

Consequences of ignoring dispersal variation in network models for landscape connectivity

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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 25th, 50th, and 75th 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.

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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.

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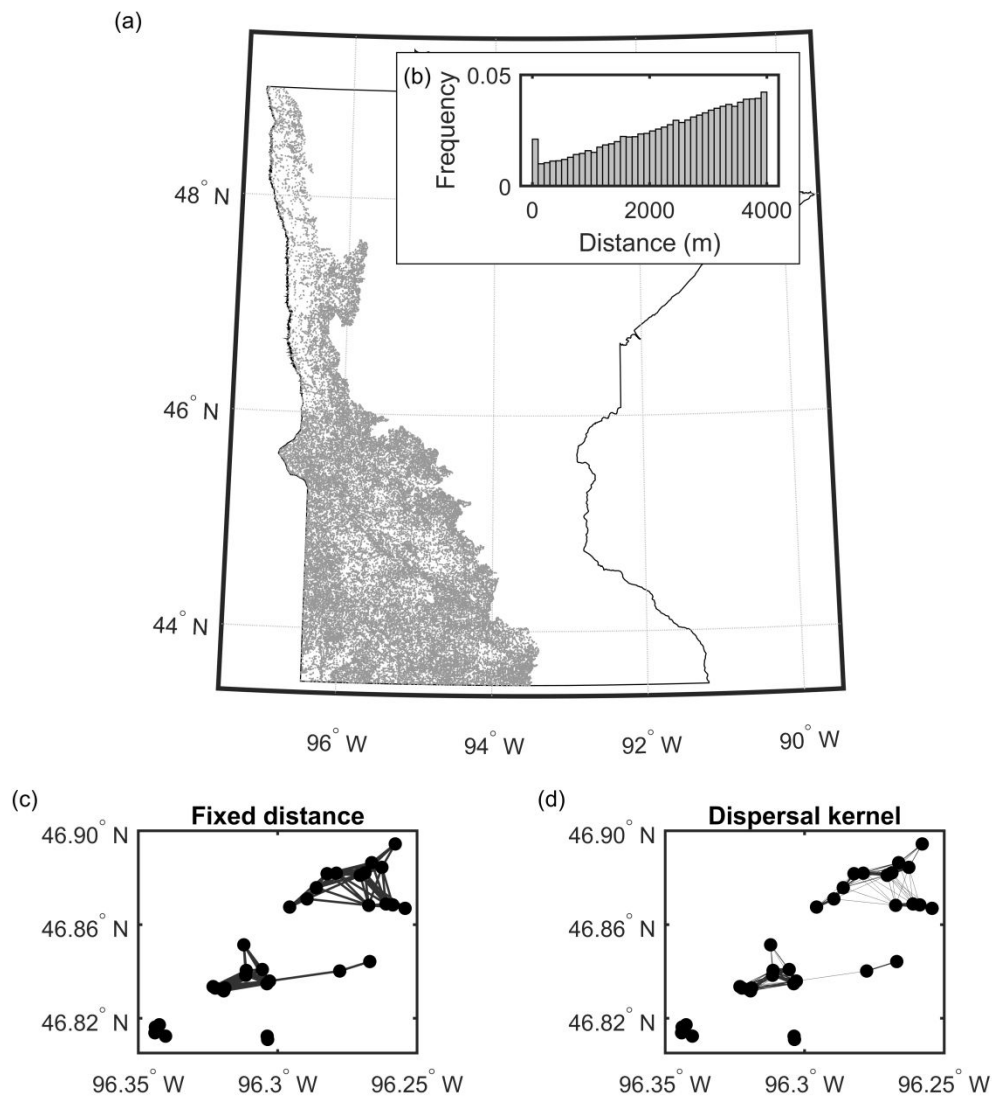
579 Figure 5. Patch-level metric values for networks with fixed dispersal distances (red), and
580 networks with dispersal kernels, ‘75%-realized’ (dark gray), ‘99%-realized’ (medium gray) and
581 ‘99.99%-realized’ (light gray). Panels show the 25th, 50th and 75th quantiles for (a) patch degree
582 centrality, 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 50th quantile for each kernel.

