

1 **Cryptic Dispersal Networks Connect Habitat Patches in ways not Captured**  
2 **by Distance**

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23

24 **Abstract**

25 Species interact with the physical world in complex ways, and life history strategies might cause  
26 species to differ in how they experience connectedness of the same landscape. As a consequence,  
27 dispersal limitation might be present but not captured by distance-based measures of  
28 connectivity. To test these ideas, we surveyed plant communities that associate with serpentine  
29 soils but differ in dispersal mode (gravity, animal, or wind), and used satellite imagery to  
30 quantify forms of landscape connectivity associated with each dispersal mode. Our data yielded  
31 two key insights: First, dispersal limitation appeared to be absent using a conventional distance-  
32 based measure of connectivity, but emerged after considering forms of landscape connectivity  
33 relevant to each dispersal mode. Second, the landscape variables that emerged as important to  
34 each dispersal mode were generally consistent with our predictions based on putative dispersal  
35 vectors, and included interactive effects that allude to the altered efficacy of animal dispersal in  
36 invaded landscapes. Our results have broad implications for understanding how ecological  
37 communities reorganize as landscapes are fragmented, patches are lost, and the function of  
38 dispersal life histories is altered.

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47 **Introduction**

48 Ecologists have long-sought to quantify the importance of dispersal limitation in ecological  
49 communities (Borcard et al. 2004; Gilbert and Lechowicz 2004; Cottenie 2005) for two main  
50 reasons. First, the presence of dispersal limitation can cause local species richness to fall short of  
51 what a given environment can support (Germain et al. 2017), and second, the failure of  
52 propagules to reach suitable sites generates spatial turnover in species richness and composition  
53 that contribute to regional biodiversity (Hurtt and Pacala 1995; Mouquet and Loreau 2003).  
54 Towards this goal, numerous statistical tools have been developed to isolate the relative  
55 explanatory power of dispersal vs. environment from field data (*e.g.*, (Peres-Neto et al. 2006;  
56 Prugh 2009)), typically testing for and interpreting an effect of distance among local  
57 communities on species occupancy, richness, or composition as evidence of dispersal limitation  
58 (Hanski 1994a; Cottenie 2005; Prugh et al. 2008). If spatial distance among sites is assumed to  
59 be the best proxy of restricted dispersal, then the absence of significant distance effects on  
60 diversity patterns is interpreted as evidence that dispersal is not limiting at the spatial scales  
61 examined (*e.g.*, (Freestone and Inouye 2006)) – that is, that species have access to all habitat  
62 patches, and that variation in species occupancy and richness patterns reflect variation in local  
63 environmental conditions.

64 An alternative but rarely considered explanation for non-significant distance effects is  
65 that isolation by distance is not the spatial variable most relevant to dispersal – habitat patches  
66 might be close in space but poorly connected by dispersal due to other landscape features, such  
67 as physical barriers. Though this idea has been explored in aquatic ecosystems for which there is  
68 obvious network structure (*e.g.*, riverine networks (Beisner et al. 2006; Brown and Swan 2010))  
69 or directionality to dispersal (*e.g.*, water currents (White et al. 2010)), it has not been explored in

70 terrestrial systems for which dispersal barriers may be cryptic and thus difficult to identify and  
71 measure. Although isolation by distance is likely the most important factor limiting dispersal in  
72 many ecosystems (*e.g.*, oceanic islands), exploring alternative dispersal pathways can reveal  
73 hidden constraints to how species move across and interact with their landscapes, and might  
74 explain why distance effects are generally weak in terrestrial ecosystems; a recent synthesis of  
75 1,015 animal surveys found that spatial isolation was a poor predictor of patch occupancy for  
76 most species (Prugh et al. 2008).

77         If dispersal is constrained in a greater range of ways other than by distances among  
78 habitat patches, then, intriguingly, species might differ in how they experience the spatial  
79 connectedness of the same physical landscape based on dispersal life histories (Beisner et al.  
80 2006). In plants, for example, species possess a range of adaptations to disperse, called dispersal  
81 syndromes or “modes”, such as dispersal by gravity, animals, or wind. Previous research of  
82 understory herbs in aspen stands clearly demonstrates that dispersal mode dictates how  
83 constrained plant species distributions are by the size and spatial isolation of habitat patches,  
84 even without accounting for additional sources of trait variation (*e.g.*, seed size) among species  
85 within dispersal modes (Jones et al. 2015). In that study, however, the effect of dispersal mode  
86 on species distributions was not consistent with a simple difference in dispersal ability among  
87 modes (*i.e.*, dispersal ability: gravity < wind < animal (Jones et al. 2015)), as hypothesized if  
88 distances among habitat patches was the only cause of spatial isolation. We contend that linking  
89 species distributions to the spatial distribution of dispersal vector movement might be the  
90 missing piece needed to understand the mechanisms that underlie the spatial distribution and  
91 composition of biodiversity, for plants and potentially other terrestrial organisms. Identifying  
92 spatial constraints on species distributions is key to understanding the processes that underlie

93 fundamental patterns in ecology, such as species-area relationships (Shen et al. 2009), as well as  
94 to forecast how ecological communities might reorganize as the spatial and environmental  
95 structure of landscapes is altered by humans (Gonzalez et al. 2011; Frishkoff et al. 2016).

