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HERBIVORES AND EDAPHIC FACTORS CONSTRAIN THE REALIZED NICHE OF A NATIVE PLANT

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Abstract. Biotic interactions, such as competition and herbivory, can limit plant species ranges to a subset of edaphically suitable habitats, termed the realized niche. Here we explored the role that herbivores play in restricting the niche of serpentine ecotypes of the native California annual *Collinsia sparsiflora*. We planted seeds from four populations into a range of natural field environments that varied in the presence/absence of naturally occurring *C. sparsiflora* and in predicted suitability for growth and survival of the serpentine ecotype of *C. sparsiflora*. Path analysis was then used to model the direct and herbivore-mediated indirect effects of environmental variables on the survival of *C. sparsiflora* serpentine ecotypes. We found that *C. sparsiflora* received more herbivory when planted into areas where serpentine ecotypes of *C. sparsiflora* were not predicted to persist, and that increased herbivory was associated with decreased survival, suggesting that herbivores may limit the distribution of *C. sparsiflora* serpentine ecotypes. Additionally, we demonstrated that edaphic environmental variables impacted the survival of *C. sparsiflora* serpentine ecotypes both directly and indirectly, by altering interactions with herbivores. These indirect effects were probably trait-mediated and probably occurred because edaphic factors may influence plant traits that, in turn, alter attractiveness to herbivores. Although the magnitude of direct effects exceeded the magnitude of indirect effects, many strong herbivore-mediated indirect effects were detected. Thus, interactions between the abiotic environment and insect herbivory contributed to restricting the niche of *C. sparsiflora* serpentine ecotypes to a subset of available habitat.

Key words: Collinsia sparsiflora; *ecological niche modeling; ecotypes; herbivory; indirect effect; local adaptation; path analysis; plant–insect interaction; niche, serpentine soils.*

INTRODUCTION

Plant populations are patchily distributed across the landscape. Identifying the abiotic and biotic factors that contribute to this patchiness and limit species distributions remains a central issue in ecology. The niche concept is a useful framework for considering both the local distribution and ecological tolerance of a species. The fundamental niche describes the range of environments that an organism can inhabit based on physiological tolerances (Hutchinson 1959, Holt 2003). Rates of dispersal across the habitat and biotic interactions with other species may further alter the actual area occupied, termed the realized niche (Hutchinson 1959). Species interactions often vary across environmental gradients (e.g., Bertness and Ellison 1987, Louda and Rodman 1996). As a result, interspecific interactions that decrease population growth rates, such as competition (Bertness and Ellison 1987, Davis et al. 1998, Choler et al. 2001), predation (Davis et al. 1998), disease (Augspurger and Kelly 1984), and herbivory (Parker and Root 1981, Smith 1987, Louda and Rodman 1996, Harley 2003, DeWalt et al. 2004), can restrict the observed distributions of focal species to a subset of otherwise suitable habitats. Similarly, the presence of mutualists can allow for the expansion of species distributions to otherwise unsuitable habitats (i.e., facilitation; Choler et al. 2001, Bruno et al. 2003).

Herbivory often decreases individual plant fitness (Marquis 1984, reviewed in Huntly 1991), and in several systems, herbivores limit the abundance (Smith 1987, Rand 2002) or population growth rates of their host plants (Ehrlen 1995, Louda and Potvin 1995, Fagan and Bishop 2000, Bishop 2002). Several other studies provide evidence that the combination of spatial variation in herbivory and strong demographic effects of herbivores restricts plant distributions to a subset of available habitats (Parker and Root 1981, Louda and Rodman 1996, Harley 2003, DeWalt et al. 2004). However, strong impacts of herbivores on plant distributions and

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population dynamics are documented most frequently when plants are grown outside their typical distribution (e.g., biological control studies, reviewed in Crawley [1989*a*], or transplant experiments; see DeWalt et al. [2004]), or in other recently altered environments (e.g., Bishop 2002, Fagan et al. 2004). Although several studies have documented demographic impacts of herbivores on plant populations in native, undisturbed habitats (Louda 1982, Doak 1992, Louda and Potvin 1995, Louda and Rodman 1996, Root 1996, Kauffman and Maron 2006), in many cases, the demographic impacts of herbivory may be underestimated, potentially because plant populations under intense herbivory have already been excluded and/or have evolved anti-herbivore defenses to minimize strong herbivore impacts (Harper 1969, Connell 1980, DeWalt et al. 2004). Thus, the strongest herbivore effects on population dynamics often can be detected only when the plant population has been perturbed from its natural state. Accordingly, experimental plantings into patches that are unoccupied, but within the fundamental niche of the plant species, are valuable for investigating the effects of herbivory on plant population dynamics and plant distributions (Crawley 1990).

There are two distinct ecotypes of the native California annual *Collinsia sparsiflora* that grow in close proximity but occupy different habitats (serpentine vs. non-serpentine soils). In a previous study, we constructed a niche model describing the distribution of the serpentine ecotype of *C. sparsiflora* and then experimentally tested the niche model by planting *C. sparsiflora* seeds into plots where environmental variables associated with the *C. sparsiflora* distribution had been described (e.g., *C. sparsiflora* presence/absence, calcium : magnesium ratio, phosphorus, slope, aspect, and biomass; see Wright et al. 2006*a*). We found that the niche model, based on descriptive data, successfully predicted the survival of *C. sparsiflora* serpentine ecotypes but did not predict the survival of the non-serpentine ecotype.

