Conservation Biology

Contributed Paper

Consequences of ignoring dispersal variation in network models for landscape connectivity

Lauren L. Sullivan,[1,2*] Matthew J. Michalska-Smith,[3,4] Katie P. Sperry,[2,5] David A. Moeller,[6] and Allison K. Shaw[2]

[1]Division of Biological Sciences, University of Missouri, Columbia, MO, U.S.A.
[2]Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, MN, U.S.A.
[3]Department of Veterinary Population Medicine, University of Minnesota, Saint Paul, MN, U.S.A.
[4]Department of Plant Pathology, University of Minnesota, Saint Paul, MN, U.S.A.
[5]Marine and Environmental Sciences, Northeastern University, Boston, MA, U.S.A.
[6]Department of Plant and Microbial Biology, University of Minnesota, Saint Paul, MN, U.S.A.

Abstract: Habitat loss and fragmentation can negatively influence population persistence and biodiversity, but the effects can be mitigated if species successfully disperse between isolated habitat patches. Network models are the primary tool for quantifying landscape connectivity, yet in practice, an overly simplistic view of species dispersal is applied. These models often ignore individual variation in dispersal ability under the assumption that all individuals move the same fixed distance with equal probability. We developed a modeling approach to address this problem. We incorporated dispersal kernels into network models to determine how individual variation in dispersal alters understanding of landscape-level connectivity and implemented our approach on a fragmented grassland landscape in Minnesota. Ignoring dispersal variation consistently overestimated a population's robustness to local extinctions and underestimated its robustness to local habitat loss. Furthermore, a simplified view of dispersal underestimated the amount of habitat substructure for small populations but overestimated habitat substructure for large populations. Our results demonstrate that considering biologically realistic dispersal alters understanding of landscape connectivity in ecological theory and conservation practice.

Keywords: fragmentation, grasslands, graph theory, network models, population size, weighted networks

Consecuencias de la Omisión de la Variación en la Dispersión en los Modelos de Redes para la Conectividad de Paisajes

Resumen: La pérdida y la fragmentación del hábitat pueden influir negativamente la persistencia de poblaciones y biodiversidad. Sin embargo, estos efectos pueden ser mitigados si las especies tienen una dispersión exitosa entre los fragmentos aislados de hábitat. Los modelos de redes son la herramienta principal para la cuantificación de la conectividad del paisaje, no obstante en la práctica, se tiende a usar una visión excesivamente simplista de la dispersión de especies. Es común que estos modelos ignoren la variación que existe entre individuos en sus habilidades de dispersión y que asuman que todos los individuos se pueden mover la misma distancia y con la misma probabilidad. En este estudio, desarrollamos una estrategia de modelaje para (minimizar o aminorar) estas limitaciones incorporando kernels de dispersión dentro de los modelos de redes para determinar cómo la variación individual de la dispersión altera el entendimiento de la conectividad a nivel de paisaje. Como un ejemplo, implementamos esta estrategia en un paisaje de pastizal fragmentado en Minnesota. Omitir la variación en la dispersión generó una sobreestimación sistemática de la robustez de la población ante las extinciones locales y una subestimación de la robustez ante la pérdida local del hábitat. Además, una visión simplificada de la dispersión subestimó la complejidad de hábitat para las poblaciones pequeñas, sin emgargo sobreestimó la complejidad para las poblaciones grandes. Nuestros resultados demuestran que incorporar parámetros que describan una dispersión

---

*Address correspondence to L. L. Sullivan, email sullivanll@missouri.edu
Article impact statement: Including biologically meaningful dispersal in network models alters understanding of connectivity between fragmented habitat patches.
Paper submitted May 8, 2019; revised manuscript accepted September 18, 2020.

Conservation Biology, Volume 35, No. 3, 944–954
© 2020 Society for Conservation Biology
DOI: 10.1111/cobi.13640

biológica realista tiene implicaciones importantes en la teoría de conectividad de paisajes e implementación de practicas de conservación.

Palabras Clave: fragmentación, modelos de redes, pastizales, redes ponderadas, tamaño poblacional, teoría de gráficos

摘要: 生境丧失和破碎化会对种群续存和生物多样性产生负面影响, 但如果物种成功扩散到孤立的栖息地斑块, 则可以缓解这种影响。网络模型是量化景观连接度的主要工具, 但在实际应用中, 物种扩散往往被过度简化。这些模型通常假设所有个体以相同的概率移动相同的固定距离, 而忽略了个体扩散能力的变异。本研究开发了一种建模方法来解决这个问题。我们在网络模型中加入了个体扩散函数, 以确定个体扩散能力差异如何改变对景观尺度连接度的理解, 并把我们的方法应用在明尼苏达州的一个破碎化的草原景观中。结果显示, 忽略个体扩散的变异会导致高估种群产生局部灭绝的稳健性, 且低估种群应对局部栖息地丧失能力的稳健性。此外, 简化扩散模型还会低估小种群栖息地亚结构的数量, 并高估大种群栖息地亚结构数量。我们的研究结果表明, 考虑生物学上实际的扩散能力, 可以改变生态学理论和保护实践中对景观连接度的认识。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 破碎化, 草地, 图论, 网络模型, 种群大小, 加权网络

Introduction

Loss of habitat is one of the largest anthropogenic threats to Earth's planetary systems (Rockström 2009), and contributes to major declines in biodiversity (Newbold et al. 2016) and other ecosystem services (Haddad et al. 2015). Habitat loss fundamentally alters landscapes by simultaneously decreasing the overall amount of native habitat and changing how the remaining habitat patches are arranged with respect to each other through fragmentation per se (Fahrig 2017). The negative effects of fragmentation (Fletcher et al. 2018) can be mitigated if species are still able to move between physically isolated habitat patches to maintain population connectivity. However, the extent of species' movement among patches remains an open question (Fahrig 2017). Thus, a complete understanding of the degree to which current (Haddad et al. 2015) and ongoing (Wright & Wimberly 2013) fragmentation disrupts connectivity requires accounting for potential species movement among patches.

Recent work examining how organisms move among fragmented patches draws on network modeling (e.g. Saura & Rubio 2010; Fletcher et al. 2013; Ziółkowska et al. 2014; Wimberly et al. 2018). This approach converts spatial data on habitat locations to networks (or graphs), in which nodes represent habitat patches and 2 patches are connected by an edge if organisms can disperse between them (Urban & Keitt 2001). These networks can be analyzed to inform conservation decisions by calculating patch-based or network-based connectivity metrics and by identifying sets of patches that are connected via dispersal and function as a unit (termed *components*). Network modeling has enabled researchers and managers to infer connectivity, identify habitat patches with high conservation value, and quantify the scale of dispersal necessary to maintain connectivity (e.g. O'Brien et al. 2006; Saura & Rubio 2010; Creech et al. 2014). Generally, although models that infer connectivity tend to take into account detailed information about matrix quality between habitat patches and potential ease of flow through this matrix (Moilanen & Hanski 1998; McRae et al. 2008; Wimberly et al. 2018), they are often based on simplistic assumptions about species' movement dynamics. Specifically, network models, particularly unweighted or binary networks that simply consider whether or not patches are connected, tend to define species' dispersal as a single fixed distance, which effectively assumes that all individuals are equally able to disperse up to that distance, but unable to disperse past that distance. Building network models based on the same sets of simplifying assumptions limits one's ability to understand how a broad range of biological factors (such as dispersal behavior) influence connectivity, which is especially problematic because dispersal variation can have many consequences (Snell et al. 2019; Shaw 2020). Simplified dispersal assumptions may over- or underestimate the degree of connectivity or fail to capture important connectivity patterns altogether, thereby preventing accurate estimations of landscape-level habitat use.

