Divergent Perspectives on Landscape Connectivity Reveal Consistent Effects from Genes to Communities

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Abstract Landscape connectivity is increasingly emphasized due to its relevance for interpreting effects of environmental change. Yet substantial uncertainty remains regarding the quantification of connectivity and the extent to which connectivity influences biodiversity. We review and synthesize 370 articles published since 2005 on the quantification and effects of landscape connectivity on biodiversity. We find a notable change in the quantification of connectivity from structural to functional approaches, a rise in network approaches, and a decline in approaches based on metapopulation theory. Most studies (54 %) did not test for the effects of connectivity, but of those that did, 91 % found effects on biodiversity, with over five times as many positive as negative effects reported. These effects were largely consistent across levels of biological organization, despite diverse perspectives on movement and connectivity across these domains. Nevertheless, we argue that several outstanding issues need to be addressed to advance our understanding of the effects of connectivity and its importance for conservation. These issues include the need for greater emphasis on estimating connectivity effects, explicitly incorporating the problem of scale, capturing impacts of movement processes relevant to different levels of organization, proper accounting

of uncertainty, and isolating connectivity effects relative to other issues influencing biodiversity.

Keywords Conservation planning · Dispersal · Habitat fragmentation · Habitat loss · Graph theory · Network

Introduction

Landscape connectivity, or the degree to which the landscape impedes or facilitates movement of organisms [1], is a fundamental concept of landscape ecology, movement biology, and conservation [2, 3]. Landscape connectivity can influence individuals, populations and communities through a variety of mechanisms, including demographic rescue, inbreeding avoidance, colonization of unoccupied habitat, altered species interactions, and spread of disease [4, 5]. Connectivity is also highly relevant for conservation aimed at ameliorating negative impacts of human-induced environmental change on biodiversity [2, 6, 7].

While connectivity is increasingly embraced and emphasized in ecology, evolution, and conservation, there is considerable uncertainty regarding the accuracy of connectivity mapping and the extent to which connectivity influences populations and communities [8–11]. For example, independent field validations of predicted connectivity models often highlight that such models perform poorly [9, 12]. Several theoretical models and empirical results also suggest that the effects of connectivity may be less important than other aspects of landscape structure, such as habitat amount [13], habitat quality [14], or temporal changes in habitat [15]. For instance, Lindell and Maurer [16] showed that immigration rates driven by variation in connectivity play a much smaller role than local patch quality in determining population size. While major strides have been made regarding the effects of corridors and stepping

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stones in experimental systems [17–19], it remains unclear how such effects translate to broader spatial scales. These issues have led to suggestions that the degree of uncertainty around the importance of connectivity is large relative to other factors, such that connectivity should be a lower priority for large-scale conservation relative to other known threats, such as declining habitat area or illegal poaching [20–22].

Here we review and synthesize evidence for the effects of landscape connectivity. To do so, we first formally describe the diverse perspectives on the quantification of connectivity and its effects. Second, we briefly review concepts and theory relevant to understanding the effects of connectivity for different levels of organization (i.e., individuals, populations, and communities). Third, we assess trends in the quantification of connectivity and evidence for its effects by systematically reviewing the landscape connectivity literature over the past 10 years (2005–2015). We conclude by discussing challenges and opportunities for furthering our understanding of the effects of connectivity on biodiversity and make recommendations for fostering more rapid progress in our understanding of the role of connectivity in landscapes.

Understanding the Effects of Connectivity

Terms and Definitions for Connectivity and its Effects

The term ‘landscape connectivity’ has been used loosely in ecology, evolution, and conservation. While definitions of landscape connectivity vary [23, 24], all emphasize movement and/or flow across landscapes [25, 26]. Kool et al. [25] highlighted that all approaches to population connectivity emphasize inter-population relationships. More broadly, we argue that all notions of connectivity are built upon relational data, or information that describes linkages or flow between two or more locations.

In recent years, there has been an explosion of approaches and metrics for quantifying, describing, and mapping landscape connectivity [27–32]. Calabrese and Fagan [23] classified connectivity metrics into three general categories: structural, potential, and actual connectivity (Table 1). Structural connectivity describes aspects of landscape configuration assumed to be relevant for flow and movement, without attempting to capture species- or process-specific variability. Potential and actual connectivity attempt to capture functional aspects of connectivity, or functional connectivity, where movement or flow is explicitly integrated into the interpretation of connectivity. Potential connectivity uses secondary (indirect) information regarding species- or process-specific movements and flow. Actual (or realized) connectivity measures movement and flow directly in order to quantify landscape connectivity. We prefer to use the term ‘realized’ connectivity in these situations, to

reflect that this interpretation captures the realization of connectivity on the landscape, analogous to the realized niche [33].