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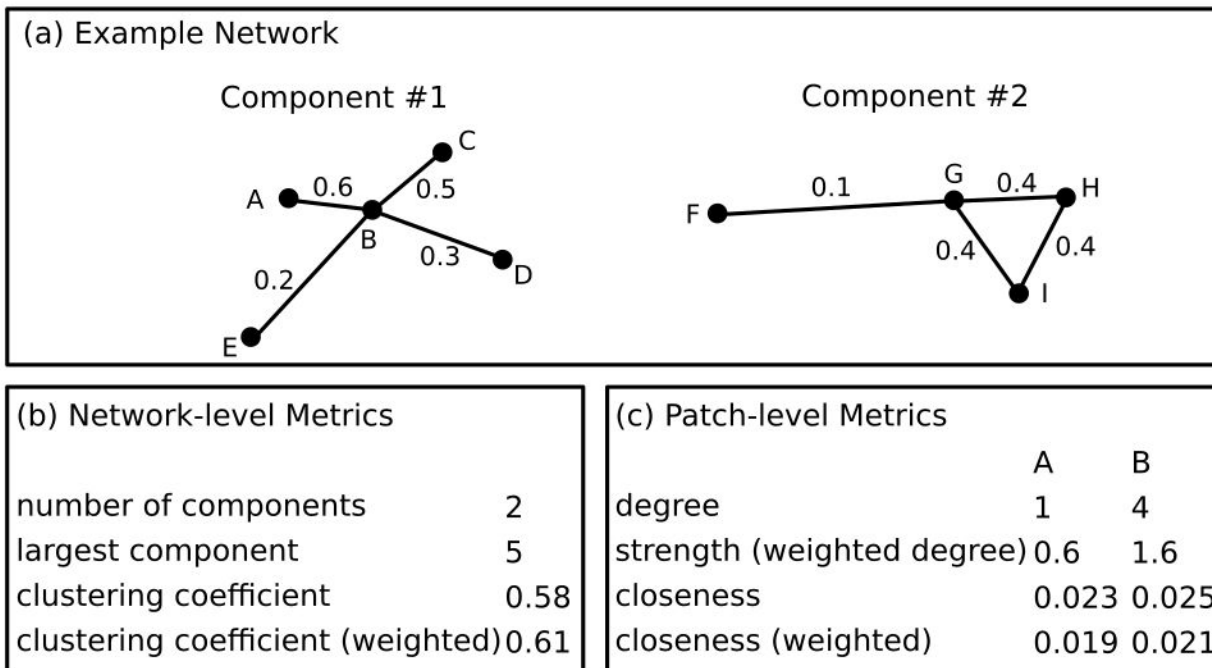
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 596 proportion of dispersers between patches.

