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Cryptic dispersal networks shape biodiversity in an invaded landscape

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Abstract. Species interact with the physical world in complex ways, and life-history strategies could cause species to differ in how they experience the connectedness of the same landscape. As a consequence, dispersal limitation might be present but not captured by distance-based measures of connectivity. To test these ideas, we surveyed plant communities that live on discrete patches of serpentine habitat embedded within an invaded nonserpentine habitat matrix. Species in these communities differ in dispersal mode (gravity, animal, or wind); thus we used satellite imagery to quantify landscape features that might differentially influence connectivity for some dispersal- mode groups over others (surface streams, animal paths). Our data yielded two key insights: first, dispersal limitation appeared to be absent using a conventional distance-based measure of connectivity, but emerged after considering forms of landscape connectivity relevant to each dispersal mode. Second, the landscape variables that emerged as most important to each dispersal mode were generally consistent with our predictions based on species' putative dispersal vectors, but also included unexpected interactive effects. For example, the richness of animal-dispersed species was positively associated with animal connectivity when patches were close in space, but when patches were isolated, animals had a strong negative effect. This finding alludes to the reduced ability of animals to disperse seeds between suitable patches in invaded landscapes because of increased inter-patch distances. Real landscapes include complex spatial flows of energy and matter, which, as our work demonstrates, sets up ecological opportunity for organisms to differ in how they disperse in a common landscape.

Key words: connectivity; dispersal mode; fragmentation; invasion biology; McLaughlin Natural Reserve; serpentine grassland.

INTRODUCTION

Ecologists have long sought to quantify the importance of dispersal limitation in ecological communities (Borcard et al. 2004, Gilbert and Lechowicz 2004, Cottenie 2005) for two main reasons. First, the presence of dispersal limitation can cause local species richness to fall short of what a given environment can support (Foster and Tilman 2003, Germain et al. 2017), and second, the failure of propagules to reach suitable sites can generate spatial turnover in species composition that contributes to regional biodiversity (Hurtt and Pacala 1995, Mouquet and Loreau 2003). Numerous statistical tools have been developed to isolate the relative explanatory power of dispersal vs. environment from field data (e.g., Peres-Neto et al. 2006, Prugh 2009), typically testing for and interpreting an effect of distance among local communities on species occupancy, richness, or composition as evidence of dispersal limitation (Hanski 1994*b*, Cottenie 2005, Prugh et al. 2008). If spatial distance among sites is assumed to be the best proxy of restricted dispersal, then the absence of significant negative effects of distance between habitat patches on diversity is interpreted as evidence that dispersal is not limiting at the spatial scales examined (e.g., Freestone and Inouye 2006)—that is, that species have access to all habitat patches, and that variation in species occupancy and richness patterns reflect variation in local environmental conditions.

An alternative but often overlooked explanation for nonsignificant distance effects is that simple Euclidean distance is not the spatial variable most relevant to dispersal—habitat patches might be close in space but poorly connected by dispersal because of other landscape features, such as physical barriers. Though this idea has been explored in aquatic ecosystems for which there is obvious network structure (e.g., riverine networks; Beisner et al. 2006, Brown and Swan 2010) or directionality to

dispersal (e.g., water currents; White et al. 2010), it has not been explored in terrestrial systems for which dispersal barriers may be cryptic and thus difficult to identify and measure (Lowe and McPeek 2014). Although Euclidean distance is likely the most important factor limiting dispersal in many ecosystems (e.g., oceanic islands), exploring alternative dispersal pathways can reveal hidden constraints to how species move across and interact with their landscapes, and might explain why distance effects are generally weak in terrestrial ecosystems. For example, a recent synthesis of 1,015 studies that examined predictors of animal species' distributions found that spatial isolation was a poor predictor of patch occupancy (Prugh et al. 2008).

If dispersal is constrained by factors other than distances among habitat patches, then species with different dispersal life histories might differ in how they experience the spatial connectedness of the same physical landscape (Grainger et al. 2017). In plants, for example, species possess a range of adaptations to disperse, called dispersal syndromes or "modes," such as dispersal by gravity, animals, or wind. Previous research with understory herbs in aspen stands demonstrates that dispersal mode dictates how constrained plant species distributions are by the size and spatial isolation of habitat patches (Jones et al. 2015). In that study, however, the effect of dispersal mode on species distributions was not consistent with a simple difference in dispersal ability (i.e., dispersal ability: gravity < wind < animal; Jones et al. 2015), as hypothesized if distances among habitat patches were the only cause of spatial isolation. We contend that linking species distributions to the spatial flows in the movement of dispersal vectors might be the missing piece needed to understand the mechanisms that underlie the spatial distribution and composition of biodiversity, for plants and potentially other terrestrial organisms. Identifying spatial constraints on species distributions is key to understanding the processes that underlie fundamental patterns in ecology, such as species–area relationships (Shen et al. 2009), as well as to forecast how ecological communities might reorganize as the spatial and environmental structure of landscapes is altered by humans (Gonzalez et al. 2011).

We explored alternative forms of landscape connectivity to understand the distribution of biodiversity in a natural patch network of plants that associate with serpentine soils. Serpentine soils form via the emergence and erosion of the Earth's mantle into discrete patches embedded within a matrix of nonserpentine soil. Serpentine soils are hypothesized to act as "islands" of refuge for native plant species to escape the "sea" of European grasses that now dominate Californian landscapes (Harrison and Rajakaruna 2011, Gilbert and Levine 2013). The plant communities that associate with serpentine soils are an emerging model system to understand the mechanisms that underlie the spatial scaling of biodiversity (Harrison and Rajakaruna 2011, Anacker and Harrison 2012), the interaction between local and regional

processes (Harrison 1999, Harrison et al. 2006), and the community impacts of species invasions (Gilbert and Levine 2013, Case et al. 2016). Recent experimental work demonstrates that dispersal limits plant diversity at our study site (Germain et al. 2017), yet as we will discuss, we find no evidence of spatial distance as a proxy for dispersal limitation through our observational data; this contradiction motivates our examination of other landscape features relevant to dispersal. Specifically, the absence of tall vegetation in serpentine grasslands allows landscape features, such as hydrological networks and animal paths, to be captured via satellite imagery (Fig. 1a). Although a rich literature explores the effect of dispersal mode on the spatial distribution of biodiversity (e.g., Damschen et al. 2008, De Bie et al. 2012), ours is the first study to our knowledge to use satellite imagery to link dispersal modes to movement of dispersal vectors.

