

Understanding the consequences of seed dispersal in a heterogeneous environment

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Abstract. Plant distributions are in part determined by environmental heterogeneity on both large (landscape) and small (several meters) spatial scales. Plant populations can respond to environmental heterogeneity via genetic differentiation between large distinct patches, and via phenotypic plasticity in response to heterogeneity occurring at small scales relative to dispersal distance. As a result, the level of environmental heterogeneity experienced across generations, as determined by seed dispersal distance, may itself be under selection. Selection could act to increase or decrease seed dispersal distance, depending on patterns of heterogeneity in environmental quality with distance from a maternal home site. Serpentine soils, which impose harsh and variable abiotic stress on non-adapted plants, have been partially invaded by *Erodium cicutarium* in northern California, USA. Using nearby grassland sites characterized as either serpentine or non-serpentine, we collected seeds from dense patches of *E. cicutarium* on both soil types in spring 2004 and subsequently dispersed those seeds to one of four distances from their maternal home site (0, 0.5, 1, or 10 m). We examined distance-dependent patterns of variation in offspring lifetime fitness, conspecific density, soil availability, soil water content, and aboveground grass and forb biomass. ANOVA revealed a distinct fitness peak when seeds were dispersed 0.5 m from their maternal home site on serpentine patches. In non-serpentine patches, fitness was reduced only for seeds placed back into the maternal home site. Conspecific density was uniformly high within 1 m of a maternal home site on both soils, whereas soil water content and grass biomass were significantly heterogeneous among dispersal distances only on serpentine soils. Structural equation modeling and multigroup analysis revealed significantly stronger direct and indirect effects linking abiotic and biotic variation to offspring performance on serpentine soils than on non-serpentine soils, indicating the potential for soil-specific selection on seed dispersal distance in this invasive species.

Key words: *environmental heterogeneity; Erodium cicutarium; invasive species; multigroup analysis; phenotypic plasticity; seed dispersal; serpentine soils; structural equation modeling.*

INTRODUCTION

Environmental heterogeneity is ubiquitous in natural systems, and in part determines the distributions of plant species on continental and local spatial scales. Continental range limits are primarily determined by geographic barriers to dispersal (Case et al. 2005) and climatic variation (Parmesan 2006). However, the local distribution of plant populations within a landscape is determined by dispersal and spatial patterns of heterogeneity along environmental axes that define the niche of a species (e.g., competition, nutrient, light, and water availability; for review see Brown et al. 1996). In addition to shaping local species distributions, the interaction between seed dispersal and micro-environmental variation in these factors dictates both population dynamics and patterns of selection within species

(Bell and Lechowicz 1991, Lechowicz and Bell 1991, Stratton 1994).

The spatial scale of environmental heterogeneity, relative to gene flow, should determine the nature of plant population responses to that heterogeneity. These responses will include some combination of adaptive genetic differentiation, the expression of adaptive phenotypic plasticity by individuals, and nonrandom distributions generated by dispersal, establishment, and local extinction. Adaptive genetic differentiation among plant populations, where selection differs strongly between distinct environments, has been demonstrated in many plant species (reviewed by Linhart and Grant 1996 and Kawecki and Ebert 2004). Alternatively, plant lineages experiencing fine-grained spatial heterogeneity can potentially persist in a variety of microhabitats via adaptive phenotypic plasticity, in which a single genotype produces appropriate alternative phenotypes in response to different environments (Bradshaw and Hardwick 1989). The balance between these contrasting responses hinges on the spatial and temporal scales of environmental heterogeneity relative to gene flow, and

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on the degree to which there are tradeoffs between fitness in alternative environments (Via and Lande 1985). A few studies have used experimental plantings to document the spatial scales at which fine-scaled (0.1–10 m) environmental heterogeneity leads to changes in selection pressures on plant populations (Maddox and Antonovics 1983, Antonovics et al. 1987, Stratton 1994). Environmental heterogeneity that influences plant phenotype, fitness, or patterns of selection on small spatial scales (0.1–10 m) has been demonstrated in populations of *Impatiens capensis* and *Impatiens pallida* growing in undisturbed old growth forest understory (Bell and Lechowicz 1991, Lechowicz and Bell 1991).

Where habitats vary in patterns of spatial heterogeneity, seed dispersal distance is likely to be under habitat-specific selection, since dispersal in space (as well as in time; Venable and Lawlor 1980) will alter the distribution of environments experienced by subsequent generations. To foster our understanding of how natural patterns of environmental heterogeneity exert selection on dispersal and plasticity, a logical first step is to document the spatial scale of relevant environmental variation, relative to the scale of dispersal by seeds away from their maternal parent (Stratton 1994, Kalisz et al. 2001).

Theoretical models and empirical studies have both been used to build an understanding of how selection might be expected to act on seed dispersal, given predictable variation in the types of environmental challenges experienced by progeny that disperse different distances from the maternal parent. In many natural systems there is a strong negative relationship between distance from the maternal home site and conspecific seedling density (Janzen 1978, Augspurger 1983a, Donohue 1997). Models that incorporate the intraspecific and kin competition that might result from this pattern generally predict selection for increased dispersal distance (Venable and Brown 1993, Rousset and Gandon 2002, Muller-Landau et al. 2003). However, when distance-dependent changes in environmental quality and predictability are included in the models, selection can favor increased, decreased, or intermediate dispersal distances (Janzen 1970, Hamilton and May 1977, Venable and Brown 1988, 1993, McPeck and Holt 1992, Levin and Muller-Landau 2000, Stocklin and Winkler 2004, Ronce et al. 2005, Kallimanis et al. 2006). High densities of competitors or natural enemies near the maternal plant may select against seeds that fail to disperse. Conversely, when a lineage is locally adapted to the maternal environment, selection may favor limited dispersal distances within a population (Schmitt and Gamble 1990, McPeck and Holt 1992, Donohue 1997, Montesinos et al. 2006). Finally, if environmental quality is temporally or spatially unpredictable, selection may favor increased dispersal distance as a bet-hedging strategy. In natural habitats, it is the balance between patterns of environmental variation and the local intensity of density-dependent interactions that likely determines the strength and direction of selection on dispersal distance.

To develop an understanding of the link between environmental heterogeneity at different spatial scales and selection on plant dispersal requires (1) identifying the relevant axes of environmental heterogeneity that affect plant fitness and (2) measuring the spatial scale of heterogeneity in these factors relative to the dispersal distance of that species. Previous experiments designed to address the relationship between offspring fitness and dispersal distance have measured the relationship between patterns of environmental variation or conspecific density, either naturally occurring (Augspurger 1983a, Soons and Heil 2002) or manipulated (Schmitt and Gamble 1990, Donohue 1997, Montesinos et al. 2006). We are unaware of any selection studies on dispersal that have measured how patterns of naturally occurring multivariate environmental heterogeneity can influence the fitness of dispersing seeds at multiple spatial scales, although this is critical for understanding how selection on dispersal distance might be influenced by heterogeneity both within and between adjacent populations.