Here, we consider the ‘effects of landscape connectivity’ to describe situations where connectivity measures (structural, potential, or realized) explain variation in biological patterns and processes. Thus, we view landscape connectivity and its effects as a set of hierarchical relationships, where structural connectivity influences movement, which in turn influences other biological processes that alter species distributions, diversity, genetic variation, ecosystem processes (e.g., pollination), or species interactions (Fig. 1). While each of these responses can be impacted by factors other than connectivity (see below), theory and concepts suggest that connectivity could have a substantial effect on these parameters. Consequently, the key to understanding the effects of landscape connectivity is to isolate how the effect of landscape on movement influences biological patterns and processes (in contrast to effects of movement variation not related to the landscape [34]).

Concepts and Theory for the Effects of Landscape Connectivity

Over the past several decades, there has been considerable theoretical development to predict and understand the effects of connectivity. Here we briefly summarize these theoretical developments across different levels of organization (individuals, populations, communities), focusing on three issues. First, how is the landscape considered? Second, what is the role of movement and how is movement predicted to influence biological patterns and processes across landscapes? Third, are there other key processes predicted to mediate the effects of movement across landscapes, and ultimately, the effects of landscape connectivity (Table 2)?

At the individual level, theoretical developments have primarily occurred in the context of applying foraging theory and related behavioral ecology theory (e.g., information theory) to landscapes [3, 35, 36]. This theory often focuses on proximate, short-term movement responses of individuals to landscape structure, such as the scale at which individuals perceive habitat and the role of different types of decision-making on dispersal and/or searching behavior through landscapes, with an emphasis on the subsequent effects of these decisions on individual fitness [37–39]. Early aspects of foraging theory were concerned with travel time between patches to explain expected residency time, which translated to an emphasis simply on distances between resource patches. More recent theoretical development has used spatially explicit simulations to capture aggregation of habitat and other structural issues of connectivity [e.g., 38]. This theoretical development has suggested that several factors may alter realized connectivity and its effects, such as high patch quality leading to little movement in landscapes of high structural connectivity [3].

Table 1 The multifarious ways in which connectivity is quantified

Concept	Metric classification	Description	How is the landscape considered?	How is movement considered?	Example of common metrics
Structural	Structural connectivity	Elements of landscape configuration assumed to be relevant for flow and movement, without attempting to capture species- or process-specific variability	Land-cover connectivity measured at the cell, patch, or landscape scale	None	Nearest neighbor, proximity index
Functional	Potential connectivity (patch-focused)	Combined attributes of landscape configuration with information on the assumed dispersal or movement distances to predict linkages	Patch-focused, but can be summarized for landscape	(Effective) dispersal distance	Metapopulation metrics, graph theory metrics
Functional	Potential connectivity (matrix-focused)	Combined attributes of landscape configuration with information on habitat use or movement to parameterize resistance surfaces for predicting linkages	Landscape mapping with grain of map as sample unit	Expert opinion, habitat use data, movement trajectories, mark-recapture	Least-cost paths or distances parameterized via resource-selection functions
Functional	Realized connectivity	Directly measuring the realized flow and/or movement of organisms to estimate the linkages between patch or landscape elements	Patch-focused or landscape mapping focused	Movement trajectories (e.g., telemetry), mark-recapture	Immigration rates, dispersal rates

Fig. 1 Hierarchical relationships regarding landscape connectivity and its effects. Landscape structure (e.g., contiguity) can describe structural connectivity, while potential connectivity occurs when landscape structure is linked to movement capacity (e.g., motion capacity, navigation capacity) of species or related processes (shown is a least-cost path). Realized (or actual) connectivity describes observed movements across landscapes, which may not reflect potential connectivity (as shown here) because of inadequate understanding of movement when interpreting potential connectivity, the impact of non-landscape processes on movement paths across landscapes, or stochastic forces. Realized connectivity can then impact a variety of biological patterns and processes

At the population level, many theoretical developments have occurred in both metapopulation ecology and population genetics. Early metapopulation theory predicted that distance among patches influenced colonization rates of unoccupied habitats and could also influence rescue effects [5]. The cumulative influence of these changes could impact the proportion of occupied habitats, depending on the ratio of local colonization and extinction rates. More recent metapopulation theory has incorporated other aspects of landscape structure, such as patch aggregation [40], matrix effects [41], and succession [42]. Related source–sink theory incorporates the effects of connectivity through variation in immigration and emigration rates, with the cumulative impacts dictated by the relative influence of immigration and emigration processes compared to local birth and death processes [43]. In this theory, landscape structure is frequently emphasized simply as the proportion of source and sink habitats on the landscape [44]. In both of these theoretical developments, propagule