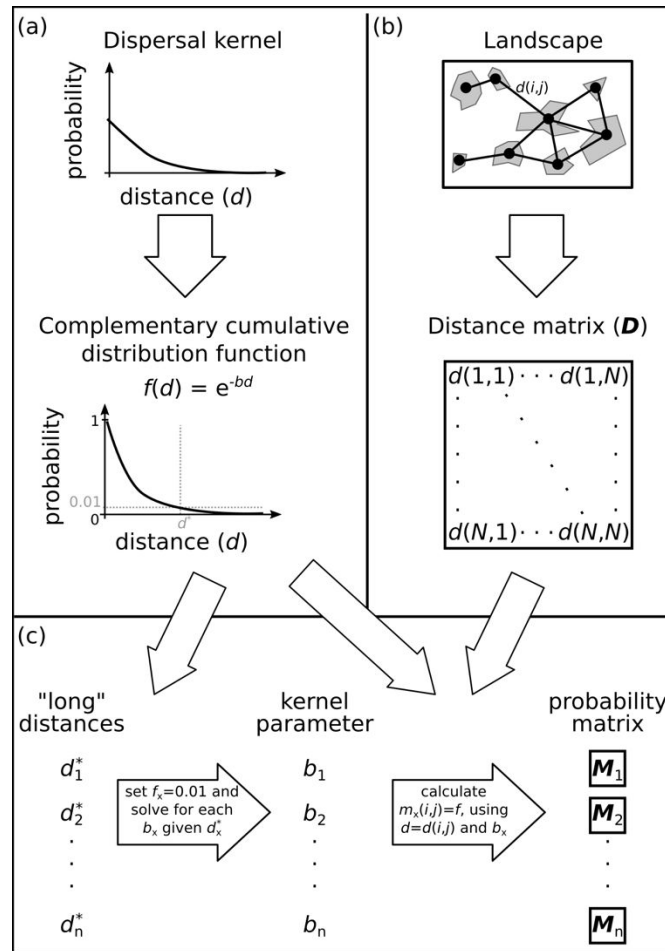
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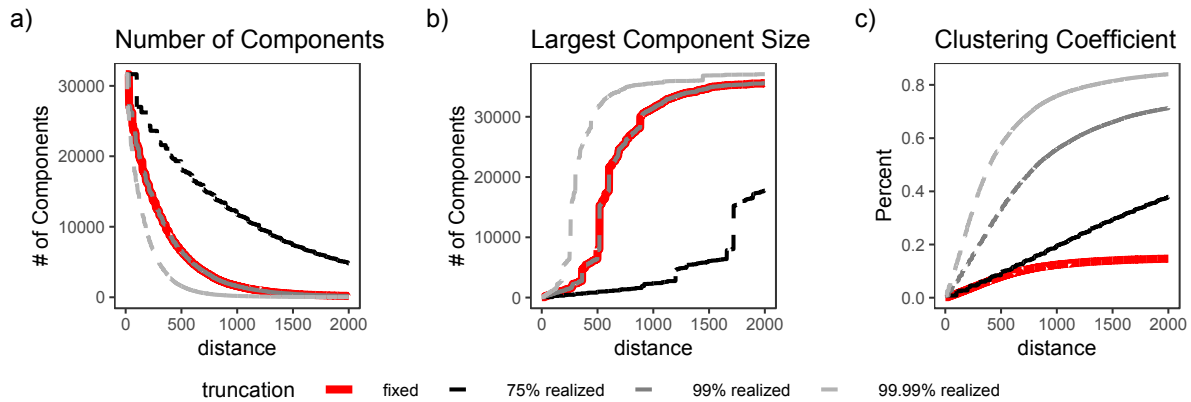
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 617 dispersal distance index $x=1 \dots n$, ($n=2000$). See Appendix S1 for full definitions of parameters.



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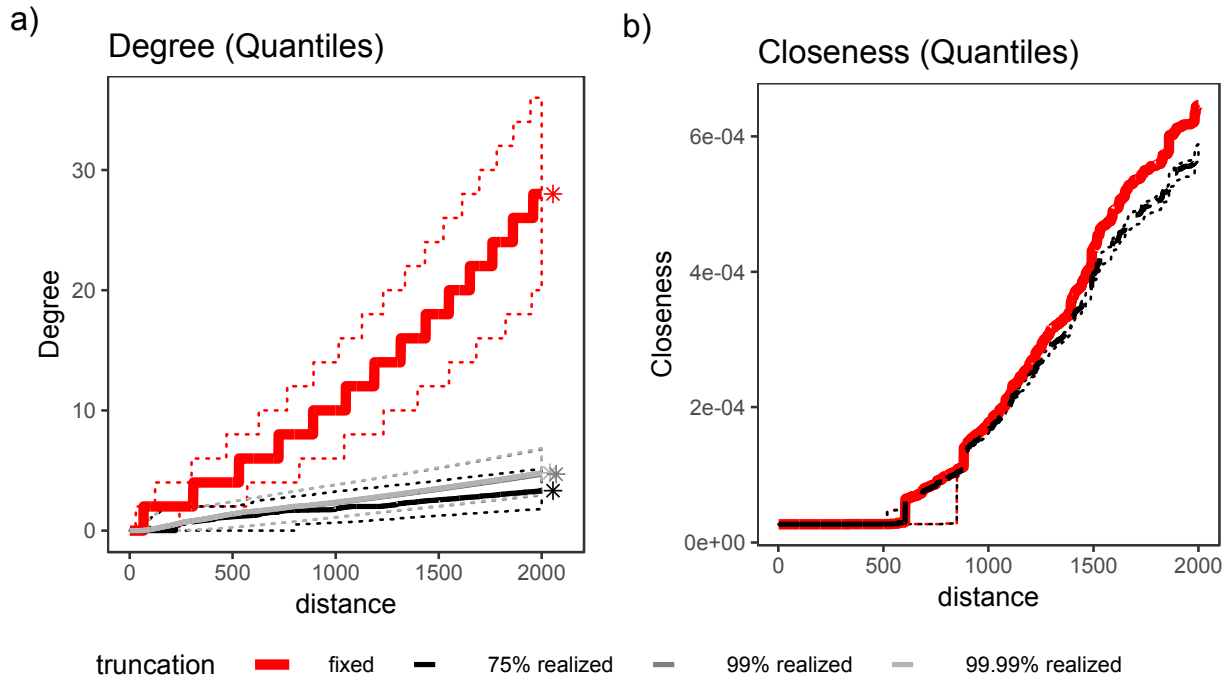
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 633 centrality, and (b) patch closeness which represent measures of robustness to local extinction. In
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 635 overlapping with the '99.99%-realized' kernel having a slightly higher degree. For clarity,
 636 asterisks represent the 50th quantile for each kernel.