An alternative to viewing dispersal as fixed is to account for variation in dispersal, thus more accurately representing movement behavior. Inherent variation among individuals (e.g., sex, personality, body condition), populations (e.g., density), and the environment (e.g., habitat quality, habitat configuration, season) can cause differences in dispersal ability (Snell et al. 2019; Shaw 2020). This dispersal variation can be captured with a dispersal kernel that describes the proportion of individuals traveling any given distance (Shoemaker et al. 2020). Dispersal kernels thus account for variation in distance traveled as well as variation in the proportion of the dispersing population traveling each distance (Kot et al. 1996). In most species, the majority of dispersing individuals travel short distances, remaining close to their source location and thus contributing to local population dynamics (Moles & Westoby 2004). Simultaneously, few individuals move longer distances, and they drive processes like colonization (Soons et al. 2004b), range expansions (Kot et al. 1996), and range shifts (Davis & Shaw 2001). This long-distance dispersal is often defined by the distance traveled by the farthest 1% of individuals (Nathan 2006). Finally, population size can influence dispersal; populations with more dispersing individuals will more fully realize the dispersal kernel and thus be more likely to successfully disperse greater distances. Although network models have the potential to account for variation in dispersal (i.e., via weighted edges [Shanafelt et al. 2017]), most are based either on the assumption of fixed dispersal (e.g. Minor et al. 2009) or have weighted edges to describe how easily an organism can move through a given matrix, ignoring dispersal variation (e.g. Ziółkowska et al. 2014; Wimberly et al. 2018). Those network models that do consider dispersal as a function of distance tend to do so based on simulated draws from dispersal kernels (Fletcher et al. 2011, 2013). Models that more fully explore weighted networks with dispersal kernels allow for a more nuanced representation of species' movement capacity and provide a better understanding of habitat connectivity and the impacts of fragmentation. A deeper understanding of connectivity would influence both the conservation of rare and threatened species that have had natural movement patterns altered by fragmentation, as well as the control of invasive species that are capable dispersers whose movement abilities can be unaltered by fragmentation (Damschen et al. 2008).

We created a series of deterministic network models to understand how variation in dispersal alters estimates of landscape connectivity. We generated networks based on fixed dispersal distances, which allowed us to compare our results with previous studies (e.g., Urban & Keitt 2001; O'Brien et al. 2006; Wimberly et al. 2018). Then, we generated networks based on dispersal kernels, which incorporated variation in dispersal and included the effect of population size. By comparing networks created either with fixed dispersal distances or with dispersal kernels, we explored how variation in dispersal alters understanding of aspects of landscape connectivity, including habitat substructure, robustness to habitat loss, and robustness to local extinction. We sought to provide a starting point for conservation managers interested in understanding how traditional methods might over- or underestimate connectivity based on simplified assumptions about dispersal. We applied these models to fragmented grasslands in Minnesota (Fig. 1), where there is renewed interest from state and local managers to consider connectivity in their restoration efforts. Minnesota managers have created plans for protecting existing grasslands and building future restorations to promote connectivity through the creation of grassland corridors (Minnesota Prairie Plan Working Group 2018), yet these plans were designed with minimal information on species movement because little is known. Thus, Minnesota grasslands are an excellent study system to demonstrate the utility of our broader approach because prior knowledge of, and interest in, connectivity exists and managers there are open to considering how to incorporate more realistic information on species' dispersal into future conservation plans (Minnesota Prairie Plan Working Group 2018; Wimberly et al. 2018; Sperry et al. 2019).

Methods

We created deterministic network models with and without dispersal kernels to draw conclusions about how including biologically meaningful knowledge of dispersal alters predictions about connectivity compared with ignoring dispersal variation. We assumed that dispersal kernels more accurately represent species movement than the assumption of fixed models where all individuals travel all distances with equal likelihood. Our models are general, and thus could apply to any species of interest, including Minnesota grasslands species across a range of dispersal distances, for example, prairie coneflower (*Echinacea angustifolia*, ~9 m) (Ison et al. 2014), ground squirrels (*Citellus tridecemlineatus*, 53–80) (Rongstad 1965), dickcissels (*Spiza americana*, 222 m) (Walk et al. 2004), and burrowing owls (*Athene cunicularia*, 2802 m) (Catlin & Rosenberg 2008) (all are mean dispersal distances).

Habitat Selection

We developed our models for the prairie region of western and southern Minnesota (also called the Prairie Parkland Province). This region was historically grassland but has been fragmented and reduced to ~1% of its original area (Minnesota Prairie Plan Working Group 2018). The spatial locations of the remaining grasslands are well documented and exist in a matrix of mostly agriculture. We refer to each separate grassland fragment as a patch throughout. To build our networks, we used a comprehensive spatial grassland habitat database for the region (The Nature Conservancy 2015). This data set combined the Minnesota Department of Natural Resources' native prairie layer, the U.S. Fish and Wildlife Services' (USFS) Habitat and Population Evaluation Team's (HAPET) 2014 reclassification data set, and the U.S. Department of Agriculture's Cropland Data Layer (CDL) data set. The USFS National Wetlands Inventory layer was used for corrections in classifying wetland and open water areas. The resulting database consisted of all grassland types, including native remnant prairie, reconstructed or disturbed grasslands, and hay or pasture fields. We included all of these grassland types in our network analysis because

