

# Consequences of ignoring dispersal variation in network models for landscape connectivity

DOI:10.1111/COBI.13640

Lauren L. Sullivan<sup>1,2</sup>, Matthew J. Michalska-Smith<sup>3,4</sup>, Katie P. Sperry<sup>2,5</sup>, David A. Moeller<sup>6</sup>, and Allison K. Shaw<sup>2</sup>

<sup>1</sup>Division of Biological Sciences, University of Missouri, Columbia, MO, U.S.A.

<sup>2</sup>Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, MN, U.S.A.

<sup>3</sup>Department of Veterinary Population Medicine, University of Minnesota, Saint Paul, MN, U.S.A.

<sup>4</sup>Department of Plant Pathology, University of Minnesota, Saint Paul, MN, U.S.A.

<sup>5</sup>Marine and Environmental Sciences, Northeastern University, Boston, MA, U.S.A.

<sup>6</sup>Department of Plant and Microbial Biology, University of Minnesota, Saint Paul, MN, U.S.A.

First published: 25 September 2020

This is the peer reviewed version of the following article:

LL Sullivan, MJ Michalska-Smith, KP Sperry, DA Moeller, and AK Shaw. "Consequences of ignoring dispersal variation in network models for landscape connectivity." *Conservation Biology* 35, no. 3 (2021): 944-954.

which has been published in final form at <https://doi.org/10.1111/cobi.13640>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions. This article may not be enhanced, enriched or otherwise transformed into a derivative work, without express permission from Wiley or by statutory rights under applicable legislation. Copyright notices must not be removed, obscured or modified. The article must be linked to Wiley's version of record on Wiley Online Library and any embedding, framing or otherwise making available the article or pages thereof by third parties from platforms, services and websites other than Wiley Online Library must be prohibited.

## 1 **Abstract**

2 Habitat loss and fragmentation can negatively impact population persistence and biodiversity,  
3 but these effects can be mitigated if species successfully disperse between isolated habitat  
4 patches. Network models are the primary tool for quantifying landscape connectivity, yet as  
5 practiced, they take an overly simplistic view of species dispersal. These models often ignore  
6 individual variation in dispersal ability, assuming all individuals move the same fixed distance  
7 with equal probability. Here we develop a modeling approach to address this problem. We  
8 incorporate dispersal kernels into network models to determine how individual variation in  
9 dispersal alters our understanding of landscape-level connectivity, and test our approach on a  
10 fragmented grassland landscape in Minnesota. We show that ignoring dispersal variation  
11 consistently overestimates a population's robustness to local extinctions while simultaneously  
12 underestimating its robustness to local habitat loss. Furthermore, a simplified view of dispersal  
13 underestimates the amount of habitat sub-structure for small populations but overestimates  
14 habitat sub-structure for large populations. Our results demonstrate that considering biologically  
15 realistic dispersal alters our understanding of landscape connectivity for ecological theory and  
16 conservation practice.

17

## 18 **Introduction**

19 Loss of habitat due to land-use alteration is one of the largest anthropogenic threats to  
20 Earth's planetary systems (Rockström 2009), contributing to major declines in biodiversity  
21 (Newbold et al. 2016) and other ecosystem services (Haddad et al. 2015). Habitat loss  
22 fundamentally alters landscapes by simultaneously decreasing the overall amount of native  
23 habitat, and changing how the remaining habitat patches are arranged with respect to each other

24 through fragmentation *per se* (Fahrig 2017). The negative effects of fragmentation (Fletcher et  
25 al. 2018) can be mitigated if species are still able to move between physically isolated habitat  
26 patches, maintaining connectivity. However, the extent of species' movement among patches  
27 remains an open question (Fahrig 2017). Thus, a complete understanding of the degree to which  
28 current (Haddad et al. 2015) and ongoing (Wright & Wimberly 2013) fragmentation disrupts  
29 connectivity requires accounting for potential species movement among patches.

30       Recent work examining how organisms move among fragmented patches draws on  
31 network modelling (e.g. Saura & Rubio 2010; Fletcher et al. 2013; Ziólkowska et al. 2014;  
32 Wimberly et al. 2018). This approach converts spatial data on habitat locations to networks (or  
33 graphs), where nodes represent habitat patches and two patches are connected by an edge if  
34 organisms can disperse between them (Urban & Keitt 2001). These networks can be analyzed to  
35 inform conservation decisions by calculating patch-based or network-based 'connectivity'  
36 metrics, and identifying sets of patches that are connected via dispersal and thus function as a  
37 unit (termed components). Network modelling has enabled researchers and managers to infer  
38 connectivity, identify habitat patches with high conservation value, and quantify the scale of  
39 dispersal necessary to maintain connectivity (e.g. O'Brien et al. 2006; Saura & Rubio 2010;  
40 Creech et al. 2014; Wimberly et al. 2018). Generally, while models that infer connectivity tend  
41 to take into account detailed information about matrix quality between habitat patches and  
42 potential ease-of-flow through this matrix (Moilanen & Hanski 1998; McRae et al. 2008;  
43 Wimberly et al. 2018), they often make simplistic assumptions about species' movement  
44 dynamics. Specifically, network models, particularly unweighted or binary networks that simply  
45 consider whether or not patches are connected, tend to define species' dispersal as a single fixed  
46 distance, effectively assuming that all individuals are equally able to disperse up to that distance,

47 and unable to disperse past that distance. Building network models with the same sets of  
48 simplifying assumptions limits our ability to understand how a broad range of biological factors  
49 (such as dispersal behavior) influence connectivity, which is especially problematic since  
50 dispersal variation can have many consequences (Snell et al. 2019; Shaw 2020). Simplified  
51 dispersal assumptions may over- or under-estimate the degree of connectivity, or fail to capture  
52 important connectivity patterns altogether, thereby preventing accurate estimations of landscape-  
53 level habitat use.

54 An alternative to viewing dispersal as fixed, is to account for variation in dispersal, thus  
55 more accurately representing movement behavior. Inherent variation among individuals (e.g. sex,  
56 personality, body condition), populations (e.g. density), and the environment (e.g. habitat quality,  
57 habitat configuration, and season) can cause differences in dispersal ability (Snell et al. 2019;  
58 Shaw 2020). This dispersal variation can be captured with a dispersal kernel, that describes the  
59 proportion of individuals traveling any given distance (Shoemaker et al. 2020). Dispersal kernels  
60 thus account for variation in distance traveled as well as variation in the proportion of the  
61 dispersing population traveling each distance (Kot et al. 1996). In most species, the majority of  
62 dispersing individuals travel short distances, remaining close to their source location and thus  
63 contributing to local population dynamics (Moles & Westoby 2004). Simultaneously, few  
64 individuals move longer distances and they drive processes like colonization (Soons et al.  
65 2004b), range expansions (Kot et al. 1996) and range shifts (Davis & Shaw 2001). This ‘long-  
66 distance dispersal’ is often defined by the distance travelled by the farthest 1% of individuals  
67 (Nathan 2006). Finally, population size can influence dispersal; populations with more  
68 dispersing individuals will more fully ‘realize’ the dispersal kernel – thus being more likely to  
69 successfully reach farther distances. Although network models have the potential to account for

70 variation in dispersal (i.e. via weighted edges, Shanafelt et al. 2017), most either assume fixed  
71 dispersal (e.g. Minor et al. 2009), or use weighted edges to describe how easily an organism can  
72 move through a given matrix, ignoring dispersal variation (e.g. Ziółkowska et al. 2014;  
73 Wimberly et al. 2018). Those network models that do consider dispersal as a function of distance  
74 tend to do so by using simulated draws from dispersal kernels (Fletcher et al. 2011, 2013).  
75 Models that more fully explore weighted networks using dispersal kernels would allow for a  
76 more nuanced representation of species' movement capacity, and provide a better understanding  
77 of habitat connectivity and the impacts of fragmentation. A deeper understanding of connectivity  
78 would influence both the conservation of rare and threatened species that have had natural  
79 movement patterns altered by fragmentation, as well as the control of invasive species that have  
80 strong movement abilities that are unaltered by fragmentation (Damschen et al. 2008).

