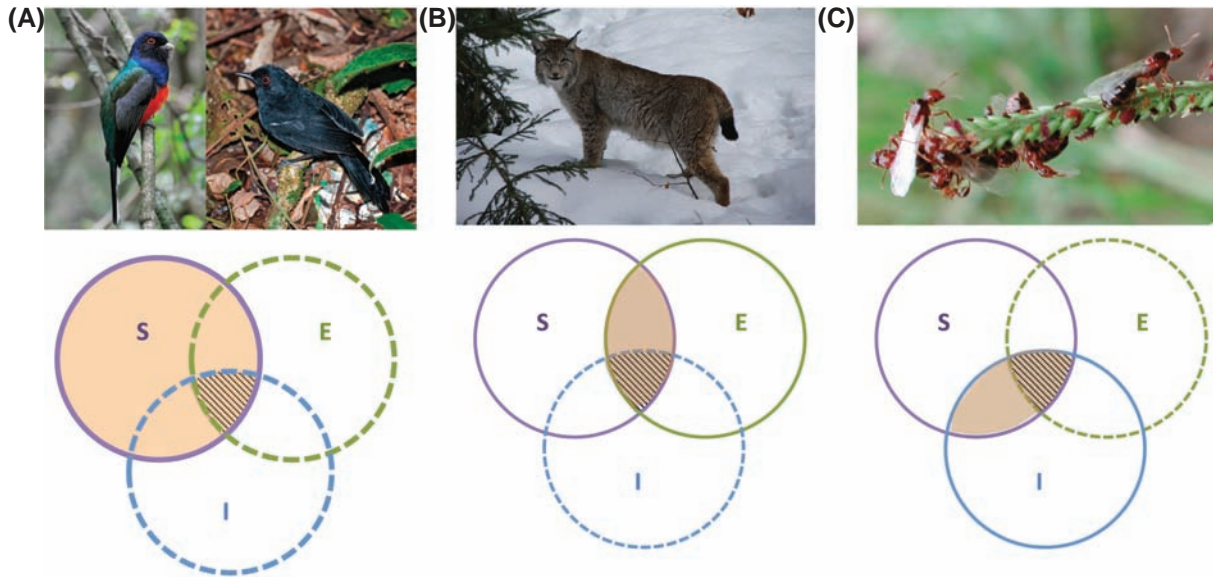


Figure 3. Three recent examples illustrate the identification of different types of constraints (shaded) for connectivity assessments. Unknown constraints are represented in the figures as dashed circles. (A) Uezu et al. (2005) used distance between habitat fragments and the presence of corridors (spatial constraints) to assess connectivity of forest birds in the Brazilian Atlantic forest landscape. (B) Kramer-Schadt et al. (2004) included daily distance travelled (spatial constraint), propensity to use different land-use types and road-induced mortality (environmental constraints) in their assessment of Eurasian lynx *Lynx lynx* connectivity in Germany. (C) Resasco et al. (2014) considered the presence of corridors (spatial constraint) and movement mode of the monogyne and polygyne social forms (intrinsic constraint) of the invasive fire ant *Solenopsis invicta*. Photo courtesy: Claudio Dias Timm, Dario Sanchez (A), Aconcongua (B), and Lamiot (C), Wikimedia Commons.

connectivity modelling with substantial focus on remotely sensed landscape characteristics, often unsupported by data on movement (Sawyer et al. 2011). Yet, recently developed technologies, such as global positioning system-based telemetry, allow for the observation of fine-scale movement data (Cagnacci et al. 2010), while analytical methods, such as individual-based and network modelling (Grimm and Railsback 2005, Minor and Urban 2008, Thurfjell et al. 2014), facilitate the incorporation of such information into connectivity assessments and predictions (Revilla and Wiegand 2008, Fletcher et al. 2011). Furthermore, landscape genetics, or the analysis of genetic information at the landscape scale, allows for the identification of specific barriers and resistant matrix types to movement and gene flow (Epps et al. 2007, Cushman et al. 2009, Spear et al. 2010). Combining these methods with small-scale observational or experimental studies on movement behaviour (Knowlton and Graham 2010) can aid in identifying constraints to successful dispersal (Stevens et al. 2006). Small-scale movements (e.g. foraging movement within home ranges or in the matrix) do not equate to landscape-scale connectivity; however, these movements can provide useful information in interpreting connectivity at larger scales (Vasudev and Fletcher 2015).