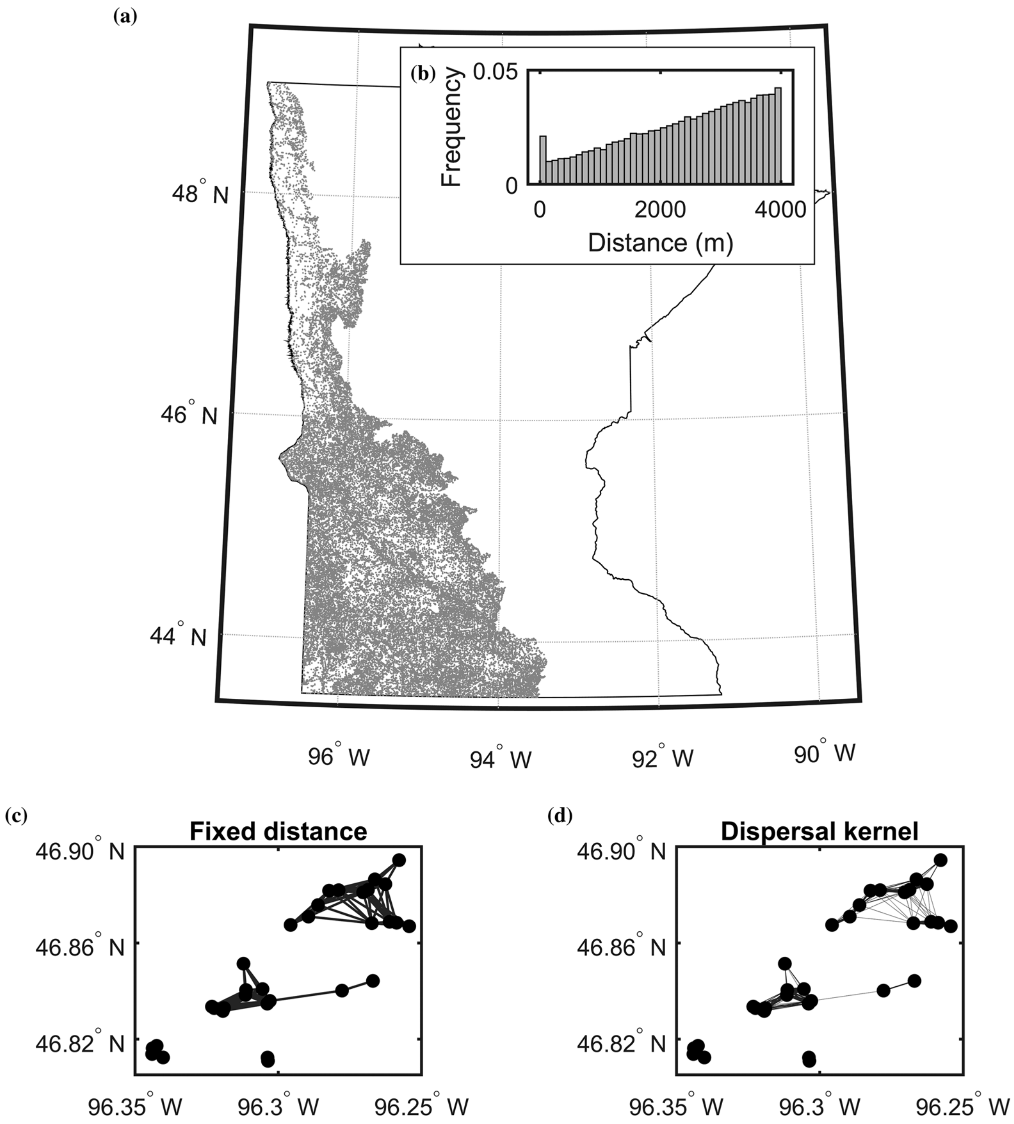
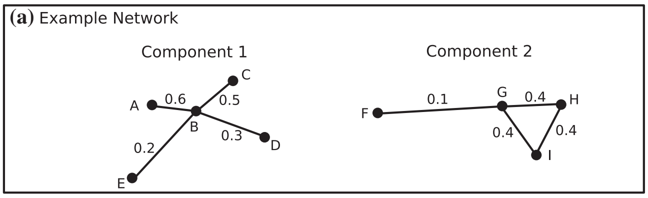


Figure 1. (a) Locations of the ~37,000 grassland patches across Minnesota (U.S.A.) used in the analysis of dispersal networks, (b) distances between habitat patches up to 4000 m (maximum in models examined), and examples of a subset of the network (Clay County) showing patches and connections under (c) a fixed distance ($d' = 2000$) and (d) dispersal kernel ($d^* = 2000$ and 99%-realized dispersal kernel). In (d) thicker lines correspond to a higher proportion of dispersers between patches.

they represent potential habitat for grassland species (e.g. birds, insects, mammals, plants). Similar to Wimberley et al. (2018), we used ArcGIS 10.4 to select patches that were 2.023 ha (5 acres) or larger. This resulted in ~37,000 grasslands ($N = 37{,}091$ patches in the network, see Appendix S1 for all parameters) to use in our connectivity analysis (Fig. 1a,b).

Networks Based on Fixed Dispersal Distances

We generated networks for our grasslands based on the assumption that organisms had no dispersal variation (i.e., all individuals traveled a fixed dispersal distance). To do this, we calculated the nearest-edge distance (i.e., the distance between the closest points) of all pairs of patches in ArcGIS with the geodesic method and set a maximum search radius of 4000m (Fig. 1c). We chose this radius, which is within the range used in similar studies (Wimberly et al. 2018), for computational simplification, but note that it is smaller than the movement ability of extremely vagile Minnesota grassland species (e.g. the red fox [*Vulpes vulpes*] disperses on average ~31,000 m [Storm et al. 1976]). We then generated 2000 networks, 1 for each fixed dispersal distance (d') that we considered (1, …, 2000 m). For each dispersal distance d, we generated a binary adjacency matrix **A** (of size $N \times N$) in which each element described whether (1) or not (0) the distance between a pair of patches was $<= d$ (i.e., whether



(b) Network-level Metrics

number of components	2
largest component	5
clustering coefficient	0.58
clustering coefficient (weighted)	0.61

(c) Patch-level Metrics

	A	B
degree	1	4
strength (weighted degree)	0.6	1.6
closeness	0.023	0.025
closeness (weighted)	0.019	0.021

Figure 2. (a) Toy dispersal network with 9 patches (A-I) and 2 components (Numbers along edges indicate probability that 2 patches are connected via dispersal and are used to calculate weighted metrics. When calculating nonweighted metrics, probability values become 1.); (b) network-level metrics calculated for the network in (a) (Only nodes B, G, H, and I are used for these calculations because the clustering coefficient only counts nodes with degree >1); and (c) patch-level metrics as calculated for 2 example patches (A and B in component 1).

an individual traveling that distance could move between these 2 patches). This generated 2000 binary adjacency matrices **A** (of size *N* x *N*) in which each element described whether (1) or not (0) 2 patches were connected for each dispersal distance. We then used each matrix to create a nondirected network in the igraph package in R (Csardi & Nepusz 2006). To guide readers through our methods, we also created a toy network (Fig. 2a).