81       Here, we create a series of deterministic network models to ask the question: how does  
82 variation in dispersal alter estimates of landscape connectivity? First, we generate networks  
83 based on fixed dispersal distances, allowing us to compare our results to previous studies (e.g.  
84 Urban & Keitt 2001; O'Brien *et al.* 2006; Wimberly *et al.* 2018). Then, we generate networks  
85 based on dispersal kernels, which incorporate variation in dispersal and include the effect of  
86 population size. By comparing networks created either with fixed dispersal distances or with  
87 dispersal kernels, we explore how variation in dispersal alters our understanding of aspects of  
88 landscape connectivity including: habitat sub-structure, robustness to habitat loss, and robustness  
89 to local extinction. Our approach provides a starting point for conservation managers interested  
90 in understanding how traditional methods might over- or under-estimate connectivity based on  
91 simplified assumptions about dispersal. We apply these models to the fragmented grasslands in  
92 Minnesota (Fig. 1), where there is renewed interest from state and local managers in considering

93 connectivity in their restoration efforts. Minnesota managers have created plans for protecting  
94 existing grasslands and building future restorations to promote connectivity through the creation  
95 of grassland corridors (Minnesota Prairie Plan Working Group 2018), yet these plans were  
96 designed with very minimal information on species movement because little is known. Thus,  
97 Minnesota grasslands are an excellent study system to demonstrate the utility of our broader  
98 approach because prior knowledge of, and interest in, connectivity exists, and managers there are  
99 open to considering how to incorporate more realistic information on species' dispersal into  
100 future conservation plans (Minnesota Prairie Plan Working Group 2018; Wimberly et al. 2018;  
101 Sperry et al. 2019).

102

### 103 **Materials and Methods**

104 We created deterministic network models with and without dispersal kernels in order to  
105 draw conclusions about how including biologically meaningful knowledge of dispersal alters  
106 predictions about connectivity as compared to ignoring dispersal variation. We assumed that  
107 dispersal kernels more accurately represent species movement than the assumption of fixed  
108 models where all individuals travel all distances with equal likelihood. Our models are general,  
109 and thus could apply to any species of interest, including Minnesota grasslands species across a  
110 range of dispersal distances: prairie coneflower (~9m; Ison et al. 2014), ground squirrels (53-  
111 80m; Rongstad 1965), dickcissels (222m; Walk et al. 2004), and burrowing owls (2802m; Catlin  
112 & Rosenberg 2008) – all indicating mean dispersal distances.

113

### 114 ***Habitat Selection***

115 We developed our models for the prairie region of western and southern Minnesota (also  
116 called the prairie parkland region). This region was historically grassland but has been  
117 fragmented and reduced to ~1% of its original area (Minnesota Prairie Plan Working Group  
118 2018). The spatial locations of the remaining grasslands are well documented, and exist in a  
119 matrix of mostly agriculture. We refer to each separate grassland fragment as a ‘patch’  
120 throughout. To build our networks, we used a comprehensive spatial grassland habitat database  
121 for the region (The Nature Conservancy 2015). This dataset combined the Minnesota  
122 Department of Natural Resources’ native prairie layer, the United States Fish and Wildlife  
123 Services’ (USFS) Habitat and Population Evaluation Team’s (HAPET) 2014 reclassification  
124 dataset, and the United States Department of Agriculture’s Cropland Data Layer (CDL) dataset.  
125 The USFS National Wetlands Inventory layer was used for corrections in classifying wetland  
126 and open water areas. The resulting database consisted of all grassland types, including native  
127 remnant prairie, reconstructed or disturbed grasslands, and hay/pasture fields. We included all of  
128 these grassland types in our network analysis because they represent potentially suitable habitat  
129 for grassland species (e.g. birds, insects, mammals, plants). Similar to Wimberley et al. (2018)  
130 we used ArcGIS 10.4 to select patches that were five acres (2.023 ha) or larger. This resulted in  
131 ~37,000 grasslands ( $N=37,091$  patches in the network, see Appendix S1 for all parameters) to  
132 use in our connectivity analysis (Fig. 1a,b).

133

#### 134 *Networks Using Fixed Dispersal Distances*

135 First, we generated networks for our grasslands assuming that organisms had no dispersal  
136 variation (i.e. all individuals traveled a fixed dispersal distance). To do this, we calculated the  
137 nearest-edge distance (i.e. the distance between the closest points) of all pairs of patches in

138 ArcGIS using the geodesic method, and a max search radius of 4000m (Fig. 1c). We chose this  
139 radius, which is within the range used in similar studies (Wimberly et al. 2018), for  
140 computational simplification, but note that it is smaller than the movement ability of extremely  
141 vagile Minnesota grassland species (e.g. the red fox disperses on average ~31,000m; Storm et al.  
142 1976). We then generated 2000 networks, one for each fixed dispersal distance ( $d'$ ) that we  
143 considered (1,...,2000m). For each dispersal distance  $d$ , we generated a binary adjacency matrix  
144  $A$  (of size  $N \times N$ ) where each element described whether (1) or not (0) the distance between a  
145 pair of patches was less than  $d$  (i.e., whether an individual traveling that distance could move  
146 between these two patches). This generated 2000 binary adjacency matrices  $A$  (of size  $N \times N$ )  
147 where each element described whether (1) or not (0) two patches were connected for each  
148 dispersal distance. We then used each matrix to create a non-directed network using the igraph  
149 package in R (Csardi & Nepusz 2006). To guide readers through our methods, we also created a  
150 'toy' network (Fig. 2a).

151

### 152 *Networks Using Dispersal Kernels*

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

$$157 \quad e^{-bd} \quad (1)$$

158 with rate parameter,  $b$ . This distribution is commonly used as a dispersal kernel since it often  
159 matches empirical data (Hovestadt et al. 2011; Shaw et al. 2019). As with the fixed distance  
160 networks, here we also considered 2000 dispersal distances. However instead of considering

161 these to be the exact distances traveled, we considered these to be the farthest 1% value ( $d^*$ ) for  
 162 defining ‘long-distance dispersal’ for our dispersal kernels. Thus we established a dispersal  
 163 kernel for each  $d_x^*$  value ( $x = 1, \dots, 2000\text{m}$ ) as follows. We determined the proportion of  
 164 individual dispersing each distance  $d$  or more, given by the complementary cumulative  
 165 distribution function (CCDF) for the exponential kernel (Fig. 3a). We set this proportion  $f$  to be  
 166 0.01, plugged in each  $d_x^*$ , and solved for the corresponding  $b_x$  value (Fig. 3c), that is

$$167 \quad b_x = \frac{-\ln(0.01)}{d_x^*}. \quad (2)$$

168 This  $b_x$  value describes a dispersal kernel where only 1% of individuals dispersed a distance of  
 169  $d_x^*$  or further. Next, we calculated the nearest-edge distance between all pairs of patches up to a  
 170 maximum distance of 4000m, resulting in a Euclidian distance matrix,  $\mathbf{D}$  (Fig. 3b). Setting a  
 171 maximum distance for these calculations (rather than calculating all pairwise distances) saved  
 172 computational time while ensuring we calculated all relevant distances needed for our kernels  
 173 below. Finally, for each dispersal distance  $d_x^*$  we converted the distance matrix,  $\mathbf{D}$ , into a matrix  
 174  $\mathbf{M}_x$ , describing the proportion of the modelled population that disperses between each patch (Fig.  
 175 3c). To do this, for each  $d_x^*$  value, we used the CCDF to calculate the proportion of individuals  
 176  $m(i,j)$  with dispersal kernel defined by  $b_x$  that would travel at least the distance  $d(i,j)$  between  
 177 each patch  $i$  and  $j$ . We then used these  $\mathbf{M}_x$  matrices to generate weighted non-directed networks,  
 178 where the weight of each edge corresponds to the proportion of dispersing individuals that can  
 179 move between the two patches the edge connects.