Niche models often define the boundaries of a species ecological niche based on the probability of occurrence, using envelope-based or non-linear methods to capture limits to distributions (Elith et al. 2006, Smolik et al. 2010). Similarly, one can identify limits to successful dispersal and define the boundaries of regions that facilitate dispersal, based on the probability of successful dispersal. Constraints to dispersal may cause inflection points in probability of

successful dispersal, which could be measured through empirical data on observed dispersal rates, transition probabilities or genetic relatedness. Empirical data on dispersal and animal movement can also be incorporated into dispersal models to assess the effects of specific factors across their parameter space on overall landscape connectivity (Kramer-Schadt et al. 2004, Revilla and Wiegand 2008). We note here that it may be difficult to map certain constraints, particularly intrinsic constraints, across large landscapes. In addition, there may be a mismatch in scale across multiple constraints that act on dispersal. Hierarchical modelling or spatially explicit individual-based modelling may be able to deal with such issues (Fletcher 2006, Revilla and Wiegand 2008).

Considering the probability of dispersal success as analogous to probability of occupancy suggests that a number of analytical tools used in ecological niche modelling and species distribution modelling may be transferrable to identifying and mapping dispersal constraints. For instance, thresholds for determining locations that allow for successful dispersal (on the basis of dispersal probabilities) can be evaluated using techniques that determine optimal thresholds for different types of prediction errors and associated ‘confusion matrices’ (Liu et al. 2005). Viewing dispersal modelling in such a manner allows us to make decisions on whether to minimize false positive or negative error rates (Elith et al. 2006). The cumulative nature of dispersal suggests that methods such as estimating cumulative hazards to dispersal through survival modelling (Merrill et al. 2010) may also prove useful for capturing dispersal constraints. Finally, insights obtained on species dispersal constraints can be used to direct further research efforts in an approach analogous to the iterative sampling approach of ecological niche modelling (Guisan et al. 2006).

Despite considerable theoretical knowledge on potential limitations to dispersal and recent methodological advances, there exists little information on the context-specific relevance of these limitations to connectivity (but see Ball and Goldingay 2008). While network models and resistance-distance models, frequently used to model connectivity, can account for various limits to successful dispersal, they do so in an implicit manner. In addition, as currently applied in spatial ecology, these models are not sufficient to address all types of constraints we discuss, partly because they focus on spatial sampling units rather than individual-based sampling units. As a consequence, such approaches may over-predict connectivity (Fletcher et al. 2011). In fact, as pointed out by Sawyer et al. (2011) and Zeller et al. (2012), connectivity models are often based on data of questionable relevance to animal movement. The process-based approach emphasized by the SEI framework highlights the need for future research to be aimed at identifying the relative importance of various spatial, environmental and intrinsic factors in limiting successful dispersal, and explicitly incorporating these factors into connectivity models.

### Constraint-based connectivity conservation

Connectivity is included as an explicit objective in many conservation programs (Lindenmayer et al. 2008, Doerr et al. 2011). In this context, it is worthwhile to revisit and state explicitly the central question being addressed while practicing connectivity conservation. We note how a similar exercise facilitated the clarification of central goals in the field of niche modelling, and the tailoring of goals subtly to suit different conservation objectives, particularly in the face of climate change (Peterson et al. 2011). As connectivity conservation is currently practiced, it can be argued that we typically ask, ‘where do animals potentially disperse?’ We contend that an equally important question for connectivity conservation should be, ‘what are the limiting factors to successful dispersal across landscapes?’ Traditionally, objectives are phrased within the geographic space, for instance, conserving dispersal routes between pre-determined population fragments. In an alternative approach, conservation objectives may emphasize ameliorating current or potential anthropogenic limitations to dispersal. Further, we suggest that approaching connectivity conservation from the perspective of dispersal constraints emphasizes that conservation efforts might productively focus on the most imminent threat to connectivity (Fig. 1B). Threat-based conservation approaches might achieve greater success at facilitating successful dispersal than traditional approaches to connectivity conservation in some situations (Fig. 1B).

