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Review

The value of considering demographic contributions to connectivity: a review

Joseph Drake, Xavier Lambin and Chris Sutherland

C. Sutherland (https://orcid.org/0000-0003-2073-1751) ✉ (css6@st-andrews.ac.uk), Centre for Research into Ecological and Environmental Modelling, Univ. of St Andrews, Scotland, UK. – J. Drake (https://orcid.org/0000-0003-0458-3533), Organismal and Evolutionary Biology Interdisciplinary Program, Univ. of Massachusetts-Amherst, Massachusetts, USA. CS and JD also at: Dept. of Environmental Conservation, Univ. of Massachusetts, USA. – X. Lambin (https://orcid.org/0000-0003-4643-2653), School of Biological Sciences, Univ. of Aberdeen, Scotland, UK.

Connectivity is a central concept in ecology, wildlife management, and conservation science. Understanding the role of connectivity in determining species persistence is increasingly important in the face of escalating anthropogenic impacts on climate and habitat. These connectivity augmenting processes can severely impact species distributions and community and ecosystem functioning.

One general definition of connectivity is that it is an emergent process arising from a set of spatial interdependencies between individuals or populations, and increasingly realistic representations of connectivity are being sought. Generally, connectivity consists of a structural component, relating to the distribution of suitable and unsuitable habitat, and a functional component, relating to movement behavior, yet the interaction of both components often better describes ecological processes. Additionally, although implied by 'movement', demographic measures such as the occurrence or abundance of organisms are regularly overlooked when quantifying connectivity. Integrating such demographic contributions based on the knowledge of species distribution patterns is critical to understanding the dynamics of spatially structured populations.

Demographically-informed connectivity draws from fundamental concepts in metapopulation ecology while maintaining important conceptual developments from landscape ecology, and the methodological development of spatially-explicit hierarchical statistical models that have the potential to overcome modeling and data challenges. Together, this offers a promising framework for developing ecologically realistic connectivity metrics.

This review synthesizes existing approaches for quantifying connectivity and advocates for demographically-informed connectivity as a general framework for addressing current problems across ecological fields reliant on connectivity-driven processes such as population ecology, conservation biology and landscape ecology. Using supporting simulations to highlight the consequences of commonly made assumptions that overlook important demographic contributions, we show that even small amounts of demographic information can greatly improve model performance. Ultimately, we argue demographic measures are central to extending the concept of connectivity and resolves long-standing challenges associated with accurately quantifying the influence of connectivity on fundamental ecological processes.

Introduction

The ability to accurately measure connectivity is crucial for managing habitat loss and fragmentation (Rayfield et al. 2011, Wasserman et al. 2012, Haddad et al. 2015, 2016) in order to preserve genetic diversity and promote population persistence (Hilty et al. 2020). Connectivity, conceptually, is the strength of links among locations mediated by effective dispersal (Calabrese and Fagan 2004) and how the environment facilitates or hinders those links (Taylor et al. 1993). Therefore, connectivity is a property of a landscape that emerges from the set of spatial dependencies that arise between individuals and populations within a particular landscape (or seascape, etc., Kool et al. 2013). Beyond this general definition, however, the ability to effectively quantify how, when, and to what extent, connectivity contributes to ecological processes has been beset by semantic uncertainties (Kool et al. 2013) and debate (Tischendorf and Fahrig 2000, 2001, Moilanen and Hanski 2001).

Such uncertainty and debate is fueled, in part, by a diversity of ecological sub-disciplines and conservation applications that draw upon the concept and seek to quantify connectivity through a continually increasing array of models and metrics (Kindlmann and Burel 2008, Rayfield et al. 2011, Fletcher et al. 2016). Population dynamics (Clinchy et al. 2002), disease networks (Margosian et al. 2009), forestry planning (Banks et al. 2005), wildlife management (Horváth et al. 2019), conservation reserve design (Blowes and Connolly 2012, Gupta et al. 2019), spatial conservation planning (Daigle et al. 2020), invasive species mitigation (Drake et al. 2017a), landscape genetics (Marrotte et al. 2017) and more, all invoke the concept of connectivity, but often in different contexts and spatiotemporal scales. While we acknowledge that such context-dependency makes it unrealistic to find a single connectivity metric that would satisfy all applications, idiosyncratic uses of connectivity have proliferated into a loosely related set of tools. Therefore, we find it pertinent to synthesize the properties of connectivity to understand how common assumptions in various modeling approaches influence estimates of connectivity.

Connectivity is traditionally considered to be a function of two core components: a structural component, relating to the distribution of suitable and unsuitable habitat (Calabrese and Fagan 2004), and a functional component, relating to the influence of the landscape matrix on dispersal success (Kindlmann and Burel 2008, Rayfield et al. 2011). Comprehensive quantification of connectivity (i.e. the probability of an organism successfully leaving point A and arriving at point B, including what goes on in between), should ideally consider both structural and functional components. The consideration of both the available habitat and the movement behavior can be described as 'potential' connectivity

(Calabrese and Fagan 2004) and can be applied to identify potential corridors or pinch points (Ziółkowska et al. 2012), and other useful conservation planning indices such as the probability of connectivity (Saura and Pascual-Hortal 2007). However, this approach is arguably incomplete because the underlying distributions of populations are often not incorporated (Moilanen and Nieminen 2002). Indeed, spatially explicit information about the distribution (e.g. occupancy), size (e.g. abundance) or demography (e.g. survival) of a population or set of populations is crucial for understanding how and why both structural and functional components of connectivity influence ecological dynamics across time and space. Changes in any one of these components can contribute to shifts in the emergent connectivity and the resulting ecological processes in important, yet hitherto unexplored, ways. For example, landscapes and populations change through space and time, and at different spatial and temporal scales, and the judicious inclusion of information about the dynamics of both in connectivity modeling is likely to provide greater insight about their relative contribution to the spatiotemporal dynamics of spatially structured populations.

Through our synthesis, we have identified a third component that is garnering increasing recognition when describing connectivity, i.e. landscape connectivity is the combination of structural, functional and demographic components (Fig. 1). Connectivity is a representation of movement processes, through the lens of dispersal, by individuals among focal habitats (Matthysen 2012, Baguette et al. 2013). These patches contain varying qualities of habitat and exist in the landscape where movement between them responds to the intervening matrix. Incorporating a demographic weighting to established components based on the spatiotemporal distribution of the populations producing dispersers allows for a dynamic and demographically-informed view of connectivity, which we refer to as demographically-weighted connectivity (Fig. 1).

Specifically, we advocate demographically-weighted connectivity as a dynamic framework synthesized from contributions across ecological and conservation literature for understanding the role of connectivity-driven processes that cuts across discrepancies among sub-disciplines. Further, using simulation, we explore key demographic assumptions (representing increasing amounts of biological realism found in connectivity studies) to demonstrate the value of incorporating demographic components of connectivity and the consequences for ignoring it. This simulation highlights the importance of estimating key parameters that control the scale of colonization and dispersal and their probabilities. Such a focused approach on connectivity and its core components should allow for increased integration across sub-disciplines and help progress the search for general ecological processes (Rapacciuolo and Blois 2019). We reassert that
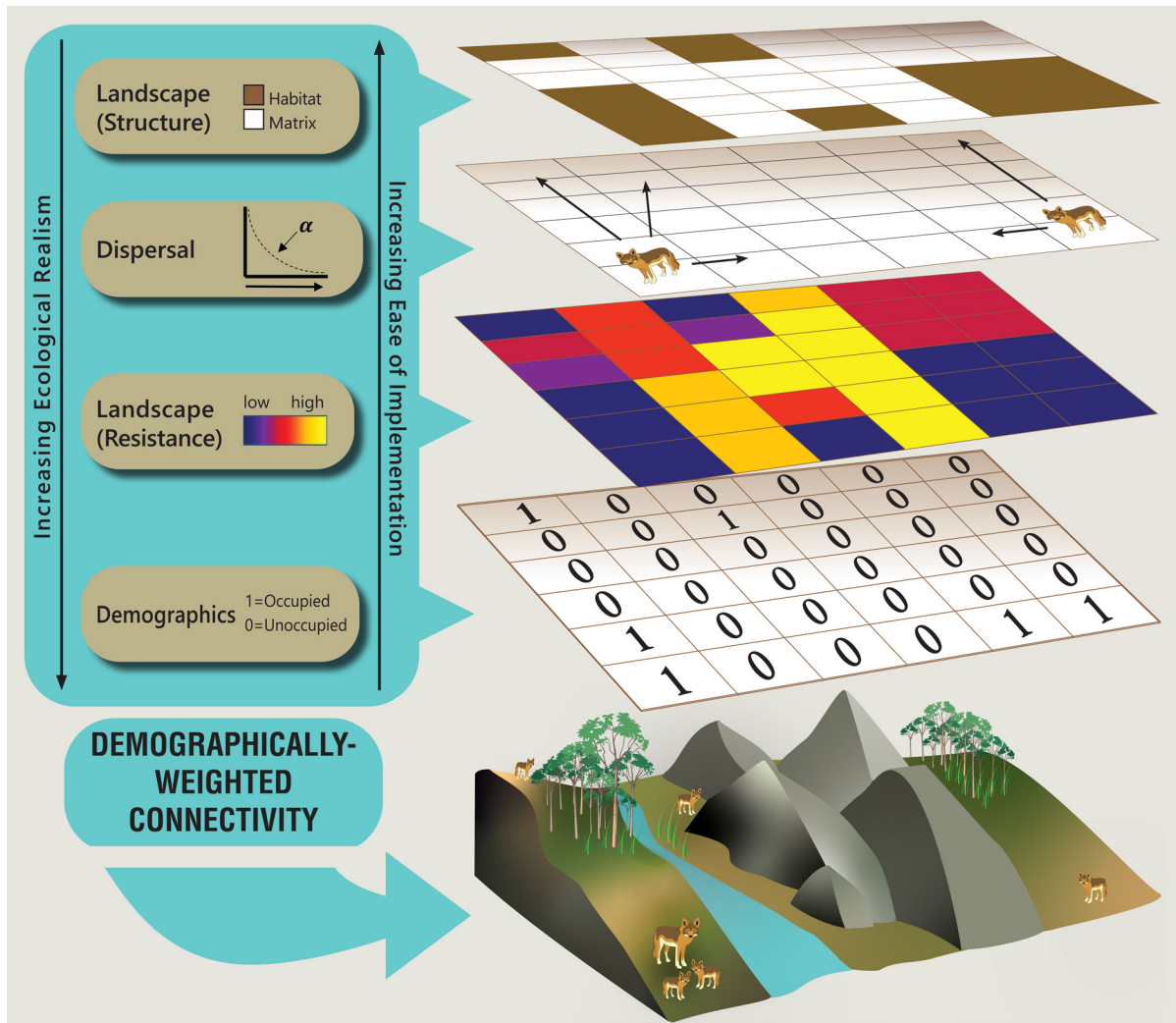
Figure 1. Demographically-weighted connectivity considers three core components of connectivity: landscape (structure and resistance), the dispersal process and population demographic information. Landscape connectivity has often been seen as a static process among habitat patches on the landscape. Connectivity not only influences population dynamics but is influenced by them. Connectivity in the landscape shifts across space and time coincident with the spatiotemporal distribution of organisms. While some habitat may be within effective dispersal range (α) of an organism (Box 2), others may be functionally isolated due to a landscape that is resistant to successful dispersal. Even when such habitat is within the dispersal capability of another parcel of habitat, only when populations of organisms are there, and capable of dispersing, would habitat be functionally connected. The data used to weight connectivity may take the form of simple occurrence data (as shown here), but also abundance, number or breeders, fecundity or any other demographic representation that is hypothesized to relate to the dispersal process and impact connectivity. Demographically-weighted connectivity thus provides an extended conceptual representation of landscape connectivity that considers, explicitly, the population dynamics and demographics which can influence connectivity and the ecological processes dependent upon it. Image designed by Tina Sotis based on research by Drake et al. (2021).

individual decisions and population dynamics are not only a product of connectivity but also an important determinant of connectivity.