180 Finally, we explored the influence of population size on connectivity metrics. A dispersal  
 181 kernel describes the distribution of distances that would be observed across a very large number  
 182 of dispersal events. However, since species vary in population size and fecundity, they will also  
 183 vary in how well the kernel is ‘realized’. These differences will appear most strongly for the low-

184 probability longer distances (the dispersal kernel tail); a species with a smaller population size or  
185 lower fecundity will have fewer realized dispersal events and thus across the population there  
186 will be fewer dispersal distances represented by the tail of the kernel. To mimic different  
187 population sizes with our models, we thresholded the matrix  $M$  at three values, by keeping the  
188 75% highest dispersal probabilities (i.e. setting to zero all dispersal probabilities less than 25%;  
189 ‘75%-realized’, representing a small population), 99% (‘99%-realized’, medium population), and  
190 99.99% (‘99.99%-realized’, large population). This is equivalent to truncating the dispersal  
191 kernel at three increasingly long maximum distances, but does not incorporate uncertainty and  
192 represents the simplifying assumption that small populations are less likely to reach longer  
193 distances than large populations. Imposing a maximum dispersal distance also kept the dispersal  
194 kernel from becoming infinite (i.e. there is a very small proportion of individuals dispersing  
195 infinitely far). We note that an alternative approach to examining population size is to multiply  
196 all weighted edges within the network by these proportions (for large populations, 0.9999, for  
197 medium populations 0.99, for small populations 0.75), and then conduct network analyses. This  
198 approach leads to qualitatively similar results for patch-level metrics to those we present here  
199 (Appendix S2).

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

204

205 ***Connectivity Metrics***

206 *Network-level Metrics*

207 For each network generated with fixed dispersal (non-weighted) and dispersal kernels  
208 (weighted), we calculated three network-level metrics (Fig. 2b), to quantify different aspects of  
209 network structure and connectivity. The first two metrics do not take into account weights and  
210 thus were calculated the same way for both non-weighted (binary) and weighted networks. (1)  
211 Number of components, (see Appendix S3 for igraph functions): two patches are in the same  
212 component if they are connected by an edge; fully isolated patches are their own component.  
213 Patches in different components are isolated from each other, thus the number of separate  
214 components in a network provides a rough sense of overall fragmentation across the network  
215 (Calabrese & Fagan 2004). (2) Maximum component size: the number of patches in the largest  
216 component of the network provides a measure of effective network size (Urban & Keitt 2001).  
217 Both the number of components and the size of the largest component represent an estimate of  
218 the amount of habitat sub-structure present. (3) Average clustering coefficient: this metric  
219 quantifies the extent to which a network contains well-connected clusters of patches and thus  
220 provides an estimate of local landscape connectivity. In non-weighted networks, for a given  
221 patch  $i$ , that is connected to  $k_i$  neighboring patches (see patch-level metrics below), there can be  
222 at most

$$223 \quad (1/2) k_i (k_i - 1) \quad (3)$$

224 connections among its neighboring patches. The clustering coefficient for this patch is the  
225 fraction of those possible connections that actually occur (Watts & Strogatz 1998), a metric used  
226 to quantify the local connectivity for landscape networks (Wimberly et al. 2018). Average  
227 clustering coefficient can be considered a measure of robustness to habitat loss, as networks with  
228 higher clustering will more easily maintain their sub-structure even as habitat fragmentation  
229 removes either edges or patches. For weighted networks, we used weighted distances between

230 patches based on dispersal proportion (Csardi & Nepusz 2006). This weighted clustering  
 231 coefficient is calculated as

$$232 \quad \frac{1}{s_i(k_i - 1)} \sum_{j,h} \left\{ \frac{1}{2} [m(i,j) + m(i,h)] a(i,j) a(i,h) a(j,h) \right\} \quad (4)$$

233 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  
 234 of the weighted matrix  $\mathbf{M}$ , and  $a(i,j)$  are the elements of the adjacency matrix  $\mathbf{A}$ . We note that  
 235 there was little difference between the mean and median values for clustering coefficient, except  
 236 for small to moderate dispersal distances in the ‘75%-realized’ kernels where the mean value was  
 237 larger than the median value (Appendix S4).

238

#### 239 *Patch-level Metrics*

240 For each patch within each network, we also calculated two patch-level metrics (Fig. 2c),  
 241 and summarized them by looking at the 25<sup>th</sup>, 50<sup>th</sup>, and 75<sup>th</sup> quantiles of all values for patches  
 242 within each network. (1) Degree centrality: for non-weighted networks, this metric is calculated  
 243 as the number of connected neighbors each patch has ( $k_i$ ), i.e. the number of patches that an  
 244 individual could potentially reach via dispersal as defined by the model (Wimberly et al. 2018).  
 245 For weighted networks we calculated strength, the weighted version of degree centrality, as

$$246 \quad s_i = \sum_j m(i,j) \quad (5)$$

247 where  $m(i,j)$  are the elements of the weighted matrix  $\mathbf{M}$  for all connected neighbors  $j$  of patch  $i$ .  
 248 Degree centrality or strength quantifies the number of colonization opportunities to or from each  
 249 patch and represents a measure of short-term robustness to local (patch-level) extinction. Patches  
 250 with low degree/strength are likely to be isolated and vulnerable to reductions in species richness  
 251 as any local extinction would be unlikely to be recovered by recolonization from other patches.

252 (2) Closeness centrality: for non-weighted networks, this metric quantifies the importance of  
 253 each patch  $i$  for overall connectivity in the network as

$$254 \quad \frac{1}{\sum_{i \neq j} p_{ij}} \quad (6)$$

255 where  $p_{ij}$  is the shortest path, or the number of steps (i.e. sequential dispersal events) it takes to  
 256 reach every other patch  $j$  in the network from the focal patch. If two patches are not connected  
 257 (i.e.  $p_{ij}$  is infinite), the total number of patches ( $N$ ) is used instead of  $p_{ij}$  for this pair. Thus  
 258 closeness is a measure of the average number of sequential dispersal events required to  
 259 recolonize the network, and represents a measure of long-term robustness to local extinction. We  
 260 chose closeness as our centrality metric (rather than ‘betweenness’ as used by Minor and Urban  
 261 (2007)) because closeness more accurately represents dispersing organisms that do not always  
 262 take the most efficient route between patches (Borgatti 2005). For weighted networks, we  
 263 calculated a weighted version of closeness, as

$$264 \quad \frac{1}{\sum_{i \neq j} q_{ij}} \quad (7)$$

265 where  $q_{ij}$  is the sum of inverse probabilities  $m^{-1}$  along the shortest path between patch  $i$  and patch  
 266  $j$ . Since the inverse of the proportion of dispersers gives an expected number of events needed  
 267 (e.g., a 0.5 proportion of dispersers would take about 2 dispersal events), weighted closeness is  
 268 again a measure of long-term robustness to local extinction because it tallies the expected  
 269 number of sequential dispersal events required to recolonize the entire network. As for non-  
 270 weighted networks, if two patches are not connected, the total number of patches ( $N$ ) is used  
 271 instead of  $q_{ij}$  for that pair. Note that this correction for unconnected patches (while a suitable  
 272 approximation for non-weighted networks) is actually an underestimate of the number of  
 273 sequential dispersal events for weighted networks. Since the degree to which it underestimates  
 274 dispersal events (and thus overestimates weighted closeness) interacts with the different

275 population sizes we considered, there is no meaningful way to compare across different  
276 truncations of the dispersal kernels for this metric. Thus, we only calculated weighted clustering  
277 coefficient for the networks based on the ‘99%-realized’ dispersal kernels.