96 We explored alternative forms of landscape connectivity to understand the distribution of  
97 biodiversity in a natural patch-network of plants that associate with serpentine soils. Serpentine  
98 soils form via the emergence and erosion of the Earth's mantle into discrete patches embedded  
99 within a matrix of non-serpentine soil. Serpentine soils are hypothesized to act as "islands" of  
100 refuge for native plant species to escape the "sea" of European grasses that now dominate  
101 Californian landscapes (Harrison and Rajakaruna 2011; Gilbert and Levine 2013). The annual  
102 plant communities that associate with serpentine soils are an emerging model system to  
103 understand the mechanisms that underlie the spatial scaling of biodiversity (Anacker and  
104 Harrison 2012; Germain et al. 2017), the interaction between local and regional processes  
105 (Harrison 1999; Harrison et al. 2006), and the community impacts of species invasions (Gilbert  
106 and Levine 2013; Case et al. 2016). Recent experimental work has demonstrated that dispersal  
107 limits plant diversity at our study site (fig. 1), yet we find no evidence of spatial distance as a  
108 proxy for dispersal limitation through our observational data (table A2); this contradiction  
109 motivates our examination of other landscape features relevant to dispersal. Specifically, the  
110 absence of tall vegetation in serpentine grasslands allowed landscape features, such as  
111 hydrological networks and animal paths, to be captured via satellite imagery (fig. 2).

112 We surveyed plant communities on serpentine patches and in the non-serpentine matrix,  
113 categorized species by dispersal mode, and estimated habitat patch characteristics relevant to  
114 different modes of dispersal. We used these data to answer two questions: (1) Are there  
115 landscape features that characterize habitat patch connectivity better than distance among habitat

116 patches, and (2) does dispersal mode influence how species respond to these features? If species  
117 experience different landscape constraints, then we predict that the richness of species belonging  
118 to different dispersal modes will be highest in habitat patches highly connected by their  
119 respective dispersal vectors. Specifically, we predict that hydrological networks, animal paths,  
120 and distance would explain the richness of species dispersed by gravity, animals, and wind,  
121 respectively. As a case study, we also explore the spatial distribution of patch occupancy patterns  
122 of *Plantago erecta* (California plantain), a small-statured annual with seed morphologies  
123 consistent with a mixed dispersal strategy (*i.e.*, dispersal via water and animals (Germain et al.  
124 2017)). If our models are correct, then we predict that *P. erecta*'s distributions would be  
125 explained by forms of habitat connectivity shown to be important to both dispersal modes.

126 Our analyses of species richness fall into a general class of 'incidence function' models  
127 (Prugh 2009), the basis of which was first developed by Levins (Levins 1969) and later adapted  
128 by Hanski (Hanski 1994*a*, 1994*b*) to test species' extinction and colonization as a function of  
129 patch size and isolation by distance, respectively. These models have achieved broad success at  
130 understanding the population and metapopulation persistence of a diversity of organisms in  
131 fragmented landscapes (*e.g.*, butterflies [28], pikas (Moilanen et al. 1998)), with applications to  
132 landscape management and conservation planning (Wahlberg et al. 1996).

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## Materials and Methods

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### *Study System*

136 Our study took place at the 2800-ha McLaughlin Natural Reserve (<http://nrs.ucdavis.edu/mcl/>) in  
137 Northern California, at the boundary of Lake, Yolo, and Napa counties (38°51'47.01"N,  
138 122°21'48.87"W). The landscape is characterized by patches of serpentine soil interspersed

139 among a matrix of non-serpentine soil. Serpentine (ultramafic) soils are derived from the Earth's  
140 mantle in regions where it becomes exposed, such as along the San Andreas Fault, and are  
141 identified by Ca/Mg ratios  $< 1$  (Anacker 2014). Calcium is essential to plant growth, and is  
142 captured less efficiently in the presence of magnesium. Low Ca/Mg ratios, coupled with low soil  
143 fertility, high heavy metal content, and poor soil moisture retention, present a harsh growing  
144 environment for plants. Yet, serpentine soils support a rich diversity of native and endemic plant  
145 species (Anacker 2014), and are hypothesized to act as spatial refugia for native species to  
146 escape the competitive effects of the exotic European plants that now dominate the non-  
147 serpentine matrix (Gilbert and Levine 2013).

