

## Patterns of seed dispersal syndromes on serpentine soils: examining the roles of habitat patchiness, soil infertility and correlated functional traits

Marko J. Spasojevic, Ellen I. Damschen & Susan Harrison

To cite this article: Marko J. Spasojevic, Ellen I. Damschen & Susan Harrison (2014) Patterns of seed dispersal syndromes on serpentine soils: examining the roles of habitat patchiness, soil infertility and correlated functional traits, *Plant Ecology & Diversity*, 7:3, 401-410, DOI: 10.1080/17550874.2012.678506

To link to this article: <https://doi.org/10.1080/17550874.2012.678506>



View supplementary material [↗](#)



Published online: 10 Oct 2012.



Submit your article to this journal [↗](#)



Article views: 507



View related articles [↗](#)



View Crossmark data [↗](#)



Citing articles: 5 View citing articles [↗](#)

## Patterns of seed dispersal syndromes on serpentine soils: examining the roles of habitat patchiness, soil infertility and correlated functional traits

Marko J. Spasojevic<sup>a\*</sup>, Ellen I. Damschen<sup>b</sup> and Susan Harrison<sup>a</sup>

<sup>a</sup>Department of Environmental Science and Policy, University of California, Davis, USA; <sup>b</sup>Department of Zoology, University of Wisconsin-Madison, Madison, USA

(Received 8 September 2011; final version received 18 March 2012)

**Background:** It is critical to understand the ecological factors shaping seed dispersal in plant communities in order to predict their fate in the face of global change. Communities restricted to patchy habitats may contain more species with ‘directed’ dispersal syndromes that facilitate successful seed dispersal to other patches; however, habitat quality may constrain the presence of and efficiency of dispersal syndromes found within those habitats.

**Aims:** The aim of this study was to hypothesise that if habitat patchiness is an important filter on dispersal syndromes, ‘directed’ vertebrate dispersal should be more prevalent in serpentine habitats because of their patchiness. Alternatively, if habitat quality is more important, wind dispersal should be more prevalent in serpentine habitats because of their low fertility.

**Methods:** Using three datasets representing grassland, chaparral and forest vegetation types, we analysed differences in the composition of dispersal syndromes (vertebrate, wind, passive, water and ant) between communities on patchy infertile serpentine soils and on continuous, fertile non-serpentine soils. Our analyses also accounted for correlated functional traits and phylogenetic relatedness.

**Results:** Across and within all three vegetation types, serpentine communities had significantly higher proportions of wind dispersed and lower proportions of vertebrate-dispersed species. These patterns were not independent of functional traits. Proportions of the other dispersal syndromes did not differ.

**Conclusions:** Our results suggest that on low-fertility soils, habitat quality may outweigh habitat patchiness as a filter on the availability of dispersal syndromes, potentially adding to the vulnerability of such communities to stochastic extinctions and global change.

**Keywords:** directed dispersal; dispersal syndromes; habitat patchiness; plant functional traits; phylogenetic relatedness; serpentine

### Introduction

Human-induced changes to ecosystems are currently affecting many species around the world via alterations in land-use, habitat fragmentation and changes in temperature and precipitation patterns (Parmesan 2006). Whilst some species may have traits that allow them to persist in situ in response to such changes, others are dispersing to more suitable habitats (Parmesan and Yohe 2003; Parmesan 2006); however, species that cannot persist may lack suitable habitats to disperse to, or are unable to disperse far enough to cope with many of the above changes to ecosystems (Thomas et al. 2004; Parmesan 2006). Understanding environmental factors influencing the distributions of dispersal syndromes within and among communities can help predict the fate of species and communities in the future (Parmesan 2006; Engler et al. 2009). Community assembly theory provides a framework for understanding how multiple factors may influence the distribution of dispersal syndromes within plant communities (Ozinga et al. 2004). The composition of dispersal syndromes within and among communities is influenced by both the spatial distribution of suitable habitats across the landscape (MacArthur and Wilson 1967; Leibold et al. 2004; Holyoak et al. 2005)

and by the environmental conditions of a given habitat (Willson et al. 1990; Ozinga et al. 2004; Flinn et al. 2010). Understanding the relative influence of habitat patchiness and habitat quality is critical because in a rapidly changing environment, our ability to predict patterns of species persistence or extinction, and community disassembly and reassembly, will depend on how habitat patchiness and habitat quality shape the composition of dispersal syndromes within communities.

The distribution of habitats across the landscape is known to play an important role in determining the composition of dispersal syndromes within a community (Hamilton and May 1977; Howe and Smallwood 1982; Flinn et al. 2010). Metacommunity theory suggests that this is especially true in complex landscapes where communities are restricted to patchy or island-like habitats (Leibold et al. 2004; Holyoak et al. 2005). Dispersal can connect similar communities in separate isolated patches of habitat, which can counteract the effects of local processes such as environmental filtering or competition (Mouquet and Loreau 2003; Chase et al. 2005). Dispersal among patches can enable species to persist in unfavourable ‘sink’ habitats as a result of dispersal from more favourable ‘source’

\*Corresponding author. Email: [mspasoje@ucdavis.edu](mailto:mspasoje@ucdavis.edu)

habitats (Amarasekare et al. 2004); however, the effect of dispersal in influencing the structure of communities in patchy habitats is dependent on the dispersal ability of the species present within those patches (Leibold et al. 2004; Holyoak et al. 2005). Species found in patchy habitats may be those that have longer-distance dispersal syndromes (vertebrate, water and wind dispersal syndromes) allowing them to disperse to and maintain populations in isolated habitat fragments (Levine and Murrell 2003; Vandvik and Goldberg 2006).

Recent work considering the relative efficiency of long-distance dispersal syndromes suggests that certain long-distance dispersal syndromes can be more effectively directed to sites suitable for recruitment (Howe and Smallwood 1982; Wenny 2001; Spiegel and Nathan 2007; Spiegel and Nathan 2010). Thus, species that are restricted to highly patchy habitats may require dispersal methods that are especially efficient at dispersing to those patches (directed dispersal). Birds and mammals have been found to preferentially disperse seeds to favourable microsites for germination (Wenny and Levey 1998; Dean and Milton 2000; Purves and Dushoff 2005; Briggs et al. 2009). Therefore, in patchy habitats directed vertebrate dispersal may be expected to be more common, whilst the frequency of less directed dispersal syndromes, such as wind dispersal, may be lower (Howe and Smallwood 1982; Wenny 2001; Spiegel and Nathan 2010).