Networks Based on Dispersal Kernels

We also generated networks for our grasslands assuming that individual organisms varied in their dispersal ability (i.e. their movement was described by a dispersal kernel [Fig. 1d]). Specifically, we used the exponential distribution (Fig. 3a) in which the proportion of individuals traveling any distance d is

$$e^{-bd}, \tag{1}$$

where b is the rate parameter. This distribution is commonly used as a dispersal kernel because it often matches empirical data (Hovestadt et al. 2011; Shaw et al. 2019). As with the fixed distance networks, we also considered 2000 dispersal distances. However instead of considering these to be the exact distances traveled, we considered these to be the farthest 1% value (d^*) for defining long-distance dispersal for our dispersal kernels. Thus we established a dispersal kernel for each $d_x{}^*$ value ($x = 1, \ldots, 2000$ m) as follows. We determined the proportion of individual dispersing each distance d or more, given by the complementary cumulative distribution function (CCDF) for the exponential kernel (Fig. 3a). We set this proportion f to be 0.01, plugged in each $d_x{}^*$, and solved for the corresponding b_x value (Fig. 3c), that is

$$b_x = \frac{-\ln(0.01)}{d_x^*}. \tag{2}$$

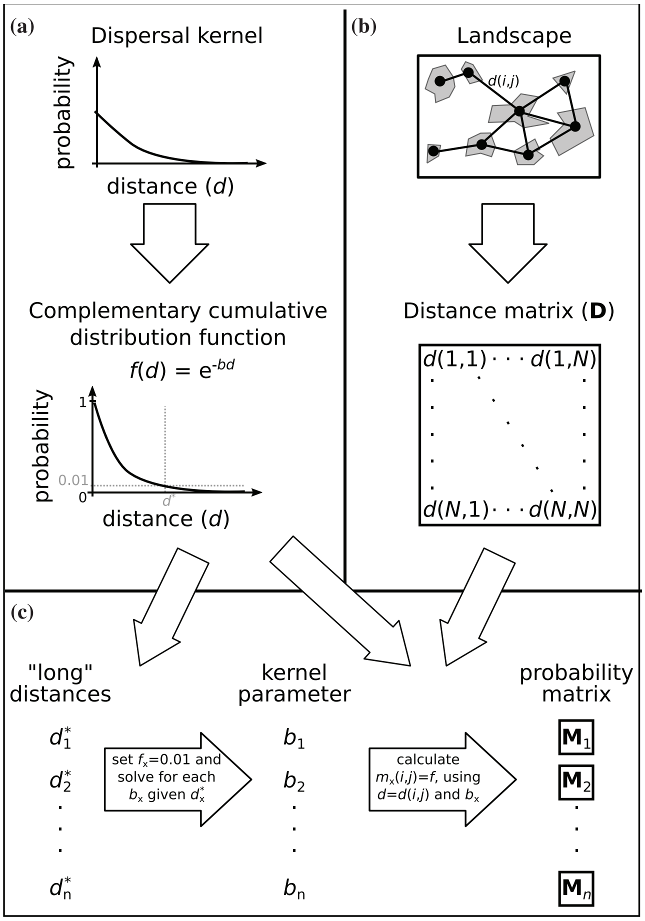


Figure 3. Schematic for building networks from dispersal kernels: (a) dispersal kernel (proportion of population traveling a distance d*) used to calculate the complementary cumulative density function (CCDF) (*f*, proportion of individuals traveling a distance* d *or more;* d*, *long-distance dispersal – [1%] individuals traveling* d *or more); (b) landscape of* N *patches used to calculate the physical distance between all pairs of patches* i *and* j *(i.e., distance matrix [**D**]); and (c) the deterministic map from each long distance (*$d_x{}^*$*) to corresponding dispersal kernel parameter (*b_x*) (caculated by setting* f_x *to 0.01) and then to the weighted matrix (**M**$_x$, proportion of individuals dispersing between all pairs of patches* i *and* j*) (using* f *and **D**), where* x *is the dispersal distance index* x = *1,…,*n (n = *2000). See Appendix S1 for full definitions of parameters.*

This b_x value describes a dispersal kernel for which only 1% of individuals dispersed a distance of d_x^* or farther. Next, we calculated the nearest-edge distance between all pairs of patches up to a maximum distance of 4000 m, resulting in a Euclidian distance matrix, **D** (Fig. 3b). Setting a maximum distance for these calculations (rather than calculating all pairwise distances) saved computational time while ensuring we calculated all relevant distances needed for our kernels below. Finally, for each dispersal distance d_x^* we converted the distance matrix, **D**, into a matrix $\mathbf{M}_x$ to describe the proportion of the modeled population that disperses between each patch (Fig. 3c). To do this, for each d_x^* value, we used the CCDF to calculate the proportion of individuals $m(i,j)$ with dispersal kernel defined by b_x that would travel at least the distance $d(i,j)$ between each patch i and j. We then used these $\mathbf{M}_x$ matrices to generate weighted nondirected networks in which the weight of each edge corresponded to the proportion of dispersing individuals that could move between the 2 patches the edge connected.

Finally, we explored the influence of population size on connectivity metrics. A dispersal kernel describes the distribution of distances that would be observed across a very large number of dispersal events. However, because species vary in population size and fecundity, they will also vary in how well the kernel is realized . These differences will appear most strongly for the low-probability long distances (the dispersal kernel tail). A species with a small population size or low fecundity will have few realized dispersal events and thus across the population there will be few dispersal distances represented by the tail of the kernel. To mimic different population sizes with our models, we set the **M** threshold at 3 values by keeping the 75% (all dispersal probabilities < 25% set to 0, i.e., 75% realized, a small population), 99% (99% realized, medium population), and 99.99% (99.99% realized, large population) highest dispersing proportion. This is equivalent to truncating the dispersal kernel at 3 increasingly long maximum distances, but does not incorporate uncertainty and represents the simplifying assumption that small populations are less likely to reach longer distances than large populations. Imposing a maximum dispersal distance also kept the dispersal kernel from becoming infinite (i.e., there is a very small proportion of individuals dispersing infinitely far). An alternative approach to examining population size is to multiply all weighted edges within the network by these proportions (0.9999 for large populations, 0.99 for medium populations, 0.75 for small populations) and then conduct network analyses. This approach leads to qualitatively similar results for patch-level metrics to those we present here (Appendix S2).

In total, we considered 2000 different measures of long-distance dispersal and 3 different measures of population size, generating 6000 weighted networks. As above, we calculated network and patch-level metrics for each network, some of which were modified to accommodate the weighted network structure.