Demographic connectivity: synthesizing core contributions

Demographically-informed connectivity draws from fundamental concepts in metapopulation ecology (Hanski 1994, Hanski and Ovaskainen 2000, Ovaskainen and Hanski 2001)

while maintaining important conceptual developments from landscape ecology (Turner 2005), and the methodological development of spatially-explicit hierarchical statistical models that have the potential to overcome modeling and data challenges (Box 1). Ecological connectivity has traditionally been approached from either a structural or functional perspective (Taylor et al. 1993, 2006). This false dichotomy masks a complex gradient of ecological assumptions about connectivity. Instead, we argue that, in addition, connectivity metrics should consider demographic weighting, when applicable, across this gradient. Although movement is implied

Box 1. The current state of demographic connectivity modeling, a spatially realistic metapopulation perspective

Spatially realistic metapopulation theory (SMT) has the potential to act as a unifying force in ecological research (Hanski and Gilpin 1991, Hanski and Ovaskainen 2003), providing a strong conceptual basis and analytical framework for the conservation of fragmented species. Its implementation through the stochastic patch occupancy framework (SPOM; Moilanen 1999, Ovaskainen and Hanski 2004) has allowed the exploration of connectivity's influence on (meta)population dynamics through the lens of dispersal. It has historically been difficult to implement (Baguette 2004, Sutherland et al. 2014), but recent advances have increased the popularity and utility of SMT.

Connectivity in SPOMs is often modelled as a function of dispersal from occupied patches in the spatially explicit patch network (Hanski 1994) and often relies on an assumption of abundance scaling with patch size. This approach is often criticized, because when this assumption does not hold, it can cause erroneous inference, performing poorly as a connectivity predictor (Prugh 2009). While this model has classically relied on such assumptions, occupancy models that are used to estimate dispersal and infer connectivity would benefit from more direct inclusion of demographic data (Clinchy et al. 2002). This can be achieved with the flexibility of Bayesian hierarchical modeling (Risk et al. 2011, Sutherland et al. 2014, Howell et al. 2020a).

Bayesian hierarchical modeling has allowed for the accounting for imperfect detection (Royle and Kery 2007, Guillera-Arroita 2017, MacKenzie et al. 2018) and estimation of missing data (O'Hara et al. 2002, Risk et al. 2011, Sutherland et al. 2014), making traditionally error-prone data easier to analyze. Although the need to incorporate more detailed demographic data is not always needed (Chandler et al. 2015), the inclusion of population size and structure can lead to more accurate representations of connectivity and population dynamics structure (Pellet et al. 2007, Sutherland et al. 2012). Weighting of model components can inherently increase acknowledgement of spatiotemporal heterogeneity of spatially structured populations (Thomas and Kunin 1999), allowing the combination of temporal dynamism and demographic weighting to produce more dynamic representations of connectivity (Drake et al. in review).

Inclusion of other core components of demographic connectivity has been facilitated by the conditional flexibility of hierarchical modeling (Royle and Dorazio 2009). First, the internal state of patch dynamics, often overlooked by classical SPOMs (Holt 1992), can be estimated through the use of sub-models (Sutherland et al. 2014), thus directly addressing the population size/structure to patch area relationship directly (Bender et al. 1998). Second, recent advances by Howell et al. (2018) has allowed the generalization of SMT to allow landscape resistance to be included in the model. This addresses a perennial criticism of the metapopulation framework in general (With 2004), allowing more mechanistic understanding of the dispersal process and acknowledging non-Euclidean movement, reducing the reliance on expert opinion. As well, the inclusion of non-Euclidean dispersal and demographics address both system-scale and local issues of population dynamics (Howell et al. 2020a). This integration of landscape and metapopulation ecological fields has been long anticipated (Hanski and Gilpin 1991) but rarely achieved (Moilanen and Hanski 1998, With 2004, Howell et al. 2018).

to qualitatively achieve measures of functional connectivity, demographic measures (e.g. occupancy, abundance; see below) have historically rarely been considered in investigations of connectivity (Prugh et al. 2008), but an increasing awareness for their need is developing (Fletcher et al. 2019). Next, taking recent developments and historic contributions from the literature, we develop the justification and importance of considering demographic contributions for a more holistic connectivity by discussing each component of connectivity in turn.

Dispersal

Dispersal, the movement of individuals and propagules that may have consequences for gene flow across space (Ronce 2007), links populations, making it essential to connectivity and, as a result, local colonization–extinction dynamics and the maintenance of gene flow and genetic diversity (Bowler and Benton 2005, Crooks and Sanjayan 2006, Baguette et al.

2013). However, lack of empirical dispersal knowledge is often cited as a serious impediment to research (Driscoll et al. 2014), particularly in applications of connectivity (Zeller et al. 2012). For example, when available, sample sizes are often small and lack power, and pooling likely masks important sex-, age- and stage-specific variation (Elliot et al. 2014a). Yet, it is the inclusion of information about dispersal that makes connectivity metrics functional. This is true whether considering fluid dispersed propagules (Munoz 2004), plants (Auffret et al. 2017), small flying insects (Jangjoo et al. 2016), anadromous fish (Bradbury et al. 2014) or large predatory mammals (Zeller et al. 2018). The constraints that impact dispersal for any given species will impact both the potential or realized connectivity that emerges from the landscape structure (Vasudev et al. 2015). Understanding dispersal is therefore key to accurately characterizing the intersection of, and mechanistic link between, landscape structure and population connectivity.

Unfortunately, this presents a limited perspective of an assumed measure of functional connectivity that often ignores

the underlying population distribution. This is evident in applications of landscape resistance mapping. For example, when predicting functional connectivity for bullfrogs, *Lithobates catesbeianus*, in the Sonoran Desert, Drake et al. (2017b) produced resistance estimates to illustrate landscape-scale shifts in potentially connected habitat, regardless of occupancy state. Such demographically-naïve approaches are widely applied and, while useful, represent hypotheses of connectivity that are prone to biases (Zeller et al. 2012) resulting from a mischaracterization of the underlying distribution and behavior of individuals, i.e. of potential dispersers (Riotte-Lambert and Laroche 2021). Indeed, including information on known occurrences, and hence a refined representation of dispersal sources, can generate altogether different characterizations of landscape connectivity and of management priorities (Cushman et al. 2013, Drake et al. 2017a). Overlooking the underlying distribution of potential dispersers is likely to overstate state-specific dispersal of a landscape and introduces biases in the characterization of connectivity which will be more strongly felt in more heterogeneous, spatially-structured populations (Box 2).

Dispersal has three stages: emigration, transfer and immigration, each a multi-faceted context-dependent process. Despite the importance of each stage and the fact that each plays out at, and is influenced by, factors at characteristic spatial and temporal scales (Clobert et al. 2012), functional connectivity approaches have often viewed dispersal solely through the lens of the transfer stage (Diniz et al. 2020). Data at each stage can be limited, but data on the transfer stage are often scarcest (Cozzi et al. 2018); assumptions outnumber data in model representation of this movement. Such scarcity begets the use of proxies, such as functional connectivity, for these largely latent processes.

In fact, recognizing what controls emigration and immigration may provide insight and may be as, if not more, important for estimating connectivity (Vasudev and Fletcher 2016). Variation in emigration rates has been linked to inbreeding avoidance and kin competition (Lambin et al. 2001, Bowler and Benton 2005), area-dependence (Wang and Altermatt 2019) and habitat quality (Hui et al. 2012). Likewise, immigration may depend on conspecific attraction (Matthysen 2005) and perception of site habitat quality (Betts et al. 2008), rather than solely the distance traveled from natal patches (Telfer et al. 2001). The balancing of dispersal costs and benefits is multi-causal and there is potential for a dynamic feedback loop whereby each of these demographic processes can be influenced by, and contribute to, variation in local- and landscape-level connectivity. Thus, factors such as the distribution and abundance of a population and dispersal behavior introduce a spatiotemporal dynamism to the concept of connectivity that has been often overlooked (Drake et al. unpubl.).

Where information on the processes influencing dispersal's transfer stage is limited, patterns gleaned from observed emigration and immigration may provide a reasonable alternative source of dispersal data. Occupancy-based statistical methods can be used to interpret patterns of colonization and extinction (Hanski and Ovaskainen 2003, Ovaskainen and Hanski 2004) and have been commonly used to infer the scale and rate of dispersal (Sutherland et al. 2012, Driscoll et al. 2014). Analytical advances have gone a long way towards the integration of even simple demographic data such as occupancy or abundance to increase the mechanistic understanding of connectivity and its contribution to ecological processes, including predictions of how landscape features influence movement (Vasudev et al. 2015; Box 1). Moreover, advances in data collection have shown that a variety of sampling methods, including determining presence and absence of species through non-invasive methods such as hair snares (Dixon et al. 2006), scat samples (Long et al. 2007) and even environmental DNA (Sales et al. 2020), can increase our ability to examine the impact of connectivity more accurately through the dispersal process for single species and for entire communities (Baguette et al. 2013, Rapacciuolo and Blois 2019). The rapid advances in sampling technology and analytical methods have revolutionized ecological monitoring and modeling such that landscape-scale inference about species occurrence and abundance distributions is commonplace. Considering how valuable this information can be to refining measures of connectivity, we advocate for an integration of landscape-scale estimates of population state variables into connectivity research (Sutherland et al. 2015, Morin et al. 2017, Meyer et al. 2020).

Landscape

For spatially structured populations, the landscape is often divided thematically into the habitat patch and the inter-patch matrix (Dilts et al. 2016). This paradigm is applicable across a wide assortment of environments, not solely in terrestrial ones (Baguette et al. 2013, Boulanger et al. 2020). The focal patch or patch network is often defined by breeding habitat (Compton et al. 2007) or stepping-stones of suitable habitat too small for long-term occupancy (Saura et al. 2014); these patches are surrounded by unsuitable inter-patch matrix typically not permanently occupied by focal species. The amount and relative position of patches defines the landscape structure but rarely reflects the realized distribution of populations or whether they are functionally connected via the intervening matrix. It is worth noting that the patch-matrix landscape model represents one (a binary) end of a spectrum, while continuously occupied landscapes (e.g. gradients of habitat suitability) represents the other end. All landscapes exist along this gradient, depending on the degree of landscape heterogeneity. Therefore, while demographically-weighted connectivity may seem to stem from a patch-centric view, these ideas are not limited to the binary matrix perspective.