We surveyed plant communities on serpentine patches and in the nonserpentine matrix, categorized species by dispersal mode, and estimated habitat patch characteristics relevant to different modes of dispersal. We used these data to answer three questions: (1) Is the nonserpentine habitat matrix so impermeable that species in serpentine habitat patches exist as metapopulations? (2) Are there landscape features that characterize habitat patch connectivity better than interpatch distance? (3) Does dispersal mode influence how species respond to those landscape features? If species experience different landscape-scale constraints to dispersal, we predict that the richness of species belonging to different dispersal modes will be highest in habitat patches highly connected by their putative dispersal vectors. Specifically, we predict that hydrological networks, animal paths, and distance would explain the richness of species dispersed by gravity, animals, and wind, respectively.

METHODS

Study system

Our study took place at the 2,800-ha McLaughlin Natural Reserve (http://nrs.ucdavis.edu/mcl/) in Northern California, at the boundary of Lake, Yolo, and Napa counties (38°51′47.01″ N, 122°21′48.87″ W). The landscape is characterized by patches of serpentine soil interspersed within a matrix of nonserpentine soil. Serpentine (ultramafic) soils are derived from the Earth's mantle in regions where it becomes exposed, such as along the San Andreas Fault, and are identified by Ca/Mg ratios < 1 (Harrison and Rajakaruna 2011). Calcium is essential to plant growth and is captured less efficiently in the presence of magnesium. Low Ca/Mg ratios, coupled with low soil fertility, high heavy-metal content, and poor soil moisture retention, create a harsh growing environment for plants. Yet, serpentine soils support a rich diversity of native and endemic plant species and are hypothesized to act as spatial refugia for native species to escape
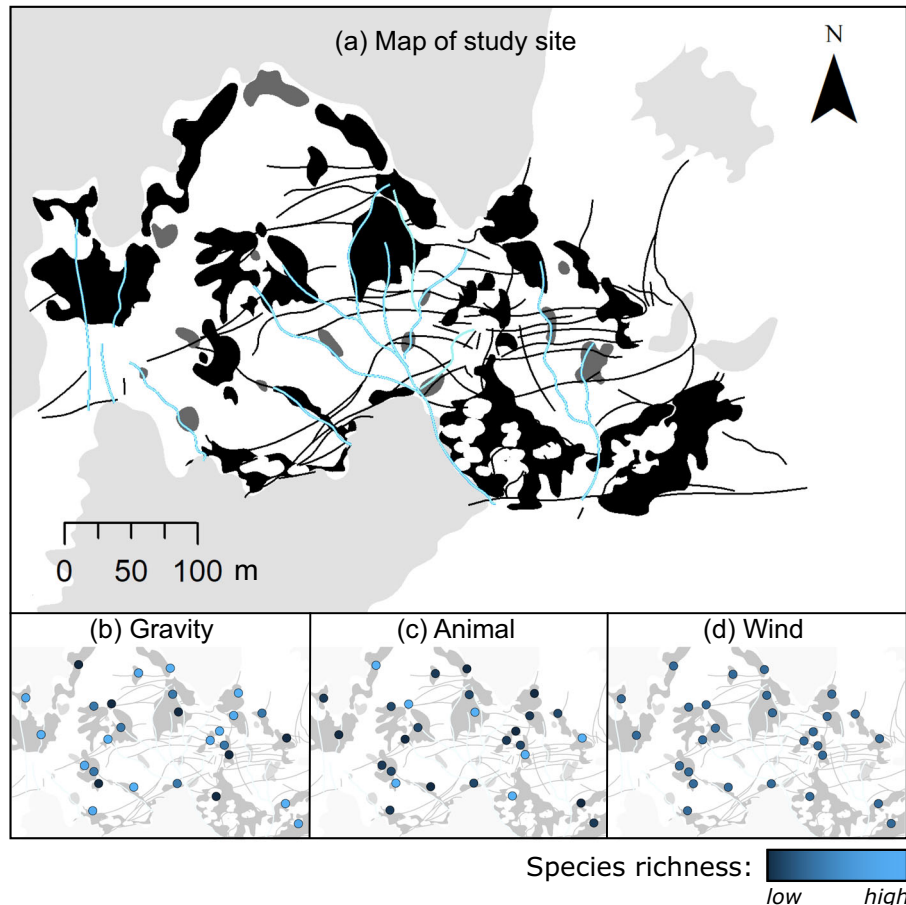
Fig. 1. Map of (a) sampled (black) and unsampled (dark gray) habitat patches at our 18-ha study site within McLaughlin Reserve, California, with (b)–(d) species richness of each dispersal mode group per habitat patch predicted by the fixed effects in our reduced connectivity models (Appendix S1: Table S4). (a) In the map, thin black lines are animal paths and thick blue lines are surface runoff, both traced from satellite imagery. The habitat matrix (white) is nonserpentine soils dominated by European grasses, such as *Avena barbata*, and the site boundaries are either road or chaparral (light grey). (b) Points correspond to locations of sampled serpentine patches. A Google Earth satellite image is shown in Appendix S1: Fig. S2.

the competitive effects of exotic European plants that now dominate the nonserpentine matrix (Gilbert and Levine 2013).