Network-Level Connectivity Metrics

For each network generated with fixed dispersal (nonweighted) and dispersal kernels (weighted), we calculated 3 network-level metrics (Fig. 2b) to quantify different aspects of network structure and connectivity. The first 2 metrics (number of components and maximum component size) do not take into account weights and thus were calculated the same way for both nonweighted (binary) and weighted networks. For number of components (see Appendix S3 for igraph functions), 2 patches were in the same component if they were connected by an edge; fully isolated patches were their own component. Patches in different components were isolated from each other; thus, the number of separate components in a network provided a rough sense of overall fragmentation across the network (Calabrese & Fagan 2004). For maximum component size, the number of patches in the largest component of the network provided a measure of effective network size (Urban & Keitt 2001). Both the number of components and the size of the largest component represented an estimate of the amount of habitat substructure present. Average clustering coefficient quantifies the extent to which a network contains well-connected clusters of patches and thus provides an estimate of local landscape connectivity. In nonweighted networks, for a given patch i that is connected to k_i neighboring patches (see patch-level metrics below), there can be at most

$$\left(1/2\right) k_i(k_i - 1) \tag{3}$$

connections among its neighboring patches. The clustering coefficient for this patch is the fraction of those possible connections that actually occur (Watts & Strogatz 1998), a metric used to quantify the local connectivity for landscape networks (Wimberly et al. 2018). Average clustering coefficient can be considered a measure of robustness to habitat loss because networks with higher clustering will more easily maintain their substructure even as habitat fragmentation removes either edges or patches. For weighted networks, we used weighted distances between patches based on dispersal proportion (Csardi & Nepusz 2006). This weighted clustering coefficient is calculated as

$$\frac{1}{s_i\left(k_i - 1\right)} \sum_{j,h} \left\{ \frac{1}{2} \left[m\left(i, j\right) + m\left(i, h\right) \right] a\left(i, j\right) a\left(i, h\right) a\left(j, h\right) \right\}, \tag{4}$$

where s_i is the strength of patch i (see below), k_i is the degree of patch i, $m(i,j)$ are the elements of the weighted matrix **M**, and $a(i,j)$ are the elements of the adjacency matrix **A**. There was little difference between the mean and median values for clustering coefficient, except for small to moderate dispersal distances in the 75%-realized kernels where the mean value was larger than the median value (Appendix S4).

Patch-Level Connectivity Metrics

For each patch within each network, we also calculated 2 patch-level metrics (degree and closeness centrality) (Fig. 2c) and summarized them by looking at the 25th, 50th, and 75th quantiles of all values for patches within each network. For nonweighted networks, degree centrality was calculated as the number of connected neighbors each patch has (k_i), that is, the number of patches that an individual could potentially reach via dispersal as defined by the model (Wimberly et al. 2018). For weighted networks we calculated strength, the weighted version of degree centrality, as

$$s_i = \sum_j m\left(i, j\right), \tag{5}$$

where $m(i,j)$ are the elements of the weighted matrix $\mathbf{M}$ for all connected neighbors j of patch i.

Degree centrality or strength quantifies the number of colonization opportunities to or from each patch and represents a measure of short-term robustness to local (patch-level) extinction. Patches with low degree or strength are likely to be isolated and vulnerable to reductions in species richness because any local extinction would be unlikely to be recovered by recolonization from other patches. For nonweighted networks, closeness centrality quantifies the importance of each patch i for overall connectivity in the network as

$$\frac{1}{\sum_{i\neq j} p_{ij}} \tag{6}$$

where p_{ij} is the shortest path or the number of steps (i.e., sequential dispersal events) it takes to reach every other patch j in the network from the focal patch. If 2 patches are not connected (i.e., p_{ij} is infinite), the total number of patches (N) is used instead of p_{ij} for this pair. Thus closeness is a measure of the average number of sequential dispersal events required to recolonize the network and represents a measure of long-term robustness to local extinction. We chose closeness as our centrality metric (rather than betweenness as used by Minor & Urban [2007]) because closeness more accurately represents dispersing organisms that do not always take the most efficient route between patches (Borgatti 2005). For weighted networks, we calculated a weighted version of closeness, as

$$\frac{1}{\sum_{i\neq j} q_{ij}}, \tag{7}$$

where q_{ij} is the sum of inverse probabilities m^{-1} along the shortest path between patch i and patch j. Because the inverse of the proportion of dispersers gives an expected number of events needed (e.g., a 0.5 proportion of dispersers would take about 2 dispersal events), weighted closeness is again a measure of long-term robustness to local extinction because it tallies the expected number of sequential dispersal events required to recolonize the entire network. As for nonweighted networks, if 2 patches are not connected, the total number of patches (N) is used instead of q_{ij} for that pair. This correction for unconnected patches (while a suitable approximation for nonweighted networks) is actually an underestimate of the number of sequential dispersal events for weighted networks. Because the degree to which it underestimates dispersal events (and thus overestimates weighted closeness) interacts with the different population sizes we considered, there is no meaningful way to compare across different truncations of the dispersal kernels for this metric. Thus, we only calculated weighted clustering coefficient for the networks based on the 99%-realized dispersal kernels.

All analyses were run in R 3.4.4 (R Core Team 2017).

Results

Network-Level Metrics

Networks were less fragmented (i.e., had less habitat substructure) for large dispersal distances, resulting in fewer components (Fig. 4a) and larger largest components (Fig. 4b). These relationships were starkest for networks created from dispersal kernels with long realized kernel tails (i.e. large population size or high fecundity). In other words, the 99.99%-realized kernel showed the fastest drop in the number of components and the fastest increase in size of the largest component with increasing d^*, whereas the 75%-realized dispersal kernel showed a markedly slower decrease in the number of components and slower increase in maximum component size with increasing d^*. The fixed dispersal distance produced accurate estimates for populations of intermediate size (the 99%-realized dispersal kernel) (Fig. 4a & b). Intuitively, this result occurs because a network from a fixed dispersal distance of d' is structurally equivalent to a network with a 99%-realized dispersal kernel with distance d^* (the same patches are connected in both when considering nonweighted [or binary] network metrics such as the number of components and largest component size). However, fixed dispersal distance underestimated habitat substructure for smaller populations (75% realized) and overestimated habitat substructure for larger populations (99.99% realized).

Networks were also more connected for larger dispersal distances; they had higher clustering coefficients (Fig. 4c). In other words, populations with larger dispersal distances were more robust to habitat loss leading to