Structural representations of landscape connectivity that focus solely on spatial structure of the patch network and overlook the underlying spatial distribution of individuals can generate biased representations of inter-patch connections (Lookingbill et al. 2010, Martensen et al. 2017). The simplifying assumptions of structural models can be useful

Box 2. Illustration of bias emerging from common connectivity modeling assumptions

We conducted a simulation (code available in Supporting information) of spatially-explicit patch occupancy dynamics in a homogenous matrix to determine how commonly applied assumptions about demography influences the ability to recover parameter estimates that influence connectivity. Using a metapopulation as an archetypal spatially structured system and the well-established stochastic patch occupancy model (SPOM; Ovaskainen and Hanski 2004) as pedagogical demonstration, we iteratively relax spatiotemporal invariance and realism of demographic contributions.

We initialized the metapopulation simulation with each patch having an occupancy probability of ψ. These colonization–extinction rates are Markovian, i.e. they are conditional on the occupancy states, z, in the previous year for any given patch i:

$$\psi_{i,t} = \left(1 - z_{i,t-1}\right) C_{i,t-1} + z_{i,t-1}\left(1 - \varepsilon_{i,t-1}\right)$$

where ε is the probability of extinction ($\varepsilon = 0.4$) and C is the colonization probability. For every occupied patch, we generated local population size (N_i) by simulating a random Poisson variable according to an expected area–abundance relationship. This allowed for stochasticity in spatiotemporal abundances:

$$N_{it} \sim \text{Pois}\left(\exp\left(\beta_0 + \beta_1 \times A_{it}\right) \times z_{it}\right)$$

where β_0 is the intercept ($\beta_0 = -1$) and β_1 is the slope parameter relating area to abundance, and the multiplication by z_{it}, the occupancy state, ensures only occupied sites have non-zero abundances. Patch areas were generated from a Uniform(1,3) distribution.

Transition rates themselves are a function of the number of individuals in a patch, i.e. they have a demographic basis:

$$C_{i,t} = 1 - \exp\left(-\gamma \times S_{i,t}\right)$$

γ is the per capita effective dispersal rate and $S_{i,t}$ is the measure of connectivity:

$$S_{it}^* = \sum_{j \neq i} X_{it-1} \times \exp\left(-\alpha d_{ij}\right)$$

where the exponentiated term $-\alpha d_{ij}$ is what makes this representation of connectivity spatially explicit, being a decreasing function of increasing interpatch distances, d_{ij}, scaled by the parameter α. Also, X_{it} represents a series of increasingly realistic demographic weightings (below).

We explore sensitivities by considering variation in time series length ($t = 5, 10$), patch network size (sizes = 30, 100) and area–abundance relationship ($\beta_1 = 1, 2$). In addition to this area–abundance relationship scenario, we generated abundances to have the same overall mean and variance but without the area–abundance relationship (this we refer to as 'disrupting' the relationship). We explored additional combinations of parameters including additional values, which are reported in Supporting information, although the results and scenarios used here are representative of general patterns.

Varying both total abundance and heterogeneity of populations sizes allowed us to consider how different population structures in the landscape impact recovery of parameter estimates. Varying the dispersal rate ($\gamma = 0.2, 0.03$) and the slope of the area:abundance relationship (β_1) to estimate abundance allowed us to examine scenarios reflecting diverse metapopulations; from low population sizes with relatively low variance (ranging approximately from 1 to 11 mean = 2.72) such as those found in carnivores (Benson et al. 2016) to the those with high abundance and variance (ranging approximately from 1 to 154, mean = 20.09).

The patch area–disperser abundance relationship has been a core incidence function model assumption (Hanski 1994) that has recently received increased scrutiny (Ozgul et al. 2009). This disruption of the area–abundance relationship may reflect biologically realistic scenarios where this relationship may not exist (Prugh et al. 2008) and provide insight into bias introduced into modeling populations that do not conform to this assumption (Hovel and Lipcius 2001).

We consider five formulations of the data-generating model that represents increasingly unrealistic assumptions about connectivity. First, we fit the data generating model (N_{it}) described above that included abundance effects on connectivity. Second, we approximate abundance with occupancy-weighted patch sizes ($A_i z_{it}$). Third, we approximate abundance with occupancy state only (z_{it}), ignoring any potential information contained in the size of the patch. Fourth, we approximate abundance with unweighted patch size (A_i), ignoring the occupancy state. Finally, we fit a model that assumes all patch contribute to connectivity equally by ignoring patch size and demographic contributions (U).

These simulations were carried out in R (<www.r-project.org>), using the NIMBLE package (de Valpine et al. 2017); each model combination was run 500 times, each run iterated 30 000 times with 10 000 burn-in and a single chain. We wish to note that these simulations were computationally intensive, requiring multiple processor cores to work over several days or weeks depending on the settings applied. Extended description of the model can be found in Supporting information.

Influence of demography for parameter recovery

Here we focus specifically on the ability to recover the parameter α, the spatial scale parameter of the dispersal kernel that represents the spatial scale of connectivity. Dispersal kernels are central to representing spatial population processes (Nathan et al. 2012). We use a negative exponential version (but other forms may be used; Supporting information) of the incidence function model (Hanski 1994). This form relates the dispersal process to connectivity through the scaling parameter α, representative of the mean dispersal distance (Moilanen and Nieminen 2002). To determine the impact of increasing demographic assumptions on modelling connectivity, we calculated the mean estimator bias of the median connectivity parameter α for each of the 120 possible outcomes.

Unsurprisingly, the data-generating model, N_{it}, performed well and was unbiased in each scenario (mean bias < 0.05; Supporting information). Estimates of α were more biased in high abundance scenarios than in low abundance scenarios. The amount of bias propagation i.e. increasing bias for longer time series and more patches, was inversely proportional to the amount of demographic information included (inset Fig. 1). In fact, model z, which only used occupancy weighting, was the only model to reduce bias as data increased by year and patch number, and was able to have an acceptable amount of bias (from 5 year, 30 patches = 0.06 to 10 years, 100 patches = 0.024) even where the area–abundance relationship was disrupted in the low abundance variant; the high abundance variant of models weighted with z also reduced bias as spatial and temporal data increased. This may be due to the ability of occupancy data to capture the dispersal process through temporal patterns of colonization–extinction across the landscape.
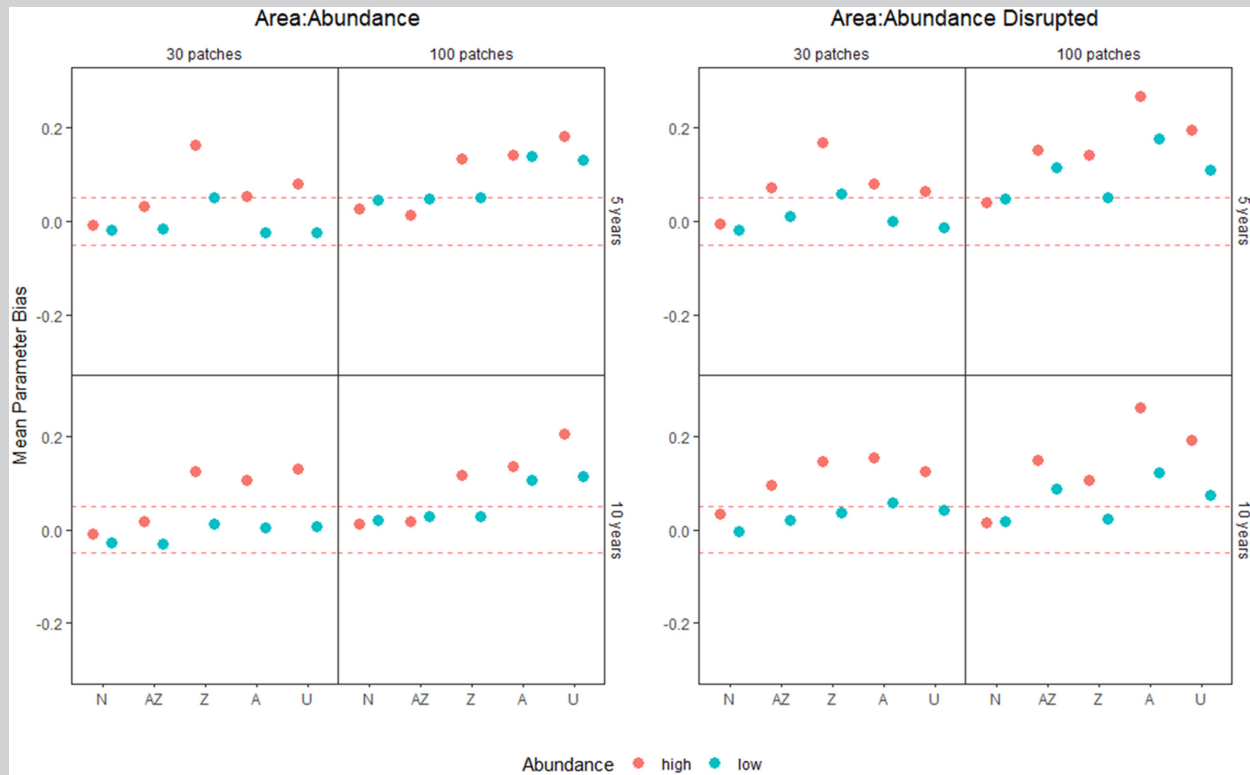
When the area–abundance relationship held, model $A_i z_{it}$ exhibited negligible bias, whereas, when this relationship was disrupted, only low abundance variants in smaller patch networks with fewer years of data maintained reasonable bias in the estimator. As the amount of assumptions for patch data increased both spatially and temporally, so did the bias. Of note is that the uninformed model U generally performed worse than model A_i when the area–abundance relationship held, but, unsurprisingly when this was disrupted, area weighting for connectivity models resulted in the greatest bias recorded (10 years, 100 patches = 0.262), performing less consistently than an unweighted metric (10 years, 100 patches = 0.192).

This exploration of several key assumptions found in connectivity studies show that disregarding demographic information can bias parameter estimates and reduce model consistency. Further, this trend appears to couple with corresponding parameter coverage performance with decreasing demographic data lending to decreased coverage (Supporting information). Information such as disperser abundance and structure of the populations in relation to the patch network can each have impacts individually or compounding to recover accurate connectivity assessments. As connectivity models become less general, results indicate that overestimation of parameter α (inset Fig. 1), i.e. the overestimation of species ability to disperse, and hence a bias to connectivity, could lead to misguided conservation decisions. The results of this simulation suggest that although increased demographic fidelity allows for less biased parameter estimates, the choice to include any demographic information (e.g. occupancy) may be more important than neglecting the state variable in favor of area-based approximations or a demographically uninformed model. We prescribe care to be taken when invoking an area-based assumption for connectivity unless system or species-specific patch size to abundance relationships have been empirically confirmed.

This simulation also shows how powerful the SPOM framework can be at integrating demographic connectivity for describing ecological processes (Box 1) as well as the importance of demographic connectivity itself in recovering accurate parameter estimations. While this simulation framework provides a useful perspective on parameter recovery, we use it as a pedagogical tool. If applied towards hypotheses in real world systems, it also provides a useful testing framework to extend to other models and methods pertaining to heterogeneity in connectivity on the landscape. Model selection methods such as information criterion may also be applied to explore the intersection of model parsimony and mechanistic explanations of animal behavior and landscape connectivity. Also, the model is further generalizable through the inclusion of other biologically informative distances, such as least cost paths, as pointed out by Hanski (1994) and implemented by Howell et al. (2018). As well, imperfect detection is likely to be complicating factor for real data and this model could be extended to account for such observational error (Sutherland et al. 2014, Chandler et al. 2015). This simulation shows a reflection of the current state of connectivity modeling and the implications these common assumptions can have on inference. There is room for improvement and many of the works referenced throughout this manuscript show that it is a possible and worthwhile pursuit.

when demographic data, such as the occupancy, is limited or absent (Urban and Keitt 2001), but may under-estimate connectivity when the distinction between patch and matrix is not clear (Wiens 2001). This is particularly true for continuously-distributed organisms that use a wide variety of habitat (Dilts et al. 2016) or when a single patch dominates the network and ecological processes (Cavanaugh et al. 2014).