Current conservation practice predominantly encompasses constraints to dispersal arising from habitat configuration (Moilanen et al. 2009, Worboys et al. 2010, Sawyer et al. 2011), such that conservation strategies based on these spatial constraints, or informed by models that incorporate only spatial constraints, may focus conservation efforts on areas that are not amenable to successful dispersal (illustrated in Fig. 1A). Corridors and stepping-stones (Worboys et al. 2010), in effectively decreasing the distance between fragments, also address spatial constraints to dispersal.

Conservation strategies that encompass environmental or intrinsic constraints may be more suited to facilitate successful dispersal in certain contexts (Manning et al. 2006, Ball and Goldingay 2008) and can greatly expand the current repertoire of connectivity conservation interventions. We illustrate below, using the example of a wide-ranging species for which spatial constraints are negligible, how the threat-based approach of the SEI framework can provide insights into dispersal limitations in heterogeneous landscapes, aid in prioritizing conservation interventions, and identify innovative conservation strategies for the facilitation of connectivity.

### Identifying and mapping dispersal constraints: an example of a wide-ranging species

We highlight the utility of the SEI framework in understanding constraints to successful dispersal for the African elephant *Loxodonta africana*. We focus on two factors identified using satellite-telemetry as constraints for elephant dispersal in a landscape located at the boundaries of Botswana, Namibia and Zambia: a) availability of water, and b) the presence of wildlife fences and other human-induced movement barriers (Cushman et al. 2010). Traditional consideration of species dispersal requirements as an approximation of the occupied niche is not valid for elephants, as the species is known to traverse non-habitat land cover types across large distances (Cushman et al. 2010). Moreover, due to the wide-ranging nature of the species, spatial constraints pose a limitation to elephant dispersal only at very large scales. Models or conservation interventions that only focus on spatial constraints are therefore likely to greatly over-predict dispersal.

The presence of water, an environmental constraint, has been shown to influence elephant movement (Loarie et al. 2009, Cushman et al. 2010), and Cushman et al. (2010) incorporated this limitation into landscape resistance analyses to map potential dispersal routes that follow existing water bodies (Fig. 4A, B). Furthermore, Loarie et al. (2009) used telemetry data from 73 elephants to quantify this relationship in a manner amenable for envelope-based approaches used in niche modelling; all recorded locations of elephants were within 60 km of a permanent water source, while 93% of recorded locations in the dry season were within 15 km of a water source. Incorporating this environmental constraint into dispersal assessments would result in restricting locations that allow for successful dispersal to areas adjacent to water sources.

Wildlife fences and other human-induced barriers restrict the movement of individual elephants due to mortality from electrocution and persecution by humans (Cushman et al. 2010). Individual elephants differentially perceive fences and other anthropogenic deterrents as barriers to movement (intrinsic constraints), segregating into risk-averse individuals, for whom fences pose an absolute barrier to dispersal, and risk-prone individuals, for whom fences do not represent a movement barrier (Thouless and Sakwa 1995, O’Connell-Rodwell et al. 2000). Cushman et al. (2010) evaluated the ‘barrier effect’ of fences and other anthropogenic deterrents by mapping potential dispersal routes for elephants in the presence and absence of such deterrents (Fig. 4A, B, source: Fig. 19.6 in Cushman et al. 2010). We suggest that the two