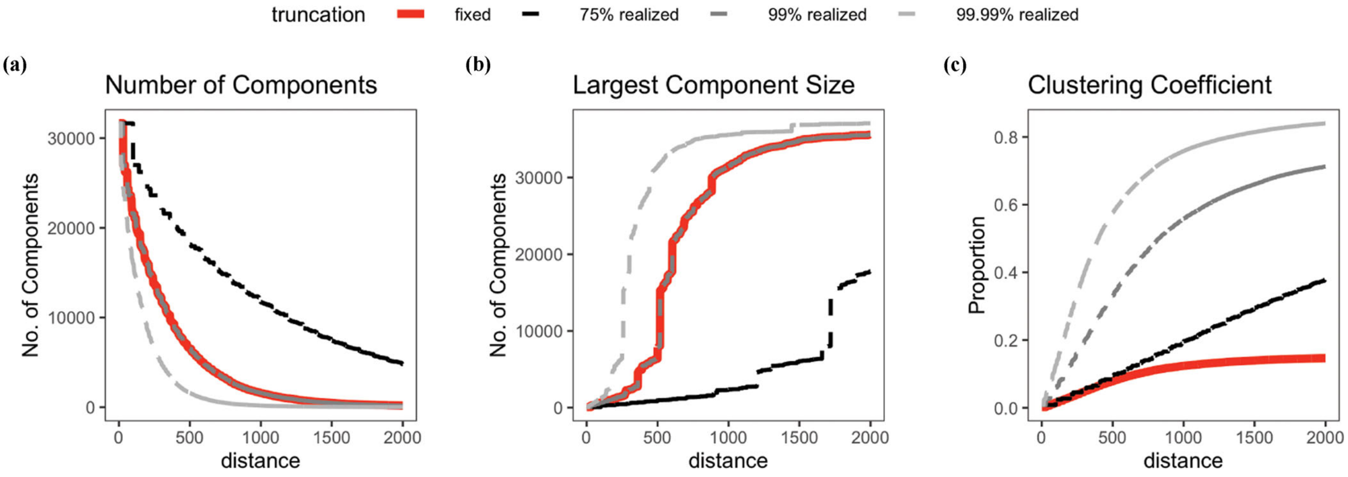


Figure 4. Network-level metric values for networks with fixed dispersal distances (red) and with the exponential dispersal kernel at different tail truncations, 75% realized (dark gray), 99% realized (medium gray), and 99.99% realized (light gray), which represent increasing abilities for long-distance dispersal: (a) number of components, (b) size of the largest component, which represent measures of habitat substructure, and (c) clustering coefficient, which represents robustness to habitat loss.

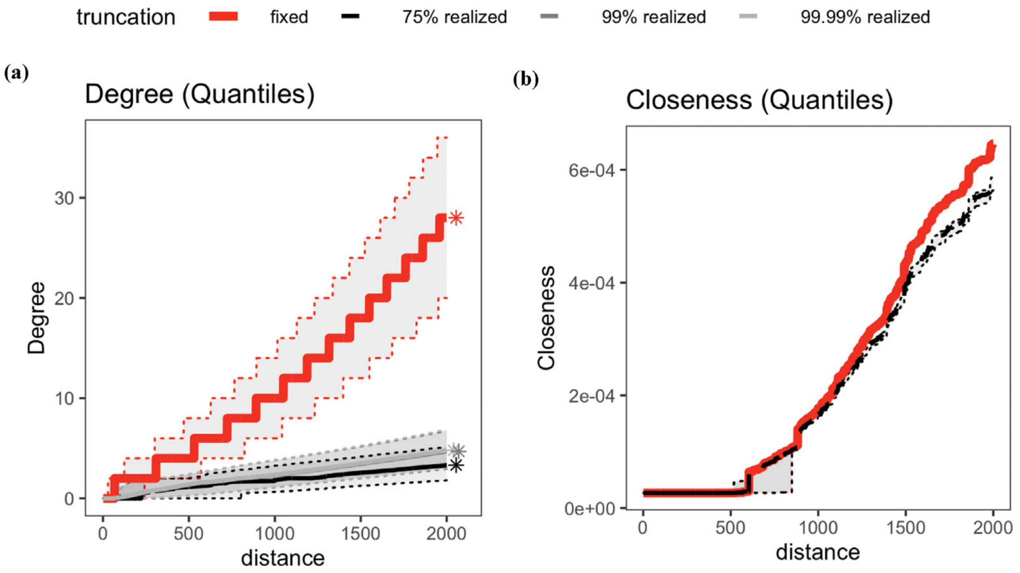


Figure 5. Patch-level metric values for networks with fixed dispersal distances (red) and networks with different dispersal kernels, 75% realized (dark gray), 99% realized (medium gray), and 99.99% realized (light gray). Panels show the 25th, 50th (asterisks), and 75th quantiles for (a) patch degree centrality and (b) patch closeness, which are measures of robustness to local extinction. In (a) 99%-realized kernel and 99.99%-realized kernel nearly overlap with 99.99%-realized kernel, which has a slightly higher degree.

lost patches or connections. However, the fixed dispersal distance consistently underestimated robustness to habitat loss compared with all 3 populations sizes (75%-, 99%-, 99.99%-realized dispersal kernels) (Fig. 4c). The largest difference occurred for the largest population sizes (99.99%-realized kernel). The fixed network and the 75%-realized kernel produced similar results for low dispersal distances, but the clustering coefficient then plateaued for the fixed distance, whereas the 75%-realized kernel continued to increase for large dispersal distances.

Patch-Level Metrics

Patches in networks with large dispersal distances were on average connected to more neighbor patches (higher degree centrality) (Fig. 5a) and represented a high short-term robustness to local extinctions. Networks from fixed dispersal distances consistently overpredicted robustness compared with networks from dispersal kernels, a gap that increased with dispersal distance. In other words, fixed kernel networks systematically overpredicted the number of neighbors (and thus expected number of recolonization opportunities) each patch had compared with dispersal kernel networks. Within the dispersal kernel networks, the smallest populations (75%-realized kernel) had patches with the lowest robustness, followed by medium (99%-realized kernal) and large (99.99%-realized kernal) population sizes. However, these ranges overlapped substantially. Similarly, patches in networks with large dispersal distances had high closeness values (Fig. 5b). Fixed dispersal distances consistently overpredicted closeness and thus underpredicted the number of sequential dispersal events needed to recolonize a network following extinction, compared with the networks created with dispersal kernels.

Discussion

We built deterministic network models from fixed dispersal distances and dispersal kernels, and contrasted them to more fully explore how weighted networks that use dispersal kernels affect estimates of landscape connectivity. As with other simulation-based connectivity models that incorporate dispersal variation (Palmer et al. 2014), we found that network models based on dispersal kernels generated a markedly different understanding of population connectivity than network models based on a fixed dispersal distance (Figs. 4–5, Appendix S5). Specifically, using fixed dispersal consistently overestimated a population's robustness to local extinctions while underestimating robustness to habitat fragmentation. Our results from fixed dispersal distances qualitatively matched similar network analyses for other grasslands (Wimberly et al. 2018) and for forests (Urban & Keitt 2001), suggesting that current habitat management based on fixed dispersal networks is applying inaccurate estimates of population connectivity. Because there is ample evidence that most organisms have substantial variation in dispersal (e.g. Baguette 2003; Krkošek et al. 2007; Sullivan et al. 2018), connectivity models must account for such variation by using dispersal kernels. Other network models that use dispersal kernels to match empirical movement data show these methods to be a good approximation of movement ability (Fletcher et al. 2011, 2013). These findings have implications for managers who plan for conservation based on connectivity metrics. Some species of concern may need more total habitat, whereas others rely on continual recolonization and thus would differ in whether fixed models over- or underestimated their connectivity.