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EDITOR COMMENTS

Comment: I appreciate the effort you have taken to address this issue. However, at least some of the journal's readers may raise a similar objection. I do hope you will persist with this discussion, because I think the manuscript is greatly improved by your efforts to date. I also believe you understand the reviewer's concern, and will understand the basis for their dis-satisfaction with the remedies you have applied. The reviewer is quite flexible about how this issue may be addressed, and it need not necessarily be overwhelmingly burdensome to deal with it. Please give it some additional, careful thought and see what you can come up with that will give them and other potential readers, satisfaction on this remaining point.

Response: We appreciate you continuing to work with us to improve this paper. We have done what we believe the reviewer wanted us to do, and you will see some of the resulting figures make sense, and have thus been included in the supplemental information. As before, the results are quantitatively different from our approach, but very qualitatively similar. However some of the results from the suggested changes by the reviewer make sense with Network Theory and the math behind it, but do not make sense for a manager on the ground attempting to understand the connectivity of their landscape. Thus we have opted to leave those figures out of the manuscript, but have described why we only include the ones we do in the supplement. See below for a full response.

REVIEWER 3 COMMENTS

Comment: I clarify that I do not have an issue with the 4000m cutoff, and see it as reasonable for computational ease, especially as the authors clarify that the probability of dispersal to this distance is exceedingly low.

Response: Great! We are happy the reviewer agrees with our 4000m cutoff.

Comment: My concern is solely on the imposition of an artificial threshold (the 0.99, and 0.75 cutoffs) for the population sizes (henceforth, population-size-cutoffs). In particular, in a paper that aims to address issues that a dispersal threshold brings to network analyses. I thank the authors for taking the time to understand my concern and try out the approach suggested.

I have gone through Appendix S2: Authors first step: "We re-ran our models where instead of truncating the dispersal kernel tail for increasingly small populations, we multiplied the weights of each edge by three percentages to represent different population sizes (i.e. weights for large populations were multiplied by 0.9999, weights for medium populations were multiplied by 0.99, and weights for small populations were multiplied by 0.75)." -- this is the approach I suggest *in entirety*, and will in itself (alone) provide a modified value of links for smaller populations.

The following 2nd step undertaken by the authors: "Then, we used those same cutoff values (0.9999, 0.99, and 0.75) as our limit for what was considered connected in our network models

for each corresponding population size. " -- is not part of what I recommend, and takes the authors right back to an artificial threshold. ie., this second step negates the utility of the first step.

Response: Thank you for this clarification! We have been able to re-run the models as you suggest by following just step 1.

Comment: To explain again my concern to the authors:

- The premise of the paper is that a single dispersal distance imposes an artificial threshold on linkages between populations that is unrealistic. The authors posit that this artificial threshold is problematic. I agree.

- I applaud the authors on their approach to address this and think that their overall methodological approach is beneficial and useful.