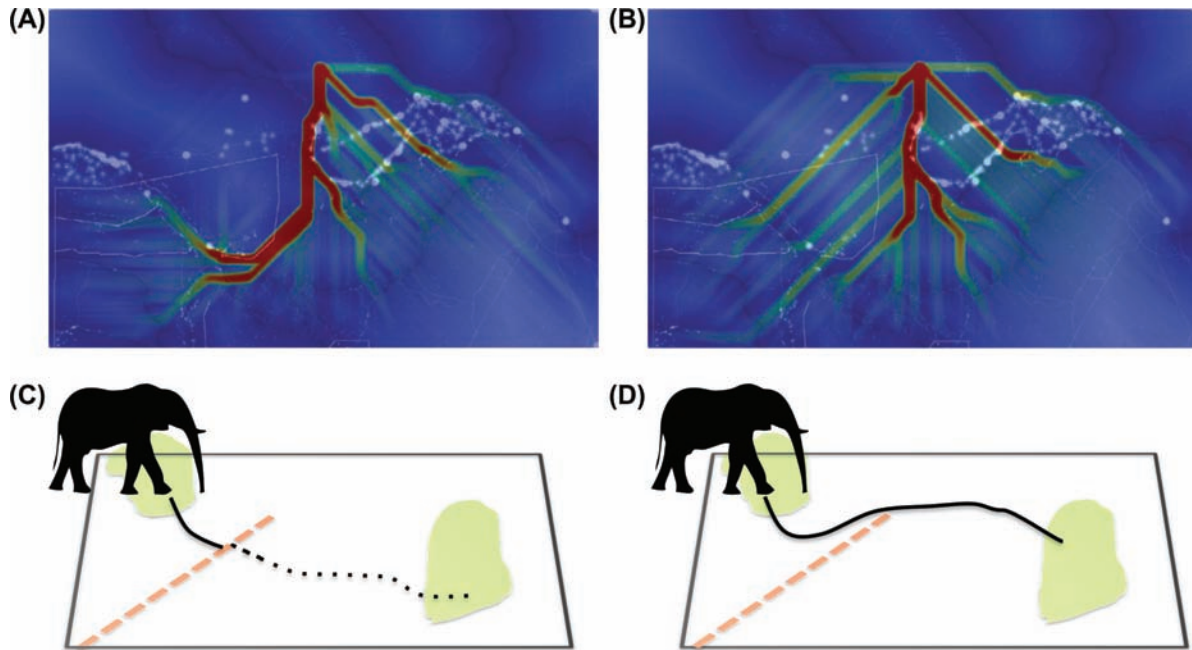


Figure 4. Locations of successful dispersal for the African elephant *Loxodonta africana* in a landscape located at the boundaries of Botswana, Namibia and Zambia are constrained by the availability of water and the presence of anthropogenic deterrents (e.g. wildlife fences, Cushman et al. 2010). Dispersal routes, shown in red, are seen to follow the existing water body passing vertically through the centre of the landscape (A, B). Landscape resistance maps produced by Cushman et al. (2010) in the presence (A) and absence (B) of anthropogenic deterrents can be considered as representing locations of successful dispersal for elephants that consider such deterrents as a barrier (A), and those that do not (B). Fences (an anthropogenic deterrent, shown as orange dashed lines in (C) and (D)) can either have mortality or behavioural effects on elephants. (C) Mortality effects at fences are caused by electrocution or persecution by humans, while (D) behavioural effects occur when individual elephants modify their movement path on perceiving the threat posed by wildlife fences. One such potential movement path of dispersing animals between two habitat fragments (shown in green) in a hypothetical landscape is shown in both figures as black lines, the dotted black line representing a projection of the movement paths in the absence of mortality. (A) and (B) reproduced from Cushman et al. 2010 with permission.

maps can be viewed as representing locations of successful dispersal for the aforementioned two categories of individuals in the elephant population, respectively (Fig. 4A, B, reproduced from Fig. 19.6 in Cushman et al. 2010 with permission). Furthermore, fences act as a constraint to successful dispersal through both the augmentation of mortality costs of dispersal (Fig. 4C) and the alteration of movement paths (Fig. 4D).