In addition to the distribution of habitats across the landscape, environmental conditions can also shape dispersal syndromes either directly or indirectly. Resource availability may constrain the availability and efficiency of dispersal syndromes (Willson et al. 1990; Ozinga et al. 2004; Flinn et al. 2010). On patches of infertile soil, lower resource availability may lead to lower abundances of vertebrates, which may, in turn, lead to a lesser prevalence of vertebrate dispersal (Hughes and Westoby 1992; Edwards et al. 2006). In addition, the open vegetation structure on infertile soils may promote the efficiency of wind dispersal (Howe and Smallwood 1982; Nathan et al. 2008). Furthermore, lower water availability can hinder the production of fleshy fruit dispersed by vertebrates (Tabarelli et al. 2003; Almeida-Neto et al. 2008). Lastly, dispersal syndromes may be functionally and/or phylogenetically non-independent of resource acquisition/tolerance traits, such that traits that allow a species to persist in a given habitat may be correlated with particular dispersal syndromes. Thus, dispersal syndromes may be indirectly constrained by traits required in low-resource environments (i.e., slow growth, high investment in below-ground structures) making it difficult to distinguish the direct causal relationship of the environment on dispersal syndromes (Westoby et al. 1996; Ronce 2007). Strategies of seed dispersal and resource acquisition may be part of broader trait syndromes that are strongly associated with particular phylogenetic groups, the distributions of which may reflect their biogeographic histories, further complicating attempts at direct functional interpretation (Herrera 1992).

Several studies have assessed the importance of directed dispersal in anthropogenically fragmented landscapes (e.g., Cheptou et al. 2008; Montoya et al. 2008), whilst others have considered the influence of environmental conditions on dispersal syndromes (e.g., Willson et al. 1990; Ozinga et al. 2004); however, we are aware of no study to date that has simultaneously considered spatial and environmental influences on the distribution of dispersal syndromes across communities, whilst also accounting for correlated functional traits and phylogenetic relationships. Here we compare the composition of dispersal syndromes of communities in patches of infertile serpentine soil to the dispersal syndromes of communities in a landscape of more fertile soils. Serpentine soils provide a unique opportunity to simultaneously test the importance of habitat patchiness, habitat quality and correlated functional traits and phylogenies on the composition of dispersal syndromes within plant communities. One of the challenges in evaluating the role of directed dispersal is that suitable locations for species are often unknown (Wenny 2001). Serpentine affinities in the California Floristic Province are well known (Safford et al. 2005), making it possible for us to directly test predictions of the role of directed dispersal on how habitat patchiness and environmental constraints should affect dispersal syndromes.

Using data from >450 species in three structural vegetation types (forest, chaparral and grassland), we examined the roles of habitat patchiness and environmental conditions in shaping the dispersal potential of plant communities. We asked (1) does the composition of dispersal syndromes differ between serpentine and non-serpentine communities within each structural vegetation type? If so, we then ask (2) are the differences in dispersal syndromes more consistent with habitat patchiness or soil fertility as a filter? If habitat patchiness has acted as an ecological filter on the composition of dispersal syndromes, we predict a greater prevalence of longer-distance dispersal syndromes (vertebrate, wind and water) in serpentine communities, or alternatively, a greater prevalence of directed dispersal syndromes (vertebrate dispersal, less wind dispersal) on serpentine; however, if soil fertility has been the most important filter, we predict a greater prevalence of wind dispersal on serpentine. Next, to examine habitat patchiness without the confounding influence of soil fertility, we asked (3) whether either long-distance or directed dispersal was more prevalent or more isolated (<5 ha) than on more continuous (>500 ha) patches of serpentine. We then asked (4) whether the dispersal syndrome patterns we found were confounded by, or independent of, variation in resource acquisition traits or phylogenetic relatedness between serpentine and non-serpentine communities. Lastly, (5) we compared dispersal syndromes among structural vegetation types within each soil type.

## Methods

We combined data from three studies that compared community structure in adjacent habitats on serpentine (i.e.,

ultramafic) and non-serpentine (i.e., non-ultramafic) rocks and soils. The grassland data were collected at the Donald and Sylvia McLaughlin University of California Natural Reserve in Napa and Lake Counties California (Harrison 1999b). These data consist of 38 sites on serpentine soil and 42 on non-serpentine soil surveyed in 1999–2011 (data used here are from 2009) using five 1-m<sup>2</sup> plots per site spaced every 10 m along a 50-m transect (Harrison 1999b). The chaparral data were collected in Lake, Sonoma and Napa Counties, California (Harrison 1997, 1999a). These data consist of sites on small patches of serpentine (24 sites on separate outcrops of 3–5 ha), sites on large patches of serpentine (24 sites within four outcrops of >500 ha), and sites on continuous non-serpentine (24 sites in natural vegetation interspersed among the serpentine outcrops) surveyed in 1997 surveyed using 50-m line transects (Harrison 1997, 1999a). The forest data were collected in coniferous forest and woodland habitats in the Siskiyou Mountains of southwestern Oregon (Damschen et al. 2010). These data consist of 53 sites on non-serpentine and 55 on serpentine ( $n=108$ ) surveyed in 2007 using 25 1-m<sup>2</sup> plots per site along a 50-m transect (Damschen et al. 2010). These three data sets were merged for analysis. The combined data set included 511 species including ferns, graminoids, herbs, shrubs, vines and trees. Because only presence/absence data were available from the chaparral study, we used presence/absence data from all three studies in the combined data set. Whilst these datasets differ slightly in sampling intensity, similar areas were sampled in each dataset and none of these methods should favour species with a particular dispersal syndrome.

We were able to find dispersal syndrome data on 466 of the 511 species (Appendix 1) from published sources (Andersen 1993; Gutterman 1994; Matlack 1994; Fuller and del Moral 2003; Haugo 2006; Lengyel et al. 2009; Sawyer et al. 2009) and the Kew Royal Botanical Gardens Seed Information Database (Royal Botanic Gardens 2008). Species without dispersal syndrome information were dropped from the dataset. These species tended to be rare species unlikely to contribute to the overall patterns. We categorised seed dispersal syndromes into five broad categories: passive, wind, water, vertebrate and ant. Passive dispersal syndromes included seed dispersed by ballistic (ballochory) methods and unassisted dispersal (no particular dispersal method). Wind dispersal syndrome included both wind- (anemochory) and tumbling-dispersed seeds. Water dispersal syndrome only included water-dispersed seeds (hydrochory). Vertebrate dispersal syndrome included adhesive mammal dispersal (epizoochory) and dispersal by ingestion for both mammals and birds (endozoochory). Finally, ant dispersal syndrome only included ant-dispersed seeds (myrmecochory). We did not consider dispersal mechanisms to be mutually exclusive (species could have multiple dispersal syndromes: polychory: 215 out of 511 species). Also, because we did not have data indicating primary dispersal syndromes for all species, we did not assign primary or secondary dispersal modes and included all assigned dispersal syndromes for a

species. We then calculated the relative proportion of each dispersal syndrome (0 to 100) within each plot by dividing the total number of occurrences of a given dispersal syndrome by the total number of occurrences of all dispersal syndromes for each plot and multiplying by 100. We classified dispersal syndromes as either long- (wind, vertebrate and water) or short-distance (ant and passive) following Nathan et al. (2008), and calculated the relative proportion of long-distance dispersal syndromes in each plot as above. Whilst seeds with long-distance dispersal syndromes do not always disperse long distances, this classification describes potential differences in dispersal distance (Cain et al. 2000; Nathan et al. 2008).