Table 2 Hypothesized effects of landscape connectivity on organisms

Level of organization	Effects	How is the landscape considered?	How is the movement process considered?	Other key processes predicted to alter outcomes	Scale		Primary theory*
					Temporal	Spatial	
Individual	Fitness, physiology, behavior	Effective distance	Movement trajectories, dispersal	Resource quality, perception, individual variation	Short	Small	Foraging theory, information theory
Population	Distribution, demography	Effective distance, patch area	Colonization, immigration	Propagule pressure, habitat quality, extinction rate	Short	Moderate	Metapopulation, source-sink
	Gene flow	Effective distance, barriers	Effective dispersal	Migration-selection balance, post-dispersal reproduction, genetic drift	Long	Large	Neutral theory
Community	Species interactions	Effective distance between patches and species	Interspecific variation in dispersal	Proximity and movement of recipient species	Short	Moderate	Metacommunity
	Diversity and richness of species	Effective distance, patch area	Interspecific variation in immigration rates	Extinction rate, species sorting	Moderate	Large	Island biogeography, metacommunity

* Landscape ecologists have extended each of these theoretical developments in recent years

pressure is emphasized, either indirectly via variation in patch size, or directly through estimates of population abundance. Landscape ecology theory focusing on populations has also highlighted the role of the matrix in terms of disperser mortality and movements near patch boundaries [13, 45].

For population genetics, early theory incorporated migration, or the extent to which a local population's alleles are replaced by immigrant alleles, as a probabilistic process between subpopulations. Propagule movement is a critical component of migration, with effective dispersal required for successful post-dispersal reproduction [46]. Migration was integral to early theory as a contrast to local selection [47], thereby emphasizing the balancing role of movement and local processes on genetic outcomes. Geographic distance and some aspects of habitat configuration (e.g., stepping stones) were soon incorporated, which predicted increased genetic homogenization at shorter distances and more connected subpopulations [48, 49]. Yet barriers to dispersal were generally considered in the context of species boundaries rather than affecting connectivity within species [50]. With the establishment of neutral theory of population genetics [51], the role of migration has been shown to have a direct effect on pairwise genetic distance, where the genetic distance between populations cannot be large unless the migration rate is very low [52], emphasizing that only infrequent effective dispersal events are required for small genetic distances [26]. More recently, landscape genetics theory has emphasized the role of the landscape matrix, such as isolation-by-resistance relationships [53]. There is also increasing emphasis on integrating both population-level and individual-level genetic variation with spatial statistics to better capture complex landscape structure and isolate the roles of movement on genetic structure, despite a general lack of theoretical development [54].

At the community level, much of the theoretical underpinnings on effects of connectivity stems from island biogeography and metacommunity ecology. In island biogeography, MacArthur and Wilson [55] identify several aspects of the landscape (island configuration) that can influence immigration rates of species. These include distance to mainland, aggregation of islands, and the presence of corridors and stepping stones, each of which is highly relevant when interpreting landscape connectivity [56, 57]. Variation in immigration rates can then influence overall species diversity, but this effect is contingent on the ratio of immigration to local extinction rates. Classic island biogeography theory neglected aspects of the landscape matrix on predictions of connectivity, although recent theory has attempted to capture such issues [58]. Metacommunity theory also provides several paradigms for understanding spatial variation in communities, with each paradigm providing a different emphasis on the role of dispersal and immigration relative to local niche and stochastic processes [59]. For some paradigms, such as species sorting, dispersal (and as an extension, landscape connectivity) is

thought to play a minor role in structuring communities, whereas in others, such as the patch-dynamics paradigm, it is thought to be crucial [59]. Less theory has focused on the effects of connectivity for species interactions, although there is some notable development regarding the effects of connectivity on competition and predation [e.g., 60]. For instance, predator–prey theory frequently invokes the idea of spatial refugia for prey as a key element in the outcome of predator–prey interactions [61].

This diverse theory focusing on different levels of organization shares common themes, yet connectivity is often interpreted differently in terms of the role of movement and the way the landscape is considered. Movement has been invoked differently in these theoretical developments, with some requiring that movements result in individuals recruiting into a new breeding population (e.g., population genetics theory) and others simply requiring that individuals move through a location of habitat (e.g., behavioral ecology theory). Furthermore, movement is frequently interpreted at different temporal and spatial scales [26] (Table 2). The incorporation of landscape structure on this diverse theoretical development has also varied in terms of the complexity of landscape structure being considered and the scales at which connectivity is interpreted [24, 62] (Table 2). While recent theory tends to consistently emphasize the role of the matrix, other issues such as landscape barriers have not been consistently treated among theoretical developments. For instance, connectivity barriers that generate population structure are often emphasized in genetics, yet in population ecology such structure is less frequently emphasized in our understanding of connectivity [but see 57, 63]. Importantly, each line of theoretical development outlines key non-connectivity issues that can alter the effects of connectivity, particularly the role of local processes and conditions (e.g., species sorting, selection).