The SEI approach to understanding connectivity emphasizes the explicit consideration of constraints to successful dispersal. Focusing on the foremost threat to movement, we might consider that the intersection between the presence of fences (environmental constraint) and the perception of these barriers as an untenable risk by a portion of the population (intrinsic constraint) limits and modifies patterns of dispersal in the species (Fig. 4). Directing conservation efforts towards these identified constraints might include a) the mitigation of conflict that induces the erection of wildlife fences and b) alternative methods of cattle fencing that restrict the movement of cattle, but do not negatively influence animal movement routes. Novel strategies such as these might better manage connectivity than conventional strategies.

Furthermore, differentiating between the mortality and behavioural effects of the wildlife fences facilitates a more mechanistic understanding of the constraints to successful dispersal. For individuals who do not consider the wildlife

fence as a barrier, we might consider areas of high mortality risk associated with fences as potential dispersal traps (Fig. 1A). If these individuals are intrinsically associated with heightened exploratory behaviour or ‘boldness’ (Fraser et al. 2001), or belong to a particular age-sex class (Sukumar and Gadgil 1988), these suspected dispersal traps could have substantial influence on the overall viability of populations in the landscape. In revealing these potential detrimental effects of anthropogenic threats to connectivity and in directing conservation strategies to be more threat-based, the SEI approach may help guide appropriate management of connectivity for this endangered species.

## Conclusions

The growing emphasis on connectivity is evident in the shifting focus from single populations to heterogeneous landscapes, encompassing dispersal processes as well as the human-dominated matrix within which these processes largely occur (Worboys et al. 2010). However, despite our theoretical understanding of dispersal, a vast literature on connectivity modelling, and on-ground efforts in managing connectivity (Worboys et al. 2010, Clobert et al. 2012), the veracity and rigor of existing connectivity modelling and conservation has been repeatedly questioned (Sawyer et al. 2011, Zeller et al. 2012). Sharpening our focus on

constraints to successful dispersal may spur the integration of key processes into modelling, conservation prioritization and interventions through the productive implementation of existing and new methodologies (Cagnacci et al. 2010, Knowlton and Graham 2010). Such a process-based approach may ultimately lead to a deeper understanding of how species utilize resources and disperse across landscapes, alter monitoring and assessments of the success of connectivity conservation, and may help identify how and why connectivity limits populations and communities. In this manner, we expect that the SEI framework will help facilitate these goals with ongoing environmental change.

*Acknowledgements* – We acknowledge financial support from the Alumni Fellowship, Univ. of Florida (DV and VRG), the Univ. of Florida and the National Science Foundation (DEB-1343144; RJF), and the Bay and Paul Foundation (MK). We thank J. D. Austin, K. Sieving, M. Christman, K. Kainer, U. Ramakrishnan, J. Watling, and J. Resasco and editors and reviewers for constructive feedback that helped improve the manuscript.