To assess relationships between dispersal syndromes and resource acquisition traits, we used data on plant height, specific leaf area (SLA), leaf water content (LWC), and wood density (Harrison et al. unpublished data, collected as per Cornelissen et al. 2003). We chose these resource-related traits because they are known to vary amongst species along gradients of soil fertility and climate (Cornwell and Ackerly 2009; Ordóñez et al. 2009). Plant height is often allometrically related to overall plant size (biomass, rooting depth, lateral spread) as well as to competitive interactions for light (Westoby 1998; Aan et al. 2006). Specific leaf area is associated with leaf life span and tissue N (Reich et al. 1997) and with an allocation strategy including fast relative growth rate and high photosynthetic capacity per unit leaf area (Westoby et al. 2002). Leaf water content is associated with a slower relative growth rate (Garnier and Laurent 1994; Vile et al. 2006) and tolerance to low water availability (Farooq et al. 2009). Wood density is correlated with resistance to drought stress (Hacke et al. 2001).

#### Statistical analysis

To quantify differences in the composition of dispersal syndromes among soil types (serpentine and non-serpentine across all three vegetation types) we used a non-metric multidimensional scaling (NMDS) using Bray–Curtis dissimilarity among plots in R. Bray–Curtis dissimilarity is a semi-metric measure of dissimilarity used for continuous numerical data and does not group samples by shared zeros in the dataset (Beals 1984). ‘Stress’ is a measure of departure from monotonicity in the relationship between the dissimilarity in the original  $n$ -dimensional space and distance in two-dimensional ordination space (Kruskal and Wish 1978). In general, stress values <0.1 correspond to a good indication of the similarities between samples, whereas stress values >0.2 indicate a poor relationship (Clarke 1993). Stress values do not affect analyses conducted on dissimilarity matrices, only how well the dissimilarity among sites is represented in a two-dimensional figure (Clarke 1993).

We then used permutational analysis of variance (perMANOVA: Anderson 2001) on the above Bray–Curtis dissimilarity matrix in the Vegan package (Oksanen et al. 2010) in R (R Development Core Team 2010) to test



for differences in the composition of dispersal syndromes among: (1) serpentine and non-serpentine soil, both within and among vegetation types; (2) vegetation types; and (3) patchier and more continuous serpentine (i.e. very small versus large patches) within the chaparral vegetation type. Permutational analysis of variance is very similar to an ANOVA but analyses differences in species composition rather than species numbers (Anderson 2001). We then assessed homogeneity of variance in the perMANOVA by calculating beta-dispersion for each of the above analyses (Anderson 2006), using betadisp in the Vegan package (Oksanen et al. 2010) in R (R Development Core Team 2010). Additionally, we used indicator species analysis (Dufrene and Legendre 1997) to ask which dispersal syndromes were related to significant differences in dispersal syndrome composition among groups. To assess whether dispersal syndromes might vary amongst habitats because they are correlated with resource acquisition traits, we used both individual trait values and the first principal component score of all traits to describe the suite of traits. Principal component analysis was conducted in JMP version 9. Because the first principal component described most of the variation in the suite of traits among individual species, we use that axis score as a measure of stress-tolerance/resource-acquisition strategy.

To test for differences in plant functional traits amongst soil types, we used a generalised linear model for each trait with each trait as a response variable and soil type and vegetation type as main effects. We tested for an interaction between soil type and vegetation type. All traits were log-transformed to meet the assumptions of normality.

To test for differences in dispersal syndromes amongst soil types when taking into account vegetation type and correlated functional traits, we used a generalised linear mixed model (GLMM) for each dispersal syndrome separately with a proportion of the dispersal syndrome in a community plot as the response variable, and soil type, vegetation type and principal component 1 (PC1) as the main effects. Ant, water and long-distance dispersal syndromes were untransformed and fit with a Poisson distribution. Vertebrate dispersal was log-transformed to meet the assumptions of normality (it had no zeros) and then fit using a normal distribution. Passive and wind dispersion were log-transformed and then fit with a Poisson distribution. We initially ran a fully factorial model and then re-ran the model excluding all non-significant interactions. We then re-ran the analysis substituting each of the individual traits for PC1. We subsequently ran a similar analysis for the serpentine chaparral data where we categorised sites into small (patchy) and large (continuous) patches of serpentine. We then ran a similar model using the proportion of long-distance dispersal syndromes as the response variable and treated the variables as above. Analyses were conducted using JMP version 9.

To test whether dispersal syndromes were likely to be linked, through patterns of shared inheritance, to other potential soil type adaptations, we used phylogenetic independent contrasts. We generated a phylogenetic supertree

using the software Phylomatic (Webb and Donoghue 2005) and set all branch lengths equal to one. Then, using the comparative analysis by independent contrasts (CAIC) as implemented in R (Purvis and Rambaut 1995), we tested for phylogenetic non-independence between dispersal syndromes and soil tolerance (i.e., whether a species was found or not found on serpentine). We only conducted this analysis for wind and vertebrate dispersal because these were the only dispersal syndromes showing significant differences between soil and vegetation types.

## Results

Across all three vegetation types, the composition of dispersal syndromes differed between communities on serpentine and non-serpentine soils ( $F_{1,259} = 23.40$ ,  $P < 0.01$ ; Figure 1A). Similarly, within each vegetation type, serpentine and non-serpentine communities significantly differed in composition of dispersal syndromes (forest:  $F_{1,107} = 18.03$ ,  $P < 0.01$ , Figure 1B; grassland:  $F_{1,79} = 32.05$ ,  $P < 0.01$ , Figure 1C; chaparral:  $F_{1,71} = 9.54$ ,  $P < 0.01$ , Figure 1D). Lastly, within chaparral serpentine communities there was no significant difference between the composition of dispersal syndromes and between small and large patches of serpentine ( $F_{1,47} = 2.16$ ,  $P = 0.09$ , Figure 1D). Supporting the assumption of homogeneity of variance, there was no difference in beta-dispersion of the composition of dispersal syndromes between serpentine and non-serpentine across in forests ( $F_{1,107} = 2.25$ ,  $P = 0.14$ ), grasslands ( $F_{1,79} = 0.05$ ,  $P = 0.81$ ), chaparral ( $F_{1,71} = 1.16$ ,  $P = 0.32$ ), or small and large patches of serpentine ( $F_{1,47} = 0.22$ ,  $P = 0.64$ ). Indicator species analysis suggested that the differences amongst serpentine and non-serpentine communities were due to lower vertebrate dispersal ( $P < 0.01$  both across all vegetation types and within each vegetation types) and higher wind dispersal ( $P < 0.01$  both across all vegetation types and within each vegetation types) on serpentine soils. Passive, water and ant dispersal did not differ among soil types ( $\chi^2 = 1.29$ ,  $P = 0.72$ ;  $\chi^2 = 0.81$ ,  $P = 0.34$ ; and  $\chi^2 = 2.68$ ,  $P = 0.10$ , respectively, Figure 2).