Given that variation in the interpretation of connectivity and non-connectivity-related issues might play variable roles across these levels of organization, we might expect the effects of connectivity to differ depending on the level of organization considered. While several notable examples of the effects of connectivity exist [e.g., 19, 64], it remains unclear to what extent landscape connectivity effects across levels of organization are being determined in nature, as well as whether such effects are consistent across these domains.

Literature Review of the Evidence of Connectivity Effects

Methods

We systematically reviewed articles to evaluate recent evidence for the effects of landscape connectivity. Using the ISI Web of Science, we compiled articles using the search phrase

“‘landscape connectivity’ AND ecology” from 2005 to the present (search date, July 26, 2015), which resulted in 624 articles. We assumed that this search would yield few false-positive errors, but errors of omission would likely be higher. As such, we consider these articles to be a representative sample of research focusing on landscape connectivity over the past decade, but emphasize that this search did not capture all articles on connectivity. For example, we likely omitted studies important for understanding movement processes (e.g., seed dispersal) that did not make explicit reference to landscape connectivity. We included only empirical articles in our review (i.e., those that included at least some portion of empirical data) and removed review or theoretical articles from our analyses.

From these empirical articles, we determined how connectivity was quantified, and whether and how effects of connectivity were measured. We classified descriptions of landscape connectivity for each article into one of three categories: 1) structural connectivity, 2) potential connectivity, and 3) realized connectivity [23]. Structural connectivity included investigations that considered land-use or land cover connectedness without considering the movement process. Potential connectivity included investigations that parameterized metrics of connectivity based on information about movement or flow. This included species-specific or non-species-specific information such as average dispersal distances in metapopulation measures, assuming that some land cover types are generally impermeable to many species (e.g., urban areas), or parameterizing resistance surfaces based on expert opinion, habitat use, or radio telemetry. Consequently, investigations that used movement data (e.g., telemetry) to parameterize resistance surfaces, but then subsequently used such surfaces to quantify linkages among locations, were labeled as potential connectivity because the connectivity measurements were not based on observed movements between locations of interest. Realized connectivity included investigations where observed movement was used to describe linkages and quantify landscape connectivity directly, such as the use of mark–recapture or radiotelemetry data [9, 65].

We also further classified the quantification of connectivity based on different types of common metrics including the use of FRAGSTATS and related programs (e.g., ‘proximity’ index [66]), metapopulation theory [67], individual-based models [68], graph theory [69], least-cost measures [70], and circuit theory [28]. Note that the last two approaches are also based on graph theory and related network concepts, but emphasize the use of resistance maps [71]. For our analysis, we reserved the use of the term ‘graph theory’ for its applications to patch/population networks [9, 30, 69, 72]. Finally, for investigations that measured movement, we classified movement into three types that were used repeatedly in the literature: 1) colonization, immigration, and emigration rates; 2) dispersal (movement from natal to breeding locations or movements between

breeding locations); and 3) gap-crossing, which could include crossing forest gaps or roads, or movement through underpasses. We also classified movement based on the primary types of data used: either colonization (changes in species occurrence), mark–recapture, or individual trajectories. Each of these approaches provides different information regarding movement and landscape structure and its relationship to potential effects (Tables 1, 2).

Given quantification of landscape connectivity, we then determined whether articles addressed potential effects of connectivity by relating landscape connectivity measures to biological patterns and processes. Patterns and processes we considered include species distribution (occurrence, abundance, density), population demography (survival, reproduction, population viability), species interactions (e.g., predation), community structure (diversity, turnover), genetics (e.g., genetic differentiation, genetic distance measures), and individual-level processes (e.g., physiology, behavior). We considered genetics measures, such as genetic divergence, as potential effects of landscape connectivity because such measures are impacted by both movement- and non-movement-related processes [26]. We note that these summaries regarding observed effects may include some bias, as we were more likely to identify articles finding effects of connectivity given the search terms we used.