## References

- Adriaensen, F. et al. 2003. The application of ‘least-cost’ modelling as a functional landscape model. – *Landscape Urban Plann.* 64: 233–247.
- Apte, S. et al. 2000. Jumping ship: a stepping stone event mediating transfer of a non-indigenous species via a potentially unsuitable environment. – *Biol. Invasions* 2: 75–79.
- Baguette, M. et al. 2013. Individual dispersal, landscape connectivity and ecological networks. – *Biol. Rev.* 88: 310–326.
- Ball, T. M. and Goldingay, R. L. 2008. Can wooden poles be used to reconnect habitat for a gliding mammal? – *Landscape Urban Plann.* 87: 140–146.
- Barve, N. et al. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. – *Ecol. Model.* 222: 1810–1819.
- Belisle, M. 2005. Measuring landscape connectivity: the challenge of behavioral landscape ecology. – *Ecology* 86: 1988–1995.
- Benard, M. F. and McCauley, S. J. 2008. Integrating across life-history stages: consequences of natal habitat effects on dispersal. – *Am. Nat.* 171: 553–567.
- Bitume, E. V. et al. 2014. Dispersal distance is influenced by parental and grand-parental density. – *Proc. R. Soc. B* 281: 20141061.
- Bonte, D. and de la Peña, E. 2009. Evolution of body condition-dependant dispersal in metapopulations. – *J. Evol. Biol.* 22: 1242–1251.
- Bonte, D. et al. 2012. Costs of dispersal. – *Biol. Rev.* 87: 290–312.
- Bowler, D. E. and Benton, T. G. 2009. Variation in dispersal mortality and dispersal propensity among individuals: the effects of age, sex and resource availability. – *J. Anim. Ecol.* 78: 1234–1241.
- Bowne, D. et al. 1999. Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). – *Landscape Ecol.* 14: 53–65.
- Cagnacci, F. et al. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. – *Phil. Trans. R. Soc. B* 365: 2157–2162.
- Calabrese, J. and Fagan, W. 2004. A comparison-shopper’s guide to connectivity metrics. – *Front. Ecol. Environ.* 2: 529–536.
- Carlo, T. A. and Morales, J. M. 2008. Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. – *J. Ecol.* 96: 609–618.
- Chase, J. M. and Leibold, M. A. 2003. *Ecological niches: linking classical and contemporary approaches*. – Univ. of Chicago Press.
- Ciuti, S. et al. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. – *PLoS One* 7: e50611.
- Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. – *Ecol. Lett.* 12: 197–209.
- Clobert, J. et al. 2012. *Dispersal ecology and evolution*. – Oxford Univ. Press.
- Cushman, S. A. et al. 2009. Use of empirically derived source-destination models to map regional conservation corridors. – *Conserv. Biol.* 23: 368–376.
- Cushman, S. A. et al. 2010. Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. – In: Cushman, S. A. and Huettmann, F. (eds), *Spatial complexity, informatics, and wildlife conservation*. Springer, pp. 349–367.
- Doerr, V. A. J. et al. 2011. Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson et al. – *J. Appl. Ecol.* 48: 143–147.
- Doligez, B. et al. 2002. Public information and breeding habitat selection in a wild bird population. – *Science* 297: 1168–1170.
- Dullinger, S. et al. 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. – *J. Ecol.* 92: 241–252.
- Elith, J. et al. 2006. Novel methods improve prediction of species’ distributions from occurrence data. – *Ecography* 29: 129–151.
- Engler, R. and Guisan, A. 2009. MigClim: predicting plant distribution and dispersal in a changing environment. – *Divers. Distrib.* 15: 590–601.
- Epps, C. W. et al. 2007. Optimizing dispersal and corridor models using landscape genetics. – *J. Appl. Ecol.* 44: 714–724.
- Eycott, A. E. et al. 2012. A meta-analysis on the impact of different matrix structures on species movement rates. – *Landscape Ecol.* 27: 1263–1278.
- Fletcher, R. J. 2006. Emergent properties of conspecific attraction in fragmented landscapes. – *Am. Nat.* 168: 207–219.
- Fletcher, R. J. 2009. Does attraction to conspecifics explain the patch-size effect? An experimental test. – *Oikos* 118: 1139–1147.
- Fletcher, R. J. et al. 2011. Social network models predict movement and connectivity in ecological landscapes. – *Proc. Natl Acad. Sci. USA* 108: 19282–19287.
- Fletcher, R. J. et al. 2013. Signal detection theory clarifies the concept of perceptual range and its relevance to landscape connectivity. – *Landscape Ecol.* 28: 57–67.
- Fletcher, R. J. et al. 2014. The matrix alters the role of path redundancy on patch colonization rates. – *Ecology* 95: 1444–1450.
- Frair, J. L. et al. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. – *J. Appl. Ecol.* 45: 1504–1513.
- Fraser, D. F. et al. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. – *Am. Nat.* 158: 124–135.
- Gilroy, J. J. and Sutherland, W. J. 2007. Beyond ecological traps: perceptual errors and undervalued resources. – *Trends Ecol. Evol.* 22: 351–356.
- Grimbacher, P. S. and Catterall, C. P. 2007. How much do site age, habitat structure and spatial isolation influence the restoration of rainforest beetle species assemblages? – *Biol. Conserv.* 135: 107–118.
- Grimm, V. and Railsback, S. F. 2005. *Individual-based modeling and ecology*. – Princeton Univ. Press.