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#### *Field Survey and Data Collection*

150 Plant surveys and all fieldwork were conducted in early May 2017, at approximately peak  
151 flowering. We haphazardly selected 28 serpentine habitat patches out of all 42 patches in a 18 ha  
152 region of the reserve, ranging from 31 to 4533 m<sup>2</sup> in size and 0.75 to 356 m away from their  
153 nearest neighbor patch (fig. 2). At each patch, we surveyed a transect of five 0.75 x 0.75 m<sup>2</sup>  
154 plots: one plot in the patch centre, one plot halfway between each edge and the patch centre, one  
155 plot 1 m into the non-serpentine matrix, and one plot 5 m into the matrix (fig. A1). In other  
156 words, the distances among plots within patches were scaled by patch size, whereas the two  
157 matrix plots were fixed distances from the patch edge. We recorded the presences of all species  
158 in each plot, and made note of species that covered more than 25% of a plot by area (usually one  
159 to three species). In total, 77 plant species were present in our surveys, 72 of which could be  
160 identified; the five unidentified species occurred once each, had no distinguishing features to  
161 assess dispersal mode with certainty (*i.e.*, only a single basal leaf) and were discarded from all

162 analyses that required information on dispersal mode. Sampling the same total area for all habitat  
163 patches regardless of patch size is a standard sampling method to prevent confounding patch size  
164 with sampling intensity (Cook et al. 2002).

165 Species' dispersal modes (dispersal via wind, gravity, or animals) were categorized based  
166 on previous research (Spasojevic et al. 2014) and updated here based on seed/diaspore  
167 morphology and if more detailed information on dispersal modes was available (table A1).  
168 Wind-dispersed species were identified by the presence of a pappus or seed wings, whereas  
169 animal-dispersed species had morphologies for attachment to passing animals, such as burrs,  
170 awns, or hairs. Species categorized as gravity dispersed had seeds that lacked any apparent  
171 mechanism for dispersing by wind or animals, and tended to have smooth, spherical diaspores  
172 conducive to downslope dispersal via rain and gravity. We include ant-dispersed species as  
173 gravity dispersed given that ants disperse seeds at very small spatial scales and are unlikely to  
174 contribute to regional occupancy patterns (Thomson et al. 2011), as well as species with reduced  
175 pappi that were biomechanically unlikely to confer wind dispersal (e.g., *Lasthenia californica*).  
176 One species, *Plantago erecta* (California plantain), was previously categorized as being  
177 dispersed by water (Spasojevic et al. 2014). However, *P. erecta* seeds produce a sticky mucilage  
178 that might also allow dispersal by animals (observation noted in (Germain et al. 2017)). As such,  
179 we categorize this species as being animal-dispersed but also explore the occupancy patterns of  
180 this species in depth as a case study of a species with two potential dispersal modes.

181 Species were additionally categorized as patch- or matrix-associated (table A1) to  
182 identify and account for species that were unlikely constrained to serpentine habitat patches  
183 (Cook et al. 2002; Jones et al. 2015). 'Matrix-associated' species included both matrix specialists  
184 and generalists that show no affinity for habitat type. Species were considered matrix-associated



185 if they were equally or more common in matrix plots than in the patch plots. Twelve species met  
186 these criteria, including *Avena fatua*, *Bromus hordeaceus*, and *Lotus wrangelianus*. Species  
187 richness (fig. A2A) and composition (fig. A2B) differed among serpentine habitat patches and  
188 the non-serpentine matrix (both  $P < 0.001$ ), confirming that serpentine plant communities are  
189 distinct and thus constrained to the serpentine habitat-patch network.

190 We estimated habitat patch characteristics in the field and using ArcGIS on GoogleEarth  
191 images. In ArcGIS, we delineated all serpentine patches within our study region, including the  
192 28 surveyed patches and 14 unsurveyed patches; these delineations allowed us to calculate patch  
193 size and patch connectivity. Patch connectivity was estimated using edge-to-edge distances  
194 between patch  $i$  and all other  $j$  patches (including the unsampled patches), weighted by a  
195 negative exponential dispersal kernel using eq. 1 (Hanski 1994a, 1994b; Jones et al. 2015):

196

$$197 \text{ connectivity}_i = \sum_{j \neq i}^n A \cdot e^{-d_{ij}/\alpha} \quad (\text{eq. 1})$$

198

199 where  $A$  is the area of patch  $j$ ,  $d$  is the Euclidean distance in meters between patch  $i$  and  $j$ , and  $\alpha$   
200 is the mean dispersal distance, set to 5 m for all species. In other words, patch  $i$  is most  
201 connected when it is in close proximity to many large patches. Our connectivity measure falls  
202 into a general class of measures called incidence function models, which have been shown to  
203 perform equally well or better than alternative measures (*i.e.*, nearest-neighbour or buffer  
204 measures (Prugh 2009).