It is well established that the matrix matters (Ricketts 2001, Brady et al. 2009, Ruffell et al. 2017), and that overlooking properties of the intervening matrix poses challenges to estimating connectivity (Calabrese and Fagan 2004). For example, barriers to movement limit the colonization potential and reduce the neighborhood's disperser pool, thus limiting patch-specific contributions to network connectivity and ultimately limiting gene flow (Kimmig et al. 2020). So, while functionally isolated patches that are not occupied or are occupied and produce no emigrants are assumed to contribute to network connectivity under the structural paradigm, in reality, they make no contribution to actual connectivity. The consequences of not acknowledging such 'zombie patches' is the equivalent of introducing false positive errors which could lead to bias in key model components and erroneous estimates of connectivity (Box 2). Further, considering occupancy dynamics for functional connectivity better reflects both the dispersal pool, through the inclusion of occupancy states and the dispersal process, through colonization–extinction dynamics (Sutherland et al. 2014, Chandler et al. 2015). Thus, in the same way demographic data provides mechanistic interpretations of structural connectivity, it can also offer a mechanistic interpretation of functional connectivity.

Functional connectivity seeks to introduce biological realism by invoking increasingly realistic movement rules. Often this is through the use of landscape resistances that introduce variable strengths of spatial dependencies beyond Euclidean distance based measures (Zeller et al. 2012, Graves et al. 2014, Diniz et al. 2020). Resulting resistance surfaces are often modelled via cost–distance methods (Adriaensen et al. 2003) or circuit theory applications (McRae 2006, McRae et al. 2008), that seek to quantify the interaction between movement and landscape structure. Thus, the objective of functional connectivity metrics is to identify inter-patch corridors with lower resistance to movement than the rest of the matrix (Beier and Noss 2008). As applied, many existing approaches to connectivity modeling represent hypotheses of naïve function that assume populations, and hence dispersers, are uniformly distributed through the landscape. In reality these dispersers are more likely to exhibit spatial heterogeneity (Zeller et al. 2018). This raises concerns about how well existing approaches represent the dispersal process, and the value of the resulting resistance surfaces in applied settings (Beier and Noss 2008, Laliberté and St-Laurent 2020). Noteworthy exceptions include the rarely applied weighting schemes available in the application of circuit theory (McRae et al. 2008, Dickson et al. 2019) and the development of a unified framework for connectivity that can integrate species distribution information (Fletcher et al. 2019).

While conceptually appealing, resistance models are challenging to parameterize due to the lack of information at the transfer stage, and if mis-specified, can be poor predictors of connectivity (Janin et al. 2009, Keeley et al. 2017), especially

when parameterized using expert opinion (Koen et al. 2012, Zeller et al. 2012). Empirical estimates can be derived from techniques such as GPS telemetry, mark–recapture or genetic data (Epps et al. 2007, Graves et al. 2014, Sutherland et al. 2015), or indirectly from observed locations of focal organisms. For example, Zeller et al. (2018) found that movement corridors were best recovered using resistance surfaces estimated by cost–distance pathways informed by GPS data, but also suggesting that circuit-theory based algorithms be used to infer dispersal if opportunistic presence-only data is the data available.

Another emerging interest is the existence of short- and long-term habitat shifts in response to disturbances, wildfire, climate change and fragmentation (Bishop-Taylor et al. 2018, Littlefield et al. 2019). Accounting for temporal variation in habitat structure and its influence on connectivity by considering long term and ephemeral changes in landscapes (Ruiz et al. 2014, Zeigler and Fagan 2014, Drake et al. 2017b, Bishop-Taylor et al. 2018) are likely to become increasingly important as more species undergo climate-induced range reductions (Littlefield et al. 2017) and loss of habitat and the subsequent increasing landscape resistance and reducing structural and functional connectivity (Dilts et al. 2016). In fact, like spatiotemporal (meta)population dynamics, shifts in the extent, structure, and quality of habitat is an important contributor to spatiotemporal variation in connectivity (i.e. connectivity dynamics, Zeller et al. 2020). In a study of fragmented Brazilian Atlantic Forest patches, Martensen et al. (2017) showed that temporal changes in patch size resulted in up to 150% increase in connectivity between patches compared to static snapshots of habitat availability. It is worth noting that the authors did not account for underlying occupancy dynamics which are predicted to be linked to patch size (Hanski 1998). In general, both functional and structural measures of connectivity do not have spatial or temporal dynamics built into their conceptual interpretations. Spatial habitat variability over ecological time scales is not equal to short-term changes in populations within that habitat, which, we argue, renders the domain incomplete because, a patch is not a population. Integrating aspects of the underlying population state directly resolves this concern.

Demographic weighting

Ideally, weighting connectivity measures via locale-specific demographic contributions would not be necessary if all movements could be observed completely which we suggest is unlikely in practice. Thus, information on spatiotemporal changes in the distribution or size of a population, which provides a measure of dispersers and their contribution to ecological processes, should be used to inform connectivity. Integrating spatiotemporal heterogeneity in population size and hence in the production of dispersers, which we refer to as demographic-weighting, directly and explicitly introduces spatiotemporal dynamism into connectivity modeling (Sutherland et al. 2014, Drake et al. unpubl.). Such dynamism is crucial to identify the 'actual connectivity' between

extant populations amongst occupied habitat (Calabrese and Fagan 2004). Examples of relevant and now commonly estimated demographic data useful for weighing the contribution of patches to connectivity are occupancy, a local state variable that describes the distribution of populations and whether they contribute to colonization–extinction dynamics (Chandler et al. 2015, Howell et al. 2018), and population size, the number of potential dispersing life stages in occupied patches (Sutherland et al. 2014). Alternatives to occupancy and abundance may include the number of reproductively active individuals (Robertson et al. 2019), fecundity (Castorani et al. 2015, 2017), the number of successful reproducers (Robertson et al. 2018), stage-structure (Sutherland et al. 2012), conspecific condition (Clobert et al. 2009, Cote and Clobert 2010), dispersal syndrome of individuals (Jones et al. 2015, Edelsparre et al. 2018, Fobert et al. 2019), individual condition (Shima and Swearer 2009, Marshall et al. 2010) and individual behavioral expression (Cote and Clobert 2007, Brown et al. 2017). Each has in common the fact that they have the potential to vary spatially and therefore influence the number of potential dispersers, and hence connectivity.

These examples build upon earlier approaches to spatially realistic modeling in landscape ecology and metapopulation ecology. Hanski (1994) introduced a realistic metapopulation model that accounted for simple occupancy states in the measure of connectivity between patches. This model also used a Euclidean distance but suggested that any meaningful biological distance could be included (Box 1). This model also accounted for variation in habitat amount or quality (Hanski 1994), but was focused on within-patch metrics. Conservation practitioners often focused on identifying corridors through interpatch matrix informed by coarse population distributions to identify source locations and potential bottlenecks (Larkin et al. 2004). More recently, researchers have integrated species distribution models with information on dispersal to advance the realism of landscape connectivity, particularly useful for exploring predictions of range shift abilities in accordance with shifting habitats due to climate change (Ofori et al. 2017). These methods have, however, historically conflated the impact of landscape on movement and the mortality of dispersing individuals when quantifying resistance and connectivity (Zeller et al. 2012). Fletcher et al. (2019) used spatially absorbing Markov chains to disentangle these processes and improve least-cost path and circuit theory modeling, allowing multiscale temporal predictions as well as quantification of demographic parameters related to connectivity. Identifying such divergent causal mechanisms (avoidance versus mortality) and their influence on ecological processes may be important for understanding how demography impacts spatiotemporal heterogeneity in connectivity and vice versa.

Spatiotemporal heterogeneity is an inherent characteristic of any spatially structured population, and where such heterogeneity is prevalent, the assumption that all populations contribute equally to connectivity is difficult to justify (Prugh et al. 2008, Box 2). This concern is regularly alleviated

using theoretically justified proxies of population size such as patch size, and while surrogates likely capture longer term average population sizes, they fail to capture temporal stochasticity resulting from local population dynamics or whether the species is even present. In this regard, such proxies may result in misrepresentations of connectivity, potentially similar to those in structural measures. For instance, while simple patch occupancy may be enough to increase the accuracy of dispersal estimates, Clinchy et al. (2002) found that occurrence data masked population declines such that the population dynamic processes of pika could not be inferred without more detailed demographic data. Ultimately, connectivity measures that do not consider the spatial distribution of dispersers, may be overly simplistic for many ecological questions or management goals (Lambin et al. 2004).

Consequences of ignoring demography

Demographic proxies

The use of patch size as a surrogate for population size is common in ecology, especially in landscape-scale investigations. This is largely due to the time-, labor- and cost-intensive nature of gathering demographic data at spatial and temporal scales that are representative of landscape-scale or population-level processes. However, the relationship between patch size and abundance are not always linear (Deza and Anderson 2010) or even positive (Hovel and Lipcius 2001), and the strength of the relationship can be taxon- (Pellet et al. 2007) or stage-specific (Sutherland et al. 2012). Indeed, there is accumulating evidence suggesting that, when measuring connectivity, area-abundance assumptions do not hold and that demographic information representing real-time heterogeneity in abundance is preferred (Moilanen and Nieminen 2002, Prugh 2009).

In addition to the spatial misrepresentation of local abundances, area approximations that use a single measure of patch size implicitly assume a degree of temporal invariance with the potential to mask local dynamics (Sutherland et al. 2012). In this case, large patches will dominate, and potentially bias, inferences about network dynamics regardless of their internal state (Cavanaugh et al. 2014). Moreover, density-dependent factors (e.g. dispersal, local population dynamics) are completely overlooked, despite their importance in determining both local and regional (meta)population dynamics (Eriksson et al. 2014, Spanowicz and Jaeger 2019). Attempts at addressing the deficiencies of the static measures, such as incorporating time-varying measures of habitat quality (Clinchy et al. 2002), are also likely to mischaracterize the response of either local population size or potential emigrants and overlook important thresholds (Harman et al. 2020).

Notwithstanding, population size is itself a proxy for the number of dispersers, which drives connectivity between patches. Dispersal rates can be sex-specific (Trochet et al. 2016) and/or stage-structured (Sutherland et al. 2014, Tucker et al. 2017). Further, different demographic life stages within the same habitat patch, may experience the landscape differently during the transfer stage of dispersal, and per-capita contribution to connectivity varies accordingly (Baguette et al. 2013). For example, in African lions, *Panthera leo*, differences in levels of risk aversion result in substantially different estimates of sex- and age-specific landscape resistance (Elliot et al. 2014b). Increases in mortality risk to dispersing individuals, whether due to human–wildlife conflict, predation, or exposure, can be masked in resistance surfaces (Fletcher et al. 2019), especially if demographic data are ignored when smaller and younger individuals experience increased mortality risk (Sibly et al. 1997). Such attention to demographic details also helps decipher effective dispersal which leads to successful habitat colonization and reproduction, a potentially crucial aspect to correctly interpret conservation objectives and ecological questions (Greenwood and Harvey 1982, Vasudev and Fletcher 2016). A failure to consider demographic determinants of connectivity has the potential, therefore, to lead to unsound management decisions (Elliot et al. 2014b).