278 All analyses were run in R v3.4.4 (R Core Team 2017), data and code are available at the  
279 Dryad Digital Repository xxxxx.

280

## 281 **Results**

### 282 *Network-level Metrics*

283 Networks were less fragmented (had less habitat sub-structure) for larger dispersal  
284 distances, with fewer components (Fig. 4a) and larger largest components (Fig. 4b). These  
285 relationships were starkest for networks created from dispersal kernels with longer realized  
286 kernel tails (i.e. larger population size or higher fecundity). In other words, the ‘99.99%-realized’  
287 kernel showed the fastest drop in the number of components, and the fastest increase in size of  
288 largest component with increasing  $d^*$ , while the ‘75%-realized’ dispersal kernel showed a  
289 markedly slower decrease in the number of components and slower increase in maximum  
290 component size with increasing  $d^*$ . The fixed dispersal distance produced accurate estimates for  
291 populations of intermediate size (the ‘99%-realized’ dispersal kernel, Fig. 4a-b). Intuitively, this  
292 result occurs because a network from a fixed dispersal distance of  $d'$  is structurally equivalent to  
293 a network with a ‘99%-realized’ dispersal kernel with distance  $d^*$  (the same patches are  
294 connected in both when considering non-weighted (or binary) network metrics like the number  
295 of components and largest component size). However, fixed dispersal distance underestimated  
296 habitat sub-structure for smaller populations (‘75%-realized’) and overestimated habitat sub-  
297 structure for larger populations (‘99.99%-realized’).

298 Networks were also more connected for larger dispersal distances, with higher clustering  
299 coefficients (Fig. 4c). In other words, populations with larger dispersal distances are more robust  
300 to habitat loss leading to lost patches or connections. However, the fixed dispersal distance  
301 consistently underestimated robustness to habitat loss compared to all three population sizes  
302 ('75%-, 99%-, 99.99%-realized' dispersal kernels, Fig. 4c), with the largest difference for the  
303 largest population sizes ('99.99%-realized' kernel). The fixed network and the '75%-realized'  
304 kernel produced similar results for low dispersal distances, but the clustering coefficient then  
305 plateaued for the fixed distance while the '75%-realized' kernel continued to increase for larger  
306 dispersal distances.

307

#### 308 *Patch-level Metrics*

309 Patches in networks with larger dispersal distances were on average connected to more  
310 neighbor patches (higher degree centrality, Fig. 5a), representing a higher short-term robustness  
311 to local extinctions. Networks from fixed dispersal distances consistently overpredicted  
312 robustness compared to networks from dispersal kernels, a gap that increased with dispersal  
313 distance. In other words, fixed kernel networks systematically overpredict the number of  
314 neighbors (and thus expected number of recolonization opportunities) each patch has, compared  
315 to dispersal kernel networks. Within the dispersal kernel networks, smallest populations ('75%-  
316 realized' kernel) had patches with the lowest robustness, followed by medium ('99%-realized')  
317 and large ('99.99%-realized') population sizes, however these ranges overlapped substantially.  
318 Similarly, patches in networks with larger dispersal distances had higher closeness values (Fig.  
319 5b). Fixed dispersal distances consistently overpredicted closeness, and thus underpredicted the

320 number of sequential dispersal events needed to recolonize a network following extinction,  
321 compared to the networks created with dispersal kernels.

322

## 323 **Discussion**

324 We built deterministic network models from fixed dispersal distances and dispersal  
325 kernels, and contrasted them to more fully explore how weighted networks that use dispersal  
326 kernels affect estimates of landscape connectivity. As with other simulation-based connectivity  
327 models that incorporate dispersal variation (Palmer et al. 2014), we found that network models  
328 based on dispersal kernels generated a markedly different understanding of population  
329 connectivity than network models based on a fixed dispersal distance (Figs. 4-5, Appendix S5).  
330 Specifically, using fixed dispersal consistently overestimated a population's robustness to local  
331 extinctions while simultaneously underestimating robustness to habitat fragmentation. Our  
332 results from fixed dispersal distances qualitatively match similar network analyses for other  
333 grasslands (Wimberly *et al.* 2008) and for forests (Urban & Keitt 2001), suggesting that current  
334 habitat management using fixed dispersal networks is based on inaccurate estimates of  
335 population connectivity. As there is ample evidence that most organisms have substantial  
336 variation in dispersal (e.g. Baguette 2003; Krkošek et al. 2007; Sullivan et al. 2018), connectivity  
337 models must account for such variation by using dispersal kernels. Other network models that  
338 use dispersal kernels to match empirical movement data find these methods to be a good  
339 approximation of movement ability (Fletcher et al. 2011, 2013). These findings have  
340 implications for managers that plan for conservation based on connectivity metrics. Some  
341 species of concern may need more total habitat, while others rely on continual recolonization and  
342 thus would differ in whether fixed models over- or underestimated their connectivity.

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

353           In light of our results, explicit consideration of conservation goals can help guide the  
354 appropriate use of dispersal kernels for management and planning. Inherent in the use of  
355 dispersal kernels is the understanding that most individuals move shorter distances, and few  
356 individuals move farther distances. Therefore, the conservation goals at the heart of maintaining  
357 connectivity should take population size into account when appropriate. For example, often the  
358 goal of promoting connectivity between patches is to build a functioning meta-population for  
359 rare species where individuals can move freely and breed between patches (Hanski 1998). As  
360 rare or threatened species are often dispersal-limited due to small population sizes and low  
361 fecundity (Baur 2014), considering a less realized dispersal kernel (i.e. '75%-realized') could  
362 more accurately represent likely connectivity outcomes for this particular goal. Moreover, if  
363 small population sizes are of serious concern, other methods might need to be incorporated,  
364 including individual based models (Grimm & Railsback 2005). Another goal of maintaining  
365 connectivity might be to allow for the possibility of species' response to climate change via

366 range shifts (Krosby et al. 2010). Range expansions often proceed through the dispersal of a few  
367 individuals over a long distance (Davis & Shaw 2001). To successfully track climate change,  
368 large populations must produce the few individuals that disperse long distances, thus a more  
369 realized dispersal kernel (i.e. '99.99%-realized') would be more appropriate to include in  
370 network models to achieve this goal. Consideration of these highly realized dispersal kernels is  
371 also appropriate for controlling invasive species like the cane toad, which have high movement  
372 ability (Perkins et al. 2013). Finally, for sessile organisms like plants, managers might be  
373 interested in distinguishing between maintaining high genetic diversity to decrease the  
374 probability of inbreeding depression - which requires the movement of gametes (i.e. pollen),  
375 versus allowing for species recolonization to increase species diversity - which requires the  
376 movement of individuals (i.e. seeds) (Elistrand 1992; Brudvig et al. 2009). In this case managers  
377 should consider defining dispersal kernels that represent pollen and seed dispersal separately in  
378 order to match their management goals. When looking to define dispersal kernels, managers can  
379 use measurement-based (e.g. Stevens et al. 2010), trait-based (e.g. Soons et al. 2004a), or  
380 genetic-based approaches (e.g. Bacles et al. 2006) to estimate kernels.