Results

From our systematic sample of the literature over the past 10 years, 370 of the 624 articles reviewed were empirical investigations on connectivity. Based on our search terms, the number of empirical investigations has risen consistently over time, from 8 articles in 2005 to over 60 articles per year in 2013–2014. The topics covered in these articles were diverse, including habitat fragmentation [73], land planning [74], urbanization [75], climate change [76], impacts of roads [77], habitat restoration [63], imperiled species management [78], and spread of invasives [79].

Quantifying Connectivity Of the 370 empirical articles, 122 (33 %) quantified structural connectivity, with the remainder quantifying aspects of functional connectivity. Of those quantifying functional connectivity, 228 quantified potential connectivity (55 used a ‘generic species’ approach rather than species-specific information on movement), whereas only 20 quantified realized connectivity across landscapes. We note that 71 articles (19 %) incorporated some aspect of movement, yet 51 of these used movement data to parameterize potential connectivity models (e.g., local steps between successive locations to parameterize least-cost path models) rather than using movement to infer realized connectivity among locations (e.g., dispersal rates, movements among protected areas). Over this time period, there was an increase in the

number of investigations quantifying potential connectivity and a decrease in the use of structural connectivity measures (Fig. 2a). We found a general decline in the use of FRAGSTATS [66] and metapopulation approaches for quantifying connectivity, and a concomitant rise in the use of network approaches (graph theory, least-cost approaches, and circuit theory), with over 70 % of investigations in the last 2 years of our review using network approaches (Fig 2b). Note that some graph-based measures are directly derived from metapopulation concepts (and are small extensions of metapopulation measures [69]), yet articles rarely invoked metapopulation concepts in their use of these measures. Individual-based models were rarely used for quantifying connectivity (2 % of empirical studies; Fig. 2b).

Measuring and Understanding Effects One hundred and seventy one of the 370 articles, or approximately 46 % of empirical articles, tested for effects of connectivity. Among these articles, connectivity was most frequently used to explain variation in species distribution (abundance, occurrence, density), genetic measures (e.g., heterozygosity), or community diversity measures (e.g., species richness; Fig. 3a). Even though the number of studies assessing effects increased over time, we found no substantial trends regarding the proportion of studies testing for effects, the evidence for effects (positive or negative), or the level of organization being considered (*unpublished results*).

Of those studies that measured effects, there was evidence for the general expectations from theory (Table 2), with examples of connectivity leading to increased likelihood of occurrence [80], less genetic differentiation [81], and greater species richness [82]. Overall, 154 (91 % of the investigations testing for effects) found at least some evidence for effects of connectivity. Effects were similarly observed with distribution (90 %; 69 of 77 articles), genetics (89 %; 42 of 47 articles), and diversity (92 %; 33 of 36 articles) response variables. Some of these investigations reported tests for several response variables, with inconsistent effects [e.g., 83]. Effects reported were generally positive (e.g., increasing connectivity leading to increases in occurrence or abundance, gene flow, or diversity), with over five times as many investigations reporting positive effects as negative effects (141 positive; 25 negative; 67 no effects). Nearly all articles testing for effects with genetics reported positive effects of connectivity, while others were slightly more variable, with articles focused on species interactions showing the greatest proportion of negative effects (Fig. 3). Of these articles testing effects, most used potential connectivity measures, but this varied by level of organization (Fig. 3).

For investigations testing effects, we found great variation in the number of investigations that incorporated movement data and in the type of movement data considered for different levels of organization, which were not always consistent with

Fig. 2 Trends in the quantification of landscape connectivity, January 2005–July 2015. **a** Structural connectivity measures have tended to decline in recent years, while potential connectivity measures tended to increase. **b** Different types of approaches have also changed over time, with an increase in network approaches (graph theory, least-cost, circuit theory)

theoretical developments (Table 2). In general, investigations on individual behavior, species interactions, and diversity rarely used movement data (Fig. 4). Investigations on effects on genetics tended to more frequently use information on individual movement trajectories (e.g., from GPS telemetry), but the relationship of those types of data to effective dispersal, which is the crucial process for genetics, is unclear (Table 2). Investigations on population distribution and demography were more varied in their use of movement data, which ranged from data on gap-crossing movements and dispersal (taken from mark–recapture studies), to directly measuring colonization or immigration rates (Fig. 4).

Discussion

We found that the literature reported generally consistent effects of connectivity across levels of organization, despite the fact that each of these domains tends to treat the problem of connectivity differently (Table 2). Yet we argue that there are still many outstanding challenges for understanding and predicting the effects of connectivity. These challenges reflect the need to appropriately quantify connectivity in ways that capture underlying processes of relevance to different levels of organization, and to appropriately quantify (and isolate) the effects of landscape connectivity relative to other issues that can drive variation in biological patterns and processes across landscapes.

How Should Connectivity be Quantified?