Using common proxies for demography in connectivity can lead to bias (Box 2), but demographic data is hard and/or expensive to collect. Our simulation demonstrates what may occur if you fail to account for demographic variation or other additional (un)known sources of bias/variation. Rather than forgoing connectivity research due to this, there is potential for an application of Bayesian hierarchical modeling (Box 1) to help account for this bias using a random effects parameterization. For example, Fletcher et al. (2011), used random effects to help account for variation in dispersal. Such an approach may help increase the robustness of connectivity models (Drake et al. in review) to bias but are unfortunately phenomenological and may be less powerful than including demographic data directly.

Ultimately, connectivity is a dynamic property of an embedded population-landscape system. Populations vary in space and time and are often structured such that contributions to ecological dynamics are not equal among individuals. This is no different for connectivity, and as such, direct measures of the functional component of the local population in space and time are critically important because they represent fundamental spatiotemporal contributions to emergent landscape connectivity.

Sources of error and structural weaknesses

Missing information about the functional state of a patch can arise in several ways, each with specific implications for inference about occupancy, dispersal, and hence, connectivity. One main source of error is the false negative error associated with imperfect detection: the assumption that a patch is not occupied after failing to detect a species at a site when it is actually present (Mackenzie et al. 2002, MacKenzie et al. 2003, Guillera-Arroita and Lahoz-Monfort 2012). Missing a patch completely, or assuming it isn't occupied (note that both overlook contributions to connectivity), overestimates dispersal rates and colonization in metapopulations and hence

biases estimates of connectivity (Moilanen 2002). Imperfect detection also skews resistance estimates of landscape features (Graves et al. 2014) and masks important demographic information resulting in biased estimates of dispersal and inferred connectivity when these observational errors are left unaccounted in models (MacKenzie et al. 2018). False positives can also occur, and while they are another important source of bias (Moilanen 2002, Miller et al. 2011), they are assumed to be less common (MacKenzie et al. 2018).

Interestingly, however, unweighted measures of connectivity, of which many are, systematically introduce false positives by failing to acknowledge the underlying spatiotemporal distribution of the population. Under the classical description of structural connectivity, where all viable patches are assumed to be hosting populations, landscape connectivity is overstated due to the inclusion of contributions from unoccupied parts of the landscape. Even when weighting schemes are incorporated similar errors can occur. For example, the estimated mean dispersal distance for the water vole, *Arvicola amphibius*, when assuming data perfectly represented patch states compared to when errors were explicitly acknowledged was 12.4 km and 2.10 km, respectively (Sutherland et al. 2012, 2014). The latter is more reflective of estimated dispersal confirmed by mark–recapture, telemetry and genetic analyses (Stoddart 1970, Telfer et al. 2003, Aars et al. 2006, Fisher et al. 2009). More generally, contributions to connectivity are biased if area does not correlate to occupancy state or abundance (Box 2), or when occupancy states do not distinguish between functional states such as breeding and non-breeding populations (Sutherland et al. 2013). Sources of errors and biases in the underlying patch state such as erroneously missing or considering the functional importance of a patch, or misrepresentations of the functional component, erodes the connectivity signal resulting in, at best, estimates of connectivity and associated dynamics with high uncertainty, or at worst, biased estimates of connectivity (Prugh 2009). Recent advances in how data are collected and analyzed have naturally facilitated the integration of demographic data and methods for addressing imperfect detection upon which the concept of demographically informed connectivity has been synthesized (Sutherland et al. 2015, Morin et al. 2017, Meyer et al. 2020, Box 1).

The temporal scales of demographically-weighted connectivity

Long-term planning for promoting the persistence of species is often the end-goal for management actions, yet conservation planning is often based on relatively short time scales (e.g. annually) and therefore requires demonstration of success at corresponding scales. Demographically-weighted connectivity is most likely to be important at this scale of generations and 10's of generations, i.e. at the scale of (meta)population dynamics which is driven by dispersal and colonization–extinction dynamics. For example, when considering species invasions or reintroductions, where small beachheads of organisms can lead to system-wide occupancy (Howell et al.

2020a), this framework may be especially useful as an addition to others, as the acknowledgement of demographic states or population distributions may be crucial to understanding colonization, persistence and quickly shifting distribution of organisms though time in such systems.

Spatiotemporally shifting populations, when considered in connectivity analyses, can help account for the impact of intermittent or cyclic environmental disturbances and population dynamics (Lambin et al. 2001, Howell et al. 2020b, Zeller et al. 2020). This may come through shifts in organismal ranges, potentially due to spatiotemporally correlated extinctions and colonization events shifting the whole system's configuration. Such a scenario shifts the numbers and distribution of dispersers, and resulting genetic diversity, across time and space. For example, current genetic spatial structure may be the result of past demographic structure and dispersal patterns (Driscoll and Hardy 2005), reflecting a connectivity that no longer exists on the landscape. This may result from a temporal lag in observed genetic structure due to loss of connectivity compared to the observed structure when the connectivity is facilitated by the removal of barriers to dispersal (Landguth et al. 2010, Driscoll et al. 2014). As well, demographic insights to connectivity, such as density dependent dispersal can be useful in determining the ability for species to track long-term climate change driven range shifts (Best et al. 2007). Determining the eco-evolutionary consequences of such shifts will be critical in the wake of large scale disturbances and environmental change (Dytham et al. 2014); demographically-weighted connectivity metrics can help identify key population processes and critical habitat, as well as reduce bias in estimates of dispersal and population dynamics (Sutherland et al. 2014).

Conservation actions often aim to achieve long term persistence of species, habitats or communities, even when constrained by the need for short term results. While we have focused on demographic-connectivity metrics, other metrics of 'potential' connectivity may still be appropriate to conservation planning; particularly those metrics that emerge at the landscape scale from finer pair-wise metrics. This approach to connectivity may incorporate behavioral data (such as mean dispersal), but may not consider the demographic state (e.g. occupancy or distribution) of a species across the available habitat. One such example is metapopulation capacity (Hanski and Ovaskainen 2000), which has been used to explore the ability of a specific spatial aggregation of habitat to allow long term persistence of a species. Such measures are likely to provide insights into landscapes and habitat patches contributions to long-term population viability (Visconti and Elkin 2009). Such tools are capable of identifying land for reserve designs (Strimas-Mackey and Brodie 2018) but often still rely on connectivity measures and proxies to determine population dynamics and persistence (Cabeza and Moilanen 2001).

The idea that demographics matter to connectivity, even at short time scales, and that the distribution of populations impacts connectivity inference is well supported in our simulation study (Box 2, Supporting information). We demonstrated that as demographic data was abstracted out of models

to greater degrees, the amount of bias increased, both as the number of patches or years increased. Particularly, if the population to area relationship does not hold, bias can emerge quickly and appeared to continue to propagate (Box 2, Fig. 1). Likewise, when connectivity was demographically-weighted, the distribution of dispersers was accounted for, resulting in negligible bias in parameter estimates (Box 2, Fig. 1).

Eco-evolutionary and management implications

Dispersal's central role in life history is under strong selection (Ronce 2007). This leads to changes in dispersal phenotypes tied to changes in the costs of dispersal and potentially shifting dispersal life stage, relative probability of effective dispersal success, and dispersal propensity (Legrand et al. 2017). Changes in dispersal phenotype will impact functional connectivity, i.e. the response to landscape and demographics (Legrand et al. 2017). Eco-evolutionary feedbacks driven by changes to functional connectivity and response to the landscape and conspecifics would, in turn, impact dispersal (Fronhofer and Altermatt 2017). This feedback may increase dispersal, for example, through the adaptation to more efficient use of matrix allowing increased long-distance dispersal success (Bonte et al. 2012). If increased isolation increases dispersal costs, which in turn reduces colonization, this will likely decrease the magnitude of and selection for dispersal syndromes, shifting populations to increased residency instead (Matthysen et al. 1995, Legrand et al. 2017). However, Hanski and Mononen (2011) identified that simply changing model parameter values alters this prediction, especially when model assumptions are not reflective of the species biology (e.g. breakdowns in patch area abundance assumptions). Such work that explores dispersal and evolution often make these assumptions about connectivity out of necessity, sometimes reflecting spatiotemporal invariance or demographic naivety. As with Hanski and Mononen (2011), a re-parameterization of connectivity models explicitly considering demography, and associated demographically-weighted connectivity feedbacks, also have the potential to alter standing expectations about the evolution of dispersal, particularly in the face of continued habitat fragmentation and loss (Thomas 2000, Cote et al. 2017).

The contribution of habitat fragmentation and habitat loss, or specifically the associated reductions in connectivity and gene flow (Mills and Allendorf 1996), is a major conservation concern (Soulé 1987). Also the reduction in dispersal or connectivity between patches (Griffen and Drake 2008) can decrease potential for viable adaptations to future disturbances for the whole population (Kimura et al. 1963, Bonte et al. 2018). This limits the distribution of dispersal phenotypes and genetic diversity, ultimately reducing the effective population size (Palstra and Ruzzante 2008), again increasing potential inbreeding risks and genetic drift. A potential, catastrophic scenario is mutational meltdown, the accumulation of deleterious mutations, happening in an expedited fashion in highly fragmented and increasingly isolated populations, leading potentially to metapopulation

collapse (Higgins and Lynch 2001). Static, structural, or other forms of connectivity that rely on area assumptions, would likely miss demographically driven shifts in connectivity, resulting in overestimated persistence (Wang and Whitlock 2003). As well, the increase in realistic estimates of dispersal rates by inclusion of demographic data that address population processes (Sutherland et al. 2014) can help resolve problems of cryptic population genetic interactions that emerge at shorter time scales, but have long-term eco-evolutionary consequences for conservation (Lowe et al. 2017).

As climate change, invasions, fragmentation and other threats force species to adapt or shift their range (Shine et al. 2011, Cote et al. 2017, Maher et al. 2017, Littlefield et al. 2019), the role of connectivity in shaping species' responses will be a function of the combined effects of genetic bottlenecks, local adaptation, colonization–extinction dynamics and dispersal barriers (Parmesan 2006, Saura et al. 2014, Bonte et al. 2018, Senner et al. 2018, Bani et al. 2019). Now, more than ever, moving beyond unrealistic assumptions and unrepresentative surrogates, and parameterizing connectivity models with accurate information on the underlying processes that give rise to, and respond to, connectivity is paramount (Lowe et al. 2017). In turn, viewing realized connectivity as inherently reliant on demographic inputs will offer greater insight about the eco-evolutionary consequences of connectivity and the mechanisms controlling persistence of (meta)populations (Kinnison and Hairston 2007). Indeed, we suggest that demographically-informed connectivity provides a conceptual framework (Fig. 1) along with associated modeling innovations to better quantify connectivity with wide ranging basic and applied implications.