The magnitude of differences between fixed and dispersal kernel connectivity metrics depended on how we modeled the tail of the dispersal kernel, which reflected a examining different population sizes of organisms. The underestimate of robustness to habitat fragmentation (clustering) was the largest for large populations (99.99%-realized dispersal kernel) (Fig. 4c). In contrast, the overestimate of robustness to local extinction (degree centrality) was similar for all population sizes, but slightly larger for small populations (75%-realized dispersal kernel) (Fig. 5a). Degree centrality estimates the expected number of patches that can be colonized with a single set of dispersal events. Because fixed dispersal is effectively based on the assumption of perfect dispersal (patches within a fixed distance will always be reached), networks with fixed dispersal will always overestimate colonization ability.

In light of our results, explicit consideration of conservation goals can help guide the appropriate use of dispersal kernels for management and planning. Inherent in the use of dispersal kernels is the understanding that most individuals move short distances and few individuals move far. Therefore, the conservation goals at the heart of maintaining connectivity should take population size into account when appropriate. For example, often the goal of promoting connectivity between patches is to build a functioning metapopulation for rare species where individuals can move freely and breed between patches (Hanski 1998). Because rare or threatened species are often dispersal limited due to small population sizes and low fecundity (Baur 2014), considering a less realized dispersal kernel (i.e., 75% realized) could more accurately represent likely connectivity outcomes for this particular goal. Moreover, if small population sizes are of serious concern, other methods might need to be incorporated, including individual based models (Grimm & Railsback 2005). Another goal of maintaining connectivity may be to allow for the possibility of species' response to climate change via range shifts (Krosby et al. 2010). Range expansions often proceed through the dispersal of a few individuals over a long distance (Davis & Shaw 2001). To successfully track climate change, large populations must produce the few individuals that disperse long distances; thus, a more realized dispersal kernel (i.e., 99.99% realized) would be more appropriate to include in network models to achieve this goal. Consideration of these highly realized dispersal kernels is also appropriate for controlling invasive species, such as the cane toad (*Rhinella marina*), that have high movement ability (Perkins et al. 2013). Finally, for sessile organisms such as plants, managers may be interested in distinguishing between maintaining high genetic diversity to decrease the probability of inbreeding depression—which requires the movement of gametes (i.e., pollen)—versus allowing for species recolonization to increase species diversity—

which requires the movement of individuals (i.e. seeds) (Elistrand 1992; Brudvig et al. 2009). In this case, managers should consider defining dispersal kernels that represent pollen and seed dispersal separately in order to match their management goals. When looking to define dispersal kernels, managers can use measurement-based (e.g., Stevens et al. 2010), trait-based (e.g., Soons et al. 2004a), or genetic-based approaches (e.g., Bacles et al. 2006) to estimate kernels.

Grasslands are globally important, yet they are among the most threatened due to land-use conversion and fragmentation (Soons et al. 2005; Newbold et al. 2016). Our network models help elucidate how likely species are able to move between grassland patches and maintain connectivity at a broader scale. Our results are comparable to those of Wimberly et al. (2018), who determined connectivity of the grasslands in the Prairie Coteau region of Minnesota and the Dakotas, but used a fixed dispersal distance. Extrapolating their results based on our findings from network models with dispersal kernels, one might expect that for species with large population sizes there may be increased connectivity, with fewer, larger components that are more robust to fragmentation than what Wimberly et al. (2018) found. One might expect the opposite for species with small populations. To aid Minnesota grassland managers, we created a web-based app to allow for the direct application of network models to existing grasslands in Minnesota (Sperry et al. 2019). This approach could be easily updated to incorporate known dispersal kernel information for species of interest (e.g., grassland plant species [Sullivan et al. 2018]), patch prioritization, or matrix quality between patches (Castillo et al. 2016), which would afford a more targeted understanding of which species can maintain connectivity and which may require assistance moving between patches.

To determine whether and where connectivity is maintained between isolated habitat fragments, one must account for how organisms move in a biologically meaningful way. We took steps toward this goal by considering variability in dispersal in network models by incorporating fully explored dispersal kernels to determine how this alters the view of network-based connectivity relative to standard methods that are based on a fixed dispersal distance. Because interspecific dispersal variation is also common, future work should examine how dispersal varies across species (e.g., when different species have different dispersal kernel shapes) and when there is directionality in dispersal to understand more fully how interspecific variation affects connectivity. We found that models ignoring dispersal variation simultaneously overestimated robustness to local extinctions while underestimating robustness to habitat loss, relative to models that accounted for dispersal variation. The magnitude of these differences depends on both biological traits of the species of interest, particularly population size, and dispersal distance.

Acknowledgments

This work was supported by the Legislative-Citizen Commission on Minnesota Resources (LCCMR) Environmental and Natural Resources Trust Fund (ENRTF) grant (M.L. 2016, Chp. 186, Sec. 2, Subd. 08b). We thank R. Johnson for help with GIS data layers; UMN Theory Group for topical discussions; L. Dee, D. Leach, N. Narayanan Venkatanarayanan, Z. Radford, R. Shaw, J. Sherman, T. Weiss-Lehman, and 4 anonymous reviewers for helpful comments on the manuscript. The Minnesota Supercomputing Institute (http://msi.umn.edu) at University of Minnesota provided resources that contributed to the research results reported in this article.

Supporting Information

Additional information is available online in the Supporting Information section at the end of the online article. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Data and code are available at the Zenodo Digital Repository https://zenodo.org/record/4279644#.X7VYcFlMG3d.

Literature Cited

Bacles CFE, Lowe AJ, Ennos RA. 2006. Effective seed dispersal across a fragmented landscape. Science **311:**628.

Baguette M. 2003. Long distance dispersal and landscape occupancy in a metapopulation of the Cranberry Fritillary butterfly. Ecography **26:**153–160.

Baur B. 2014. Dispersal-limited species - A challenge for ecological restoration. Basic and Applied Ecology **15:**559–564.

Borgatti SP. 2005. Centrality and network flow. Social Networks **27:**55–71.

Brudvig LA, Damschen EI, Tewksbury JJ, Haddad NM, Levey DJ. 2009. Landscape connectivity promotes plant biodiversity spillover into non-target habitats. Proceedings of the National Academy of Sciences of the United States of America **106:**9328–9332.

Calabrese JM, Fagan WF. 2004. A comparison-shopper' s guide to connectivity metrics. Frontiers in Ecology and the Environment **2:**529–536.

Castillo JA, Epps CW, Jeffress MR, Ray C, Rodhouse TJ, Schwalm D. 2016. Replicated Landscape genetic and network analyses reveal wide variation in functional connectivity for American pikas. Ecological Applications **26:**1660–1676.

Catlin DH, Rosenberg DK. 2008. Breeding dispersal and nesting behavior of burrowing owls following experimental nest predation. The American Midland Naturalist **159:**7.

Creech TG, Epps CW, Monello RJ, Wehausen JD. 2014. Using network theory to prioritize management in a desert bighorn sheep metapopulation. Landscape Ecology **29:**605–619.

Csardi G, Nepusz T. 2006. The igraph software package for complex network research. InterJournal Complex Sy:1695.