- Guisan, A. et al. 2006. Using niche-based models to improve the sampling of rare species. – *Conserv. Biol.* 20: 501–511.
- Guisan, A. et al. 2013. Predicting species distributions for conservation decisions. – *Ecol. Lett.* 16: 1424–1235.
- Hanson, J. S. et al. 1990. Landscape fragmentation and dispersal in a model of riparian forest dynamics. – *Ecol. Model.* 49: 277–296.
- Harris, R. and Reed, J. 2002. Behavioral barriers to non-migratory movements of birds. – *Ann. Zool. Fenn.* 39: 275–290.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. – *Proc. Natl Acad. Sci. USA* 106: 19659–19665.
- Johnson, C. J. et al. 2002. A multiscale behavioral approach to understanding the movements of woodland caribou. – *Ecol. Appl.* 12: 1840–1860.
- Kneitel, J. M. and Chase, J. M. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. – *Ecol. Lett.* 7: 69–80.
- Knowlton, J. L. and Graham, C. H. 2010. Using behavioral landscape ecology to predict species' responses to land-use and climate change. – *Biol. Conserv.* 143: 1342–1354.
- Kramer-Schadt, S. et al. 2004. Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. – *J. Appl. Ecol.* 41: 711–723.
- Kupfer, J. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. – *Global Ecol. Biogeogr.* 15: 8–20.
- Lawler, J. J. et al. 2013. Projected climate-driven faunal movement routes. – *Ecol. Lett.* 16: 1014–1022.
- Lindenmayer, D. B. and Fischer, J. 2007. Tackling the habitat fragmentation panchreston. – *Trends Ecol. Evol.* 22: 127–132.
- Lindenmayer, D. et al. 2008. A checklist for ecological management of landscapes for conservation. – *Ecol. Lett.* 11: 78–91.
- Liu, C. et al. 2005. Selecting thresholds of occurrence in the prediction of species distributions. – *Ecography* 28: 385–393.
- Loarie, S. R. et al. 2009. Fences and artificial water affect African savannah elephant movement patterns. – *Biol. Conserv.* 142: 3086–3098.
- Lowe, W. H. and Allendorf, F. W. 2010. What can genetics tell us about population connectivity? – *Mol. Ecol.* 19: 3038–3051.
- MacArthur, R. H. and Wilson, E. O. 1967. *The theory of island biogeography*. – Princeton Univ. Press.
- Manning, A. D. et al. 2006. Scattered trees are keystone structures – implications for conservation. – *Biol. Conserv.* 132: 311–321.
- Merrill, E. et al. 2010. Building a mechanistic understanding of predation with GPS-based movement data. – *Phil. Trans. R. Soc. B* 365: 2279–2288.
- Minor, E. S. and Urban, D. L. 2008. A graph-theory framework for evaluating landscape connectivity and conservation planning. – *Conserv. Biol.* 22: 297–307.
- Moilanen, A. et al. 2009. The Zonation framework and software for conservation prioritization. – In: Moilanen, A. et al. (eds), *Spatial conservation prioritization: quantitative methods and computational tools*. Oxford Univ. Press, pp. 196–210.
- Nathan, R. and Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. – *Trends Ecol. Evol.* 15: 278–285.
- Nathan, R. et al. 2008. A movement ecology paradigm for unifying organismal movement research. – *Proc. Natl Acad. Sci. USA* 105: 19052–19059.
- O'Connell-Rodwell, C. E. et al. 2000. Living with the modern conservation paradigm: can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. – *Biol. Conserv.* 93: 381–391.
- Orrock, J. L. et al. 2008. Consumptive and nonconsumptive effects of predators on metacommunities of competing prey. – *Ecology* 89: 2426–2435.
- Peterson, A. T. et al. 2011. *Ecological niches and geographic distributions*. – Princeton Univ. Press.
- Prevedello, J. A. et al. 2011. Does land use affect perceptual range? Evidence from two marsupials of the Atlantic Forest. – *J. Zool.* 284: 53–59.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. – *Ecol. Lett.* 3: 349–361.