Looking forward

Our review suggests that while both structural (e.g. available habitat) and functional (i.e. dispersal ability) connectivity paradigms are important, demographic weighting is a comparably, if not more, important dimension of connectivity. Our simulations illustrate the consequences of assuming all patches contribute equally to connectivity (Box 2). The ability to accurately characterize connectivity dynamics increases when unrealistic assumptions about the underlying population are relaxed through demographic-weighting. The simulations also suggest that inferences about the impact of connectivity on both short- and long-term population dynamics (and by extension genetic diversity) are likely to be biased if demographic contributions are ignored. While connectivity is obviously model-, situational-, species-, landscape-, and demographically-dependent, the generalities we derive are important for guiding future research.

Empirical modelling (Box 1) and simulations (Box 2) clearly demonstrate the value of integrating demographic information to increase mechanistic descriptions of connectivity, yet studies such as these are still limited in number

and further work is needed. For example, stage-structured dispersal, area-based population scaling assumptions, and accounting for individual heterogeneity in dispersal need to be considered in more studies to better understand spatiotemporal heterogeneity to dynamic connectivity across landscapes (Zeller et al. 2020). Managing populations fragmented by increasingly inhospitable matrix and its subsequent increase in resistance to connectivity will be necessary as anthropogenic landscape changes accelerate. Thus, the role of the disperser, the variation of dispersal behavior in response to landscape, the complex interaction of ecological and evolutionary processes, and the demographic influences upon them, is central to mitigating the detrimental effects of habitat loss and isolation (Burgess et al. 2014, Poli et al. 2020). However, perhaps more important is to ensure that these processes are accurately represented in models that are used to make predictions about connectivity and support specific conservation actions.

We also believe that demographic landscape connectivity falls naturally within the larger toolbox of existing approaches for understanding eco-evolutionary processes. In fact, many of the most interesting ecological questions and pressing conservation concerns may only be tractable with complementary methods, such as demographic connectivity modeling and landscape genetic techniques (Cushman et al. 2018, Wan et al. 2018, Zeller et al. 2018, Peterman et al. 2019). Not only can demographically-weighted connectivity be used to improve understanding of individual species, but across taxa as well (Cushman and Landguth 2012). We predict that it can help identify multi-species generalities of connectivity for community-level inference (Brennan et al. 2020) and for uncovering connectivity trends for biodiversity in general (Hartfelder et al. 2020). Terrestrial ecologists may do well to look to marine systems for examples of demographically- or population-based connectivity in dynamic environments and vice versa (Cowen and Sponaugle 2009, Castorani et al. 2015, Zeller et al. 2020). Demographic connectivity can help refocus sub-disciplines of ecology and conservation sciences to integrate data and methods (Howell et al. 2018) across spatiotemporal scales to provide inference and insight into fundamental ecological processes controlling biodiversity assembly rules like selection and dispersal (Pinto and MacDougall 2010, Rapacciuolo and Blois 2019).

The IUCN recently issued guidelines for connectivity conservation (Hilty et al. 2020). We agree that a focus on connectivity as a concept, and the central role it plays in mitigating global biodiversity loss is absolutely essential. We do note, however, that the guidelines put forth by the IUCN make very little mention of the demographic basis of connectivity and view populations as being a result of connectivity rather than acknowledging that population dynamics and connectivity are explicitly linked and should be treated as such. Claims that less than 10% of protected lands are viably 'connected' for biodiversity conservation (Ward et al. 2020) are concerning, but acknowledgment of the demographic nature of connectivity is required to reaffirm if such claims are optimistic or pessimistic.

Conclusion

The connectivity paradigm has too often been suggested to be solely the driver of population dynamics and not to be driven by them. This is a remnant of the 'if we build it, they will come' mentality (Hilderbrand et al. 2005). Such 'field-of-dreams' hypotheses may be born out as Shakespearean tragedy. In an age of expanding rates of extinction (McCallum 2007, Ceballos et al. 2015, Sánchez-Bayo and Wyckhuys 2019), in a not too distant future, the world may no longer have the necessary reservoirs of biodiversity to abide such thinking. Instead, we must continue to elucidate how populations are connected: the more populations, the more chance for connectivity and recolonization of conserved habitat. Our framework addresses this directly. If we are not careful, we may conserve 'Nature's Stage' (Beier et al. 2015) so perfectly that it lay set for 'The Tempest' (Shakespeare 1623), yet no survivors may yet cling to the fragments of our shipwreck whom may take their cue and enter stage-right.

Here we have presented a general conceptual synthesis of existing approaches for measuring and estimating connectivity through the integration of information about the landscape, dispersal, and, importantly, demographic contributions – demographically-weighted connectivity. It is our hope that this review will lead to further integration of demographic information into connectivity frameworks and will facilitate the crosstalk between sub-disciplines of ecology themselves. Indeed, demographically-informed connectivity helps us prevent Prospero's hubris, moving the quantification of connectivity's influence on ecological processes forward, instead of losing our way in the coming storm.

Author contributions

Joseph Drake: Conceptualization (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead). **Xavier Lambin**: Conceptualization (equal); Writing – review and editing (equal). **Chris Sutherland**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing – review and editing (equal).

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Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6hdr7sr16> (Drake et al. 2021).

References

Aars, J. et al. 2006. Widespread gene flow and high genetic variability in populations of water voles *Arvicola terrestris* in patchy habitats. – Mol. Ecol. 15: 1455–1466.

Adriaensen, F. et al. 2003. The application of 'least-cost' modelling as a functional landscape model. – Landsc. Urban Plan. 64: 233–247.

Auffret, A. G. et al. 2017. Plant functional connectivity – integrating landscape structure and effective dispersal. – J. Ecol. 105: 1648–1656.

Baguette, M. 2004. The classical metapopulation theory and the real, natural world: a critical appraisal. – Basic Appl. Ecol. 5: 213–224.

Baguette, M. et al. 2013. Individual dispersal, landscape connectivity and ecological networks. – Biol. Rev. 88: 310–326.

Bani, R. et al. 2019. Dispersal traits interact with dynamic connectivity to affect metapopulation growth and stability. – Theor. Ecol. 12: 111–127.

Banks, S. C. et al. 2005. The effects of habitat fragmentation via forestry plantation establishment on spatial genotypic structure in the small marsupial carnivore, Antechinus agilis. – Mol. Ecol. 14: 1667–1680.

Beier, P. and Noss, R. F. 2008. Do habitat corridors provide connectivity? – Conserv. Biol. 12: 1241–1252.

Beier, P. et al. 2015. Conserving natures stage: introduction. – Conserv. Biol. 29: 613–617.

Bender, D. J. et al. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. – Ecology 79: 517.

Benson, J. F. et al. 2016. Interactions between demography, genetics and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. – Proc. R. Soc. B 283: 20160957.

Best, A. S. et al. 2007. Which species will succesfully track climate change? The influence of intraspecific competition and density dependent dispersal on range shifting dynamics. – Oikos 116: 1531–1539.

Betts, M. G. et al. 2008. Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. – Ecography 31: 592–600.

Bishop-Taylor, R. et al. 2018. Evaluating static and dynamic landscape connectivity modelling using a 25-year remote sensing time series. – Landsc. Ecol. 33: 625–640.

Blowes, S. A. and Connolly, S. R. 2012. Risk spreading, connectivity and optimal reserve spacing. – Ecol. Appl. 22: 311–321.

Bonte, D. et al. 2012. Costs of dispersal. – Biol. Rev. Camb. Phil. Soc. 87: 290–312.

Bonte, D. et al. 2018. Eco-evolutionary feedbacks following changes in spatial connectedness. – Curr. Opin. Insect Sci. 29: 64–70.

Boulanger, E. et al. 2020. Spatial graphs highlight how multi-generational dispersal shapes landscape genetic patterns. – Ecography 43: 1–13.

Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – Biol. Rev. 80: 205–225.

Bradbury, I. R. et al. 2014. Landscape structure and climatic variation determine Atlantic salmon genetic connectivity in the northwest Atlantic. – Can. J. Fish. Aquat. Sci. 71: 246–258.

Brady, M. J. et al. 2009. Habitat attributes of landscape mosaics along a gradient of matrix development intensity: matrix management matters. – Landsc. Ecol. 24: 879–891.

Brennan, A. et al. 2020. Characterizing multispecies connectivity across a transfrontier conservation landscape. – J. Appl. Ecol. 57: 1700–1710.

Brown, L. M. et al. 2017. Using animal movement behavior to categorize land cover and predict consequences for connectivity and patch residence times. – Landsc. Ecol. 32: 1657–1670.

Burgess, S. C. et al. 2014. Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected-area design. – Ecol. Appl. 24: 257–270.

Cabeza, M. and Moilanen, A. 2001. Design of reserve networks and the persistence of biodiversity. – Trends Ecol. Evol. 16: 242–248.

Calabrese, J. M. and Fagan, W. F. 2004. A comparison-shopper's guide to connectivity metrics. – Front. Ecol. Environ. 2: 529–536.

Castorani, M. C. N. et al. 2015. Connectivity structures local population dynamics: a long-term empirical test in a large metapopulation system. – Ecology 96: 3141–3152.

Castorani, M. C. N. et al. 2017. Fluctuations in population fecundity drive variation in demographic connectivity and metapopulation dynamics. – Proc. R. Soc. B 284: 20162086.

Cavanaugh, K. C. et al. 2014. Patch definition in metapopulation analysis: a graph theory approach to solve the mega-patch problem. – Ecology 95: 316–328.

Ceballos, G. et al. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. – Sci. Adv. 1: 9–13.

Chandler, R. B. et al. 2015. Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. – J. Appl. Ecol. 52: 1325–1333.

Clinchy, M. et al. 2002. Pattern does not equal process: what does patch occupancy really tell us about metapopulation dynamics? – Am. Nat. 159: 351–362.

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. – Univ. of Oxford Press.

Compton, B. W. et al. 2007. A resistant-kernel model of connectivity for amphibians that breed in vernal pools. – Conserv. Biol. 21: 788–799.

Cote, J. and Clobert, J. 2007. Social personalities influence natal dispersal in a lizard. – Proc. R. Soc. B 274: 383–390.

Cote, J. and Clobert, J. 2010. Risky dispersal: avoiding kin competition despite uncertainty. – Ecology 91: 1485–1493.

Cote, J. et al. 2017. Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. – Ecography 40: 56–73.

Cowen, R. K. and Sponaugle, S. 2009. Larval dispersal and marine population connectivity. – Annu. Rev. Mar. Sci. 1: 443–466.

Cozzi, G. et al. 2018. Socially informed dispersal in a territorial cooperative breeder. – J. Anim. Ecol. 87: 1–12.

Crooks, K. and Sanjayan, M. 2006. Connectivity conservation: maintaining connections for nature. – In: Crooks, K. and Sanjayan, M. (eds), Connectivity conservation, 1st edn. Cambridge Univ. Press, pp. 1–19.

Cushman, S. A. and Landguth, E. L. 2012. Multi-taxa population connectivity in the northern Rocky Mountains. – Ecol. Model. 231: 101–112.

Cushman, S. A. et al. 2013. Biological corridors and connectivity. – In: Key topics in conservation biology 2, Hoboken, NJ: Wiley-Blackwell, pp. 384–404.

Cushman, S. A. et al. 2018. Editorial: The least cost path from landscape genetics to landscape genomics: challenges and opportunities to explore NGS data in a spatially explicit context. – Front. Genet. 9: e.2018.00215.

Daigle, R. M. et al. 2020. Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect. – Methods Ecol. Evol. 11: 570–579.

de Valpine, P. et al. 2017. Programming with models: writing statistical algorithms for general model structures with NIMBLE. – J. Comput. Graph. Stat. 26: 403–413.