A critical step toward understanding the effects of landscape connectivity is the reliable quantification of connectivity. While several reviews have contrasted metrics used to

Fig. 3 **a** The frequency of effects considered in empirical investigations of landscape connectivity, January 2005–July 2015. **b** The proportion of articles that found evidence for positive and negative effects. **c** The number of positive and negative effects as a function of the way in which connectivity was quantified. Individual refers to investigations that tested for effects on individual behavior and physiology. Distribution includes investigations on occurrence or abundance of

species. Demography includes investigations on demographic parameters and (meta)population viability. Genetics includes investigations on heterozygosity, allelic richness, differentiation, etc. Species interactions include investigations where the focus was on pairwise interaction between species (e.g., pollination, seed dispersal). Diversity includes investigations on species richness and composition, as well as common diversity metrics (e.g., Shannon's index)

Fig. 4 How movements were considered in investigations on the effects of landscape connectivity, January 2005–July 2015. Shown is the frequency of studies that tested for effects on individuals, populations, and communities as a function of movement data considered ($N=29$ studies measuring movement), where the first three types of movement data focus on the movement process, while the last two emphasize the movement technique used. Colonization refers to studies that directly measured colonization, immigration, or emigration rates. Dispersal refers to investigations that explicitly measured dispersal events, typically through the use of mark–recapture techniques. Gap-crossing includes investigations measuring crossing events such as gaps in forests or underpass crossings. Mark–recapture refers to investigations that used mark–recapture techniques to estimate movement (some of which were dispersal events, while others were shorter-term movements not associated with breeding). Trajectory refers to the use of either telemetry data or direct observations of movement trajectories

quantify connectivity [23, 30, 32, 72], our review shows the extent to which different types of measures have been used to assess the effects of connectivity in recent years.

The recent increase in the use of functional connectivity measures is undoubtedly a positive step forward, because all major conceptual and theoretical developments of connectivity emphasize movement or flow [1, 84]. This was mirrored by a decrease in FRAGSTATS-type metrics that largely quantify structural connectivity. Within measures capturing functional connectivity, we found a notable decline in the use of metapopulation measures in favor of network approaches. Graph-based measures of potential connectivity are currently the most common approaches for quantifying connectivity, but these approaches are not without criticism [8, 85]. Some of these measures have little biological underpinning [85], whereas others are often parameterized based on unrealistic assumptions about movement [9]. We also emphasize that graph-based measures that have proven more useful (e.g., ‘flux’, ‘probability of connectivity’ [69, 74]) rely heavily on metapopulation concepts, with the primary differences being in new ways to capture indirect flow on networks [74] and the potential decomposition of different components of functional connectivity [27]. Graph-theoretic measures that focus on ‘habitat reachability’ have shown much promise, in part because they incorporate issues of habitat area that theory suggests is relevant for population connectivity [5]. Yet for

interpreting effects of landscape connectivity relative to other landscape factors, such measures may implicitly confound area effects not related to connectivity with reachability [27]. Other network approaches, such as least-cost paths, make strong assumptions about organism movement [86]. These approaches appear to emerge more from advancements in Geographic Information Systems (GIS) and computing power than advancements in our understanding of movement ecology [86]. Circuit theory approaches provide a balanced compromise, based on the similarity of flow of electricity through circuits with random walks [28], yet better integration of more general random walk theory and movement ecology into our quantification of landscape connectivity is still needed.

For approaches that rely on resistance or friction maps, there is an increasing awareness of the need to use movement data for interpreting resistance rather than relying on expert opinion or habitat use information [71], which may not be consistent with the relationship of the niche concept to landscape connectivity [87]. In this way, Harju et al. [80] provided a novel example, where they used hidden Markov models to objectively identify dispersal phases in movement trajectories by sage grouse (*Centrocercus urophasianus*), and subsequently determined how landscape variables explained movement during the dispersal phase to parameterize resistance surfaces. Furthermore, the assumption that movement rates through the matrix is simply an issue of ease of movement may not always be tenable [3, 71, 87]. The matrix can have complex effects on both movement and mortality [13, 18], which are seldom considered in the quantification of connectivity.