There was no difference in the proportion of species with long distance dispersal (wind, vertebrate and water combined) syndromes between serpentine and non-serpentine ( $\chi^2 = 0.02$ ,  $P = 0.89$ ) or between small isolated patches and more continuous patches of serpentine ( $\chi^2 = 1.83$ ,  $P = 0.18$ ); however, the proportion of long-distance dispersal syndromes differed among vegetation types ( $\chi^2 = 315.12$ ,  $P < 0.001$ ), with forest having the highest ( $75.2\% \pm 0.67$  s.e.) and grassland and chaparral having similar levels ( $58.1\% \pm 0.83$  s.e. and  $56.90\% \pm 0.78$  s.e., respectively).

Dispersal syndromes did not differ significantly in the predicted direction between small isolated patches and more continuous patches of serpentine. The only significant difference was a significantly lower proportion of water dispersal on small isolated patches ( $\chi^2 = 5.71$ ,  $P = 0.02$ ).

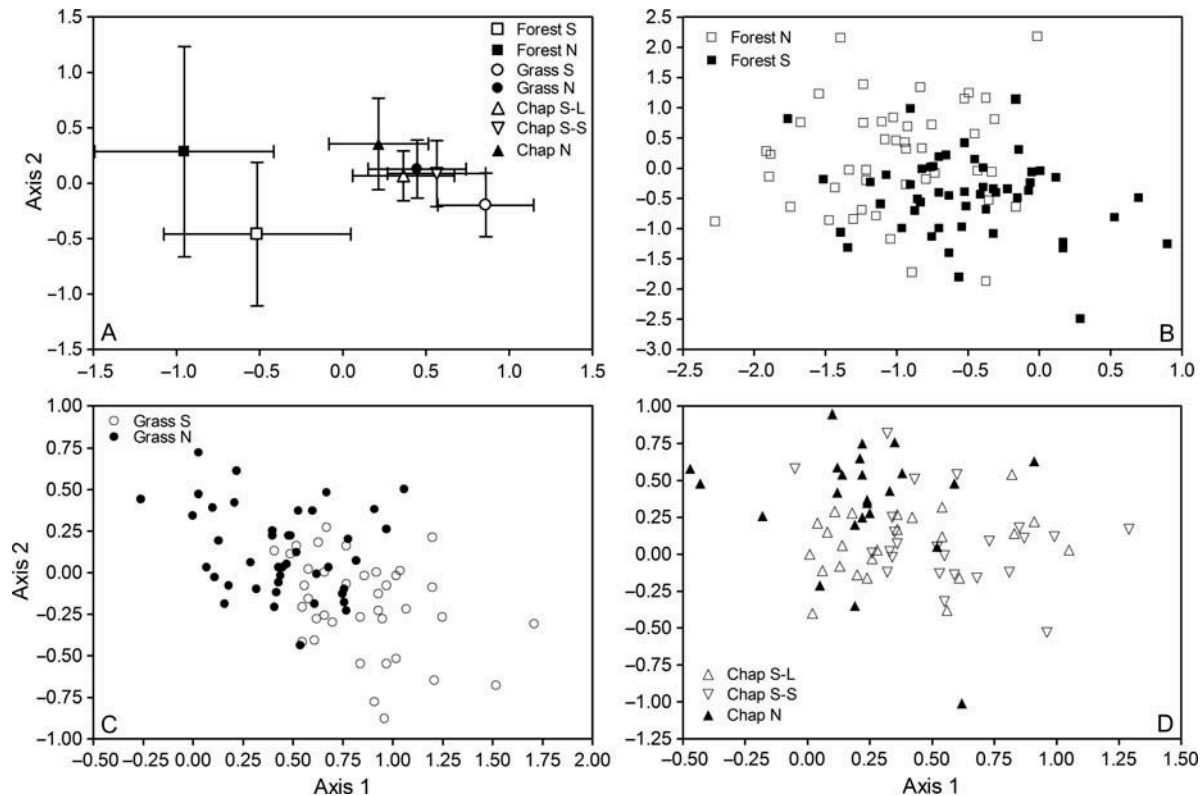


Figure 1. Patterns of dissimilarity in dispersal syndromes among soil types and vegetation types. (A) Non-metric multidimensional scaling plot of mean dissimilarity ( $\pm 1$  SD) in dispersal syndrome composition among community types; (B) dissimilarity among sites within forest vegetation; (C) grassland vegetation; and (D) chaparral vegetation. Open symbols represent serpentine communities and closed symbols represent non-serpentine communities. Squares represent forest habitat, circles represent grassland habitat and triangles represent chaparral habitat (both small patches: inverted open triangles; large patches: regular open triangles). In all panels S represents serpentine and N represent non-serpentine. Stress = 0.17 for all figures.

Functional traits differed between soils; both plant height and SLA were higher on non-serpentine than serpentine soils across all three vegetation types ( $F_{1,254} = 105.98$ ,  $P < 0.0001$  and  $F_{1,254} = 206.14$ ,  $P < 0.001$ , respectively). Leaf water content did not differ between serpentine and non-serpentine soils across all vegetation types ( $F_{1,254} = 0.01$ ,  $P = 0.93$ ) but was significantly higher on non-serpentine than serpentine soils in grasslands and chaparral ( $F_{1,78} = 18.45$ ,  $P < 0.001$  and  $F_{1,70} = 23.95$ ,  $P < 0.001$ , respectively). Principal component 1 accounted for 66.4% of the variation in the functional trait data and was associated with SLA (loading score: 0.81), LWC (loading score:  $-0.95$ ) and height (loading score: 0.64). A high PC1 score indicated high SLA, taller plants and low LWC (a resource-acquisitive strategy), and a low PC1 score indicated the opposite (a stress-tolerant strategy) (Grime 1979; Westoby 1998). PC2 accounted for 28.4% of the variation and was associated with SLA (loading score:  $-0.53$ ) and height (loading score: 0.75).