Landscapes in which serpentine and non-serpentine soils are inter-mixed provide an excellent opportunity to examine these ideas because these two soil types differ markedly with respect to their average depth, chemistry, and water retention. Moreover, potentially dominant invasive grasses have only partially invaded serpentine soils in California (Huenneke et al. 1990), potentially resulting in distinct distributions of interspecific competition in serpentine and non-serpentine sites. To document plant responses to spatial patterns of conspecific density and environmental heterogeneity simultaneously, we conducted a multi-scale transplant experiment in adjacent populations of the invasive annual plant species *Erodium cicutarium* (L.) L'Her. that occur in contrasting soil environments within a heterogeneous landscape. To understand the consequences of dispersal, transplant treatments and environmental observations were conducted on the scale of dispersal for single maternal families in populations occurring on both serpentine and non-serpentine soils. We addressed the following questions in this study: (1) In the next generation, how does the natural density of conspecifics vary with distance from a maternal home site in each soil environment? If intraspecific competition in close proximity to the maternal home site reduces offspring fitness, we may expect to see selection for increased dispersal distance. (2) How do average attributes of the edaphic environment and plant community vary with distance from a maternal home site? Similarly, how does variability in the edaphic environment and plant community change with distance from a maternal home site? The spatial scale of heterogeneity, relative to dispersal distance, could shape patterns of selection on dispersal distance. (3) On average, how does offspring fitness vary with dispersal distance from the maternal home site? If offspring fitness varies consistently with distance from maternal home

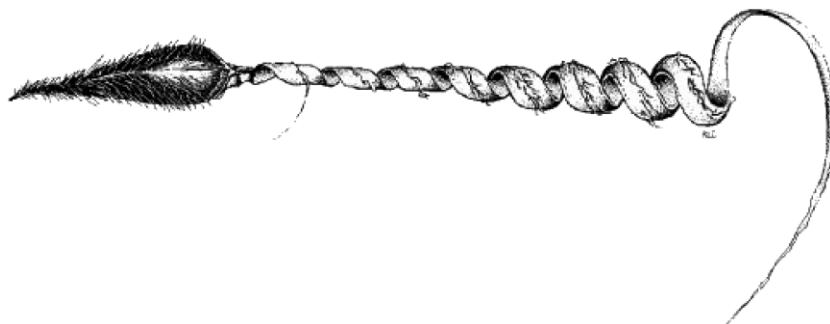


FIG. 1. Illustration of the coiled schizocarp enclosing an *Erodium cicutarium* seed, after ballistic dispersal has occurred.

sites, we may expect selection to act on traits that determine seed dispersal distance. (4) Does the relationship between dispersal distance and success differ between contrasting edaphic environments? Patterns of selection on traits determining dispersal distance could differ between soil types if the spatial scale of environmental heterogeneity differs between serpentine and non-serpentine soils. (5) Overall, do the interrelationships between the fitness of progeny, natural intra- and interspecific density, and edaphic factors differ between soil environments? Because of the extreme edaphic conditions associated with life on serpentine soils we expect to see different forms of causal association between edaphic and biotic variables, and among biotic factors, between soil types.

MATERIALS AND METHODS

Study system

Serpentine soils are characterized by high levels of heavy metals (including Ni and Cr), low levels of primary nutrients (N and P), low Ca:Mg ratios, low water availability, higher potential evapotranspiration, and wide variation in soil pH (Kruckeberg 1984). The low Ca:Mg ratio characteristic of serpentine soils creates an edaphic environment in which selective uptake of Ca ions by roots is extremely difficult. Serpentine soils impose harsh abiotic stresses on the plants growing there, and thus are generally dominated by serpentine endemics and serpentine-tolerant ecotypes (Kruckeberg 1984), with very few exotic species (Huenneke et al. 1990). Because of their high levels of endemism, serpentine habitats are of special concern for conservation (Launer and Murphy 1994, Seabloom et al. 2003).

Erodium cicutarium (L.) L'Hér. (Geraniaceae) is an annual plant of Mediterranean origin. Although its flowers are primarily self fertilized and rarely visited (B. Baythavong, *personal observation*), flower visitation could result in occasional, longer-distance, pollen movements. *Erodium cicutarium* has invaded non-serpentine grasslands throughout California (Mensing and Byrne 1998), as well as serpentine grasslands at the University of California (UC) Donald and Sylvia McLaughlin Reserve, achieving densities up to 500

individuals/m² (B. Baythavong, *personal observation*). The presence of *E. cicutarium* in both serpentine and non-serpentine grasslands provides an ideal opportunity to address the link between environmental heterogeneity and selection on dispersal distance because of the harsh conditions imposed by serpentine soils and the unique dispersal biology of *Erodium* seeds.

The dispersal characteristics of *Erodium* seeds are unusually well characterized (Stamp 1989b). *Erodium* seeds are enclosed in a schizocarp consisting of a carpel attached to a coiled awn (Fig. 1) and explosively discharge from the maternal plant (Stamp 1989b). After primary ballistic dispersal the schizocarp uncoils and coils in response to wet and dry diurnal cycles, crawling along the soil surface (hygroscopic dispersal) until it encounters and drills into a crack (Stamp 1984, 1989b). *E. moschatum* (a commonly co-occurring species which is morphologically almost indistinguishable from *E. cicutarium*) has an average ballistic dispersal distance of 50–60 cm, followed by an average of 7 cm secondary hygroscopic dispersal (Stamp 1989a). Field observations and studies of *Erodium* dispersal demonstrate that seeds enclosed in carpels are frequently moved long distances by ants and rodents (15% and 20% of seeds in experimental arrays; Stamp 1989b, Harmon and Stamp 1992).

This research was conducted in a 25-ha portion of the UC McLaughlin Reserve dubbed “the grid” (38°49'29" N, 122°20'38" W) that was surveyed in 2002 and 2003 on a 10–50 m scale for soil chemistry and plant species composition (site description *available online*).² This 500 × 500 m area encompasses many serpentine outcrops that are interspersed with non-serpentine soils. Using the grid's GIS database we selected six of the permanently marked 50-m grid points at which *E. cicutarium* occurs, based on the Ca:Mg ratio of the original soil sample collected at that point. The Ca:Mg ratio of a soil sample is a diagnostic commonly used to identify serpentine soils. We designated three of these sites (where the initial soil sample collected had a Ca:Mg < 1.0) as serpentine

² (<http://nrs.ucdavis.edu/McL/index.html>)

areas, and three sites (with Ca:Mg > 1.0) as non-serpentine areas (Appendix).