205 We estimated two alternative measures of connectivity that we hypothesized could be  
206 more appropriate for plant species that are dispersed by animals or gravity. For species that are  
207 dispersed by animals, we traced deer trails that were observable via GoogleEarth (fig. 2) using

208 ArcGIS, and used the number of trails that intersected habitat patches to estimate patch  
209 connectivity via animals. Deer exhibit path fidelity, following the path of least resistance, which  
210 is especially true in topographically challenging landscapes such as our study area, and create  
211 “highways” for a diversity of other animals to traverse landscapes, including rabbits and turkeys  
212 (Sindorf 2009). For plant species that are dispersed by gravity/water, we estimated hydrological  
213 connectivity by tracing the network of surface streams, and for each habitat patch, summed the  
214 area of all  $j$  habitat patches upslope from and connected via surface streams to each patch  $i$ .  
215 Elevation of habitat patches ranged 450-550 m a.s.l., small enough for elevational clines in  
216 climate to be unimportant. Although in some systems, habitat patches at the base of an  
217 elevational cline have increased resource inputs and thus higher productivity, productivity was  
218 not correlated with elevation ( $slope < 0.01$ ,  $P = 0.465$ ) or hydrological connectivity ( $slope = -$   
219  $0.03$ ,  $P = 0.458$ ) in our dataset. We estimated productivity as a composite measure [(1 -  
220 proportion of bare ground) x vegetation height] to non-destructively estimate the volume of plant  
221 material in each plot.

222

### 223 *Statistical Analyses*

224 To test if species composition in serpentine habitat patches was distinct from the surrounding  
225 non-serpentine matrix, we used linear mixed effects models to test differences in species  
226 composition among plots in serpentine habitat patches (“patch plots”), 1 m into the habitat  
227 matrix (“edge plots”), and 5 m into the habitat matrix (“matrix plots”). To do so, we first  
228 performed a principal coordinates analysis using Jaccard’s distances on the plot-level  
229 presence/absence data. The first and second axis scores were used as response variables in  
230 separate analyses with fixed effects of habitat type (*i.e.*, patch, edge, matrix) and ‘patch id’

231 included as a random effect to account for the non-independence of the five plots transecting  
232 each habitat patch. The ‘glht’ function in R package ‘multcomp’ was used to to perform a  
233 Tukey’s tests of compositional differences among all pairwise treatment combinations (patch vs.  
234 edge, patch vs. matrix, edge vs. matrix).

235 To examine the relationship between species richness and patch connectivity, we  
236 performed a generalized linear mixed effects model with species richness as the response, fixed  
237 effects of dispersal mode, connectivity by distance, connectivity by animals, connectivity by  
238 hydrology, patch size, and all interactions, and random effect of ‘patch id’ to account for non-  
239 independence of replicate plots within a single patch. Because there were significant higher-  
240 order interactions between dispersal mode and all connectivity measures (table A2), we  
241 performed separate analyses of biogeographic predictors for each dispersal mode. This type of  
242 analysis is highly prone to type I errors (poisson-distributed data with interacting continuous  
243 predictors), so we took several steps to identify reduced models that best fit the data. First, we  
244 performed backwards selection on each full model using the ‘step’ function in the ‘stats’  
245 package; ‘step’ sequentially drops higher order interactions until the reduced model that yields  
246 the greatest model fit (lowest AIC score) is attained. However, ‘step’ can arrive at a local  
247 minimum in AIC score that does not reflect the global minimum, which was likely for our data  
248 given the presence of significant but biologically implausible four-way interactions. For this  
249 reason, we applied ‘drop1’ to the ‘step’-reduced model to identify variables that did not  
250 significantly improve model fit even if their inclusion led to a marginal decrease in AIC scores.  
251 We cycled between ‘drop1’ and ‘step’ until a model was obtained for which all variables  
252 significantly improved model fit and led to the lowest AIC scores out of all possible reduced

253 models. We then used the function ‘Anova’ in the R package ‘car’ to test whether the reduced  
254 model was a significantly better fit to the data than an intercept-only model.