Realized connectivity is rarely quantified, which is not surprising given the challenges in such quantification. Nonetheless, there are new opportunities for quantifying realized connectivity through the use of GPS telemetry [65], new mark–recapture methods [31, 88], and new non-equilibrium genetic methods [89]. Despite an increasing integration of elements of movement into our quantification of connectivity, most approaches use this information to parameterize resistance maps that are then used to predict potential connectivity, rather than to quantify or estimate linkages across landscapes directly. While quantification of realized connectivity is challenging, without such quantification it will be difficult to validate predictions of connectivity, which is necessary for interpreting uncertainty in connectivity conservation. Furthermore, our understanding and prediction of the effects of connectivity may be limited, because effects arise from realized connectivity (and changes therein), not potential connectivity [21, 90]. LaPoint et al. [12] provided a useful alternative for validating predicted connectivity of fishers (*Martes pennanti*), where the authors evaluated predictions from least-cost and circuit theory maps with camera-trapping data in areas of high predicted connectivity (see also [81]).

Ultimately, both landscape and movement processes relevant to connectivity should be quantified in relation to the

underlying processes relevant at different levels of organization (Table 2). We found that investigations on the effects of genetic connectivity consistently considered population structuring across landscapes in addition to the roles of effective distance, while articles on other levels of investigation rarely did. Such structuring may be more critical for interpreting genetic connectivity, or conversely, this pattern could simply reflect different foci of these sub-disciplines. Because movement has variable effects depending on the spatial and temporal scales of quantification [57], the moments in the dispersal probability density function of relevance [3], and the role of post-dispersal reproduction [26], we argue that more careful scrutiny of the incorporation of movement is needed.

How Should Effects be Measured? And what Effects Should be Measured?

To understand the effects of connectivity, we emphasize that investigations should focus on measures directly related to processes predicted to be impacted by connectivity, and that connectivity effects need to be isolated and contrasted relative to other known effects for patterns and processes (e.g., habitat quality). Such measures likely vary depending on the level of organization considered when understanding connectivity (Table 2).

We found that most research aimed at understanding the effects of connectivity used measures describing species distribution or composite information on community structure (Fig. 3). These assessments were typically based on correlating metrics of connectivity to variation in species occurrence, abundance, or richness. While such investigations are useful, a large body of theory, such as niche theory [33], metacommunity theory [59], and habitat selection theory [91], emphasizes the role of non-movement related factors in driving species distributions and community structure. For example, recent niche theory for distribution modeling emphasizes movement as one of several processes influencing distributions, based solely on its constraints in terms of accessibility of areas within the niche of a species [92]. To interpret effects of connectivity using distribution data, scientists need to better isolate correlates with connectivity from other key factors known to be important for species distributions [see, e.g., 73, 75, 83].

Information on genetic differentiation is also commonly used to interpret the effects of landscape connectivity. Such information is valuable [93], and collecting such data is feasible in many systems [e.g., 81, 94]. Yet there are some challenges in using genetics for interpreting connectivity and its effects [26, 95], such as issues of temporal and spatial scale, determining the appropriate genetic response variable of interest (e.g., genetic distance versus allele sharing), and isolation of local versus landscape processes. While gene flow can be influenced not only by movement but also by post-dispersal reproduction, and may therefore fail to isolate the effect of the

landscape on movement, recent work suggests that individual movement can predict gene flow in some cases [81]. Nonetheless, recent modeling also suggests that post-dispersal mate choice and success can generate similar patterns of realized connectivity independent of movement effects [96], highlighting the need to better isolate the movement process.

Some measures that are predicted to be directly impacted by connectivity, such as colonization–extinction dynamics and range expansion rates, have been less frequently considered. Yet these measures naturally emerge from data on temporal variation in species occurrence—data that are often available. For instance, Saura et al. [56] provided a rigorous example of black woodpecker (*Dryocopus martius*) range expansion with measures of potential connectivity to predict the spread of woodpeckers across a region of Spain. Additional investigations harnessing data like these will help to further our understanding of the effects of landscape connectivity. Very few investigations have also focused on key community processes that could be impacted by connectivity, such as plant–pollinator interactions or seed dispersal (Fig. 3). In addition, most of the articles on these processes that we reviewed were primarily testing the effects of connectivity on the distributions of interacting species rather than specifically testing for effects on the interaction or process itself. In contrast, Korman et al. [97] provided a compelling illustration of changes in pollen transfer with the presence of corridors. Ultimately, processes like these may have substantial effects on the long-term functioning of ecosystems and warrant further research.

Finally, very little work has focused on interpreting the cumulative impacts of connectivity on the persistence of populations (Fig. 3a), and all of the articles from our review modeled these effects from reported empirical data rather than through direct empirical estimation of measures of population persistence. Stevens and Baguette [78] used a spatially explicit population viability analysis to understand factors influencing natterjack toad (*Bufo calamita*) viability, finding that habitat quality was of central importance, and while connectivity was also important, it was only necessary at relatively small rates of movement. These applications suggest that interpreting the relative roles of connectivity for population viability will be essential for identifying key limiting factors to guide conservation strategies [7, 22].