Dispersal syndromes were related to plant functional traits but the dispersal syndrome differences between soils were robust enough to include these traits in models. Vertebrate dispersal was positively correlated with plant height ( $F_{1,258} = 294.54$ ,  $r^2 = 0.53$ ,  $P < 0.001$ ) and negatively correlated with SLA at the community level (SLA:  $F_{1,258} = 42.70$ ,  $r^2 = 0.14$ ,  $P < 0.001$ ); however, the higher

proportion of vertebrate dispersal on non-serpentine soils remained significant in models that also included functional traits (soil effect when height included:  $\chi^2 = 38.73$ ,  $P < 0.001$ ; soil effect when SLA included:  $\chi^2 = 74.04$ ,  $P < 0.001$ ; Figure 2). These results did not change if PC1 (soil effect:  $\chi^2 = 62.41$ ,  $P < 0.001$ ) or LWC (soil effect:  $\chi^2 = 92.55$ ,  $P < 0.001$ ) was used instead because these traits were not correlated with vertebrate dispersal syndromes. Similarly, wind dispersal was positively related to SLA at the community level ( $F_{1,258} = 11.63$ ,  $r^2 = 0.04$ ,  $P < 0.001$ ) but the higher proportion of wind dispersal on serpentine remained significant in models that also included SLA ( $\chi^2 = 40.52$ ,  $P < 0.001$ , Figure 2). These results did not change if PC1 (soil effect:  $\chi^2 = 74.23$ ,  $P < 0.001$ ), height (soil effect:  $\chi^2 = 55.24$ ,  $P < 0.001$ ), or LWC (soil effect:  $\chi^2 = 90.78$ ,  $P < 0.001$ ) was used instead of SLA because these traits were not correlated with wind dispersal syndromes. When evolutionary relatedness was taken into account using phylogenetically independent contrasts, the positive species-level relationship between wind dispersal and serpentine tolerance, and the negative relationship between vertebrate dispersal and serpentine tolerance, were no longer significant ( $F_{1,35} = 0.62$ ,  $P = 0.44$ ;  $F_{1,41} = 1.22$ ,  $P = 0.28$ , respectively).

In addition to differences between serpentine and non-serpentine, there were also differences amongst the

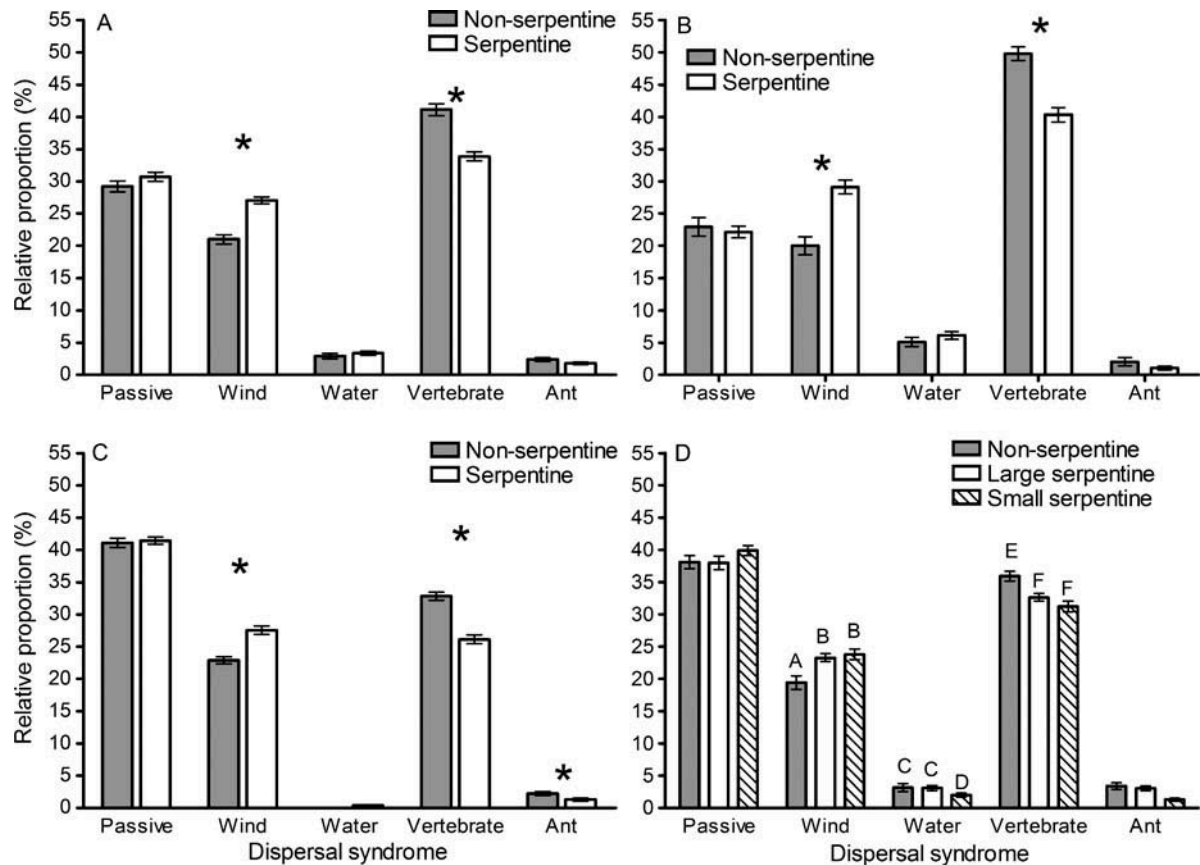


Figure 2. Distribution of dispersal syndromes among (A) soil types across all data sets; (B) soil types within forest; (C) soil types in grassland; and (D) soil types and patch size in chaparral. In all panels grey bars represent non-serpentine habitat, white bars represent serpentine habitat and hatched white bars represent patchy serpentine habitat. Stars and letters indicate significant differences  $P < 0.01$ . Error bars represent standard error.

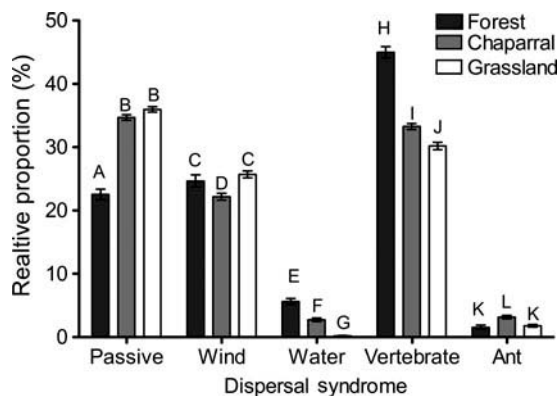


Figure 3. Differences in dispersal syndromes amongst vegetation types. Letters indicate significant differences  $P < 0.05$ . Error bars represent standard error.

three vegetation types (Figure 3). The forest vegetation type had the highest proportion of vertebrate ( $\chi^2 = 163.20$ ,  $P < 0.001$ ) and water dispersal ( $\chi^2 = 555.89$ ,  $P < 0.001$ ) and the lowest proportion of passive dispersal ( $\chi^2 = 358.68$ ,  $P < 0.001$ ). Grassland vegetation type had the lowest proportion of vertebrate ( $\chi^2 = 163.20$ ,  $P < 0.001$ ) and water dispersal syndromes ( $\chi^2 = 555.89$ ,  $P < 0.001$ ). Finally, the chaparral vegetation type

had the highest proportion of ant dispersal ( $\chi^2 = 54.16$ ,  $P < 0.001$ ) and the lowest proportion of wind dispersal ( $\chi^2 = 20.68$ ,  $P < 0.001$ ).