Experimental design

In spring 2004, we placed 25 × 25 cm pollinator exclusion cages (13 total) at the six sites to collect self-fertilized seeds from one to three localized patches of *E. cicutarium* within 10 m of each grid point. All existing flowers and fruits were removed from *E. cicutarium* plants in each patch when cages were installed to ensure that all seeds collected were the result of self-fertilization. Seeds from a given patch were bulked because the average number of seeds obtained from an individual plant in the field (approximately three seeds) was insufficient to conduct a transplant experiment. In autumn 2004, before the onset of winter rains, progeny from maternal patches that yielded at least 15 seeds were planted along a series of 10-m transects running in randomly chosen directions from their original patch location. *E. cicutarium* seeds were planted in 10 × 10 cm plots at four distances from the maternal home site along each transect: 0 m (i.e., at the original home site), 0.5 m, 1 m, and 10 m. No seeds were moved more than 10 m from their original collection location. These distances were chosen to span the lower (0 m) and upper (1 m) estimates for natural *Erodium* ballistic dispersal (Stamp 1989b), as well as a rare, longer-distance dispersal event (10 m). Depending on the number of seeds available from each collection location, we established two to six replicate transects per home site (60 total transects) and planted two to four seeds (705 total seeds) at each distance along each transect. All seeds were physically scarified to break dormancy, and were attached to wooden toothpicks using a drop of water-soluble glue to facilitate planting and seedling identification upon emergence in the field.

Throughout the growing season, emergence, survival, and the total number of viable seeds produced were recorded for each individual. In addition to monitoring experimental plants, we measured several environmental variables at each plot, including (1) aboveground biomass of neighboring forbs and grasses, (2) the number of naturally occurring *E. cicutarium* individuals within a plot following germination of experimental plants, and (3) gravimetric soil water content at bolting. To estimate soil gravimetric water content, soil cores were taken in spring 2005, after more than half of the experimental plants in a given grid location had initiated bolting. Soil cores were taken within 10 cm of the edge of each plot to avoid disturbing experimental plants and the neighboring plant community. Serpentine soils are thin and rocky, prohibiting deep soil cores. As a result, cores of the surface layer of soil, up to a maximum depth of 6 cm, were taken at each plot. Although not uniform between plots, the soil cores were representative of the upper soil surface layer available for plant growth. In subsequent analyses, the dry masses of these samples were used to estimate the depth of the top-most soil

layer. Although large individuals are capable of producing a taproot longer than 6 cm, the top layer of soil is probably an important source of nutrients and water for the majority of naturally occurring plants.

Samples for measuring biomass of the local plant community were harvested within each experimental plot beginning in mid-May 2005, after all experimental plants in a plot had senesced and been collected. All aboveground biomass was collected from each 10 × 10 cm plot and dried. The grasses and forbs in each sample were sorted, dried to a constant mass, and weighed separately.

Data analysis

Spatial scale of variation in environmental factors, conspecific density, and offspring fitness.—To characterize the spatial scale of heterogeneity that influences conspecific density and offspring lifetime fitness, we conducted mixed-model analyses of variance for each of these response variables (MIXED procedure; SAS Institute 2006). A MANOVA was used to characterize multivariate heterogeneity in aboveground grass and forb biomass, soil water content, and soil availability as a function of dispersal distance from the home site (GLM procedure; SAS Institute 2006).

All analyses of variance included the main effects of soil type (serpentine or non-serpentine), grid point nested within soil type (a random effect), home site nested within grid point (a random effect), transect nested within home site (a random effect), dispersal distance (0, 0.5, 1, or 10 m), and the two-way interactions between dispersal distance and soil type, grid point, and home site. Home site was included as a random effect because patches of *E. cicutarium* were selected haphazardly from the available patches at each grid point. A significant main effect of grid point indicates heterogeneity within each soil type on spatial scales between 50 and 400 m. Significant main effects of home site and dispersal distance indicate heterogeneity on progressively smaller spatial scales within a maximum of 50 m. A main effect of distance is of primary interest because it implies a consistent effect of seed dispersal distance from a maternal home site. Similarly, a significant interaction between soil type and dispersal distance is of interest because it indicates that patterns of variation with distance differ between serpentine and non-serpentine soils. When a significant effect of dispersal distance was apparent, or a significant interaction was detected between dispersal distance and soil type, a posteriori Tukey's tests were used to compare means.

The two to four seeds planted into each plot are subsamples that do not represent independent replicates. To avoid pseudoreplication (Hurlbert 1984), the mean number of seeds produced by individuals planted within each plot was treated as the unit of replication for analyses of offspring lifetime fitness.

None of the analyses of variance conformed to the assumptions of normality of residuals and homogeneity

of variances, and none of the data transformations we attempted reduced heteroscedasticity in any of the variables examined. As a result, weighted ANOVA was conducted for absolute fitness and intraspecific competition (Stanton and Thiede 2005). Because the home site \times dispersal distance interaction was especially heteroscedastic in both analyses, each observation was weighted by the inverse of the variance for its particular home site-by-dispersal distance combination. Weighted MANOVA for environmental variables was not feasible, since the patterns of heteroscedasticity were not consistent among the dependent variables included in the analysis. Accordingly, we conducted MANOVA on untransformed environmental variable values, and so P values should be interpreted with caution.

Dispersal-dependent coefficients of variation for offspring lifetime fitness, conspecific density and all environmental variables were calculated by dividing the variance among plots at each dispersal distance surrounding an individual home site (0.5, 1, and 10 m away) by the mean at each distance from that home site. ANOVAs of the coefficient of variation at all dispersal distances from each maternal home site were conducted to assess relative variability in offspring fitness, conspecific density, and environmental factors among dispersal distances. Univariate ANOVAs, including the fixed effects of soil type, dispersal distance and their interaction, were used to analyze the coefficient of variation in offspring fitness and conspecific density. A MANOVA with the same fixed effects was used to analyze coefficients of variation in environmental factors as a function of dispersal distance.

Relationships between variation in offspring lifetime fitness, conspecific density, and other environmental factors: model description.—A comprehensive structural equation model was created a priori based on our understanding of probable causal interactions between edaphic and biotic factors measured in this study (Fig. 2A). This model incorporates direct and indirect effects of dispersal distance, soil availability, soil water content, conspecific density, and grass and forb biomass on offspring lifetime fitness. Direct and indirect effects of dispersal distance in the model represent the effect of other unmeasured variables that are correlated with distance from a patch of *E. cicutarium*.

Relationships among environmental variables and offspring fitness on serpentine and non-serpentine soils: multigroup analysis.—A multigroup analysis was used to assess whether our structural equation model provided an adequate fit to both the serpentine and non-serpentine data sets, or, conversely, if the direct effects of dispersal distance, edaphic variables, and biotic variables differ between soil types (Grace 2006). We only considered differences between path coefficients because we were primarily interested in understanding variation in the relationships among environmental variables and offspring fitness between soil types.