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256

## Results and Discussion

257 Despite the emphasis that contemporary ecology places on dispersal as central to the dynamics  
258 and distribution of species in ecological communities (Hanski 1994a; Leibold et al. 2004),  
259 current empirical assessments of its role may not encompass the diversity of ways in which  
260 organisms experience landscape connectivity. In a patchy terrestrial plant community, we found  
261 no evidence of dispersal limitation using a distance-based estimate of patch connectivity, even  
262 after discounting the presences of species associated with the habitat matrix (*i.e.*, a non-  
263 significant effect of connectivity by distance; table A2), despite experimental evidence of its  
264 pervasiveness (fig. 1 with data from (Germain et al. 2017)). However, when separated species  
265 richness by dispersal mode (gravity, wind, animal), the spatial distributions of species richness  
266 generally corresponded to spatial patterns of dispersal vectors which connect habitat patches. We  
267 discuss these general findings, as well as several unexpected contingencies that provide a richer  
268 understanding of interacting dispersal vectors in serpentine grasslands and their altered efficacy  
269 in invaded landscapes.

270 Consistent with our prediction that the richness of gravity-dispersed species would be  
271 highest in patches highly connected by hydrology, hydrology was the only form of connectivity  
272 retained as a predictor after model selection for this group. However, the effect of hydrological  
273 connectivity was not simply a main effect, but rather, an interactive effect with patch size (*i.e.*,  
274 significant hydrological connectivity  $\times$  patch size effect [ $X^2 = 6.37$ ,  $P = 0.012$ ]), such that species  
275 richness increased with each predictor only at low values of the other (*i.e.*, fig. 3A, steep slopes  
276 connecting points 1 to 2 and points 1 to 4, but shallow slopes connecting points 3 to 4 and points

277 2 to 3). Although we did not predict this interaction *a priori*, it suggests that large,  
278 hydrologically-connected patches are locally saturated (*i.e.*, response surface decelerates from  
279 points 1 to 3, note log-scale of axes) and that these two predictors act as compensatory pathways  
280 towards reaching saturation. Our findings are consistent with recent experimental work showing  
281 that dispersal only increases species richness in small habitat patches (Schuler et al. 2017), given  
282 that populations in small patches are more prone to stochastic extinctions (Gilbert and Levine  
283 2017) which can be overcome via dispersal.

284         The model that best fit the richness data of animal-dispersed species was one that, as  
285 predicted, included the appropriate vector of dispersal: connectivity by animals. However, as  
286 with gravity-dispersed species, the best-fit model also included an interaction, in this case  
287 between connectivity by animals and connectivity by distance ( $X^2 = 7.06$ ,  $P = 0.007$ ), generating  
288 a complex response surface (fig. 3B). More species were found in serpentine patches intersected  
289 by many animal paths, but only when patches were in close proximity to one another (slope  
290 connecting points 3 to 4 in fig. 3B) – when patches were isolated, however, animals had a  
291 strongly negative effect (slope connecting points 1 to 2). What is driving the negative effect of  
292 animals in isolated patches? The answer is not likely herbivory, given that the animal-dispersed  
293 species in our dataset are generally tolerant of or well-defended against herbivory (*e.g.*, grasses,  
294 star thistle (table A1)) and given that connectivity by animals did not predict the richness of  
295 wind-dispersed species, a highly palatable group (*e.g.*, wild lettuce, dandelion (table A1)).  
296 Rather, we contend that the answer has more to do with the efficacy of animals as dispersal  
297 vectors in invaded landscapes. Seeds removed by animals in isolated habitat patches have a low  
298 probability of (i) being deposited in other habitat patches, compared to the inhospitable matrix,  
299 and of (ii) being rescued from extinction via dispersal from other patches; in other words, seeds

300 are removed but not replaced. Additionally, many of the most noxious invaders in serpentine  
301 grasslands are animal dispersed (*e.g.*, common wild oat [*Avena fatua*], barbed goatgrass  
302 [*Aegilops triuncialis*]), adding the potential for invader impacts via animal-mediated dispersal  
303 from the non-serpentine matrix, even if those invaders exist only as sink populations (Schreiber  
304 and Kelton 2005). We argue that the negative effect of dispersal via animals is likely a  
305 contemporary phenomenon, given that, prior to invasion by European grasses, a greater  
306 proportion of the landscape was suitable to species that are now restricted to occur only on  
307 serpentine patches (Gram et al. 2004; Gilbert and Levine 2013). Further support for this  
308 hypothesis comes from our finding that species richness increases with connectivity by distance  
309 only in patches highly connected by animals (slope connecting points 2 and 3), reinforcing  
310 animals as dispersal vectors, connecting patches that would otherwise be unconnected reduce  
311 close proximity.