## Discussion

Our results suggest that habitat quality may outweigh habitat patchiness as an ecological filter on the composition of seed dispersal syndromes within serpentine communities. We found that communities in low-fertility serpentine habitats had a greater proportion of less-directed wind dispersal syndromes and a lower proportion of more-directed vertebrate dispersal syndromes when compared with more productive non-serpentine habitats (Figure 2A). This pattern was found within each vegetation type (Figure 2B–D) and there were no differences in the composition of seed dispersal syndromes amongst small and large patches of serpentine in chaparral (Figure 2D). These results suggest that the patchiness of serpentine outcrops has not acted as a significant ecological filter on the composition of dispersal syndromes within serpentine communities. Furthermore, long-distance dispersal (wind, vertebrate and water) did not differ between serpentine and non-serpentine, as might have been expected if the ability to move between spatially discontinuous patches had been an important filter shaping

the composition of seed dispersal syndromes on serpentine. Our results coincide with other studies that have found strong effects of environmental filtering (e.g., elevation, moisture and light) on seed dispersal syndrome composition (Willson et al. 1990; Ozinga et al. 2004).

Whilst the greater proportion of wind dispersal syndromes and the lower proportion of vertebrate dispersal in serpentine communities generally support the role of resource availability in determining dispersal syndrome composition, there are several important co-varying factors. First, dispersal syndromes could be part of a larger set of resource-conserving traits that allow species to survive on serpentine soils. Whilst we found no evidence of correlation between dispersal syndrome and an overall suite of resource acquisition traits (PC1), we did find a significant positive relationship of vertebrate dispersal to plant height and a significant negative relationship to SLA (though weak), and a weak positive relationship of wind dispersal to SLA. Similar patterns have been found in several other studies (Andersen 1993; Navarro et al. 2009; Meers et al. 2010), suggesting that environmental filtering acts indirectly to constrain the availability of dispersal syndromes by selecting for a suite of correlated functional traits (Herrera 1992; Westoby et al. 1996; Navarro et al. 2009). Such indirect filtering on dispersal syndromes was also suggested by the results of our phylogenetic independent contrasts. We found that wind (or vertebrate) dispersal syndrome and tolerance to serpentine soils were no longer significantly correlated after phylogenetic relatedness was taken into account. This suggests that serpentine soils tend to recruit particular plant lineages that are characterised by wind (and lack of vertebrate) dispersal, which may or may not reflect any advantages of dispersal modes per se. Wind-dispersed lineages may tend to share other key functional traits that predispose them to living on serpentine or these lineages may be more prevalent on serpentine for historical reasons, similar to the findings of Herrera (1992) for seed size and sclerophylly in Mediterranean shrublands.

Our observed patterns of a greater proportion of less-directed wind dispersal syndromes and a lower proportion of more-directed vertebrate dispersal on serpentine could result from wind-dispersed plants being favoured in more open vegetation structure as has been found in several studies (Howe and Smallwood 1982; Ozinga et al. 2004; Nathan et al. 2008). Open vegetation structure is important for wind dispersal because closed vegetation structure can be a physical barrier to dispersal (Nathan and Muller-Landau 2000). Whilst this could explain the higher frequency of wind dispersal we found in sparse serpentine communities, it did not hold up when comparing across vegetation types regardless of soil type. We found the lowest proportion of wind dispersal in chaparral and similar proportions in grassland and forest (Figure 3). Wind dispersal in the forest may be favoured by increased seed release height, which has been found to be important for long-distance movement of wind-dispersed species (Soons et al. 2004).

Our observed patterns of a greater proportion of wind dispersal syndromes and a lower proportion of vertebrate

dispersal on serpentine could also result from ecological filtering resulting in a lower availability of vertebrate dispersers in infertile settings. Although we have no independent evidence for this, it seems possible due to several lines of reasoning. Fewer vertebrates are supported in less productive habitats (Siemann 1998), possibly as a result of increased chemical and physical plant defences (Strauss and Boyd 2011). For example, Ozinga et al. (2004) found a lower proportion of mammal dispersal in low-light environments, and attributed this difference in part to higher abundance of plant species with chemical compounds that deter frugivores. Similarly, heavy metals in serpentine soils can accumulate in plant tissues and fruits resulting in toxic levels for animals grazing (Miranda et al. 2009) or consuming fruits (Boyd et al. 2006), although no research has examined the impact on seed dispersers (Strauss and Boyd 2011). Finally, lower water availability on serpentine could result in lower fruit production resulting in fewer vertebrate dispersers, as found in several other habitats (Rathcke and Lacey 1985; Tabarelli et al. 2003; Almeida-Neto et al. 2008). Our results suggest the need for direct tests of the costs and benefits of vertebrate dispersal in environments of differing resource availability.

The observed dispersal syndrome differences among soil types were not consistent with patterns expected under habitat patchiness as an ecological filter (Levine and Murrell 2003; Vandvik and Goldberg 2006). Overall, long-distance dispersal (wind, water and vertebrate) was neither more nor less common on serpentine. Differences were also not consistent with predictions regarding directed dispersal (Howe and Smallwood 1982; Wenny 2001; Vander Wall and Longland 2004) because less directed (wind) dispersal was higher in the patchy serpentine environment and more directed (vertebrate) dispersal was lower (Figure 2). Directed dispersal relies on two factors being important in determining the dispersal potential of a community: preferential survival in specific locations and non-random arrival (Howe and Smallwood 1982; Wenny 2001; Vander Wall and Longland 2004). Our results suggest that non-random arrival i.e., filtering for species with particular dispersal syndromes able to reach distant sites, does not play a major role in the assembly of communities on serpentine soils (Howe and Smallwood 1982; Wenny 2001; Vander Wall and Longland 2004).