Initially, the fit of our a priori structural equation model (Fig. 2A) was assessed using the “manage groups” tool in AMOS 7.0 (SPSS, Chicago, Illinois, USA) without any equality constraints imposed across soil types. The unconstrained model provided a statistically significant fit to serpentine and non-serpentine data sets ($\chi^2 = 2.709$, $df = 2$, $P = 0.258$), enabling us to proceed with the multigroup analysis. To determine which paths differed significantly between the two data sets we imposed equality constraints on individual paths sequentially, and examined the effect of these constraints on overall model fit to both data sets (Grace 2003). After a path was constrained to be equal across groups the change in overall model chi-square was calculated. If the fit of the model was significantly worse after imposing the constraint that path was determined to be different between serpentine and non-serpentine data sets, a significant change in model fit was assessed using a single degree of freedom chi square difference test.

RESULTS

Variation in conspecific density and other environmental factors with dispersal distance.—On both serpentine and non-serpentine soils, conspecific density was significantly higher within 1 m of maternal home sites than 10 m away (Fig. 3; Table 1). In contrast, a MANOVA conducted on measured environmental factors (soil availability, soil water content, grass biomass, and forb biomass) showed distinct patterns of heterogeneity between soil types at these small spatial scales ($P < 0.0001$ for the interaction between dispersal distance and soil type; Table 2). A posteriori means comparisons within each soil type revealed no significant heterogeneity among dispersal distances on non-serpentine soils. In contrast, seeds that disperse 10 m from their maternal home site on serpentine soils encounter significantly increased grass biomass and soil moisture, compared with most seeds dispersing ≤ 1 m (Fig. 4).

Coefficients of variation for the set of measured environmental factors did not vary with distance from a maternal home site (MANOVA: $df = 8, 60$, $F = 1.05$, $P = 0.4111$). However, the coefficient of variation for conspecific density did vary with distance, such that *E. cicutarium* density is less predictable 10 m from a maternal home site than within 1 m on both soil types (ANOVA: $df = 3, 21$ $F = 6.30$, $P = 0.0051$ for the main effect of distance).

Variation in offspring lifetime fitness with dispersal distance on serpentine and non-serpentine soils.—Across the two soil types, we observed significant variation in offspring lifetime fitness with dispersal distance from a maternal home site (Table 3). A posteriori means comparisons revealed significantly higher offspring fitness in seeds dispersed 0.5 m from the maternal home site than offspring dispersed 10 m away (Fig. 5). The coefficient of variation in offspring fitness did not vary significantly with distance from a maternal home site on either soil type ($df = 3, 21$, $F = 1.38$, $P = 0.2610$).

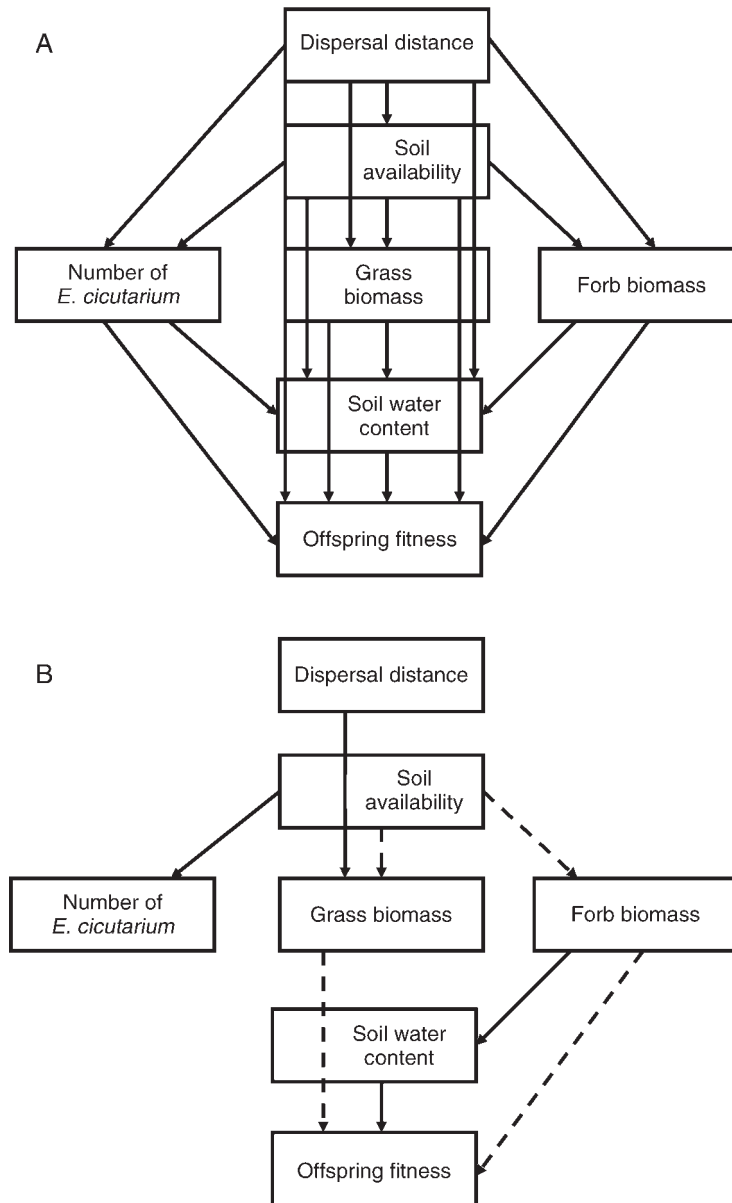


FIG. 2. (A) Structural equation model showing all hypothesized pathways linking measured variables and the lifetime fitness of dispersed progeny. The full model also included covariances linking the error terms for soil water content and soil availability, the error terms for grass and forb biomass, and the error terms for forb biomass and density of *E. cicutarium* (Geraniaceae), but these are not shown in the figure for clarity. (B) Structural equation model showing only pathways that were significantly different between serpentine and non-serpentine soils (solid arrows) and pathways that were marginally different between soil types (dashed arrows).

Given the distinct patterns of dispersal-dependent variation in environmental variables on serpentine and non-serpentine soils, we elected to explore our a priori hypothesis that selection on dispersal could differ between soil types. We conducted separate ANOVAs for offspring fitness on each soil type that included the main effects of grid point (random), maternal home site nested within grid point (random), transect nested within home site (random), and dispersal distance. Interactions between dispersal distance and grid point

and dispersal distance and home site were also included. On serpentine soils, offspring dispersed 0.5 m away from their maternal home site had significantly higher fitness than offspring dispersed 10 m away ($df = 3, 182, F = 2.64, P = 0.0510$). In contrast, offspring fitness did not vary significantly among dispersal distances on non-serpentine soils ($df = 3, 182, F = 2.40, P = 0.0692$).