Experimental test of dispersal limitation

A 2014 field experiment at McLaughlin Natural reserve found strong evidence of dispersal limitation in serpentine plant communities (Germain et al. 2017). For the current paper, we consider data from 5 of the 30 serpentine patches included in the original study that overlap with and are of the same spatial extent as our current observational research to facilitate comparisons; here, we describe methods relevant to that subset of sites. The five sites were approximately 100 m apart, and at each, we haphazardly placed a block of eight 0.75 × 0.75–m plots, each of which would receive a different dispersal treatment—for the current paper, only two of those treatments are relevant; thus we do not

describe the others. In late July, once all winter annual species had senesced and produced seed, we used garden shears to loosen all seed-containing plant material from each plot and collected it using a powerful gas-powered leaf vacuum (Stihl BG86). Because the majority of species in serpentine grassland have an annual life cycle, the vacuumed plant material contained seed of individuals that would germinate the following growing season.

Our two treatments were as follows: (1) replace the vacuumed material back onto the source plot without manipulation (control), and (2) homogenize the vacuumed material among the five sites, divide it into five equal parts, and then place the homogenized material back onto the source plots (removal of dispersal limitation). In May 2014, the growing season following our manipulations, we surveyed species richness in each plot. Treatment 1 is our control treatment, where dispersal limitation is not ameliorated and species richness should reflect a natural unaltered state. Treatment 2 removes

dispersal limitation among the five sites, so that any increase in species richness compared to the control treatment indicates the magnitude of dispersal limitation in natural communities.

Observational survey of landscape connectivity

Plant surveys and all fieldwork were conducted in early May 2017, at approximately peak flowering. We haphazardly selected 28 serpentine habitat patches out of all 42 patches in an 18-ha region of the reserve, ranging from 31 to 4,533 m^2 in size and 0.75 to 356 m away from other patches (Fig. 1). At each patch, we surveyed a transect of five 0.75×0.75–m^2 plots: one plot in the patch center, one plot halfway between each edge and the patch centre, one plot 1 m into the nonserpentine matrix, and one plot 5 m into the matrix (Appendix S1: Fig. S1). In other words, the distances among plots within patches were scaled by patch size, whereas the two matrix plots were fixed distances from the patch edge. We recorded the presence of all species in each plot and made note of species that covered more than 25% of a plot by area (usually 1–3 species). In total, 77 plant species were present in our surveys, 72 of which could be identified; the 5 unidentified species occurred once each, had no distinguishing features to assess dispersal mode with certainty (i.e., only a single basal leaf), and were discarded from analyses that required information on dispersal mode. Sampling the same total area for all habitat patches regardless of patch size is a standard sampling method to prevent confounding patch size with sampling intensity (Cook et al. 2002).

Species' dispersal modes (dispersal via wind, gravity, or attachment to animals) were categorized based on previous research (Spasojevic et al. 2014) and updated here based on seed/diaspore morphology and if more detailed information on dispersal modes was available (Appendix S1: Table S1). Wind-dispersed species were identified by the presence of a pappus or seed wings, whereas animal-dispersed species had mechanisms to attach to passing animals (e.g., burrs, awns, or hairs). Species categorized as gravity-dispersed had seeds that lacked any apparent mechanism for dispersing by wind or animals and tended to have smooth, spherical diaspores conducive to downslope dispersal via rain and gravity. We include ant-dispersed species as gravity dispersed, given that ants disperse seeds at small spatial scales and are unlikely to contribute strongly to regional occupancy patterns (Thomson et al. 2011), as well as species with reduced pappi that were biomechanically unlikely to confer wind dispersal (e.g., *Lasthenia californica*).

Species were additionally categorized as patch- or matrix-associated (Appendix S1: Table S1) to identify and account for species that were unlikely to be constrained to serpentine habitat patches (Cook et al. 2002, Jones et al. 2015). Matrix-associated species included both matrix specialists and generalists that show no affinity for habitat type. Species were considered matrix-associated if they were equally or more common in matrix plots than in the patch plots. Twelve species met these criteria, including *Avena fatua*, *Bromus hordeaceus*, and *Lotus wrangelianus*. Although one option was to use an external metric of serpentine affinity (Safford et al. 2005), our serpentine patches frequently included species that had low or no serpentine affinity, but were not present in the nonserpentine matrix, likely due to invader competition. Therefore, our occupancy-based associations, which categorized species as patch or matrix associated, were most appropriate for our research questions, as these depend on the focal community experiencing an impermeable habitat matrix regardless of known serpentine affinity.

We estimated habitat patch characteristics in the field and using ArcGIS v10.1 (ESRI.com) on GoogleEarth v7.3.2 images (Fig. 1; Appendix S1: Fig. S2). In ArcGIS, we delineated all serpentine patches within our study region, including the 28 surveyed patches and 14 unsurveyed patches; these delineations allowed us to calculate patch size and patch connectivity. Patch connectivity was estimated using distances between the edge of patch i and the closest edges of all other j patches (including unsampled patches), weighted by a negative exponential dispersal kernel using Eq. 1 (Hanski 1994*a*, *b*, Jones et al. 2015):

$$\text{connectivity}_i = \sum_{j \neq i}^{n} A \cdot e^{-d_{ij}/\alpha}, \tag{1}$$

where A is the area of patch j, d is the Euclidean distance in meters between patch i and j, and α is the mean dispersal distance, set to 5 m for all species. We note that our results are insensitive to alternative α values (reported in Appendix S1). In other words, patch i is most connected when it is in close proximity to many large patches. Our connectivity measure falls into a general class of measures called "incidence function models," which have been shown to perform equally well or better than alternative measures (i.e., nearest-neighbor or buffer measures; Prugh 2009). The basis of these models was first developed by Levins (1969) and later adapted by Hanski (1994*a*, *b*) to test species' extinction and colonization as a function of patch size and isolation by distance, respectively. These models have achieved broad success at understanding the population and metapopulation persistence of a diversity of organisms in fragmented landscapes (e.g., butterflies (Wahlberg et al. 1996) and pikas (Moilanen et al. 1998)), with applications to landscape management and conservation planning (Wahlberg et al. 1996).