In conclusion, our results suggest that the ability to move between spatially discontinuous patches has not played a strong role in determining the composition of dispersal syndromes within serpentine communities. Instead, the patterns of dispersal syndrome composition we found may be due to environmental filtering for a suite of functional traits that allow for the persistence on serpentine soils or a lower availability of vertebrate dispersers on serpentine soils. Our results, in conjunction with several other studies, (Willson et al. 1990; Ozinga et al. 2004; Tackenberg and Stocklin 2008) suggest that habitat quality may play a strong role in shaping the dispersal potential of plant communities both directly as in the above studies, or indirectly by selecting for traits that allow species to persist in lower



quality habitats. Using multiple data sets gave us the ability to distinguish effects of different aspects of the environment on dispersal syndromes including habitat quality, habitat patchiness and vegetation type. Several studies of human-fragmented landscapes have shown that species with more directed (vertebrate) dispersal are less vulnerable to fragmentation (Damschen et al. 2008; Montoya et al. 2008; Alados et al. 2010). Our results suggest that communities on discontinuous patches of low-fertility soils are not necessarily composed of good dispersers. In order to persist in the face of global change, species in these communities must be highly persistent in situ, either through seed banks (Honnay et al. 2008), stress-tolerant functional traits (Grime et al. 2000), plasticity (Nicotra et al. 2010) or genetic variation (Parmesan 2006) otherwise they may face elevated risks of extinction. Species in low-fertility communities may be high-priority candidates for managed relocation (i.e. assisted migration, assisted colonisation; Richardson et al. 2009; Vitt et al. 2010) because they are less likely to have directed dispersal syndromes that allow them to reach these locations unassisted.

### Acknowledgements

We thank Annette Bieger and Brian Anacker for determining dispersal syndromes for our species, and the handling editor and anonymous reviewers for comments on this manuscript. The studies used for this analysis were supported by National Science Foundation grants: DEB 94-24137 and DEB-0542451.

### Notes on contributors

Marko J. Spasojevic is a post-doctoral researcher. His research addresses how environmental heterogeneity, dispersal, species interactions and plant soil interactions influence the success of plant populations and the structure and function of plant communities.

Ellen I. Damschen is an assistant professor. Her research addresses the impacts of climate change, habitat fragmentation and dispersal on plant communities.

Susan Harrison is a professor. The major theme of her research is understanding the processes that shape and maintain plant species diversity at the landscape scale, where small-scale forces such as competition and facilitation interact with large-scale forces such as niche evolution and dispersal.

### References

- Aan A, Hallik L, Kull O. 2006. Photon flux partitioning among species along a productivity gradient of an herbaceous plant community. *Journal of Ecology* 94:1143–1155.
- Alados CL, Navarro T, Komac B, Pascual V, Rietkerk M. 2010. Dispersal abilities and spatial patterns in fragmented landscapes. *Biological Journal of the Linnean Society* 100:935–947.
- Almeida-Neto M, Campassi F, Galetti M, Jordano P, Oliveira A. 2008. Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates. *Global Ecology and Biogeography* 17:503–513.
- Amarasekare P, Hoopes MF, Mouquet N, Holyoak M. 2004. Mechanisms of coexistence in competitive metacommunities. *American Naturalist* 164:310–326.
- Andersen UV. 1993. Dispersal strategies of Danish seashore plants. *Ecography* 16:289–298.
- Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32–46.
- Anderson MJ. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253.
- Beals EW. 1984. Bray–Curtis ordination - an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14:1–55.
- Boyd RS, Wall MA, Jaffre T. 2006. Nettle levels in arthropods associated with Ni hyperaccumulator plants from an ultramafic site in New Caledonia. *Insect Science* 13: 271–277.
- Briggs JS, Wall SBV, Jenkins SH. 2009. Forest rodents provide directed dispersal of Jeffrey pine seeds. *Ecology* 90:675–687.
- Cain ML, Milligan BG, Strand AE. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87:1217–1227.
- Chase JM, Amarasekare P, Cottenie K, Gonzalez A, Holt RD, Holyoak M, Hoopes MF, Leibold MA, Loreau M, Mouquet N, et al. 2005. Competing theories for competitive metacommunities. In: M. Holyoak, L. M. A., and H. R. D., editors. *Metacommunities: Spatial Dynamics and Ecological Communities*. Chicago (IL): University of Chicago Press. p. 335–354.
- Cheptou PO, Carrue O, Rouifed S, Cantarel A. 2008. Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proceedings of the National Academy of Sciences of the United States of America* 105:3796–3799.
- Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.
- Cornwell WK, Ackerly DD. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79:109–126.
- Damschen EI, Brudvig LA, Haddad NM, Levey DJ, Orrock JL, Tewksbury JJ. 2008. The movement ecology and dynamics of plant communities in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 105:19078–19083.
- Damschen EI, Harrison S, Grace JB. 2010. Climate change effects on an endemic-rich edaphic flora: resurveying Robert H. Whittaker's Siskiyou sites (Oregon, USA). *Ecology* 91:3609–3619.
- Dean WRJ, Milton SJ. 2000. Directed dispersal of *Opuntia* species in the Karoo, South Africa: are crows the responsible agents? *Journal of Arid Environments* 45:305–314.
- Dufrene M, Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366.
- Edwards W, Dunlop M, Rodgerson L. 2006. The evolution of rewards: seed dispersal, seed size and elaiosome size. *Journal of Ecology* 94:687–694.
- Engler R, Randin CF, Vittoz P, Czaka T, Beniston M, Zimmermann NE, Guisan A. 2009. Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography* 32:34–45.
- Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA. 2009. Plant drought stress: effects, mechanisms and management. *Agronomy for Sustainable Development* 29:185–212.
- Flinn KM, Gouhier TC, Lechowicz MJ, Waterway MJ. 2010. The role of dispersal in shaping plant community composition