Relationship among environmental variables and offspring fitness: ecological interpretation.—A multigroup analysis of serpentine and non-serpentine data sets

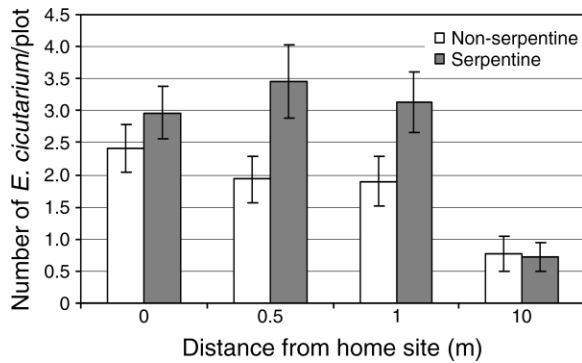


FIG. 3. Number of naturally occurring *E. cicutarium* individuals observed within plots immediately after the emergence of experimental plants on serpentine and non-serpentine soils in northern California, USA. Raw means and standard errors are shown ($N = 114$ plots for non-serpentine, 122 plots for serpentine).

revealed significant differences in several paths connecting edaphic and biotic variables (Fig. 2B). In general, paths that differed significantly between soil types were stronger on serpentine soils than on non-serpentine soils (Table 4). On non-serpentine soils dispersal distance had a moderate, negative direct effect on grass biomass. However this direct effect was reversed on serpentine soils, suggesting a soil-specific association between grass biomass and another unmeasured factor that varies with distance from patches of *E. cicutarium*. Additionally, the indirect effects of dispersal distance on all biotic variables were substantially stronger on serpentine soils than on non-serpentine soils. Increased forb biomass resulted in diminished soil water content only on non-serpentine soils, while on serpentine there was an equivalent positive association between forb biomass on soil water content, possibly as a result of the effect of an additional unmeasured factor. On non-serpentine soils there was a moderate positive effect of soil availability on *E. cicutarium* density, however increasing soil availability limited density on serpentine soils. *E. cicutarium* transplants did best in microsites with increased soil water content on non-serpentine soils. In contrast increased soil water content diminished offspring fitness on serpentine soils.

TABLE 1. ANOVA of *Erodium cicutarium* (Geraniaceae) density at germination.

Source of variation	df	F	P
Soil type	1, 2.14	0.53	0.5385
Dispersal distance	3, 9.97	4.16	0.0375
Soil type \times dispersal distance	3, 9.97	0.54	0.6629

Notes: Soil type and dispersal distance were analyzed as fixed effects. Grid location (nested within soil type), home site (nested within grid location), transect (nested within home site), and all interactions were analyzed as random effects. A posteriori Tukey tests revealed that densities of *E. cicutarium* were higher on both soil types within 1 m of a maternal home site than 10 m away.

TABLE 2. MANOVA of spatial heterogeneity for environmental variables.

Source of variation	Pillai's trace	df	F	P
Soil type	0.29398	4, 96	9.99	<0.0001
Dispersal distance	0.33019	12, 294	3.03	0.0005
Soil type \times dispersal distance	0.39250	12, 294	3.69	<0.0001

Notes: Soil type and dispersal distance were analyzed as fixed effects. Results obtained from Wilks' lambda and Hotelling-Lawley trace significance tests yielded qualitatively similar results. A posteriori Tukey tests revealed significantly greater grass biomass within 1 m of maternal home sites than sites 10 m away, and significantly lower soil water content 0.5 m and 1 m from a maternal home site than 10 m away on serpentine soils only.

In addition to the paths discussed above, four additional paths were marginally significantly different ($P < 0.09$) between the two soil types. The direct effects of soil availability on grass biomass and forb biomass were 3–5 times stronger on serpentine soils than on non-serpentine soils. Increases in soil availability limited the standing grass biomass and had a greater positive effect on forb biomass on serpentine soils. Grass biomass had a substantially stronger negative direct effect on offspring fitness on serpentine soils, suggesting competitive exclusion of *E. cicutarium* by grass on serpentine soils. Finally, forb biomass had a strong positive effect on fitness on non-serpentine soils, suggesting a common microsite affinity between forbs and *E. cicutarium*. This direct effect was weak and negative on serpentine soils.

DISCUSSION

Despite the fact that environmental heterogeneity is often important in determining plant fitness and the strength of ecological interactions, biologically relevant heterogeneity on small spatial scales (0.1–10 m) has only been examined in a few natural environments (Bell and Lechowicz 1991, Lechowicz and Bell 1991, Stratton 1994). In this study, we document dispersal-dependent offspring fitness, and contrasting patterns of environmental heterogeneity, for populations of *E. cicutarium* that have invaded serpentine and non-serpentine sites within a heterogeneous grassland matrix. Our analyses suggest that limited dispersal distances of *E. cicutarium* seeds should generally be favored. However, selection for limited dispersal distance would be driven primarily by variation in offspring fitness on serpentine soils, since offspring fitness does not vary appreciably with seed dispersal distance on non-serpentine soils. To place this observed pattern of selection into a broader context, we now consider prior hypotheses describing how intraspecific competition and environmental heterogeneity may influence selection on dispersal distance in other plant systems (Howe and Smallwood 1982).

In many plant communities, a negative correlation between conspecific seedling density and distance from the maternal home site is apparent (Janzen 1970, Augspurger 1983a, Donohue 1997). All else being equal,