We estimated two alternative measures of connectivity that we hypothesized could be more appropriate for plant species that are dispersed by animals or gravity. For species that are dispersed by animals, we traced animal trails that were observable via GoogleEarth (Fig. 1 and Appendix S1: Fig. S2) using ArcGIS and used the

number of trails that intersected habitat patches to estimate patch connectivity via animals. In topographically challenging landscapes, such as our study area, deer tend to move predictably to avoid steep uneven terrain (e.g., along ridges), resulting in consistent trampled "highways" for a diversity of animals, including rabbits and turkeys (Sindorf 2009). Counts of deer paths have been shown to provide accurate estimates of relative deer abundances (Mayle et al. 2001). Scat present in our habitat patches and on animal paths was identified as originating from deer, rabbits, and large carnivores (cougars, bobcats, and coyotes are known to visit this site).

For plant species that are dispersed by gravity/water, we estimated hydrological connectivity by tracing networks of surface streams, and for each habitat patch, summed the area of all j habitat patches upslope from and connected via surface streams to each patch i (see schematic in Appendix S1: Fig. S3). Elevation of habitat patches ranged 450–550 m above sea level, small enough for elevational clines in climate to be unimportant. Although in some systems, habitat patches at the base of an elevational cline have increased resource inputs and thus higher productivity, productivity was not correlated with elevation (slope < 0.01, $P = 0.465$) or hydrological connectivity (slope = -0.03, $P = 0.458$) in our data set. We estimated productivity as a composite measure [(1 − proportion of bare ground) × vegetation height] to estimate the volume of plant material in each plot nondestructively. We predicted that connectivity by distance would serve as the best proxy for wind dispersal, as wind moves in all directions in topographically complex landscapes (McNider and Pielke 1984).

Statistical analyses

As per Germain et al. (2017), data from our manipulative experiment were analyzed using a generalized linear mixed effects model ("glme"). Dispersal treatment was included as a fixed factor, "patch id" as a random factor (because treatments were nested within patches), and species richness as the Poisson-distributed response variable (as is appropriate for count data).

For our observational data, to determine if species composition in serpentine habitat patches was distinct from the surrounding nonserpentine matrix, we used linear mixed effects models to test for differences in species composition among plots in serpentine habitat patches (patch plots), 1 m into the habitat matrix (edge plots), and 5 m into the habitat matrix (matrix plots). To do so, we first performed a principal-coordinates analysis using Jaccard's distances on the plot-level presence/absence data. The first and second axis scores were used as response variables in separate analyses with fixed effects of habitat type (i.e., patch, edge, matrix) and patch id included as a random effect to account for the nonindependence of the five plots transecting each habitat patch. The "glht" function in R package "multcomp" was used to perform Tukey's tests of compositional differences

among all pairwise treatment combinations (patch vs. edge, patch vs. matrix, edge vs. matrix).

To examine the relationship between species richness and patch connectivity, we first performed a glme with species richness of each dispersal mode per patch as the response variable, and dispersal mode, connectivity by distance, connectivity by animals, connectivity by hydrology, patch size as fixed effects. Patch id was included as a random effect to account for the nonindependence of replicate plots within a single patch. Only plots within serpentine habitat patches were included in this analysis, as the matrix plots were a distinct plant community. Our inclusion of patch size as a fixed effect is consistent with conventional incidence function models (Prugh 2009); these are rooted in island biogeography theory, which predicts that diversity increases with patch size because of decreased extinction and increased colonization rates in large patches (MacArthur and Wilson 1967). Because there were significant interactions between dispersal mode and all connectivity measures (Appendix S1: Table S2), we performed three separate glme analyses, one for each dispersal mode, using the same model described above but omitting the dispersal mode term.

Analysis of Poisson-distributed data with interacting continuous predictors is prone to Type I errors, so we took several steps to identify reduced models that best fit the data. First, we performed backwards selection on each full model using the "step" function in the "stats" package. The function "step" sequentially drops higher-order interactions until the reduced model that yields the greatest model fit (lowest Akaike' information criteria [AIC] score) is attained. However, "step" can arrive at a local minimum in AIC score that does not reflect the global minimum, which was likely for our data given the presence of significant but biologically implausible four-way interactions. For this reason, we applied "drop1" to the "step"-reduced model to identify variables that did not significantly improve model fit even if their inclusion led to a marginal decrease in AIC scores. We cycled between "drop1" and "step" until a model was obtained for which all variables significantly improved model fit and led to the lowest AIC scores out of all possible reduced models. We then used the function "anova" in the R package "stats" to test whether the reduced model was a significantly better fit to the data than the full and intercept-only models (Appendix S1: Table S4).

Results

Species richness and composition differed among serpentine habitat patches and the nonserpentine matrix (Fig. 2), confirming that the serpentine plant community is distinct and constrained to the serpentine habitat-patch network. Specifically, we saw dramatic differences in both species richness ($\chi^2 = 29.72$, $P < 0.001$) and composition (axis 1: $\chi^2 = 327.91$, $P < 0.001$, axis 2: $\chi^2 = 53.56$, $P < 0.001$) between habitat patch and matrix plots, even though matrix plots were positioned only
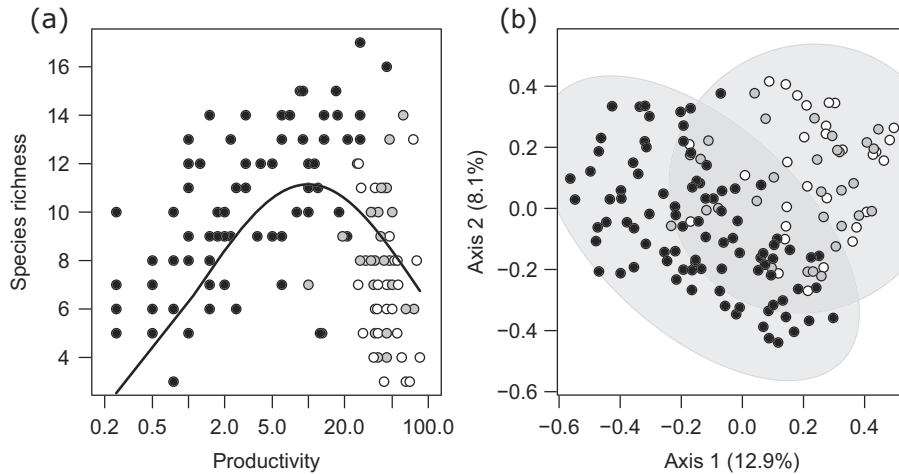
FIG. 2. Comparison of (a) species richness vs. patch productivity and (b) community composition among plots that occur in serpentine habitat patches (black points), 1 m into the nonserpentine matrix (gray points), and 5 m into the nonserpentine matrix (white points). In panel (a), the line is the fitted relationship between species richness and productivity. In panel (b), the gray regions are the 95% confidence ellipses for community composition in serpentine and nonserpentine plots.