- My contention: the same unrealism of a dispersal threshold is imposed by the authors with respect to the population-size-cutoffs - 0.99, 0.75 cutoff values for small populations. If the authors had a smaller population with a 50% cutoff, it would be almost exactly like the dispersal threshold model they say is problematic.

Hence, I would strongly recommend against using the threshold going so far as to say that it is strongly incongruent with the very premise of their paper. They are free to use *any* approach that does not impose an artificial threshold. I provide just one example approach.

Response: We now understand exactly what you were thinking with your concern. We agree this is valid, and have re-run the models with your specifications of not having a cutoff at all. And you will see below (Fig. 1), that this has worked quite well for the weighted metric of degree. We are happy to include this revised figure in our supplement, and have modified the text to drop "the second step" as you suggested above. As before, the results are quantitatively different from ours, but qualitatively quite similar. This occurs because the probability of these dispersal events past the "cutoffs" we had before are small (low probability) and thus they do not have an overly large impact on connectivity. Thus both of our approaches are valid. However, since these low probability events do matter from the standpoint of rare long-distance dispersal, we are happy to include this in our manuscript as we agree it provides an alternative way of viewing the weighted connectivity of grasslands in Minnesota.

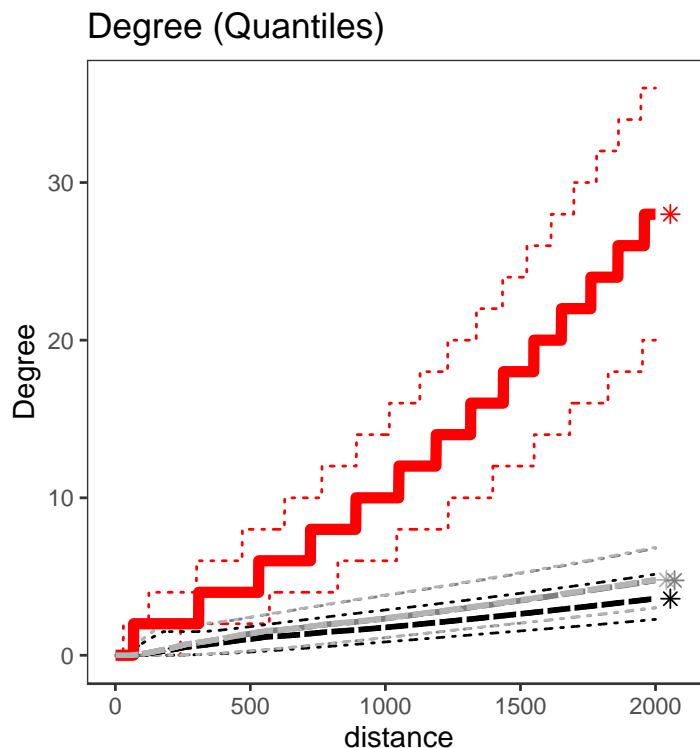


Fig 1. Updated weighted degree metric with the method proposed by the reviewer. This figure is now in the supplement

However, we must argue against including all network-level metrics (Fig. 2) with this approach in our manuscript. We believe that when you see the results, and think about how these networks are being calculated, you will agree that these results will be very misleading to managers attempting to manage for connectivity in Minnesota. For the first two network metrics we use (number of components and largest component size), the way the functions work is that they are calculated as binary networks for both weighted and non-weighted networks. (as we mention in our paper ~line 210). So, with the “no cutoff” suggested by the reviewer, this actually allows ALL patches to be connected, even if by a very very very small weight. With these binary metrics, these models show all patches we are looking at are connected in one giant component (Fig 2 a,b gray lines). While this makes sense theoretically, and we can separate in our minds that many of those patches are connected by a very small proportion, the math makes it look like all grasslands in Minnesota are connected. This is clearly misleading and is not useful to managers, as they know that this is not true. These results make it difficult for managers to parse what can help them maintain connectivity and what cannot because they would think all the patches are connected. We believe the reviewer will agree with us that these results are not helpful to readers.

There are some similar concerns with clustering coefficient (Fig 2c), as the models with “no cutoff” really overestimate the number of patches that are connected. We believe this is misleading to managers as well, however this one does work out in that the metric is not binary, so the weights are considered. We would prefer to leave this figure out of the manuscript.