381         Grasslands are globally important, yet they are among the most threatened due to land  
382 use conversion and fragmentation (Soons et al. 2005; Newbold et al. 2016). Our network models  
383 help elucidate how likely species are able to move between grassland patches and maintain  
384 connectivity at a broader scale. Our results are comparable to Wimberly et al. (2018), which  
385 determined connectivity of the grasslands in the Prairie Coteau region of Minnesota and the  
386 Dakotas, but use a fixed dispersal distance. Extrapolating their results based on our findings from  
387 network models with dispersal kernels, we might expect that for species with large population  
388 sizes there might be increased connectivity, with fewer, larger components that are more robust

389 to fragmentation than what Wimberly et al. (2018) found, but we might expect the opposite for  
390 species with smaller populations. To aid Minnesota grassland managers, we have created a web-  
391 based app to allow for the direct application of network models to existing grasslands in  
392 Minnesota (Sperry et al. 2019). This approach could be easily updated to incorporate known  
393 dispersal kernel information for species of interest (e.g. grassland plant species - Sullivan et al.  
394 2018), patch prioritization, or matrix quality between patches (Castillo et al. 2016), which would  
395 afford a more targeted understanding of which species can maintain connectivity, and which  
396 might require assistance moving between patches.

397

## 398 **Conclusions**

399 In order to understand if and where connectivity is maintained between isolated habitat  
400 fragments, we must account for how organisms move in a biologically meaningful way. We take  
401 steps toward this goal by considering variability in dispersal in network models by incorporating  
402 fully explored dispersal kernels, to determine how this alters our view of network-based  
403 connectivity as compared to standard methods that use a fixed dispersal distance. Since  
404 interspecific dispersal variation is also common, future work should examine how dispersal  
405 varies across species (e.g., when different species have different dispersal kernel shapes), and  
406 when there is directionality in dispersal to understand more fully how interspecific variation  
407 affects connectivity. We find that models ignoring dispersal variation simultaneously  
408 overestimate robustness to local extinctions while underestimating robustness to habitat loss,  
409 compared to models that account for dispersal variation. The magnitude of these differences  
410 depends both biological traits of the species of interest, particularly population size, and dispersal  
411 distance.

412 **References**

- 413
- 414 Bacles CFE, Lowe AJ, Ennos RA. 2006. Effective seed dispersal across a fragmented landscape.  
415 *Science* **311**:628.
- 416 Baguette M. 2003. Long distance dispersal and landscape occupancy in a metapopulation of the  
417 Cranberry Fritillary butterfly. *Ecography* **26**:153–160.
- 418 Baur B. 2014. Dispersal-limited species - A challenge for ecological restoration. *Basic and*  
419 *Applied Ecology* **15**:559–564.
- 420 Borgatti SP. 2005. Centrality and network flow. *Social Networks* **27**:55–71.
- 421 Brudvig LA, Damschen EI, Tewksbury JJ, Haddad NM, Levey DJ. 2009. Landscape  
422 connectivity promotes plant biodiversity spillover into non-target habitats. *Proceedings of*  
423 *the National Academy of Sciences of the United States of America* **106**:9328–32.
- 424 Calabrese JM, Fagan WF. 2004. A comparison-shopper's guide to connectivity metrics.  
425 *Frontiers in Ecology and the Environment* **2**:529–536.
- 426 Castillo JA, Epps CW, Jeffress MR, Ray C, Rodhouse TJ, Schwalm D. 2016. Replicated  
427 Landscape genetic and network analyses reveal wide variation in functional connectivity for  
428 American pikas. *Ecological Applications* **26**:1660–1676.
- 429 Catlin DH, Rosenberg DK. 2008. Breeding dispersal and nesting behavior of burrowing owls  
430 following experimental nest predation. *The American Midland Naturalist* **159**:7.
- 431 Creech TG, Epps CW, Monello RJ, Wehausen JD. 2014. Using network theory to prioritize  
432 management in a desert bighorn sheep metapopulation. *Landscape Ecology* **29**:605–619.
- 433 Csardi G, Nepusz T. 2006. The igraph software package for complex network research.  
434 *InterJournal Complex Sy*:1695.
- 435 Damschen EI, Brudvig LA, Haddad NM, Levey DJ, Orrock JL, Tewksbury JJ. 2008. The

- 436 movement ecology and dynamics of plant communities in fragmented landscapes.  
437 Proceedings of the National Academy of Sciences **105**:19078–83.
- 438 Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to Quaternary climate change.  
439 Science **292**:673–9.
- 440 Eilstrand NC. 1992. Gene flow by pollen: Implications for plant conservation genetics. *Oikos*  
441 **63**:77–86.
- 442 Fahrig L. 2017. Ecological responses to habitat fragmentation per se. Annual Review of  
443 Ecology, Evolution, and Systematics **48**:1–23.
- 444 Fletcher RJ et al. 2018. Is habitat fragmentation good for biodiversity? *Biological Conservation*  
445 **226**:9–15.
- 446 Fletcher RJ, Acevedo MA, Reichert BE, Pias KE, Kitchens WM. 2011. Social network models  
447 predict movement and connectivity in ecological landscapes. Proceedings of the National  
448 Academy of Sciences **108**:19282–19287.
- 449 Fletcher RJ, Revell A, Reichert BE, Kitchens WM, Dixon JD, Austin JD. 2013. Network  
450 modularity reveals critical scales for connectivity in ecology and evolution. *Nature*  
451 Communications **4**:1–7.
- 452 Grimm V, Railsback SF. 2005. Individual-based modeling and ecology. Princeton University  
453 Press.
- 454 Haddad NM et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems.  
455 Science Advances **1**:e1500052–e1500052.
- 456 Hanski I. 1998. Metapopulation dynamics. *Nature* **396**:41–49.
- 457 Hovestadt T, Binzenhöfer B, Nowicki P, Settele J. 2011. Do all inter-patch movements represent  
458 dispersal? A mixed kernel study of butterfly mobility in fragmented landscapes. *Journal of*

- 459        *Animal Ecology* **80**:1070–1077.
- 460 Ison JL, Wagenius S, Reitz D, Ashley M V. 2014. Mating between *Echinacea angustifolia*  
461        (*Asteraceae*) individuals increases with their flowering synchrony and spatial proximity.  
462        *American Journal of Botany* **101**:180–189.
- 463 Kot M, Lewis MA, van den Driessche P. 1996. Dispersal data and the spread of invading  
464        organisms. *Ecology* **77**:2027–2042.
- 465 Krkošek M, Lauzon-Guay J-S, Lewis MA. 2007. Relating dispersal and range expansion of  
466        California sea otters. *Theoretical Population Biology* **71**:401–407.
- 467 Krosby M, Tewksbury J, Haddad NM, Hoekstra J. 2010. Ecological connectivity for a changing  
468        climate. *Conservation Biology* **24**:1686–1689.
- 469 McRae BH, Dickson BG, Keitt TH, Shah VB. 2008. Using circuit theory to model connectivity  
470        in ecology, evolution, and conservation. *Ecology* **89**:2712–2724.
- 471 Minnesota Prairie Plan Working Group. 2018. Minnesota Prairie Conservation Plan, Second  
472        Edition.
- 473 Minor ES, Tessel SM, Engelhardt K a M, Lookingbill TR. 2009. The role of landscape  
474        connectivity in assembling exotic plant communities: a network analysis. *Ecology* **90**:1802–  
475        1809.
- 476 Minor ES, Urban DL. 2007. Graph theory as a proxy for spatially explicit population models in  
477        conservation planning. *Ecological Applications* **17**:1771–1782.
- 478 Moilanen A, Hanski I. 1998. Metapopulation dynamics: Effects of habitat quality and landscape  
479        structure. *Ecology* **79**:2503–2515.
- 480 Moles AT, Westoby M. 2004. Seedling survival and seed size: a synthesis of the literature.  
481        *Journal of Ecology* **92**:372–383.