1 m into the matrix (gray points in Fig. 2). Because matrix plots were far more productive but far less speciose than plots in habitat patches, we detected a hump-shaped productivity–diversity relationship (Fig. 2a). This is a common finding in communities characterized by competitive dominance at high levels of productivity (Mittelbach et al. 2001). Note that, compositionally, there is some overlap among habitat patch and matrix plots (Fig. 2b), which tended to be caused by matrix species (e.g., *Avena fatua*) spilling into habitat patches and not the reverse. This spillover effect increased with the number of animal paths that intersected habitat patches (Appendix S1: Fig. S4).

We found evidence of significant dispersal limitation via an experimental manipulation of dispersal but not via an observational approach. In the manipulative experiment, enhancing dispersal among habitat patches at a scale of 100 m led to an average increase of eight species per plot compared to in unmanipulated plots ($\chi^2 = 7.79$, $P = 0.005$; Fig. 3). By contrast, the observational data, which was analyzed via standard incidence function models (Eq. 1), showed that species richness was not significantly associated with connectivity by distance ($P = 0.943$), even after accounting for variance due to patch size or patch productivity (Appendix S1: Table S3).

Consistent with our hypothesis, we not only found that other forms of connectivity (i.e., hydrology, animals) significantly explained species richness patterns, but that there was a general alignment between dispersal vectors and species' putative dispersal modes. For gravity-dispersed species, hydrology was the only form of connectivity retained as a predictor after model selection for this group. However, the effect of hydrological connectivity was not simply a main effect, but rather, an interactive effect with patch size (i.e., significant hydrological connectivity × patch size effect [$\chi^2 = 6.37$,

$P = 0.012$], Fig. 4a). The model that best fit the richness data of animal-dispersed species was one that, as predicted, included connectivity by animals. However, as with gravity-dispersed species, the best-fit model also included an interaction, in this case between connectivity by animals and connectivity by distance ($\chi^2 = 7.06$, $P = 0.007$, Fig. 4b). Although we predicted that connectivity by distance would be most relevant to wind-dispersed species, species richness of this group was best predicted by an intercept-only model (Appendix S1: Table S4).

By projecting the species richness of each dispersal mode predicted by our models onto a map (Fig. 1b–d), we find that these groups differ in how they experience connectivity of the same landscape. Our models did not identify any landscape variable that might be relevant for connectivity of wind-dispersed species; therefore, our models do not predict spatial variation in habitat connectivity for species of this dispersal mode (Fig. 1d). We report the AIC values used for model comparison in each analysis in Appendix S1: Table S4.

DISCUSSION

Despite the emphasis that contemporary ecology places on dispersal as central to the dynamics and distribution of species in ecological communities (Hanski 1994b, Leibold et al. 2004), current empirical assessments of its role do not encompass the diversity of ways in which organisms experience landscape connectivity. In a patchy terrestrial plant community, we found no evidence of dispersal limitation using a distance-based estimate of patch connectivity, even after excluding species associated with the habitat matrix (i.e., a nonsignificant effect of connectivity by distance; Appendix S1: Table S3) and despite experimental evidence of its
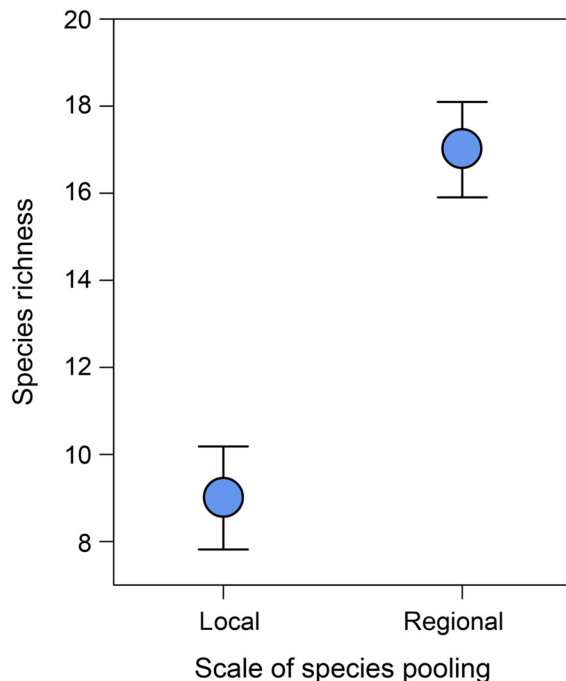
Fig. 3. Experimental evidence of dispersal limitation via pooling seeds within (local) or among (regional) habitat patches to enhance dispersal; points are means ± standard errors. The data presented here are subsetted from a larger data set (Germain et al. 2017) to include only sites within the same region as our current survey, and only plots from two treatments: (1) unmanipulated control plots (local dispersal) and (2) treatments that mixed species pools among sites within the regional extent of our survey (100-m spatial scale, regional dispersal).

pervasiveness (Fig. 3, with data from a previous study (Germain et al. 2017)). However, when species richness was separated by dispersal mode (gravity, wind, animal), the spatial distribution of species richness generally corresponded to spatial patterns of dispersal vectors that connected habitat patches. We discuss these general findings, as well as several unexpected results that provide a richer understanding of interacting dispersal vectors in serpentine grasslands and their altered efficacy in invaded landscapes.