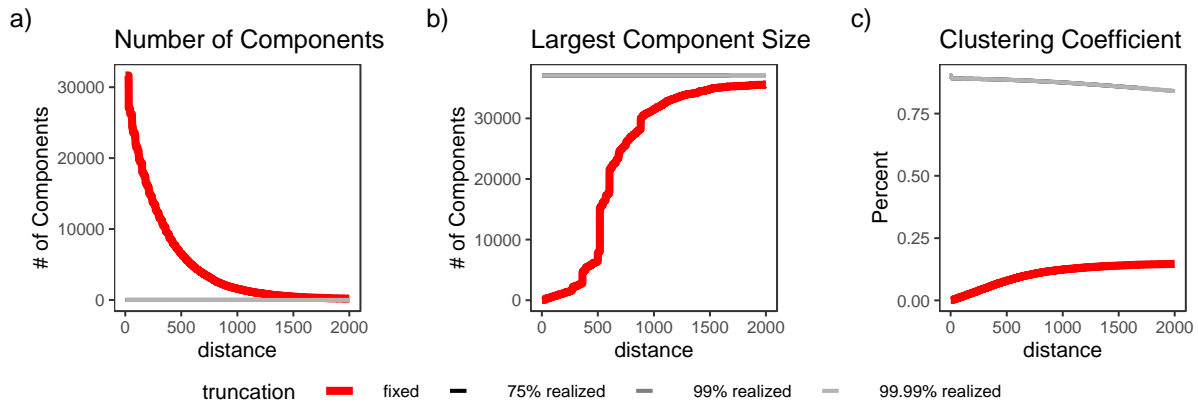


Fig 2: Network-level results for connectivity without the “artificial cutoffs”.

Comment: To the authors: I hope you understand why I am arguing so strongly against this approach you use; it imposes just the problematic artificial effect your paper aims to rectify.

Response: We understand your concerns, and recognize that there are two valid ways to look at these connectivity models. We hope we have done a satisfactory job in explaining both of the ways now. The way we have built our paper on, with the “artificial cutoffs” is perhaps theoretically not as precise, but it is likely the way that managers who are attempting to promote connectivity in their landscape are thinking. They likely cannot account for probabilities of connection < 0.0001 as in the end it does not have a lot of change in weighted connectivity measures (Fig 1 here, vs our Fig 5a in the manuscript). Thus the “cutoff” method that we have provided is likely a reasonable approach for many managers trying to make decisions, that cannot consider connectivity between patches that are connected at such low probabilities (it would be a LOT more prairies for them to consider). Therefore, we have included in the manuscript what is the most relevant information from both approaches.

Comment: I thank the authors for other changes made in the MS, and think that it has clarified their approach vis-a-vis individual variation in dispersal.

Response: You are welcome.

Comment: Response to comment on lines 73-74: "Those network models that do consider dispersal as a function of distance tend to do so by using simulated draws from dispersal kernels (Fletcher et al. 2011, 2013)." I meant this sentence is confusing and adds nothing to the introduction, so I would suggest removing it. If you would like to refer these papers as those that use dispersal kernels, you could just include a '(but see Fletcher et al. 2011, 2013)' for clarity.

I provide below a few citations where weighted networks are used in connectivity studies, which incorporates dispersal variation, and is equivalent of using a dispersal kernel, even if the specific phrase is not used, that the authors may find useful.

Creech et al 2014, Using network theory to prioritize management in a desert bighorn sheep metapopulation, *Landscape Ecology*

Castillo et al 2016 Replicated landscape genetic and network analyses reveal wide variation in

functional connectivity for American pikas. *Ecological Applications*.

Saura et al 2011 Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). *Ecological Indicators*.

Response: All of these papers estimate dispersal based on habitat flow in some way. So they do not consider the biological dispersal ability of the organism specifically (a dispersal kernel), but instead how the landscape might modify the movement of a species. We agree this is an important next step, to combine dispersal kernels with the ease-of-flow through the habitat, as we mention in the last paragraph of our discussion. We have now added Saura et al. as a reference in the text of the discussion. And we have added Creech et al. to the introduction as an excellent example of how to use network models for conservation.

For review only