312         Although we predicted that the richness of wind-dispersed species would increase with  
313 connectivity by distance, given that wind moves in all directions in topographically complex  
314 landscapes (McNider and Pielke 1984), such as our study site, we instead found that an intercept-  
315 only model best fit the data. This finding has three possible explanations, the first being that  
316 wind-dispersed species are simply not dispersal limited at the spatial scale of our surveys, and  
317 the second being the possibility that we have not adequately captured spatial variation in the  
318 movement of seeds by wind. Although we cannot weigh these two alternate explanations against  
319 each other, what we can say is that there is a high degree of variation in species richness and  
320 composition among patches for this dispersal group, including some patches that lack species  
321 from this group altogether. High spatial turnover ( $\beta$  diversity) without evidence of dispersal  
322 limitation implicates the role of local processes (Germain et al. 2013), such as environment,

323 herbivory, competition, or stochasticity. However, a more detailed examination of dispersal  
324 kernels and constraints for this group are needed.

325         The third explanation is that trait differences among wind-dispersed species, for example,  
326 short vs. tall species (Thomson et al. 2011), caused additional variation in how species  
327 experience landscape connectivity. Testing this possibility would require separate analyses of  
328 species occupancy patterns for multiple species; our data is not amenable to such an analysis,  
329 because only two wind-dispersed species occupied enough patches to reasonably fit an incidence  
330 function model (MacKenzie et al. 2005). Coarsely, though, the most common wind-dispersed  
331 species (*Microseris douglasii*), observed in 22 of the 28 sampled patches, was average in terms  
332 of plant height and the ratio of seed size to dispersal structure, though did have the largest seeds  
333 (fig. A4). Large-seeded wind-dispersed plant species disperse farther on average (Thomson et al.  
334 2011), thus seed size differences may contribute to regional occupancy patterns for this group.

335         As predicted, the distribution of *P. erecta*, a common small-statured annual with seed  
336 morphologies consistent with a mixed dispersal strategy (*i.e.*, dispersal via water and animals  
337 (Germain et al. 2017)), was explained by patch characteristics consistent with both dispersal  
338 modes. Specifically, occupancy patterns of this species were influenced by a three-way  
339 interaction between connectivity by distance, hydrology, and animals ( $\chi^2 = 5.70$ ,  $P = 0.017$ ), as  
340 well as positive main effects of hydrology and animals (both  $P \leq 0.001$ ; table 1). When patches  
341 were well-connected by hydrology, the response surface of the probability that *P. erecta* was  
342 present in patches resembled that of richness of animal-dispersed species (fig. A5B vs. fig. 3B).  
343 However, when patches were poorly connected by hydrology, occurrence probabilities generally  
344 increased with connectivity by animals (fig. A5A). This in-depth examination of single-species  
345 occupancy patterns demonstrates consilience among approaches, where connectivity measures

346 identified as important to different dispersal modes in the community level data also emerge as  
347 important predictors of a species with a mixed dispersal strategy.

348         Habitat fragmentation is the primary driver of biodiversity loss worldwide (Crooks et al.  
349 2011). In serpentine plant communities and many other ecosystems, fragmentation has occurred  
350 via the widespread invasion of non-native species, with native species now relegated to small  
351 isolated “refuge” habitat patches. Though species in refuge patches may be safe from direct  
352 competition with invaders, diversity is still challenged with the indirect effects of reduced  
353 colonization (Gilbert and Levine 2013). The extreme harshness of the competitive effect in the  
354 non-serpentine matrix is clear if we consider that (i) plots in the non-serpentine matrix were 7.1  
355 times more productive than serpentine plots yet contained 2.2 fewer species on average (fig.  
356 A2A), and that (ii) there was no difference in species composition among plots 1 m vs. 5 m into  
357 the matrix (grey vs. white points in fig. A2B) even though 1 m is within the dispersal capacities  
358 of most species. In order to prevent the non-random loss of some species over others (*e.g.*, plants  
359 dispersed by animals), landscape management plans may need to consider alternate multiple  
360 forms of habitat connectivity. Californian landscapes were invaded ~200 years ago, meaning that  
361 current communities may already reflect the compositional reorganization of some groups over  
362 others, a hypothesis that can be tested experimentally.

363

364

## Conclusion

365 Characterizing habitat connectivity is fundamental to understanding how dispersal contributes to  
366 biodiversity patterns (Leibold et al. 2004), as well as to landscape planning for conservation  
367 (Crooks and Sanjayan 2006). In a serpentine grassland, we uncover cryptic dispersal networks by  
368 linking species’ dispersal life histories to dispersal vector movement. Our results suggest that



369 ecologists should more carefully consider whether the absence of significant distance effects  
370 truly represents an absence of dispersal limitation vs. a failure to capture landscape variables that  
371 are most limiting to dispersal. Additionally, our finding that animal dispersal reduced diversity in  
372 isolated habitat patches points towards the altered functioning of ecological networks in invaded  
373 landscapes. Real landscapes include complex spatial flows of energy and matter, which as we  
374 demonstrate, sets up ecological opportunity for organisms to differ in how they interact with and  
375 experience the same landscape.