Recommendations for Future Research on Landscape Connectivity and its Effects

While we show that the effects of connectivity on populations and communities are common and generally positive, negative effects of connectivity occurred in 20 % of the articles we considered that tested for effects. This result emphasizes the need for conservation strategies to understand the effects of

landscape connectivity for the region of interest prior to interventions. To make more rapid progress in our understanding of connectivity, we have several recommendations.

First, estimating the effects of connectivity is increasingly needed. Most investigations on connectivity assume that it is of critical importance, although over half of the investigations we reviewed did not provide evidence that connectivity explained variation in ecological or evolutionary patterns and processes. While the studies we reviewed that tested for effects generally found evidence for positive effects of connectivity, several examples showed that the effects of connectivity were negative, negligible, or small relative to other issues [14, 22, 75].

Second, capturing movement issues based on the underlying theoretical developments suggests that integration of movement into connectivity should vary by discipline. Genetic connectivity, for instance, hinges on effective dispersal, or dispersal that is followed by reproduction in non-natal habitats [46], and assumptions of monotonicity between the two measurements for connectivity—dispersal and effective dispersal—may not always be valid. Lowe and Allendorf [26] also emphasize the temporal mismatches between understanding genetic connectivity, where rare, long-distance dispersal events can be crucial to connectivity, and demographic connectivity, where the numbers of dispersal events across landscapes relative to birth and death rates drive population dynamics.

Third, each of these theoretical developments emphasizes factors mediating the effects of connectivity, which should be addressed. For example, in metacommunity ecology, interpreting the role of connectivity relative to species sorting is essential for understanding community assembly [59]. In a similar vein, isolating the effect of the ‘landscape’ on connectivity relative to non-landscape factors that can ultimately drive realized connectivity is needed to appropriately understand why connectivity varies across landscapes. Belisle [3] emphasized that local patch quality can alter movement rates in landscapes with similar structures, where high-quality resources can reduce movement rates and low-quality resources can increase movement, neither of which may be driven by the landscape causing impediments to movement. For example, Fletcher et al. [90] found that for the endangered snail kite (*Rostrhamus sociabilis*), a species that can move across its entire geographic range within a few days, realized connectivity was surprisingly low, due to behavioral preference for natal habitat types by dispersers.

Fourth, spatial and temporal scale must be explicit in our understanding of connectivity. Scale can alter our interpretation of the effects of connectivity, and is particularly critical for linking connectivity ideas across levels of organization (Table 2). Spatial scale is central to evaluating the importance of landscape connectivity, because the scale at which a system is considered will alter the ‘openness’ of the system and thus the role of movement [57]. This issue has led to a call for

understanding the functional grain of landscapes and using relevant spatial grains when assessing landscape connectivity [57, 94, 95]. Temporal scales are also often implicit in landscape connectivity assessments. However, understanding the effects of landscape connectivity requires understanding the temporal scale of movements and landscape change [15, 98]. Over short time periods, connectivity may be limited based on dispersal constraints, yet over longer time periods connectivity may be much greater. Often there is a focus of simply describing the potential connectivity of a landscape and making prioritizations based on these descriptions, without understanding how current and future variation in connectivity may impact biodiversity.

Finally, connectivity assessments for conservation need to better incorporate uncertainty in understanding the importance of connectivity [7, 10–12, 21]. Because the quantification of connectivity often relies on limited information (Fig. 2), the degree of uncertainty in model outcomes can be large relative to various other issues [21]. Connectivity should not be the sole focus for such large-scale conservation strategies, but should rather be integrated into a portfolio of key issues, such as the simple conservation of habitat amount and quality [20, 21]. For example, a recent analysis of spatial conservation planning found that realized connectivity played a smaller role in patch prioritization under worst-case disturbance scenarios than did local habitat quality influencing survival [7]. Issues such as habitat area and quality are well known to be important for biodiversity conservation and have less uncertainty [21].

Conclusions

While it is well known that connectivity can potentially influence populations and communities, our understanding of the effects of connectivity has lagged advancements in the quantification and mapping of connectivity in recent years. Several challenges remain in understanding the effects of connectivity and its importance over time and space relative to other factors that influence biodiversity. These challenges have raised questions regarding the amount of uncertainty in our understanding of connectivity and its effects [7, 10–12, 21]. Nevertheless, our results emphasize that effects of connectivity are frequently observed—and predominantly positive—when they are considered in connectivity assessments. By addressing these outstanding challenges and opportunities, we will better understand the relative importance of connectivity for biodiversity and will be able to provide more effective conservation strategies.

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Compliance with Ethical Standards

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest to declare.

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