- of wetlands within an old-growth forest. *Journal of Ecology* 98:1292–1299.
- Fuller RN, del Moral R. 2003. The role of refugia and dispersal in primary succession on Mount St. Helens, Washington. *Journal of Vegetation Science* 14:637–644.
- Garnier E, Laurent G. 1994. Leaf anatomy, specific mass and water-content in congeneric annual and perennial grass species. *New Phytologist* 128:725–736.
- Grime JP. 1979. *Plant strategies and vegetation processes*. New York (NY): John Wiley.
- Grime JP, Brown VK, Thompson K, Masters GJ, Hillier SH, Clarke IP, Askew AP, Corker D, Kielty JP. 2000. The response of two contrasting limestone grasslands to simulated climate change. *Science* 289:762–765.
- Guterman Y. 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. *Botanical Review* 60: 373–425.
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloch KA. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461.
- Hamilton WD, May RM. 1977. Dispersal in stable habitats. *Nature* 269:578–581.
- Harrison S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. *Ecology* 78:1898–1906.
- Harrison S. 1999a. Local and regional diversity in a patchy landscape: native, alien and endemic herbs on serpentine. *Ecology* 80:70–80.
- Harrison S. 1999b. Native and alien species diversity at the local and regional scales in a grazed California grassland. *Oecologia* 121:99–106.
- Haugo RD. 2006. Vegetation responses to conifer encroachment in a dry, montane meadow: a chronosequence approach. In: *Forest resources [M.Sc. Thesis]*. [Seattle, WA]: University of Washington, p. 61.
- Herrera CM. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody-plants. *American Naturalist* 140:421–446.
- Holyoak M, Leibold MA, Mouquet N, Holt RD, Hoopes MF. 2005. Metacommunities a framework for large-scale community ecology. In: Holyoak M, Leibold MA, Holt RD, editors. *Metacommunities spatial dynamics and ecological communities*. Chicago (IL): The University of Chicago, p. 1–31.
- Honnay O, Bossuyt B, Jacquemyn H, Shimono A, Uchiyama K. 2008. Can a seed bank maintain the genetic variation in the above ground plant population? *Oikos* 117:1–5.
- Howe HF, Smallwood J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–228.
- Hughes L, Westoby M. 1992. Effect of diaspore characteristics on removal of seeds adapted for dispersal by ants. *Ecology* 73:1300–1312.
- Kruskal JB, Wish M. 1978. *Multidimensional scaling*. Beverly Hills (CA): Sage Publications.
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Lengyel S, Gove AD, Latimer AM, Majer JD, Dunn RR. 2009. Ants sow the seeds of global diversification in flowering plants. *Plos One* 4.
- Levine JM, Murrell DJ. 2003. The community-level consequences of seed dispersal patterns. *Annual Review of Ecology Evolution and Systematics* 34:549–574.
- MacArthur RH, Wilson EO. 1967. *The theory of island biogeography*. Princeton (NJ): Princeton University Press.
- Matlack GR. 1994. Plant-species migration in a mixed-history forest landscape in Eastern north-America. *Ecology* 75:1491–1502.
- Meers TL, Bell TL, Enright NJ, Kasel S. 2010. Do generalisations of global trade-offs in plant design apply to an Australian sclerophyllous flora? *Australian Journal of Botany* 58:257–270.
- Miranda M, Benedito JL, Blanco-Penedo I, Lopez-Lamas C, Merino A, Lopez-Alonso M. 2009. Metal accumulation in cattle raised in a serpentine-soil area: relationship between metal concentrations in soil, forage and animal tissues. *Journal of Trace Elements in Medicine and Biology* 23:231–238.
- Montoya D, Zavala MA, Rodriguez MA, Purves DW. 2008. Animal versus wind dispersal and the robustness of tree species to deforestation. *Science* 320:1502–1504.
- Mouquet N, Loreau M. 2003. Community patterns in source-sink metacommunities. *American Naturalist* 162:544–557.
- Nathan R, Muller-Landau HC. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15:278–285.
- Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A. 2008. Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution* 23:638–647.
- Navarro T, Pascual V, Alados CL, Cabezero B. 2009. Growth forms, dispersal strategies and taxonomic spectrum in a semi-arid shrubland in SE Spain. *Journal of Arid Environments* 73:103–112.
- Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M. 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* 15:684–692.
- Oksanen J, Guillaume Blanchet F, Kindt R, Legendre P, O'Hara RB, Simpson GL, Solymos P, Stevens HH, Wagner H. 2010. *Vegan: community ecology package*. 1.17–2 edition.
- Ordóñez JC, van Bodegom PM, Witte JPM, Wright IJ, Reich PB, Aerts R. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography* 18:137–149.
- Ozinga WA, Bekker RM, Schaminee JHJ, Van Groenendael JM. 2004. Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology* 92: 767–777.
- Parnesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37:637–669.
- Parnesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Purves DW, Dushoff J. 2005. Directed seed dispersal and metapopulation response to habitat loss and disturbance: application to *Eichhornia paniculata*. *Journal of Ecology* 93:658–669.
- Purvis A, Rambaut A. 1995. Comparative-analysis by independent contrasts (CAIC) - an Apple Macintosh application for analyzing comparative data. *Computer Applications in the Biosciences* 11:247–251.
- Rathcke B, Lacey EP. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16:179–214.
- Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America* 94:13730–13734.
- Richardson DM, Hellmann JJ, McLachlan JS, Sax DF, Schwartz MW, Gonzalez P, Brennan EJ, Camacho A, Root TL, Sala

- OE, et al. 2009. Multidimensional evaluation of managed relocation. *Proceedings of the National Academy of Sciences of the United States of America* 106:9721–9724.
- Ronce O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology Evolution and Systematics* 38:231–253.
- Royal Botanic Gardens, Kew. 2008. Seed information database (SID). Vol 2010, 7.1 edition.
- Safford H, Viers J, Harrison S. 2005. Serpentine endemism in the California flora: a database of serpentine affinity. *Madrono* 52:222–257.
- Sawyer J, Keeler-Wolf T, Evens J. 2009. A manual of California vegetation. 2nd ed. Sacramento (CA): California Native Plant Society.
- Siemann E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057–2070.
- Soons MB, Heil GW, Nathan R, Katul GG. 2004. Determinants of long-distance seed dispersal by wind in grasslands. *Ecology* 85:3056–3068.
- Spiegel O, Nathan R. 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters* 10:718–728.
- Spiegel O, Nathan R. 2010. Incorporating density dependence into the directed-dispersal hypothesis. *Ecology* 91:1538–1548.
- Strauss SY, Boyd RS. 2011. Herbivory and other cross-kingdom interactions on harsh soils. In: Harrison S, Rajakaruna N, editors. *Serpentine: the evolution and ecology of a model system*. Berkeley (CA): University of California Press. p. 181–199.
- Tabarelli M, Vicente A, Barbosa DCA. 2003. Variation of seed dispersal spectrum of woody plants across a rainfall gradient in north-eastern Brazil. *Journal of Arid Environments* 53:197–210.
- Tackenberg O, Stocklin J. 2008. Wind dispersal of alpine plant species: A comparison with lowland species. *Journal of Vegetation Science* 19:109–118.
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, et al. 2004. Extinction risk from climate change. *Nature* 427:145–148.
- Vander Wall SB, Longland WS. 2004. Diplochory: are two seed dispersers better than one? *Trends in Ecology & Evolution* 19:155–161.
- Vandvik V, Goldberg DE. 2006. Sources of diversity in a grassland metacommunity: quantifying the contribution of dispersal to species richness. *American Naturalist* 168:157–167.
- Vile D, Shipley B, Garnier E. 2006. Ecosystem productivity can be predicted from potential relative growth rate and species abundance. *Ecology Letters* 9:1061–1067.
- Vitt P, Havens K, Kramer AT, Sollenberger D, Yates E. 2010. Assisted migration of plants: changes in latitudes, changes in attitudes. *Biological Conservation* 143:18–27.
- Webb CO, Donoghue MJ. 2005. Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* 5:181–183.
- Wenny DG. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3:51–74.
- Wenny DG, Levey DJ. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America* 95:6204–6207.
- Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33:125–159.
- Westoby M, Leishman M, Lord J. 1996. Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 351:1309–1317.
- Willson MF, Rice BL, Westoby M. 1990. Seed dispersal spectra - a comparison of temperate plant-communities. *Journal of Vegetation Science* 1:547–562.