- 482 Nathan R. 2006. Long-distance dispersal of plants. *Science* **313**:786–788.
- 483 Newbold T et al. 2016. Has land use pushed terrestrial biodiversity beyond the planetary  
484 boundary? A global assessment. *Science* **354**:288–291.
- 485 O'Brien D, Manseau M, Fall A, Fortin MJ. 2006. Testing the importance of spatial configuration  
486 of winter habitat for woodland caribou: An application of graph theory. *Biological  
487 Conservation* **130**:70–83.
- 488 Palmer SCF, Coulon A, Travis JMJ. 2014. Inter-individual variability in dispersal behaviours  
489 impacts connectivity estimates. *Oikos* **123**:923–932.
- 490 Perkins TA, Phillips BL, Baskett ML, Hastings A. 2013. Evolution of dispersal and life history  
491 interact to drive accelerating spread of an invasive species. *Ecology Letters* **16**:1079–87.
- 492 R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna,  
493 Austria. Available from <http://www.r-project.org/>.
- 494 Rockström J. 2009. A safe operating space for humanity. *Nature* **461**:472–475.
- 495 Rongstad OJ. 1965. A life history study of thirteen-lined ground squirrels in southern Wisconsin.  
496 *Journal of Mammalogy* **46**:76–87.
- 497 Saura S, Rubio L. 2010. A common currency for the different ways in which patches and links  
498 can contribute to habitat availability and connectivity in the landscape. *Ecography* **33**:523–  
499 537.
- 500 Shanafelt DW, Salau KR, Baggio JA. 2017. Do-it-yourself networks: A novel method of  
501 generating weighted networks. *Royal Society Open Science* **4**:171227.
- 502 Shaw AK. 2020. Causes and consequences of individual variation in animal movement.  
503 *Movement Ecology* **8**.
- 504 Shaw AK, D'Aloia CC, Buston PM. 2019. The evolution of marine larval dispersal kernels in

- 505       spatially structured habitats: Analytical models, individual-based simulations, and  
506       comparisons with empirical estimates. *The American Naturalist* **3**:424–435.
- 507 Shoemaker LG et al. 2020. Integrating the underlying structure of stochasticity into community  
508       ecology. *Ecology* **101**:e02922.
- 509 Snell RS et al. 2019. Consequences of intraspecific variation in seed dispersal for plant  
510       demography, communities, evolution and global change. *AoB Plants* **11**:plz016.
- 511 Soons MB, Heil GW, Nathan R, Katul GG. 2004a. Determinants of long-distance seed dispersal  
512       by wind in grasslands. *Ecology* **85**:3056–3068.
- 513 Soons MB, Messelink JH, Jongejans E, Heil GW. 2005. Habitat fragmentation reduces grassland  
514       connectivity for both short-distance and long-distance wind-dispersed forbs. *Journal of*  
515       *Ecology* **93**:1214–1225.
- 516 Soons MB, Nathan R, Katul GG. 2004b. Human effects on long-distance wind dispersal and  
517       colonization by grassland plants. *Ecology* **85**:3069–3079.
- 518 Sperry KP, Shaw AK, Sullivan LL. 2019. Apps can help bridge restoration science and  
519       restoration practice. *Restoration Ecology*:3–6.
- 520 Stevens VM, Turlure C, Baguette M. 2010. A meta-analysis of dispersal in butterflies. *Biological*  
521       *Reviews* **85**:625–642.
- 522 Storm GL, Andrews RD, Phillips RL, Bishop RA. 1976. Morphology, reproduction, dispersal,  
523       and mortality of Midwestern Red Fox populations. *Wildlife Monographs* **49**:3–53.
- 524 Sullivan LL, Clark AT, Tilman D, Shaw AK. 2018. Mechanistically derived dispersal kernels  
525       explain species-level patterns of recruitment and succession. *Ecology* **99**:2415–2420.
- 526 The Nature Conservancy. 2015. 2015 Prairie Plan Land Cover Analysis. Minneapolis, MN.
- 527 Urban D, Keitt T. 2001. Landscape connectivity: A graph-theoretic perspective. *Ecology*

528 **82**:1205–1218.

529 Walk JW, Wentworth K, Kershner EL, Bollinger EK, Warner RE. 2004. Renesting decisions and  
530 annual fecundity of female Dickcissels (*Spiza americana*) in Illinois. *The Auk* **121**:1250–  
531 1261.

532 Watts DJ, Strogatz SH. 1998. Collective dynamics of “small-world” networks. *Nature* **393**:440–  
533 442.

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

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

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

542

543

544

545 **Figure Legends**

546 Figure 1. (a) Map of the location of the ~37,000 grassland patches across Minnesota used in our  
547 network analysis, as well as (b) the histogram showing distances between patches up to 4000m  
548 (the max our models examined). Examples of a subset of the network (from Clay County, MN)  
549 showing patches and connections under (c) the fixed distance (with  $d' = 2000$ ) and (d) dispersal  
550 kernel (with  $d^* = 2000$  and '99%-realized'). In panel (d) thicker lines correspond to a higher  
551 proportion of dispersers between patches.

552  
553 Figure 2. (a) Toy network with nine patches (points labeled A-I) and two components, where  
554 numbers along edges indicate the probability that two patches are connected via dispersal – used  
555 for calculating weighted metrics. When calculating non-weighted metrics, the probability values  
556 along connections become 1. (b) Network-level metrics calculated for this network. (Since  
557 clustering coefficient only counts nodes with degree > 1, the only nodes used for these  
558 calculations are B, G, H and I). (c) Patch-level metrics as calculated for two example patches (A  
559 and B, within component #1).

560  
561 Figure 3. Methods schematic for building networks from dispersal kernels. (a) Use the dispersal  
562 kernel (the proportion of individuals traveling a distance  $d$ ) to calculate the complementary  
563 cumulative density function (CCDF,  $f$ , the proportion of individuals traveling a distance  $d$  or  
564 more). Very few (1%) individuals travel a distance  $d^*$  or more, considered “long-distance  
565 dispersal”. (b) Use the landscape of  $N$  patches to calculate a distance matrix ( $\mathbf{D}$ , the physical  
566 distance between all pairs of patches  $i$  and  $j$ ). (c) Use the CCDF to map from each “long”  
567 distance ( $d_x^*$ ) to corresponding dispersal kernel parameter ( $b_x$ ) by setting  $f_x$  to 0.01, then use both

568 the CCDF and the distance matrix to create a corresponding weighted matrix ( $\mathbf{M}_x$ , the proportion  
569 of individuals dispersing between all pairs of patches  $i$  and  $j$ ), where  $x$  is the dispersal distance  
570 index  $x=1\dots n$ , ( $n=2000$ ). See Appendix S1 for full definitions of parameters.

571

572 Figure 4. Network-level metric values for networks with fixed dispersal distances (red) and using  
573 the exponential dispersal kernel at various tail truncations ‘75%-realized’ (dark gray), ‘99%-  
574 realized’ (medium gray) and ‘99.99%-realized’ (light gray), which represent increasing abilities  
575 for long-distance dispersal. Panels show the (a) number of components, (b) size of the largest  
576 component, which represent measures of habitat sub-structure and (c) the clustering coefficient,  
577 which represents robustness to habitat loss.