376

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381

### 382 **Author's Contributions**

383 RMG conceived of the study, RMG, NTJ, TNG designed the sampling design and performed  
384 fieldwork, NTJ did the GIS, RMG and NTJ analyzed the data, RMG, NTJ, TNG wrote the paper.

385

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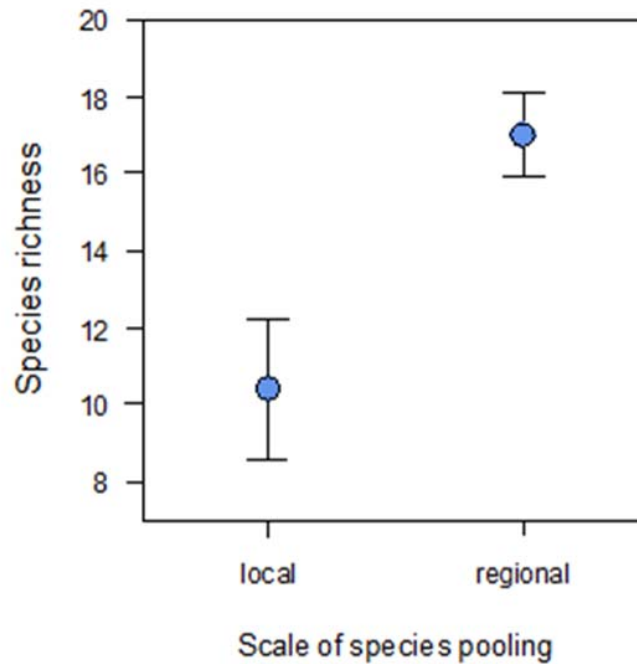
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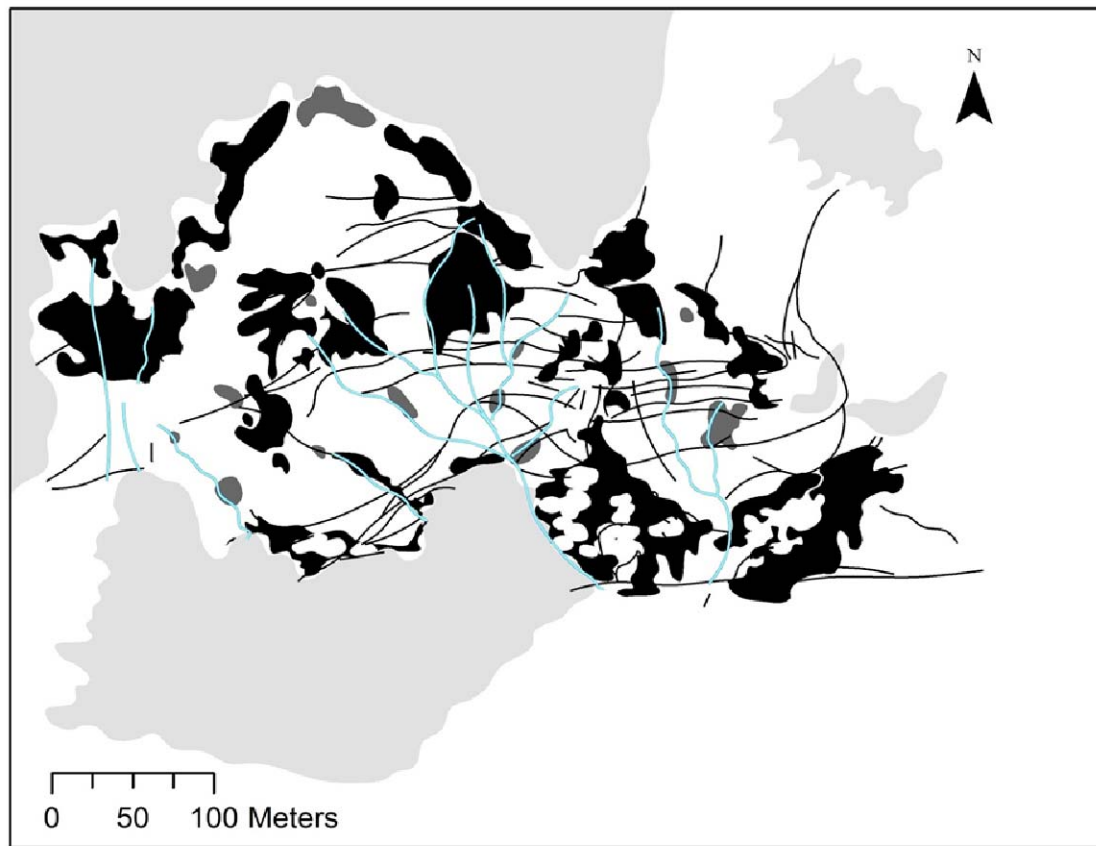
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507 **Figures and Tables**