Consistent with our prediction, the richness of gravity-dispersed species was highest in patches highly connected by hydrology, but unexpectedly, this was only true when habitat patches were small (i.e., Fig. 4a, steep slopes connecting points 1 to 2, but shallow slopes connecting points 3 to 4). Although we did not predict this interaction a priori, it suggests that large, hydrologically connected patches are locally saturated (i.e., response surface decelerates from points 1 to 3; note log-scale of axes) and that these two predictors act as compensatory pathways toward reaching saturation. Our findings are consistent with recent experimental work showing that dispersal only increases species richness in small habitat patches (Schuler et al. 2017) given that populations in

small patches are more prone to stochastic extinctions (Gilbert and Levine 2017) which can be overcome via dispersal.

More animal-dispersed species were found in serpentine patches intersected by many animal paths, but only when patches were in close proximity to one another (slope connecting points 3 to 4 in Fig. 4b)—when patches were isolated, animals had a strongly negative effect on species richness (slope connecting points 1 and 2). What is driving the negative effect of animals on the richness of animal-dispersed species in isolated patches? The answer is not likely herbivory, given that the animal-dispersed species in our data set are generally tolerant of or well-defended against herbivory (e.g., grasses, star thistle; Appendix S1: Table S1) and given that connectivity by animals did not predict the richness of wind-dispersed species, a highly palatable group (e.g., wild lettuce, dandelion [Appendix S1: Table S1]).

Rather, we hypothesize that this effect is caused by distances among patches exceeding the distances for which seeds remain attached to animals. Seeds removed by animals in isolated habitat patches have a low probability of (1) being deposited in other habitat patches, compared to the inhospitable matrix, and of (2) being rescued from extinction via dispersal from other patches. In other words, seeds are removed but not replaced. Additionally, many of the most noxious invaders in serpentine grasslands are animal dispersed (e.g., common wild oat [*Avena fatua*], barbed goatgrass [*Aegilops triuncialis*]), adding the potential for invader impacts via animal-mediated dispersal from the nonserpentine matrix, even if those invaders exist only as sink populations (Schreiber and Kelton 2005). This explanation would account for serpentine habitat patches shifting to a matrix-like composition when intersected by many animal paths (Appendix S1: Fig. S4). The negative effect of dispersal via animals is likely a contemporary phenomenon given that, prior to invasion by European grasses, a greater proportion of the landscape was suitable to species that are now restricted to serpentine patches (Gram et al. 2004, Gilbert and Levine 2013). Further support for this hypothesis comes from our finding that species richness increases with connectivity by distance only in patches that are highly connected by animals (slope connecting points 2 and 3). This result reinforces the role of animals as dispersal vectors that connect patches that would otherwise be unconnected, even if they are in close proximity.

Although we predicted that the richness of wind-dispersed species would increase with connectivity by distance, given that wind moves in all directions in topographically complex landscapes (McNider and Pielke 1984), such as our study site, we instead found that an intercept-only model best fit the data. This finding has three possible explanations, the first being that wind-dispersed species are simply not dispersal limited at the spatial scale of our surveys, and the second being that we have not adequately captured spatial variation in the movement of seeds by wind. Although we cannot

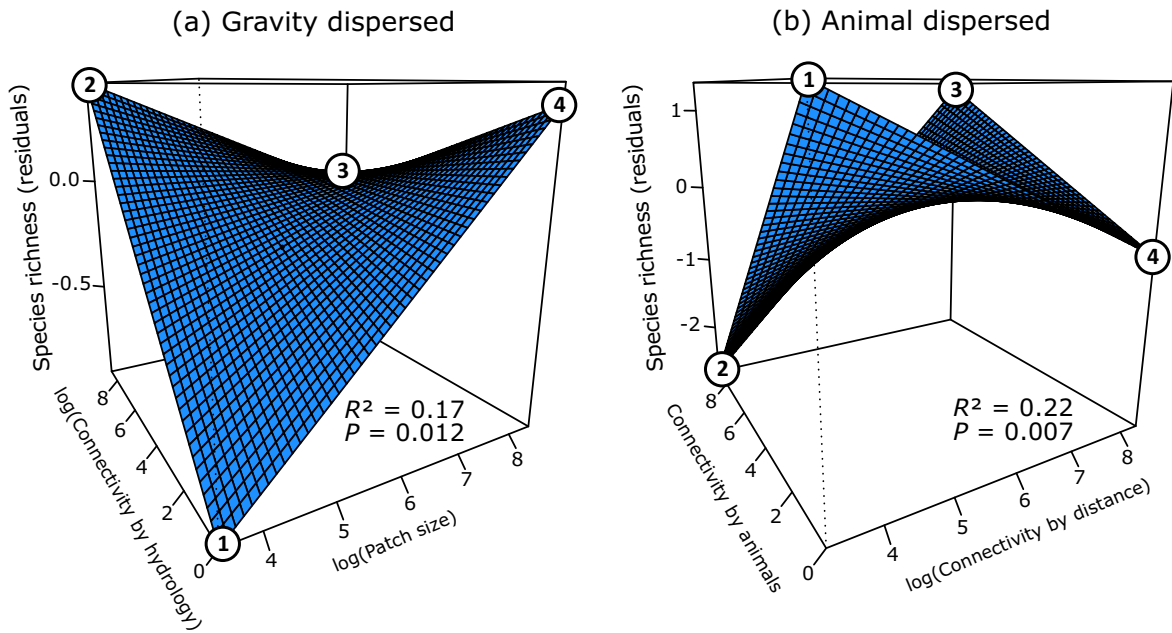## (a) Gravity dispersed

(b) Animal dispersed

FIG. 4. Species richness of (a) gravity-dispersed species, as a function of patch size and hydrological connectivity, and of (b) animal-dispersed species within serpentine habitat patches, as a function of connectivity by distance and animal connectivity. Numbered points connect different slopes to aid our description of the response surface in main text. Fitted response surfaces of species richness are shown for simplicity with residuals presented in Appendix S1: Fig. S5. The explanatory variables shown here for each group are the only fixed factors retained in the model following AIC-based model selection (described in Methods and shown in Appendix S1: Table S4).

weigh these two alternate explanations against each other, what we can say is that there is a high degree of variation in species richness and composition among patches for this dispersal group, including some patches that lack species from this group altogether. High spatial turnover (β diversity) without evidence of dispersal limitation implicates the role of local processes, such as abiotic conditions, herbivory, competition, or stochasticity (Cottenie 2005, Germain et al. 2013). However, a more detailed examination of dispersal kernels and wind patterns for this group are needed.