578

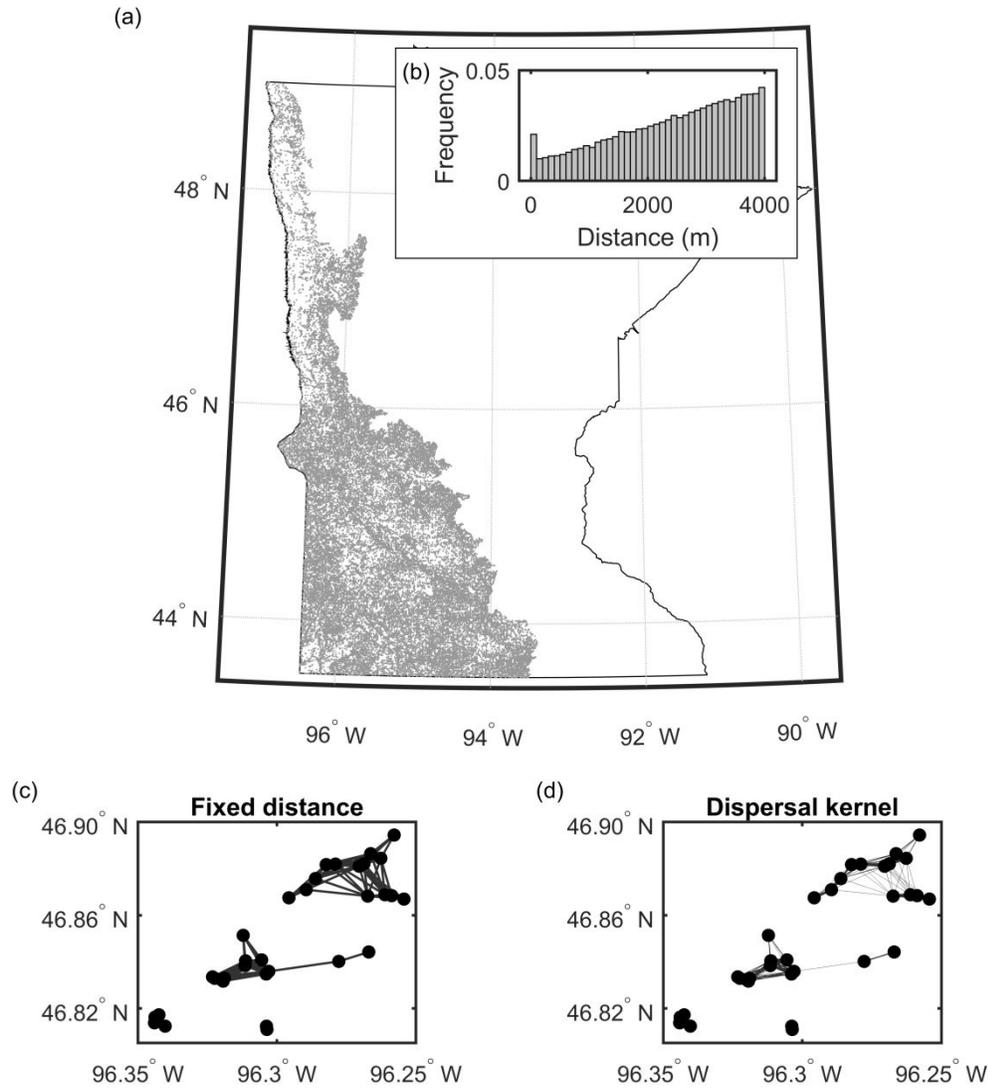
579 Figure 5. Patch-level metric values for networks with fixed dispersal distances (red), and  
580 networks with dispersal kernels, ‘75%-realized’ (dark gray), ‘99%-realized’ (medium gray) and  
581 ‘99.99%-realized’ (light gray). Panels show the 25<sup>th</sup>, 50<sup>th</sup> and 75<sup>th</sup> quantiles for (a) patch degree  
582 centrality, and (b) patch closeness which represent measures of robustness to local extinction. In  
583 panel (a), the ‘99%-realized’ (medium gray) and ‘99.99%-realized’ (light gray) are nearly  
584 overlapping with the ‘99.99%-realized’ kernel having a slightly higher degree. For clarity,  
585 asterisks represent the 50<sup>th</sup> quantile for each kernel.

586

587

588

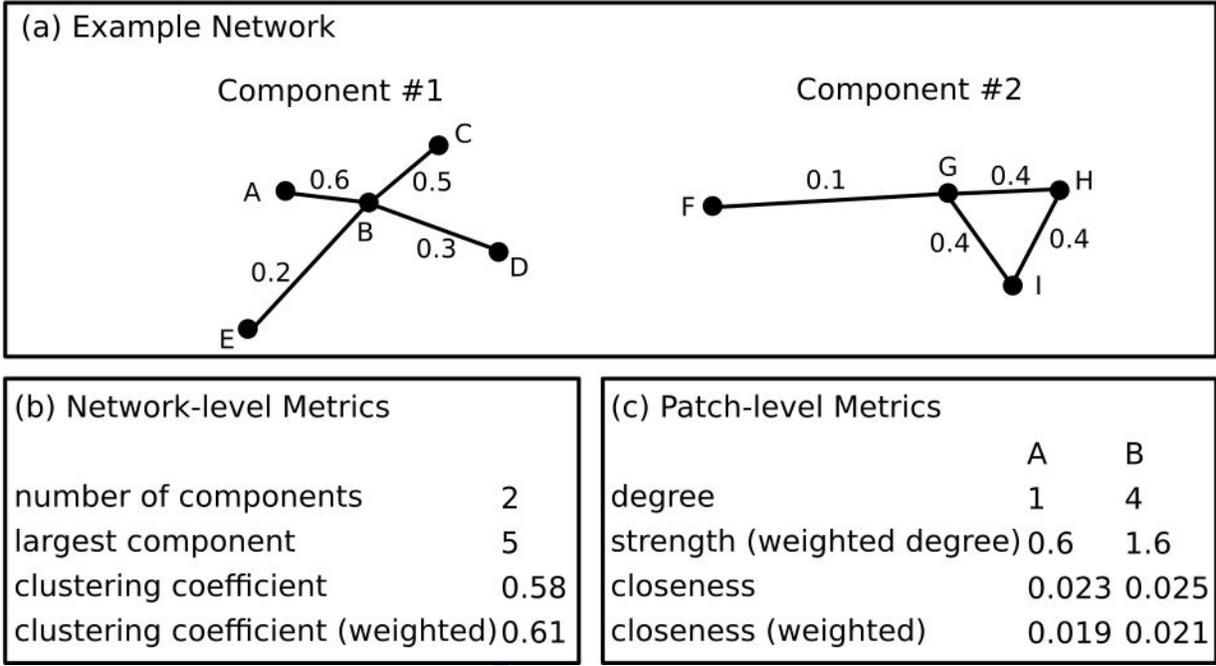
589



590

591 Figure 1. (a) Map of the location of the ~37,000 grassland patches across Minnesota used in our  
 592 network analysis, as well as (b) the histogram showing distances between patches up to 4000m  
 593 (the max our models examined). Examples of a subset of the network (from Clay County, MN)  
 594 showing patches and connections under (c) the fixed distance (with  $d' = 2000$ ) and (d) dispersal  
 595 kernel (with  $d^* = 2000$  and '99%-realized'). In panel (d) thicker lines correspond to a higher  
 596 proportion of dispersers between patches.