- Rabinowitz, A. and Zeller, K. A. 2010. A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. – *Biol. Conserv.* 143: 939–945.
- Resasco, J. et al. 2014. Landscape corridors can increase invasion by an exotic species and reduce diversity of native species. – *Ecology* 95: 2033–2039.
- Revilla, E. and Wiegand, T. 2008. Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. – *Proc. Natl Acad. Sci. USA* 105: 19120–19125.
- Sanderson, E. W. et al. 2002. A conceptual model for conservation planning based on landscape species requirements. – *Landscape Urban Plann.* 58: 41–56.
- Sawyer, S. C. et al. 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? – *J. Appl. Ecol.* 48: 668–678.
- Schultz, C. B. and Crone, E. E. 2005. Patch size and connectivity thresholds for butterfly habitat restoration. – *Conserv. Biol.* 19: 887–896.
- Selonen, V. and Hanski, I. K. 2006. Habitat exploration and use in dispersing juvenile flying squirrels. – *J. Anim. Ecol.* 75: 1440–1449.
- Skellam, J. 1951. Random dispersal in theoretical populations. – *Biometrika* 38: 196–218.
- Smolik, M. G. et al. 2010. Integrating species distribution models and interacting particle systems to predict the spread of an invasive alien plant. – *J. Biogeogr.* 37: 411–422.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. – *Ecol. Lett.* 10: 1115–1123.
- Soberón, J. and Peterson, A. T. 2005. Interpretation of models of fundamental ecological niches and species distributional areas. – *Biodivers. Inform.* 2: 1–10.
- Soberón, J. and Nakamura, M. 2009. Niches and distributional areas: concepts, methods, and assumptions. – *Proc. Natl Acad. Sci. USA* 106 (Suppl. 2): 19644–19650.
- Spear, S. F. et al. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. – *Mol. Ecol.* 19: 3576–3591.
- Stamps, J. A. 2006. The silver spoon effect and habitat selection by natal dispersers. – *Ecol. Lett.* 9: 1179–1185.
- Stevens, V. M. et al. 2006. Gene flow and functional connectivity in the natterjack toad. – *Mol. Ecol.* 15: 2333–2344.
- Stokes, E. J. et al. 2010. Monitoring great ape and elephant abundance at large spatial scales: measuring effectiveness of a conservation landscape. – *PLoS One* 5: e10294.
- Sukumar, R. and Gadgil, M. 1988. Male–female differences in foraging on crops by Asian elephants. – *Anim. Behav.* 36: 1233–1235.
- Svenning, J.-C. and Skov, F. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? – *Ecol. Lett.* 10: 453–460.
- Taylor, P. D. et al. 1993. Connectivity is a vital element of landscape structure. – *Oikos* 68: 571–573.
- Thouless, C. R. and Sakwa, J. 1995. Shocking elephants: fences and crop raiders in Laikipia district, Kenya. – *Biol. Conserv.* 72: 99–107.
- Thurfjell, H. et al. 2014. Applications of step-selection functions in ecology and conservation. – *Movement Ecol.* 2: 4.
- Uezu, A. et al. 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. – *Biol. Conserv.* 123: 507–519.
- Vasconcelos, D. and Calhoun, A. J. K. 2004. Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma*

- maculatum* (Shaw) in three restored seasonal pools in Maine. – J. Herpetol. 38: 551–561.
- Vasudev, D. and Fletcher, R. J. 2015. Incorporating movement behavior into conservation prioritization in fragmented landscapes: an example of western hoolock gibbons in Garo Hills, India. – Biol. Conserv. 181: 124–132.
- Worboys, G. L. et al. 2010. Connectivity conservation management: a global guide. – Earthscan.
- Zeller, K. A. et al. 2012. Estimating landscape resistance to movement: a review. – Landscape Ecol. 27: 777–797.
- Zollner, P. and Lima, S. 2005. Behavioral tradeoffs when dispersing across a patchy landscape. – Oikos 108: 219–230.