Deza, A. A. and Anderson, T. W. 2010. Habitat fragmentation, patch size and the recruitment and abundance of kelp forest fishes. – Mar. Ecol. Prog. Ser. 416: 229–240.

Dickson, B. G. et al. 2019. Circuit-theory applications to connectivity science and conservation. – Conserv. Biol. 33: 239–249.

Dilts, T. E. et al. 2016. Multiscale connectivity and graph theory highlight critical areas for conservation under climate change. – Ecol. Appl. 26: 1223–1237.

Diniz, M. F. et al. 2020. Landscape connectivity modeling from the perspective of animal dispersal. – Landsc. Ecol. 35: 41–58.

Dixon, J. D. et al. 2006. Effectiveness of a regional corridor in connecting two Florida black bear populations. – Conserv. Biol. 20: 155–162.

Drake, J. et al. 2017a. Graph theory as an invasive species management tool: case study in the Sonoran Desert. – Landsc. Ecol. 32: 1739–1752.

Drake, J. et al. 2017b. Using nested connectivity models to resolve management conflicts of isolated water networks in the Sonoran Desert. – Ecosphere 8: e01652.

Drake, J. et al. 2021. Data from: The value of considering demographic contributions to connectivity: a review. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.6hdr7sr16>.

Driscoll, D. A. and Hardy, C. M. 2005. Dispersal and phylogeography of the agamid lizard *Amphibolurus nobbi* in fragmented and continuous habitat. – Mol. Ecol. 14: 1613–1629.

Driscoll, D. A. et al. 2014. The trajectory of dispersal research in conservation biology. Systematic review. – PLoS One 9: e95053.

Dytham, C. et al. 2014. Changes in species' distributions during and after environmental change: which eco-evolutionary processes matter more? – Ecography 37: 1210–1217.

Edelsparre, A. H. et al. 2018. Habitat connectivity is determined by the scale of habitat loss and dispersal strategy. – Ecol. Evol. 8: 5508–5514.

Elliot, N. B. et al. 2014a. Movements vary according to dispersal stage, group size and rainfall: the case of the African lion. – Ecology 95: 2860–2869.

Elliot, N. B. et al. 2014b. The devil is in the dispersers: predictions of landscape connectivity change with demography. – J. Appl. Ecol. 51: 1169–1178.

Epps, C. W. et al. 2007. Optimizing dispersal and corridor models using landscape genetics. – J. Appl. Ecol. 44: 714–724.

Eriksson, A. et al. 2014. The emergence of the rescue effect from explicit within- and between-patch dynamics in a metapopulation. – Proc. R. Soc. B 281: 1–8.

Fisher, D. O. et al. 2009. Experimental translocation of juvenile water voles in a Scottish lowland metapopulation. – Popul. Ecol. 51: 289–295.

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. 2016. Divergent perspectives on landscape connectivity reveal consistent effects from genes to communities. – Curr. Landsc. Ecol. Rep. 1: 67–79.

Fletcher, R. J. et al. 2019. Towards a unified framework for connectivity that disentangles movement and mortality in space and time. – Ecol. Lett. 22: 1680–1689.

Fobert, E. K. et al. 2019. Dispersal and population connectivity are phenotype dependent in a marine metapopulation. – Proc. R. Soc. B 286: 20191104.

Fronhofer, E. A. and Altermatt, F. 2017. Classical metapopulation dynamics and eco-evolutionary feedbacks in dendritic networks. – Ecography 40: 1455–1466.

Graves, T. et al. 2014. Estimating landscape resistance to dispersal. – Landsc. Ecol. 29: 1201–1211.

Greenwood, P. J. and Harvey, P. 1982. The natal and breeding dispersal of birds. – Annu. Rev. Ecol. Syst. 13: 1–21.

Griffen, B. D. and Drake, J. M. 2008. A review of extinction in experimental populations. – J. Anim. Ecol. 77: 1274–1287.

Guillera-Arroita, G. 2017. Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. – Ecography 40: 281–295.

Guillera-Arroita, G. and Lahoz-Monfort, J. J. 2012. Designing studies to detect differences in species occupancy: power analysis under imperfect detection. – Methods Ecol. Evol. 3: 860–869.

Gupta, A. et al. 2019. Reserve design to optimize functional connectivity and animal density. – Conserv. Biol. 33: 1023–1034.

Haddad, N. M. et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. – Sci. Adv. 1: 1–10.

Haddad, N. M. et al. 2016. Connecting models, data and concepts to understand fragmentation's ecosystem-wide effects. – Ecography 40: 336–342.

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

Hanski, I. 1998. Metapopulation dynamics. – Nature 396: 41–49.

Hanski, I. and Gilpin, M. 1991. Metapopulation dynamics: brief history and conceptual domain. – Biol. J. Linn. Soc. 42: 3–16.

Hanski, I. and Mononen, T. 2011. Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. – Ecol. Lett. 14: 1025–1034.

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

Hanski, I. and Ovaskainen, O. 2003. Metapopulation theory for fragmented landscapes. – Theor. Popul. Biol. 64: 119–127.

Harman, R. R. et al. 2020. Frequency of occurrence and population-dynamic consequences of different forms of density-dependent emigration. – Am. Nat. 195: 851–867.

Hartfelder, J. et al. 2020. The allometry of movement predicts the connectivity of communities. – Proc. Natl Acad. Sci. USA 117: 22274–22280.

Higgins, K. and Lynch, M. 2001. Metapopulation extinction caused by mutation accumulation. – Proc. Natl Acad. Sci. USA 98: 2928–2933.

Hilderbrand, R. H. et al. 2005. The myths of restoration ecology. – Ecol. Soc. 10: 19.

Hilty, J. et al. 2020. Guidelines for conserving connectivity through ecological networks and corridors (C Groves, Ed.). – IUCN, International Union for Conservation of Nature.

Holt, R. D. 1992. A neglected face of island biogeography: the role of internal spatial dynamics in area effects. – Theor. Popul. Biol. 41: 354–371.

Horváth, Z. et al. 2019. Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. – Ecol. Lett. 22: 1019–1027.

Hovel, K. A. and Lipcius, R. N. 2001. Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. – Ecology 82: 1814–1829.

Howell, P. E. et al. 2018. Increasing connectivity between metapopulation ecology and landscape ecology. – Ecology 99: 1119–1128.

Howell, P. E. et al. 2020a. Informing amphibian conservation efforts with abundance-based metapopulation models. – Herpetologica 76: 240–250.

Howell, P. E. et al. 2020b. A statistical forecasting approach to metapopulation viability analysis. – Ecol. Appl. 30: 1–10.

Hui, C. et al. 2012. Flexible dispersal strategies in native and non-native ranges: environmental quality and the 'good-stay, bad-disperse' rule. – Ecography 35: 1024–1032.

Jangjoo, M. et al. 2016. Connectivity rescues genetic diversity after a demographic bottleneck in a butterfly population network. – Proc. Natl Acad. Sci. USA 113: 10914–10919.

Janin, A. et al. 2009. Assessing landscape connectivity with calibrated cost-distance modelling: predicting common toad distribution in a context of spreading agriculture. – J. Appl. Ecol. 46: 833–841.

Jones, N. T. et al. 2015. Dispersal mode mediates the effect of patch size and patch connectivity on metacommunity diversity. – J. Ecol. 103: 935–944.

Keeley, A. T. H. et al. 2017. Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. – Landsc. Urban Plan. 161: 90–102.

Kimmig, S. E. et al. 2020. Beyond the landscape: resistance modelling infers physical and behavioural gene flow barriers to a mobile carnivore across a metropolitan area. – Mol. Ecol. 29: 466–484.

Kimura, M. et al. 1963. The mutation load in small populations. – Genetics 48: 1303–1312.

Kindlmann, P. and Burel, F. 2008. Connectivity measures: a review. – Landsc. Ecol. 23: 879–890.

Kinnison, M. T. and Hairston, N. G. 2007. Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. – Funct. Ecol. 21: 444–454.

Koen, E. L. et al. 2012. The effect of cost surface parameterization on landscape resistance estimates. – Mol. Ecol. Resour. 12: 686–96.

Kool, J. T. et al. 2013. Population connectivity: recent advances and new perspectives. – Landsc. Ecol. 28: 165–185.

Laliberté, J. and St-Laurent, M. H. 2020. Validation of functional connectivity modeling: the Achilles' heel of landscape connectivity mapping. – Landsc. Urban Plan. 202: 103878.

Lambin, X. et al. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. – In: Clobert, J. et al. (eds), Dispersal. Oxford Univ. Press, in press.

Lambin, X. et al. 2004. Inferring pattern and process in small mammal metapopulations: insights from ecological and genetic data. – Elsevier Inc.

Landguth, E. L. et al. 2010. Quantifying the lag time to detect barriers in landscape genetics. – Mol. Ecol. 19: 4179–4191.

Larkin, J. L. et al. 2004. Landscape linkages and conservation planning for the black bear in west-central Florida. – Anim. Conserv. 7: 23–34.

Legrand, D. et al. 2017. Eco-evolutionary dynamics in fragmented landscapes. – Ecography 40: 9–25.

Littlefield, C. E. et al. 2017. Connecting today's climates to future climate analogs to facilitate movement of species under climate change. – Conserv. Biol. 31: 1397–1408.

Littlefield, C. E. et al. 2019. Connectivity for species on the move: supporting climate-driven range shifts. – Front. Ecol. Environ. 17: 270–278.

Long, R. A. et al. 2007. Comparing scat detection dogs, cameras and hair snares for surveying carnivores. – J. Wildl. Manage. 71: 2018–2025.

Lookingbill, T. R. et al. 2010. Combining a dispersal model with network theory to assess habitat connectivity. – Ecol. Appl. 20: 427–441.

Lowe, W. H. et al. 2017. Population genetics and demography unite ecology and evolution. – Trends Ecol. Evol. 32: 141–152.

MacKenzie, D. et al. 2018. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. – Academic Press.

Mackenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. – Ecology 83: 2248–2255.

MacKenzie, D. I. et al. 2003. Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. – Ecology 84: 2200–2207.

Maher, S. P. et al. 2017. Erosion of refugia in the Sierra Nevada meadows network with climate change. – Ecosphere 8: e01673.

Margosian, M. L. et al. 2009. Connectivity of the American agricultural landscape: assessing the national risk of crop pest and disease spread. – Bioscience 59: 141–151.

Marrotte, R. R. et al. 2017. Multi-species genetic connectivity in a terrestrial habitat network. – Mov. Ecol. 5: 1–11.

Marshall, D. J. et al. 2010. Phenotype-environment mismatches reduce connectivity in the sea. – Ecol. Lett. 13: 128–140.

Martensen, A. C. et al. 2017. Spatio-temporal connectivity: assessing the amount of reachable habitat in dynamic landscapes. – Methods Ecol. Evol. 8: 1253–1264.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. – Ecography 28: 403–416.

Matthysen, E. 2012. Multicausality of dispersal: a review. – In: Clobert, J. et al. (eds), Dispersal ecology and evolution. Oxford Univ. Press, pp. 3–17.

Matthysen, E. et al. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. – Oikos 72: 375–381.

McCallum, M. 2007. Amphibian decline or extinction? Current declines dwarf background extinction rate. – J. Herpetol. 41: 483–491.