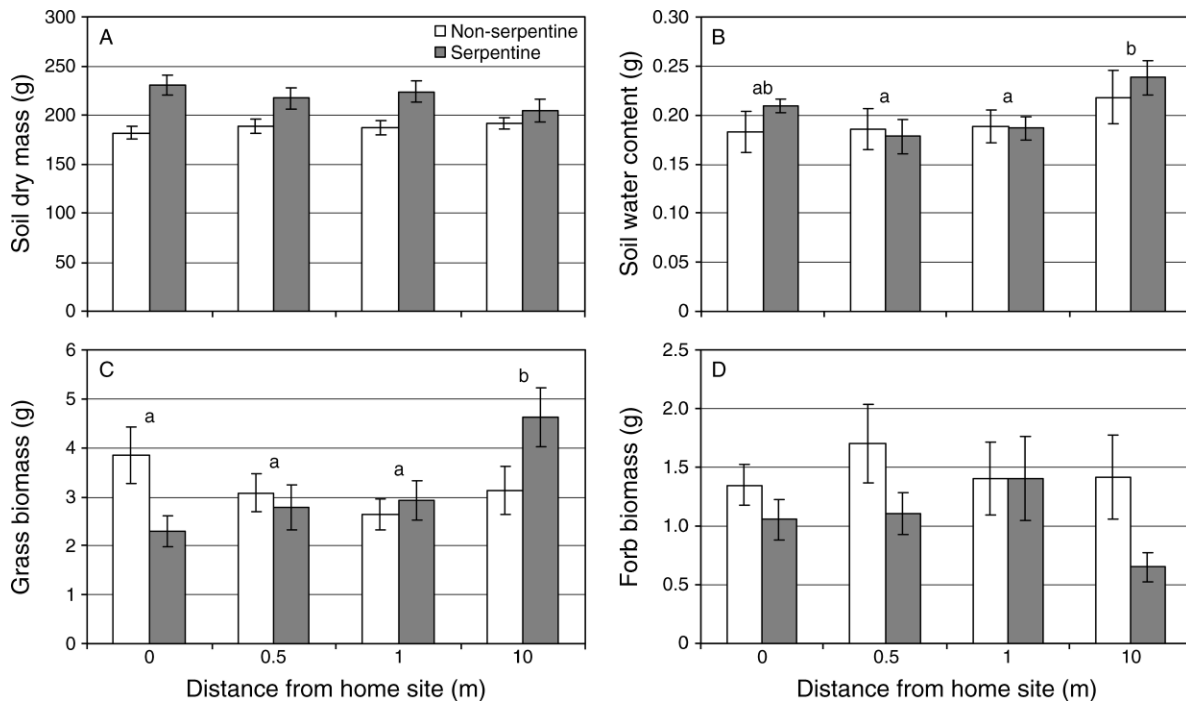


FIG. 4. (A) Soil dry mass and (B) soil gravimetric water content, and aboveground biomass of (C) grasses and (D) forbs for plots at each dispersal distance on serpentine and non-serpentine soils. Different lowercase letters indicate means are significantly different ($P < 0.05$) based on an a posteriori Tukey's test on serpentine soils. Raw means and standard errors are shown ($N = 113$ plots for non-serpentine, 116 plots for serpentine).

decreased maternal fitness due to intraspecific and even sib-sib competition in close proximity to the maternal home site is expected to select for increased dispersal (Venable and Brown 1993, Rousset and Gandon 2002, Muller-Landau et al. 2003). We found that naturally occurring densities of *E. cicutarium* are much higher within 1 m of maternal home sites on both soil types, as well as less predictable at a longer dispersal distance (10 m), but structural equation modeling indicated that intraspecific competition did not cause reduced fitness in experimentally dispersed progeny.

Multivariate analyses of variation in environmental variables revealed important differences in the patterns of small-scale edaphic heterogeneity between the soil types.

TABLE 3. ANOVA of offspring lifetime fitness.

Source of variation	df	F	P
Soil type	1, 10.9	2.01	0.1848
Dispersal distance	3, 177	3.51	0.0166
Soil type \times dispersal distance	3, 177	1.85	0.1406

Notes: Soil type and dispersal distance were analyzed as fixed effects. Grid location (nested within soil type), home site (nested within grid location), transect (nested within home site), and all interactions were analyzed as random effects. Subsequent ANOVAs were conducted separately for each soil type. A posteriori Tukey tests on subsequent ANOVAs revealed significantly higher offspring fitness at sites 0.5 m from a maternal home site than sites 10 m away on serpentine soils only.

Soil water content and grass biomass were heterogeneous on spatial scales relevant to seed dispersal distance only on serpentine soils. In contrast, coefficients of variation for these variables were equivalent at all dispersal distances, indicating that these microenvironmental factors are equally "predictable" at all dispersal distances on both soil types. The distinct patterns of heterogeneity observed between soil types, when linked to variation in the fitness of dispersed *E. cicutarium* offspring, could have impor-

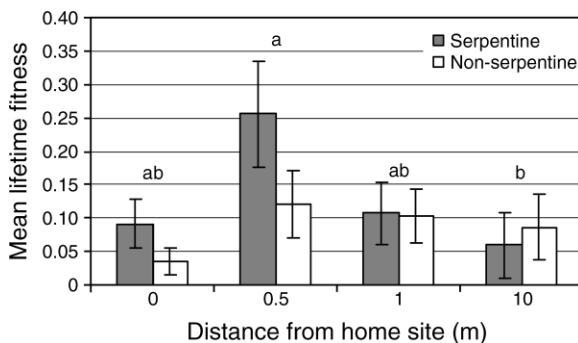


FIG. 5. Lifetime fitness of seeds dispersed to four distances from maternal home sites on serpentine and non-serpentine soils. Lifetime fitness is estimated using the total number of viable seeds an individual produced. Different lowercase letters indicate that means are significantly different ($P < 0.05$) based on an a posteriori Tukey's test on serpentine soils. Raw means and standard errors are shown ($N = 116$ plots for non-serpentine, 124 plots for serpentine).

TABLE 4. Direct and indirect effects linking edaphic, biotic, and *E. cicutarium* offspring performance variables on serpentine and non-serpentine soils.

Variables	Dispersal distance	Soil availability	Forb biomass	Grass biomass	Number of <i>E. cicutarium</i>	Soil water content
Serpentine soil						
Soil availability	-2.019	0	0	0	0	0
Forb biomass	-0.064	-0.015	0.007†	0	0	0
Grass biomass	0.197*	0.034	-0.017†	0	0	0
Number of <i>E. cicutarium</i>	-0.263	0.025	-0.012*	0	0	0
Soil water content	0.005	0	0	-0.013*	0	0.002
Offspring fitness	0.001	-0.012	0.001	0	-0.008†	-0.01
Non-serpentine soil						
Soil availability	0.647	0	0	0	0	0
Forb biomass	-0.035	0.001	0.002†	0	0	0
Grass biomass	-0.011*	-0.002	-0.003†	0	0	0
Number of <i>E. cicutarium</i>	-0.140	0.004	0.007*	0	0	0
Soil water content	0.004	0	0	-0.015*	0	0.002
Offspring fitness	0.003	-0.003	0	0	0.039†	-0.003

Notes: Direct effects presented in the table represent causal relationships, or partial regression coefficients, between one observed endogenous variable (columns) and another observed endogenous variable (rows). The values shown are for an unconstrained model that does not impose equality across the two soil types. Direct effects are shown in bold. Asterisks (*) indicate direct effects that were significantly different ($P < 0.05$) between serpentine and non-serpentine groups and daggers (†) indicate direct effects that showed marginally significant ($P < 0.09$) differences between soil types.

tant consequences for the evolutionary dynamics of plant lineages occurring on contrasting edaphic patches within this serpentine grassland mosaic.