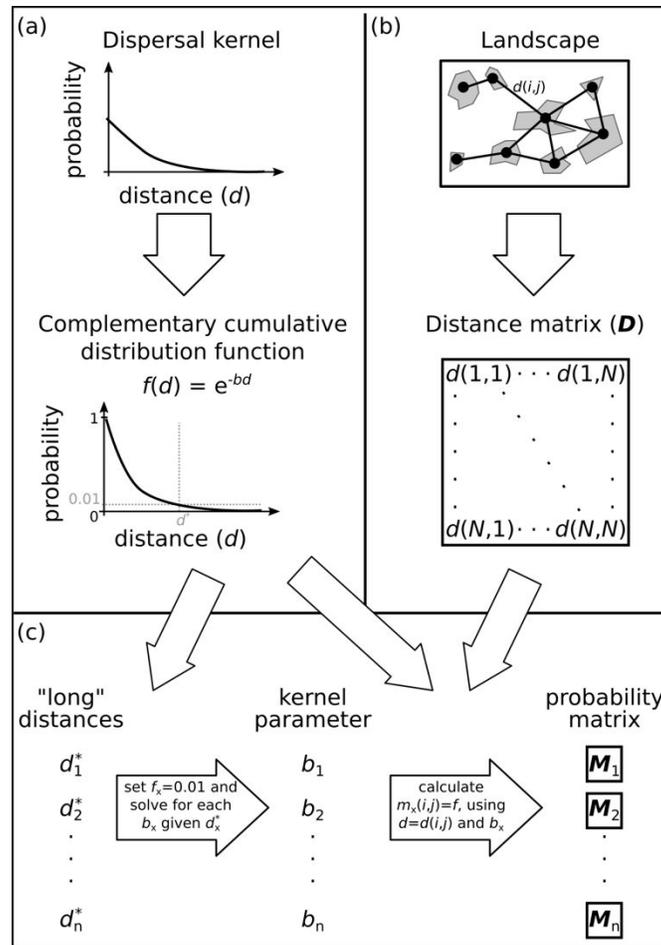
597



598

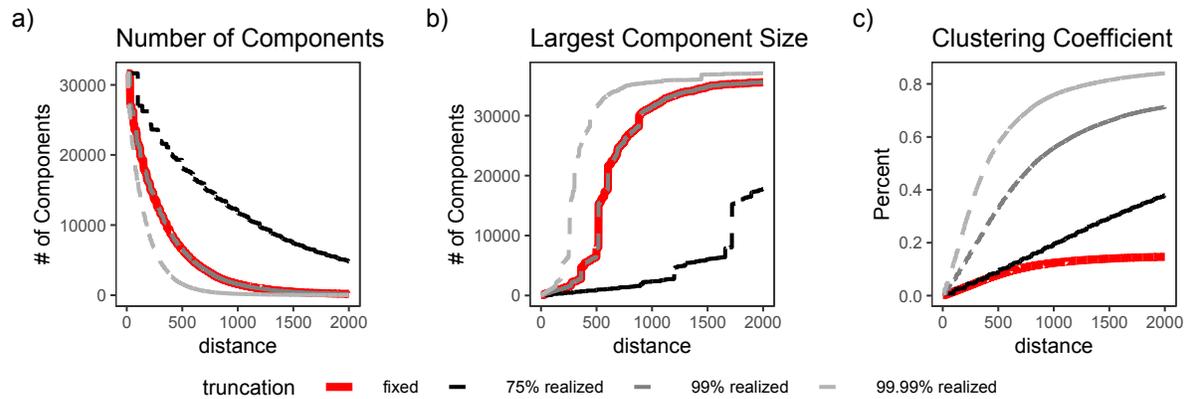
599 Figure 2. (a) Toy network with nine patches (points labeled A-I) and two components, where  
 600 numbers along edges indicate the probability that two patches are connected via dispersal – used  
 601 for calculating weighted metrics. When calculating non-weighted metrics, the probability values  
 602 along connections become 1. (b) Network-level metrics calculated for this network. (Since  
 603 clustering coefficient only counts nodes with degree>1, the only nodes used for these  
 604 calculations are B, G, H and I). (c) Patch-level metrics as calculated for two example patches (A  
 605 and B, within component #1).

606



607

608 Figure 3. Methods schematic for building networks from dispersal kernels. (a) Use the dispersal  
 609 kernel (the proportion of the population traveling a distance  $d$ ) to calculate the complementary  
 610 cumulative density function (CCDF,  $f$ , the proportion of individuals traveling a distance  $d$  or  
 611 more). Very few (1%) individuals travel a distance  $d^*$  or more, considered “long-distance  
 612 dispersal”. (b) Use the landscape of  $N$  patches to calculate a distance matrix ( $\mathbf{D}$ , the physical  
 613 distance between all pairs of patches  $i$  and  $j$ ). (c) Use the CCDF to deterministically map from  
 614 each “long” distance ( $d_x^*$ ) to corresponding dispersal kernel parameter ( $b_x$ ) by setting  $f_x$  to 0.01,  
 615 then use both the CCDF and the distance matrix to create a corresponding weighted matrix ( $\mathbf{M}_x$ ,  
 616 the proportion of individuals dispersing between all pairs of patches  $i$  and  $j$ ), where  $x$  is the  
 617 dispersal distance index  $x=1 \dots n$ , ( $n=2000$ ). See Appendix S1 for full definitions of parameters.



618

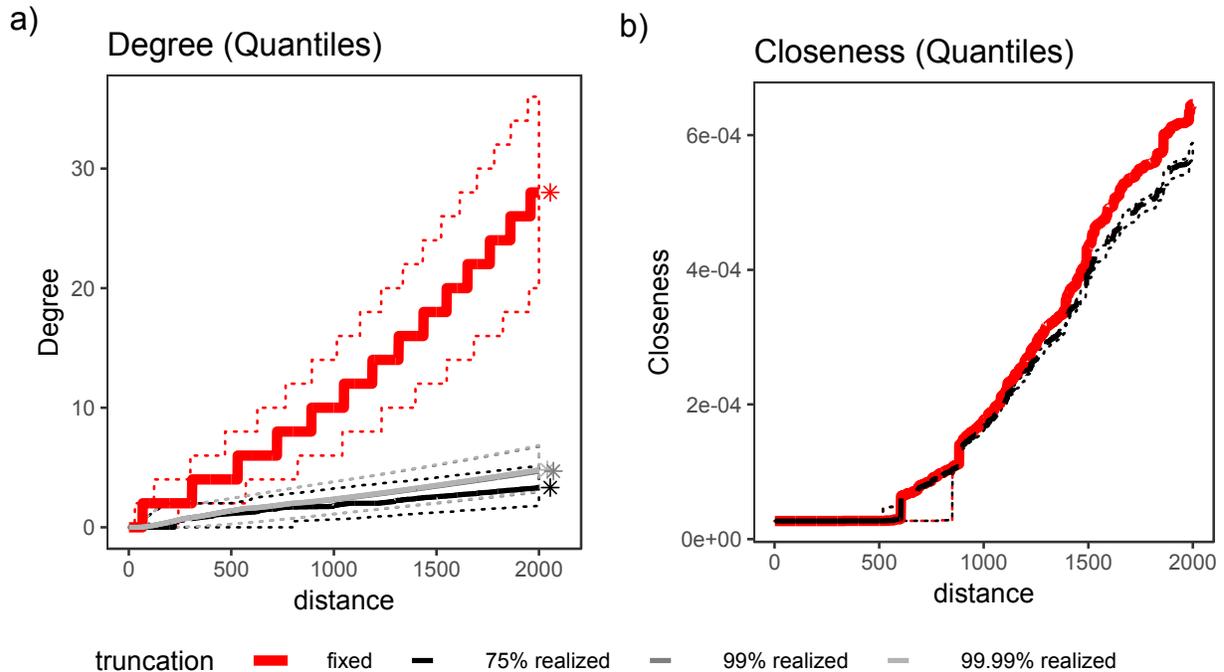
619

620 Figure 4. Network-level metric values for networks with fixed dispersal distances (red) and using  
 621 the exponential dispersal kernel at various tail truncations '75%-realized' (dark gray), '99%-  
 622 realized' (medium gray) and '99.99%-realized' (light gray), which represent increasing abilities  
 623 for long-distance dispersal. Panels show the (a) number of components, (b) size of the largest  
 624 component, which represent measures of habitat sub-structure and (c) the clustering coefficient,  
 625 which represents robustness to habitat loss.

626

627

628



629

630 Figure 5. Patch-level metric values for networks with fixed dispersal distances (red), and  
 631 networks with dispersal kernels, '75%-realized' (dark gray), '99%-realized' (medium gray) and  
 632 '99.99%-realized' (light gray). Panels show the 25<sup>th</sup>, 50<sup>th</sup> and 75<sup>th</sup> quantiles for (a) patch degree  
 633 centrality, and (b) patch closeness which represent measures of robustness to local extinction. In  
 634 panel (a), the '99%-realized' (medium gray) and '99.99%-realized' (light gray) are nearly  
 635 overlapping with the '99.99%-realized' kernel having a slightly higher degree. For clarity,  
 636 asterisks represent the 50<sup>th</sup> quantile for each kernel.

637

638

639