A third explanation is that trait differences among wind-dispersed species, for example, short vs. tall species (Thomson et al. 2011), caused additional variation in how species experience landscape connectivity. For example, large-seeded wind-dispersed plant species disperse farther on average (Thomson et al. 2011); thus seed size differences may contribute to regional occupancy patterns for this group. Testing this possibility would require separate analyses of species occupancy patterns for multiple species; our data are not amenable to such an analysis because only two wind-dispersed species occupied enough patches to reasonably fit an incidence function model (MacKenzie et al. 2005). We note, however, that our largest-seeded wind-dispersed species (*Microseris douglasii*) was also the most common, observed in 22 of the 28 sampled patches (Appendix S1: Fig. S6). This hypothesis requires future testing, as seed size is a complex trait

related to aspects of life histories other than dispersal (Moles et al. 2005).

Our approach is commonly employed to quantify how connected individual habitat patches are within a total habitat patch network (Hanski and Ovaskainen 2003), but it cannot be used to disentangle the relative importance of specific patches in maintaining total landscape connectivity. Determining the importance of individual patches in maintaining total network connectivity is invaluable to landscape management, for example, for deciding which patches to preserve if some must be lost (Estrada and Bodin 2008). To do so, alternative network metrics are applied that conceptualize habitat patches as "nodes" with links between them to represent potential dispersal pathways (i.e., "betweenness centrality"; Bodin and Saura 2010]). Although our current data set is not equipped to address this important knowledge gap, which would require information on habitat permeability, directionality of animal movement, and seed attachment times, it does suggest that the importance of any given habitat patch for total network connectivity varies among plant groups with different dispersal life histories.

Habitat fragmentation is the primary driver of biodiversity loss worldwide (Crooks et al. 2011) through reductions in habitat connectivity (Lindborg and Eriksson 2004). In serpentine plant communities and many other ecosystems, fragmentation has occurred via the widespread invasion of nonnative species, with native species now relegated to small isolated "refuge" habitat

patches. Though species in refuge patches may be safe from direct competition with invaders, diversity is still challenged with the indirect effects of reduced colonization (Gilbert and Levine 2013). The extreme harshness of the competitive effect in the nonserpentine matrix is clear if we consider that (1) plots in the nonserpentine matrix were 7.1 times more productive than serpentine plots yet contained 2.2 fewer species on average (Fig. 2a), and that (2) there was no difference in species composition among plots 1 m vs. 5 m into the matrix (gray vs. white points in Fig. 2b), even though 1 m is within the dispersal capacities of most species. In order to prevent the nonrandom loss of some species over others (e.g., plants dispersed by animals), landscape management plans may need to consider alternate forms of habitat connectivity. Californian landscapes were invaded ~200 yr ago, meaning that current communities may already reflect a compositional reorganization that favors some dispersal modes over others, a hypothesis that can be tested experimentally.

Conclusion

Characterizing habitat connectivity is fundamental to understanding how dispersal contributes to biodiversity patterns (Leibold et al. 2004), as well as to landscape planning for conservation (Crooks and Sanjayan 2006, Estrada and Bodin 2008). In a serpentine grassland, we uncovered cryptic dispersal networks by linking species' dispersal life histories to dispersal vector movement. Our results suggest that ecologists should more often consider whether the absence of significant distance effects truly represents an absence of dispersal limitation vs. an inability to capture landscape variables that are most limiting to dispersal. Additionally, our finding that animal dispersal reduced diversity in isolated habitat patches points toward the altered functioning of ecological networks in invaded landscapes. Our results have broad implications for understanding how ecological communities might reorganize as landscapes are fragmented, patches are lost, and the function of dispersal life histories is altered.

Literature Cited

Anacker, B. L., and S. P. Harrison. 2012. Historical and ecological controls on phylogenetic diversity in Californian plant communities. American Naturalist 180:257–269.

Beisner, B. E., P. R. Peres-Neto, E. S. Lindström, A. Barnett, and M. L. Longhi. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology 87:2985–2991.

Bodin, O., and S. Saura. 2010. Ranking individual habitat patches as connectivity providers: integrating network analysis and patch removal experiments. Ecological Modelling 221:2393–2405.

Borcard, D., P. Legendre, C. Avois-Jacquet, and H. Tuomisto. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85:1826–1832.

Brown, B. L., and C. M. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. Journal of Animal Ecology 79:571–580.

Case, E. J., S. Harrison, and H. V. Cornell. 2016. After an invasion: understanding variation in grassland community recovery following removal of a high-impact invader. Biological Invasions 18:371–380.

Cook, W. M., K. T. Lane, B. L. Foster, and R. D. Holt. 2002. Island theory, matrix effects and species richness patterns in habitat fragments. Ecology Letters 5:619–623.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

Crooks, K. R., C. L. Burdett, D. M. Theobald, C. Rondinini, and L. Boitani. 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philosophical Transactions of the Royal Society of London B 366:2642–2651.

Crooks, K. R., and M. Sanjayan. 2006. Connectivity conservation. Cambridge University Press, Cambridge, UK.

Damschen, E. I., L. A. Brudvig, N. M. Haddad, D. J. Levey, J. L. Orrock, and J. J. Tewksbury. 2008. The movement ecology and dynamics of plant communities in fragmented landscapes. Proceedings of the National Academy of Sciences of the United States of America 105:19078–19083.

De Bie, T. et al. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecology Letters 15:740–747.

Estrada, E., and O. Bodin. 2008. Using network centrality measures to manage landscape connectivity. Ecological Applications 18:1810–1825.