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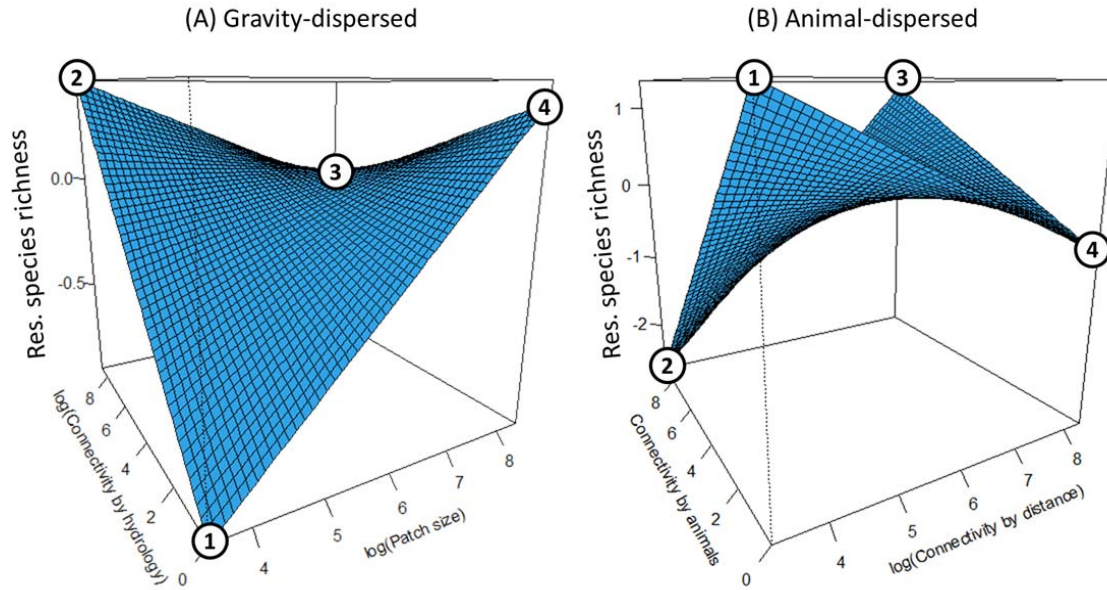
509 **Figure 1:** Experimental evidence of dispersal limitation via pooling seed banks within (local) or  
510 among (regional) habitat patches to enhance dispersal; on average, we see an increase of 7  
511 species per habitat patch with regional pooling ( $F_{1,4} = 15.2$ ,  $P = 0.0175$ ). The data presented here  
512 is subsetted from a larger dataset (Germain et al. 2017) to include only sites within the same  
513 region as our current survey, and only treatments that received locally-mixed species pools (5 m  
514 spatial scale) and those mixed among sites within the regional extent of our survey (100 m  
515 spatial scale).



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517 **Figure 2:** Map of sampled (black) and unsampled (dark gray) habitat patches at our 18-ha study  
518 site within McLaughlin Reserve, CA. Thin black lines are animal paths and thick blue lines are  
519 surface runoff, both traced from satellite imagery. The habitat matrix (white) was non-serpentine  
520 soils dominated by European grasses, such as *Avena barbata*, and the site boundaries were either  
521 road or chaparral (light grey).





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523 **Figure 3:** Species richness of (A) gravity-dispersed species, as a function of patch size and  
524 hydrological connectivity, and of (B) animal-dispersed species, as a function of connectivity by  
525 distance and animal connectivity. Numbered points connect different slopes to aid our  
526 description of the response surface in main text. Fitted response surfaces of species richness are  
527 shown for simplicity, after partialling out fixed effect of patch productivity and random effect of  
528 site ID, but residuals are shown in fig. A3.

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534 **Table 1:** Occupancy of *Plantago erecta*, a species with a mixed dispersal strategy, is explained  
535 by connectivity measures intermediate to those exhibited by species with animal and gravity  
536 dispersal

Variables	Slope	X <sup>2</sup> value	P-value
size	-2.15	0.06	0.812
distance	13.30	0.31	0.578
animals	30.99	10.44	<b>0.001</b>
hydrology	13.64	36.29	<b>&lt;0.001</b>
distance × animals	-4.70	2.15	0.143
distance × hydrology	-2.53	1.83	0.176
size × hydrology	0.47	2.82	0.093
animals × hydrology	-5.57	6.34	<b>0.012</b>
distance × animal × hydrology	0.85	5.70	<b>0.017</b>

537 *Note:* Significant *P*-values are in bold typeface. This reduced model provided a significantly  
538 better fit to the occupancy data than an intercept-only model, despite requiring an additional 9  
539 degrees of freedom (model comparison: *P* = 0.012).