We used structural equation modeling (SEM) to better understand the ecological mechanisms that contribute to variation in offspring fitness with dispersal distance. SEM and multigroup analysis enabled us to elucidate differences in the relationships among environmental variables and offspring fitness between serpentine and non-serpentine soils. On non-serpentine soils, only forb biomass had a substantial effect on offspring fitness. This positive association very likely reflects effects of unmeasured environmental variables associated with forb-rich microsites, rather than an actual facilitative effect of forbs on *E. cicutarium*, since previous experiments have demonstrated a significant positive effect of neighbor removal on *Erodium* survival and fitness in these habitats (B. Baythavong, unpublished data). All other direct and indirect effects observed on offspring fitness were of substantially smaller magnitude on non-serpentine soils than on serpentine soils. Due to a lack of consistent patterns of variation in environmental variables with distance, and the comparatively weak direct and indirect effects observed in our SEM model, we do not expect to see selection on seed dispersal distance for lineages growing on non-serpentine soils.

In contrast, on serpentine soils we found predictable structuring of environmental heterogeneity that is likely to exert selection on dispersal distance in *E. cicutarium* (Fig. 4), and structural equation modeling revealed a number of strong direct effects of edaphic variables and dispersal distance on vegetation characteristics and *E. cicutarium* density (Table 4). These causal pathways indicate that there are much stronger links between edaphic and biotic factors on serpentine soils and that

abiotic variation has a stronger effect on biotic heterogeneity there. Our experimental results support Kruckeberg's (1984) assertion that the harsh soil environment is a dominant factor determining plant community attributes on and near serpentine outcrops.

In structural equation models, as in regression-based methods, one must consider the potential role of unmeasured factors when developing causal hypotheses based on statistical findings (Grace 2006). For serpentine sites in our study, the strong direct effect of dispersal distance on *E. cicutarium* density almost certainly reflects historical accumulation of seeds in microsites favorable to *E. cicutarium*. In contrast, the direct and indirect effects of dispersal distance on the aboveground biomass of grasses and forbs imply that important, unmeasured variables (e.g., soil chemistry or macronutrient availability) vary with distance from patches of *E. cicutarium*, and that associations between species are driven in part by shared or contrasting affinities for microsite characteristics. Similarly, a direct effect of dispersal distance on offspring fitness in this annual plant could reflect the action of unmeasured ecological factors that uniquely affect *E. cicutarium*. For example, locally high densities of pathogens or other natural enemies may develop in close proximity to the maternal home site (Augsburger 1983b), and may reduce the fitness of offspring dispersed nearby. Conversely, locally high densities of beneficial soil mutualists such as mycorrhizae could enhance the fitness of offspring near the maternal home site. We did not measure any of these potential selective factors in our study, but if there were strong distance-dependent effects of either enemies or mutualists, these should have manifested as direct pathways linking dispersal distance and offspring fitness in the structural equation models (Table 4).

Theory predicts that seed dispersal distances evolve in response to patterns of environmental heterogeneity surrounding a maternal plant. Selection can favor decreased dispersal distance if the risks of dispersing long distances are too great (Schmitt and Gamble 1990, McPeck and Holt 1992, Donohue 1997, Montesinos et al. 2006). Our study suggests that selection favors limited seed dispersal distances in serpentine soil habitats, where environmental factors are predictably more favorable close to maternal home sites, but should not favor increased or reduced dispersal distance in non-serpentine soil habitats, where environmental factors do not vary consistently with distance from maternal home sites. Although this study demonstrated consistency in the location of dense patches of *E. cicutarium* across two years, it is possible that over larger time scales the location of suitable microenvironments within serpentine and non-serpentine soils may shift (Schupp 2007). Temporal variation in environmental factors may also generate selection on seed dispersal and seed dormancy on serpentine and non-serpentine soils. To thoroughly investigate the role of spatiotemporal heterogeneity in generating selection on dispersal distance would require conducting a similar experiment over much longer time scales spanning several years.

Field experiments must be conducted within contrasting natural habitats to fully understand the links between environmental heterogeneity, the response of a plant species to variation in environmental factors, and the evolutionary implications of that response. To our knowledge, ours is the first study to document differences in microenvironmental heterogeneity in soil characteristics and aboveground plant community biomass between two adjacent habitat types at spatial scales relevant to seed dispersal, and elucidate the relationship between patterns of heterogeneity and offspring fitness. The harsh chemistry of serpentine soils is often assumed to impose unique selection pressures on plants, relative to surrounding non-serpentine soils, and is thought to explain the evolution of both narrowly distributed serpentine endemics and serpentine ecotypes of broadly distributed plant species (Kruckeberg 1984, Coyne and Orr 2004). Adaptation to serpentine soils is currently an active area of research in field evolutionary ecology, and several studies have demonstrated adaptation to unusually low Ca:Mg ratios in serpentine populations (Berglund et al. 2004, Gailing et al. 2004, Brady et al. 2005, Bratteler et al. 2006, Sambatti and Rice 2006, Wright et al. 2006). Reciprocal adaptation to nearby serpentine and non-serpentine sites (e.g., Wright et al. 2006) should select for traits that reduce seed dispersal and pollen flow between the contrasting habitats. What has been less appreciated is that these soil types may impose contrasting selection on even short-range seed dispersal due to different spatial patterns of environmental heterogeneity, as demonstrated in our study.

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LITERATURE CITED

- Antonovics, J., K. Clay, and J. Schmitt. 1987. The measurement of small-scale environmental heterogeneity using clonal transplants of *Anthoxanthum odoratum* and *Danthonia spicata*. *Oecologia* 71:601–607.
- Augsburger, C. K. 1983a. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40:189–196.
- Augsburger, C. K. 1983b. Seed dispersal of the tropical tree, *Platydictyon elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* 71:759–771.
- Bell, G., and M. J. Lechowicz. 1991. The ecology and genetics of fitness in forest plants. 1. Environmental heterogeneity measured by explant trials. *Journal of Ecology* 79:663–685.
- Berglund, A. B. N., S. Dahlgren, and A. Westerbergh. 2004. Evidence for parallel evolution and site-specific selection of serpentine tolerance in *Cerastium alpinum* during the colonization of Scandinavia. *New Phytologist* 161:199–209.
- Bradshaw, A. D., and K. Hardwick. 1989. Evolution and stress: genotypic and phenotypic components. *Biological Journal of the Linnean Society* 37:137–155.
- Brady, K. U., A. R. Kruckeberg, and H. D. Bradshaw. 2005. Evolutionary ecology of plant adaptation to serpentine soils. *Annual Review of Ecology and Systematics* 36: 243–266.
- Bratteler, M., C. Lexer, and A. Widmer. 2006. Genetic architecture of traits associated with serpentine adaptation of *Silene vulgaris*. *Journal of Evolutionary Biology* 19:1149–1156.
- Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27: 597–623.
- Case, T. J., R. D. Holt, M. A. McPeck, and T. H. Keitt. 2005. The community context of species' borders: ecological and evolutionary perspectives. *Oikos* 108:28–46.
- Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer Associates, Sunderland, Massachusetts, USA.
- Donohue, K. 1997. Seed dispersal in *Cakile edentula* var. *lacustris*: decoupling the fitness effects of density and distance from the home site. *Oecologia* 110:520–527.
- Gailing, O., M. R. Macnair, and K. Bachmann. 2004. QTL mapping for a trade-off between leaf and bud production in a recombinant inbred population of *Microseris douglasii* and *M. bigelovii* (Asteraceae, Lactuceae): a potential preadaptation for the colonization of serpentine soils. *Plant Biology* 6: 440–446.
- Grace, J. B. 2003. Comparing groups using structural equations. Pages 281–296 in B. H. Pugesek, A. Tomer, and A. von Eye, editors. *Structural equation modeling: applications in ecological and evolutionary biology*. Cambridge University Press, Cambridge, UK.
- Grace, J. B. 2006. *Structural equation modeling and natural systems*. Cambridge University Press, Cambridge, UK.
- Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. *Nature* 269:578–581.