Foster, B. L., and D. Tilman. 2003. Seed limitation and the regulation of community structure in oak savanna grassland. Journal of Ecology 91:999–1007.

Freestone, A. L., and B. D. Inouye. 2006. Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. Ecology 87:2425–2432.

Germain, R. M., L. Johnson, S. Schneider, K. Cottenie, E. A. Gillis, and A. S. MacDougall. 2013. Spatial variability in plant predation determines the strength of stochastic community assembly. American Naturalist 182:169–179.

Germain, R. M., S. Y. Strauss, and B. Gilbert. 2017. Experimental dispersal reveals characteristic scales of biodiversity in a natural landscape. Proceedings of the National Academy of Sciences of the United States of America 114:4447–4452.

Gilbert, B., and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences of the United States of America 101:7651–7656.

Gilbert, B., and J. M. Levine. 2013. Plant invasions and extinction debts. Proceedings of the National Academy of Sciences of the United States of America 110:1744–1749.

Gilbert, B., and J. M. Levine. 2017. Ecological drift and the distribution of species diversity. Proceedings of the Royal Society of London B 284:20170507.

Gonzalez, A., B. Rayfield, and Z. Lindo. 2011. The disentangled bank: How loss of habitat fragments and disassembles ecological networks. American Journal of Botany 98:503–516.

Grainger, T. N., R. M. Germain, N. T. Jones, and B. Gilbert. 2017. Predators modify biogeographic constraints on species distributions in an insect metacommunity. Ecology 98:851–860.

Gram, W. K., E. T. Borer, K. L. Cottingham, E. W. Seabloom, V. L. Boucher, L. Goldwasser, F. Micheli, B. E. Kendall, and R. S. Burton. 2004. Distribution of plants in a California serpentine grassland: Are rocky hummocks spatial refuges for native species? Plant Ecology 172:159–171.

Hanski, I. 1994a. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151–162.

Hanski, I. 1994b. Patch-occupancy dynamics in fragmented landscapes. Trends in Ecology and Evolution 9:131–135.

Harrison, S. 1999. Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. Ecology 80:70–80.

Hanski, I., and O. Ovaskainen. 2003. Metapopulation theory for fragmented landscapes. Theoretical Population Biology 64:119–127.

Harrison, S., K. F. Davies, H. D. Safford, and J. H. Viers. 2006. Beta diversity and the scale-dependence of the productivity–diversity relationship: a test in the Californian serpentine flora. Journal of Ecology 94:110–117.

Harrison, S., and R. Rajakaruna, editors. 2011. Serpentine: the evolution and ecology of a model system. University of California Press, Berkeley, California, USA.

Hurtt, G. C., and S. W. Pacala. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. Journal of Theoretical Biology 176:1–12.

Jones, N. T., R. M. Germain, T. N. Grainger, A. M. Hall, L. Baldwin, and B. Gilbert. 2015. Dispersal mode mediates the effect of patch size and patch connectivity on metacommunity diversity. Journal of Ecology 103:935–944.

Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Lindborg, R., and O. Eriksson. 2004. Historical landscape connectivity affects present plant species diversity. Ecology 85:1840–1845.

Lowe, W. H., and M. A. McPeek. 2014. Is dispersal neutral? Trends in Ecology and Evolution 29:444–450.

MacArthur, R., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

MacKenzie, D. I., J. D. Nichols, N. Sutton, K. Kawanishi, and L. L. Bailey. 2005. Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86:1101–1113.

Mayle, B. A., R. J. Putman, and I. Wyllie. 2001. The use of trackway counts to establish an index of deer presence. Mammal Review 30:233–237.

McNider, R. T., and R. A. Pielke. 1984. Numerical simulation of slope and mountain flows. Journal of Climate and Applied Meteorology 23:1441–1453.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology 82:2381–2396.

Moilanen, A., A. T. Smith, and I. Hanski. 1998. Long-term dynamics in a metapopulation of the American pika. American Naturalist 152:530–542.

Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, and M. Westoby. 2005. A brief history of seed size. Science 307:576–580.

Mouquet, N., and M. Loreau. 2003. Community patterns in source–sink metacommunities. American Naturalist 162:544–557.

Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87:2614–2625.

Prugh, L. R. 2009. An evaluation of patch connectivity measures. Ecological Applications 19:1300–1310.

Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences of the United States of America 105:20770–20775.

Safford, H. D., J. H. Viers, and S. P. Harrison. 2005. Serpentine endemism in the California flora: a database of serpentine affinity. Madroño 52:222–257.

Schreiber, S. J., and M. Kelton. 2005. Sink habitats can alter ecological outcomes for competing species. Journal of Animal Ecology 74:995–1004.

Schuler, M. S., J. M. Chase, and T. M. Knight. 2017. Habitat patch size alters the importance of dispersal for species diversity in an experimental freshwater community. Ecology and Evolution 7:5774–5783.

Shen, G., M. Yu, X.-S. Hu, X. Mi, H. Ren, I.-F. Sun, and K. Ma. 2009. Species–area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. Ecology 90:3033–3041.

Sindorf, V. 2009. Animal movements: The utilization of white-tailed deer (*Odocoileus virginianus*) trails by vertebrates as a means of traversing gaps in landscape matrices. Dissertation, Cornerstone University, Grand Rapids, Michigan, USA.

Spasojevic, M. J., E. I. Damschen, and S. Harrison. 2014. Patterns of seed dispersal syndromes on serpentine soils: examining the roles of habitat patchiness, soil infertility and correlated functional traits. Plant Ecology and Diversity 7:401–410.

Thomson, F. J., A. T. Moles, T. D. Auld, and R. T. Kingsford. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. Journal of Ecology 99:1299–1307.

Wahlberg, N., A. Moilanen, and I. Hanski. 1996. Predicting the occurrence of endangered species in fragmented landscapes. Science 273:1536–1538.

White, C., K. A. Selkoe, J. Watson, D. A. Siegel, D. C. Zacherl, and R. J. Toonen. 2010. Ocean currents help explain population genetic structure. Proceedings of the Royal Society of London B 277:1685–1694.

Supporting Information