McRae, B. 2006. Isolation by resistance. – Evolution 60: 1551–1561.

McRae, B. et al. 2008. Using circuit theory to model connectivity in ecology, evolution and conservation. – Ecology 89: 2712–2724.

Meyer, N. F. V. et al. 2020. Effectiveness of Panama as an intercontinental land bridge for large mammals. – Conserv. Biol. 34: 207–219.

Miller, D. A. et al. 2011. Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. – Ecology 92: 1422–1428.

Mills, L. S. and Allendorf, F. W. 1996. The one-migrant-per-generation rule in conservation and management. – Conserv. Biol. 10: 1509–1518.

Moilanen, A. 1999. Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. – Ecology 80: 1031–1043.

Moilanen, A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. – Oikos 96: 516–530.

Moilanen, A. and Hanski, I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. – Ecology 79: 2503–2515.

Moilanen, A. and Hanski, I. 2001. On the use of connectivity measures in spatial ecology. – Oikos 95: 147–151.

Moilanen, A. and Nieminen, M. 2002. Simple connectivity measures in spatial ecology. – Ecology 83: 1131–1145.

Morin, D. J. et al. 2017. Model-based estimators of density and connectivity to inform conservation of spatially structured populations. – Ecosphere 8: e01623.

Munoz, J. 2004. Wind as a long-distance dispersal vehicle in the southern hemisphere. – Science 304: 1144–1147.

Nathan, R. et al. 2012. Dispersal kernels: review. – In: Dispersal ecology and evolution, Oxford Univ. Press, pp. 187–210.

O'Hara, R. B. et al. 2002. Bayesian analysis of metapopulation data. – Ecology 83: 2408–2415.

Ofori, B. Y. et al. 2017. Combining dispersal, landscape connectivity and habitat suitability to assess climate-induced changes in the distribution of Cunningham's skink, *Egernia cunninghami*. – PLoS One 12: e0184193.

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

Ovaskainen, O. and Hanski, I. 2004. From individual behavior to metapopulation dynamics: unifying the patchy population and classic metapopulation models. – Am. Nat. 164: 364–377.

Ozgul, A. et al. 2009. Influence of local demography on asymptotic and transient dynamics of a yellow-bellied marmot metapopulation. – Am. Nat. 173: 517–530.

Palstra, F. P. and Ruzzante, D. E. 2008. Genetic estimates of contemporary effective population size: what can they tell us about the importance of genetic stochasticity for wild population persistence? – Mol. Ecol. 17: 3428–3447.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – Annu. Rev. Ecol. Syst. 37: 637–669.

Pellet, J. et al. 2007. An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. – Biol. Conserv. 136: 483–495.

Peterman, W. E. et al. 2019. A comparison of popular approaches to optimize landscape resistance surfaces. – Landsc. Ecol. 34: 2197–2208.

Pinto, S. M. and MacDougall, A. S. 2010. Dispersal limitation and environmental structure interact to restrict the occupation of optimal habitat. – Am. Nat. 175: 675–686.

Poli, C. et al. 2020. Validating network connectivity with observed movement in experimental landscapes undergoing habitat destruction. – J. Appl. Ecol. 57: 1426–1437.

Prugh, L. R. 2009. An evaluation of patch connectivity measures. – Ecol. Appl. 19: 1300–1310.

Prugh, L. R. et al. 2008. Effect of habitat area and isolation on fragmented animal populations. – Proc. Natl Acad. Sci. USA 105: 20770–20775.

Rapacciuolo, G. and Blois, J. L. 2019. Understanding ecological change across large spatial, temporal and taxonomic scales: integrating data and methods in light of theory. – Ecography 42: 1247–1266.

Rayfield, B. et al. 2011. Connectivity for conservation: a framework to classify network measures. – Ecology 92: 847–858.

Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. – Am. Nat. 158: 87–99.

Riotte-Lambert, L. and Laroche, F. 2021. Dispersers' habitat detection and settling abilities modulate the effect of habitat amount on metapopulation resilience. – Landsc. Ecol. 36: 675–684.

Risk, B. B. et al. 2011. A robust-design formulation of the incidence function model of metapopulation dynamics applied to two species of rails. – Ecology 92: 462–474.

Robertson, E. P. et al. 2018. Isolating the roles of movement and reproduction on effective connectivity alters conservation priorities for an endangered bird. – Proc. Natl Acad. Sci. USA 115: 8591–8596.

Robertson, E. P. et al. 2019. The number of breeders explains genetic connectivity in an endangered bird. – Mol. Ecol. 28: 2746–2756.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. – Annu. Rev. Ecol. Evol. Syst. 38: 231–253.

Royle, J. A. and Kery, M. 2007. A Bayesian state-space formulation of dynamic occupancy models. – Ecology 88: 1813–1823.

Royle, J. and Dorazio, R. 2009. Hierarchical modeling and inference in ecology. Elsevier

Ruffell, J. et al. 2017. The matrix matters, but how should we manage it? Estimating the amount of high-quality matrix required to maintain biodiversity in fragmented landscapes. – Ecography 40: 171–178.

Ruiz, L. et al. 2014. Dynamic connectivity of temporary wetlands in the southern Great Plains. – Landsc. Ecol. 29: 507–516.

Sales, N. G. et al. 2020. Fishing for mammals: landscape-level monitoring of terrestrial and semi-aquatic communities using eDNA from riverine systems. – J. Appl. Ecol. 57: 707–716.

Sánchez-Bayo, F. and Wyckhuys, K. A. G. 2019. Worldwide decline of the entomofauna: a review of its drivers. – Biol. Conserv. 232: 8–27.

Saura, S. and 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. et al. 2014. Editor's choice: Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. – J. Appl. Ecol. 51: 171–182.

Senner, N. R. et al. 2018. Spatial and temporal heterogeneity in climate change limits species' dispersal capabilities and adaptive potential. – Ecography 41: 1428–1440.

Shakespeare, W. 1623. Mr William Shakespeare's comedies, histories and tragedies. – Isaac Iaggard and Ed. Blount, First Folio, London.

Shima, J. S. and Swearer, S. E. 2009. Larval quality is shaped by matrix effects: implications for connectivity in a marine metapopulation. – Ecology 90: 1255–1267.

Shine, R. et al. 2011. An evolutionary process that assembles phenotypes through space rather than through time. – Proc. Natl Acad. Sci. USA 108: 5708–5711.

Sibly, R. M. et al. 1997. Mortality rates of mammals. – J. Zool. 243: 1–12.

Soulé, M. E. 1987. Viable populations for conservation. – Cambridge Univ. Press.

Spanowicz, A. G. and Jaeger, J. A. G. 2019. Measuring landscape connectivity: on the importance of within-patch connectivity. – Landsc. Ecol. 34: 2261–2278.

Stoddart, D. M. 1970. Individual range, dispersion and dispersal in a population of water voles. – J. Anim. Ecol. 39: 403–425.

Strimas-Mackey, M. and Brodie, J. F. 2018. Reserve design to optimize the long-term persistence of multiple species. – Ecol. Appl. 28: 1354–1361.

Sutherland, C. et al. 2012. Multi-scale processes in metapopulations: contributions of stage structure, rescue effect and correlated extinctions. – Ecology 93: 2465–2473.

Sutherland, C. et al. 2013. Accounting for false positive detection error induced by transient individuals. – Wildl. Res. 40: 490–498.

Sutherland, C. et al. 2014. A demographic, spatially explicit patch occupancy model of metapopulation dynamics and persistence. – Ecology 95: 3149–3160.

Sutherland, C. et al. 2015. Modelling non-Euclidean movement and landscape connectivity in highly structured ecological networks. – Methods Ecol. Evol. 6: 169–177.

Taylor, P. D. et al. 2006. Landscape connectivity: a return to the basics. – In: Crooks and Sanjayan (eds), Connectivity Conservation. Cambridge University Press, pp. 29–43.

Taylor, P. P. D. et al. 1993. Connectivity is a vital element of landscape structure. – Oikos 68: 571–573.

Telfer, S. et al. 2001. Metapopulation processes and persistence in remnant water vole populations. – Oikos 95: 31–42.

Telfer, S. et al. 2003. Parentage assignment detects frequent and large-scale dispersal in water voles. – Mol. Ecol. 12: 1939–1949.

Thomas, C. D. 2000. Dispersal and extinction in fragmented landscapes. – Proc. R. Soc. B 267: 139–145.

Thomas, C. D. and Kunin, W. E. 1999. The spatial structure of populations. – J. Anim. Ecol. 68: 647–657.

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

Tischendorf, L. and Fahrig, L. 2001. On the use of connectivity measures in spatial ecology: a reply. – Oikos 95: 152–155.

Trochet, A. et al. 2016. Evolution of sex-biased dispersal. – Q. Rev. Biol. 91: 297–320.

Tucker, J. M. et al. 2017. Sex-biased dispersal and spatial heterogeneity affect landscape resistance to gene flow in fisher. – Ecosphere 8: e01839.

Turner, M. G. 2005. Landscape ecology: what is the state of the science? – Annu. Rev. Ecol. Evol. Syst. 36: 319–344.

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

Vasudev, D. and Fletcher, R. J. 2016. Mate choice interacts with movement limitations to influence effective dispersal. – Ecol. Model. 327: 65–73.

Vasudev, D. et al. 2015. From dispersal constraints to landscape connectivity: lessons from species distribution modeling. – Ecography 38: 967–978.

Visconti, P. and Elkin, C. 2009. Using connectivity metrics in conservation planning – when does habitat quality. – Divers. Distrib. 15: 602–612.

Wan, H. et al. 2018. Habitat fragmentation reduces genetic diversity and connectivity of the mexican spotted owl: a simulation study using empirical resistance models. – Genes 9: 403.

Wang, J. and Whitlock, M. C. 2003. Estimating effective population size and migration rates from genetic samples over space and time. – Genetics 163: 429–446.

Wang, S. and Altermatt, F. 2019. Metapopulations revisited: the area-dependence of dispersal matters. – Ecology 100: 1–11.

Ward, M. et al. 2020. Just ten percent of the global terrestrial protected area network is structurally connected via intact land. – Nat. Commun. 11: 1–10.

Wasserman, T. N. et al. 2012. Simulating the effects of climate change on population connectivity of American marten (*Martes americana*) in the northern Rocky Mountains, USA. – Landsc. Ecol. 27: 211–225.

Wiens, J. J. 2001. The landscape context of dispersal. – In: Clobert, J. et al. (eds), Dispersal. Oxford Univ. Press, pp. 96–109.

With, K. A. 2004. Metapopulation dynamics. Perspectives from landscape ecology. – In: Hanski, I. and Gaggiotti, O. E. (eds), Ecology, genetics and evolution of metapopulations, pp. 23–44.

Zeigler, S. L. and Fagan, W. F. 2014. Transient windows for connectivity in a changing world. – Mov. Ecol. 2: 1.

Zeller, K. A. et al. 2012. Estimating landscape resistance to movement: a review. – Landsc. Ecol. 27: 777–797.

Zeller, K. A. et al. 2018. Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. – Divers. Distrib. 24: 868–879.

Zeller, K. A. et al. 2020. Understanding the importance of dynamic landscape connectivity. – Land 9: 303.

Ziółkowska, E. et al. 2012. Potential habitat connectivity of European bison (*Bison bonasus*) in the Carpathians. – Biol. Conserv. 146: 188–196.