- Harmon, G. D., and N. E. Stamp. 1992. Effects of postdispersal seed predation on spatial inequality and size variability in an annual plant, *Erodium cicutarium* (Geraniaceae). *American Journal of Botany* 79:300–305.
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.
- Hueneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71:478–491.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Janzen, D. H. 1970. Herbivores and number of tree species in tropical forests. *American Naturalist* 104:501–528.
- Janzen, D. H. 1978. Bat-generated fig seed shadow in rainforest. *Biotropica* 10:121–121.
- Kalish, S., J. D. Nason, F. M. Hanzawa, and S. J. Tonsor. 2001. Spatial population genetic structure in *Trillium grandiflorum*: the roles of dispersal, mating, history, and selection. *Evolution* 55:1560–1568.
- Kallimanis, A. S., W. E. Kunin, J. M. Halley, and S. P. Sgardelis. 2006. Patchy disturbance favours longer dispersal distance. *Evolutionary Ecology Research* 8:529–541.
- Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. *Ecology Letters* 7:1225–1241.
- Kruckeberg, A. R. 1984. California serpentine: flora, vegetation, geology, soils, and management problems. University of California Press, Berkeley, California, USA.
- Launer, A. E., and D. D. Murphy. 1994. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. *Biological Conservation* 69:145–153.
- Lechowicz, M. J., and G. Bell. 1991. The ecology and genetics of fitness in forest plants. 2. Microspatial heterogeneity of the edaphic environment. *Journal of Ecology* 79:687–696.
- Levin, S. A., and H. C. Muller-Landau. 2000. The evolution of dispersal and seed size in plant communities. *Evolutionary Ecology Research* 2:409–435.
- Linhart, Y. B., and M. C. Grant. 1996. Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27:237–277.
- Maddox, G. D., and J. Antonovics. 1983. Experimental ecological genetics in *Plantago*: a structural equation approach to fitness components in *Plantago aristata* and *Plantago patagonica*. *Ecology* 64:1092–1099.
- McPeck, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140:1010–1027.
- Mensing, S., and R. Byrne. 1998. Pre-mission invasion of *Erodium cicutarium* in California. *Journal of Biogeography* 25:757–762.
- Montesinos, D., P. Garcia-Fayos, and I. Mateu. 2006. Conflicting selective forces underlying seed dispersal in the endangered plant *Silene diclinis*. *International Journal of Plant Sciences* 167:103–110.
- Muller-Landau, H. C., S. A. Levin, and J. E. Keymer. 2003. Theoretical perspectives on evolution of long-distance dispersal and the example of specialized pests. *Ecology* 84: 1957–1967.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37:637–669.
- Ronce, O., S. Brachet, I. Olivieri, P. H. Gouyon, and J. Clobert. 2005. Plastic changes in seed dispersal along ecological succession: theoretical predictions from an evolutionary model. *Journal of Ecology* 93:431–440.
- Rousset, F., and S. Gandon. 2002. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. *Journal of Evolutionary Biology* 15:515–523.
- Sambatti, J. B. M., and K. J. Rice. 2006. Local adaptation, patterns of selection, and gene flow in the Californian serpentine sunflower (*Helianthus exilis*). *Evolution* 60:696–710.
- SAS Institute. 2006. SAS version 9.1.3. SAS Institute, Cary, North Carolina, USA.
- Schmitt, J., and S. E. Gamble. 1990. The effect of distance from the parental site on offspring performance and inbreeding depression in *Impatiens capensis*: a test of the local adaptation hypothesis. *Evolution* 44:2022–2030.
- Schupp, E. W. 2007. The suitability of a site for seed dispersal is context dependent. Pages 445–462 in A. Dennis, E. W. Schupp, R. Green, and D. A. Westcott, editors. *Seed dispersal: theory and its application in a changing world*. CAB International, Wallingford, UK.
- Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecological Applications* 13:575–592.
- Soons, M. B., and G. W. Heil. 2002. Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs. *Journal of Ecology* 90:1033–1043.
- Stamp, N. E. 1984. Self-burial behavior of *Erodium cicutarium* seeds. *Journal of Ecology* 72:611–620.
- Stamp, N. E. 1989a. Efficacy of explosive vs hygroscopic seed dispersal by an annual grassland species. *American Journal of Botany* 76:555–561.
- Stamp, N. E. 1989b. Seed dispersal of 4 sympatric grassland annual species of *Erodium*. *Journal of Ecology* 77:1005–1020.
- Stanton, M. L., and D. A. Thiede. 2005. Statistical convenience vs biological insight: consequences of data transformation for the analysis of fitness variation in heterogeneous environments. *New Phytologist* 166:319–337.
- Stocklin, J., and E. Winkler. 2004. Optimum reproduction and dispersal strategies of a clonal plant in a metapopulation: a simulation study with *Hieracium pilosella*. *Evolutionary Ecology* 18:563–584.
- Stratton, D. A. 1994. Genotype-by-environment interactions for fitness of *Erigeron annuus* show fine-scale selective heterogeneity. *Evolution* 48:1607–1618.
- Venable, D. L., and J. S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* 131:360–384.
- Venable, D. L., and J. S. Brown. 1993. The population-dynamic functions of seed dispersal. *Vegetatio* 108:31–55.
- Venable, D. L., and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* 46:272–282.
- Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39: 505–522.
- Wright, J. W., M. L. Stanton, and R. Scherson. 2006. Local adaptation to serpentine and non-serpentine soils in *Collinsia sparsiflora*. *Evolutionary Ecology Research* 8:1–21.

APPENDIX

Aerial photograph of “the grid” at the University of California McLaughlin Reserve with grid points overlaid onto the landscape (*Ecological Archives* E090-148-A1).