Damschen EI, Brudvig LA, Haddad NM, Levey DJ, Orrock JL, Tewksbury JJ. 2008. The movement ecology and dynamics of plant communities in fragmented landscapes. Proceedings of the National Academy of Sciences **105:**19078–19083.

Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to Quaternary climate change. Science **292:**673–679.

Elistrand NC. 1992. Gene flow by pollen: implications for plant conservation genetics. Oikos **63:**77–86.

Fahrig L. 2017. Ecological responses to habitat fragmentation per se. Annual Review of Ecology, Evolution, and Systematics **48:**1–23.

Fletcher RJ, et al. 2018. Is habitat fragmentation good for biodiversity? Biological Conservation **226:**9–15.

Fletcher RJ, Acevedo MA, Reichert BE, Pias KE, Kitchens WM. 2011. Social network models predict movement and connectivity in ecological landscapes. Proceedings of the National Academy of Sciences **108:**19282–19287.

Fletcher RJ, Revell A, Reichert BE, Kitchens WM, Dixon JD, Austin JD. 2013. Network modularity reveals critical scales for connectivity in ecology and evolution. Nature Communications **4:**1–7.

Grimm V, Railsback SF. 2005. Individual-based modeling and ecology. Princeton and Oxford: Princeton University Press.

Haddad NM, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances **1:**e1500052–e1500052.

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

Hovestadt T, Binzenhöfer B, Nowicki P, Settele J. 2011. Do all interpatch movements represent dispersal? A mixed kernel study of butterfly mobility in fragmented landscapes. Journal of Animal Ecology **80:**1070–1077.

Ison JL, Wagenius S, Reitz D, Ashley MV. 2014. Mating between *Echinacea angustifolia* (Asteraceae) individuals increases with their flowering synchrony and spatial proximity. American Journal of Botany **101:**180–189.

Kot M, Lewis MA, van den Driessche P. 1996. Dispersal data and the spread of invading organisms. Ecology **77:**2027–2042.

Krkošek M, Lauzon-Guay J-S, Lewis MA. 2007. Relating dispersal and range expansion of California sea otters. Theoretical Population Biology **71:**401–407.

Krosby M, Tewksbury J, Haddad NM, Hoekstra J. 2010. Ecological connectivity for a changing climate. Conservation Biology **24:**1686–1689.

McRae BH, Dickson BG, Keitt TH, Shah VB. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology **89:**2712–2724.

Minnesota Prairie Plan Working Group. 2018. Minnesota prairie conservation plan. 2nd edition. Minnesota Prairie Plan Working Group, Minneapolis.

Minor ES, Tessel SM, Engelhardt K a M, Lookingbill TR. 2009. The role of landscape connectivity in assembling exotic plant communities: a network analysis. Ecology **90:**1802–1809.

Minor ES, Urban DL. 2007. Graph theory as a proxy for spatially explicit population models in conservation planning. Ecological Applications **17:**1771–1782.

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

Moles AT, Westoby M. 2004. Seedling survival and seed size: a synthesis of the literature. Journal of Ecology **92:**372–383.

Nathan R. 2006. Long-distance dispersal of plants. Science **313:**786–788.

Newbold T, et al. 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science **354:**288–291.

O'Brien D, Manseau M, Fall A, Fortin MJ. 2006. Testing the importance of spatial configuration of winter habitat for woodland caribou: an application of graph theory. Biological Conservation **130:**70–83.

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

Perkins TA, Phillips BL, Baskett ML, Hastings A. 2013. Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. Ecology Letters **16:**1079–1087.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation, Vienna. Available from http://www.r-project.org/.

Rockström J. 2009. A safe operating space for humanity. Nature **461:**472–475.

Rongstad OJ. 1965. A life history study of thirteen-lined ground squirrels in southern Wisconsin. Journal of Mammalogy **46:**76–87.

Saura S, Rubio L. 2010. A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography **33:**523–537.

Shanafelt DW, Salau KR, Baggio JA. 2017. Do-it-yourself networks: a novel method of generating weighted networks. Royal Society Open Science **4:**171227.

Shaw AK. 2020. Causes and consequences of individual variation in animal movement. Movement Ecology **8:**12. https://doi.org/10.1186/s40462-020-0197-x.

Shaw AK, D'Aloia CC, Buston PM. 2019. The evolution of marine larval dispersal kernels in spatially structured habitats: analytical models, individual-based simulations, and comparisons with empirical estimates. The American Naturalist **3:**424–435.

Shoemaker LG, et al. 2020. Integrating the underlying structure of stochasticity into community ecology. Ecology **101:**e02922.

Snell RS, et al. 2019. Consequences of intraspecific variationin seed dispersal for plant demography, communities, evolution and global change. AoB Plants **11:**plz016.

Soons MB, Heil GW, Nathan R, Katul GG. 2004*a*. Determinants of long-distance seed dispersal by wind in grasslands. Ecology **85:**3056–3068.

Soons MB, Messelink JH, Jongejans E, Heil GW. 2005. Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. Journal of Ecology **93:**1214–1225.

Soons MB, Nathan R, Katul GG. 2004*b*. Human effects on long-distance wind dispersal and colonization by grassland plants. Ecology **85:**3069–3079.

Sperry KP, Shaw AK, Sullivan LL. 2019. Apps can help bridge restoration science and restoration practice. Restoration Ecology:3–6.

Stevens VM, Turlure C, Baguette M. 2010. A meta-analysis of dispersal in butterflies. Biological Reviews **85:**625–642.

Storm GL, Andrews RD, Phillips RL, Bishop RA. 1976. Morphology, reproduction, dispersal, and mortality of Midwestern Red Fox populations. Wildlife Monographs **49:**3–53.

Sullivan LL, Clark AT, Tilman D, Shaw AK. 2018. Mechanistically derived dispersal kernels explain species-level patterns of recruitment and succession. Ecology **99:**2415–2420.

The Nature Conservancy (TNC). 2015. 2015 Prairie Plan Land Cover Analysis. TNC, Minneapolis.

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

Walk JW, Wentworth K, Kershner EL, Bollinger EK, Warner RE. 2004. Renesting decisions and annual fecundity of female Dickcissels (Spiza americana) in Illinois. The Auk **121:**1250–1261.

Watts DJ, Strogatz SH. 1998. Collective dynamics of "small-world" networks. Nature **393:**440–442.

Wimberly MC, Narem DM, Bauman PJ, Carlson BT, Ahlering MA. 2018. Grassland connectivity in fragmented agricultural landscapes of the north-central United States. Biological Conservation **217:**121–130.

Wright CK, Wimberly MC. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proceedings of the National Academy of Science **110:**4134–4139.

Ziółkowska E, Ostapowicz K, Radeloff VC, Kuemmerle T. 2014. Effects of different matrix representations and connectivity measures on habitat network assessments. Landscape Ecology **29:**1551–1570.