Here, we expand upon that work to investigate potential underlying mechanisms responsible for differences in survival of the serpentine ecotype across a heterogeneous landscape. In particular, we focus on how indirect effects, driven by differences in herbivory and differences in the fitness effects of herbivory, contribute to the documented differences in survival across locations. We employ path analyses to link variation in habitat characters with variation in herbivory and variation in survival to parse out the direct and herbivore-mediated indirect effects of habitat characteristics on the population dynamics of the serpentine ecotype of *C. sparsiflora*. We address two main questions. (1) Does the amount of herbivory or the fitness impact of herbivory vary across sites differing in predicted suitability for the persistence of *C. sparsiflora* serpentine ecotypes and/or the presence/absence of naturally occurring *C. sparsiflora*? (2) Do habitat variables known to predict the occurrence of serpentine ecotypes of *C. sparsiflora* affect survival directly or indirectly by altering interactions with herbivores? Finally, although our study focuses primarily on serpentine ecotypes, because seeds from four source populations representing both serpentine and non-serpentine ecotypes were used in the experiment, we discuss the robustness of our results across substantial intraspecific variation and the role herbivory may play in contributing to divergence in habitat use between serpentine and non-serpentine ecotypes.

MATERIALS AND METHODS

Study system

The native, annual plant *Collinsia sparsiflora* Fischer and C. Meyer (Scrophulariaceae s.l.) is patchily distributed across the McLaughlin University of California Natural Reserve in the California Coast Range, USA (data *available online*).[6] It occurs on both serpentine and non-serpentine soils in grasslands and open oak woodlands. Serpentine soils are characterized by high concentrations of heavy metals and are stressful environments for many plant species (Kruckeberg 1984, Brady et al. 2005). They also have very low calcium : magnesium (Ca:Mg) ratios, low levels of phosphorous and other nutrients, tend to be xeric, and typically support lower total plant biomass than comparable non-serpentine areas. Previous work has shown that *C. sparsiflora* populations growing in serpentine vs. non-serpentine environments have differentiated into distinct ecotypes (Wright et al. 2006*b*). We found that various generalist herbivores attack *C. sparsiflora*, including lepidopteran larvae and flea beetles (Coleoptera). Flea beetles, which were most abundant and were observed only early in the season, imposed the vast majority of damage observed in this study. Almost all herbivore damage occurred on the cotyledons and leaves produced early in the season; flowers and fruits were damaged infrequently.

Mapping the natural distribution of C. sparsiflora

In 2001, a 600 × 550 m grid (hereafter referred to as "the grid") was established across a mosaic of both serpentine and non-serpentine grasslands at the McLaughlin Reserve, with grid points every 50 m (156 grid points). Within this large grid, six smaller "gridlets" (100 × 50 m) were established to more intensively sample highly variable locations. These smaller "gridlets" were sampled at finer scales (10 m), yielding an additional 372 grid points. At each grid point ($n = 528$), data were collected on soil chemical composition and texture (22 variables; see Wright et al. [2006*b*] for a full description of these variables), soil depth, slope, aspect, biomass, and *C. sparsiflora* occurrence. *C. sparsiflora* occurrence was estimated as the presence of at least one plant in a

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[6] ⟨http://nrs.ucdavis.edu/mclaughlin.html⟩

1-m^2 quadrat located adjacent to the grid point. Because occurrence was estimated in April, toward the end of peak flowering but well within the period where fruiting plants can be observed and easily identified, occurrence data are likely to be accurate, and it is unlikely that individuals were missed. See Wright et al. (2006*a*) for details on other environmental attribute measures. The environmental variables and occurrence data were then used to construct a niche model describing the observed distribution of *C. sparsiflora* (Wright et al. 2006*a*). The final niche model included five environmental variables: slope, aspect, Ca:Mg ratio, organic matter, and phosphorus. Serpentine ecotypes were most likely to occur and persist at sites with slopes between 15 and 25 degrees, northerly aspects, soil with intermediate soil phosphorous, little organic matter, and low Ca:Mg ratios. A previous study, using the same experimental plants described here, demonstrated that the niche model successfully predicted survival of the serpentine ecotype of *C. sparsiflora* (Wright et al. 2006*a*). Although the grid included both serpentine and non-serpentine grasslands that appeared to be promising *C. sparsiflora* habitats, populations on non-serpentine soils were less common than populations growing on serpentine soils on the grid, and due to random chance, non-serpentine ecotypes were not present at the sampled grid points.

Experimental design of planting experiment

We planted *C. sparsiflora* seeds into 100 plots across the grid at the McLaughlin reserve. The 100 plots were chosen to maximize variation in the five variables included in the niche model previously described and were chosen from among the points in three highly variable "gridlets" (a subset of 198 of the 528 total grid points that were spatially clustered into three large blocks to aid in planting and data collection). Thus, the planting sites spanned a wide range of habitat quality and included both suitable sites and sites that were deemed to be outside the niche of serpentine ecotypes of *C. sparsiflora* (not expected to support growth and survival). In August 2003, we planted 40 seeds into each plot; two seeds were planted at each cell in the plot in a 5×4 array with 5 cm between cells. After germination in January 2004, seedlings were thinned to one individual per cell. Thus, there were a maximum of 20 plants in each plot, with five plants from each of four source populations: NS1, NS2, S1, and S3. The four source populations were collected from sites within the McLaughlin reserve and represented two distinct ecotypes that are locally adapted to different soil types: S, serpentine; NS, non-serpentine (see Wright et al. [2006*b*] for a full description of these source populations). The soil environment is extremely heterogeneous across the reserve, and seed source populations were relatively close together (<1 km); however, prior reciprocal transplant and common garden experiments indicate that there is a genetic basis to phenotypic differences between populations (Wright et al. 2006*b*, Wright and Stanton 2007). The seeds used in this experiment were the selfed progeny of field-collected seeds (32 maternal families per population) grown for one generation in a common greenhouse environment in order to reduce maternal effects resulting from differences in the source population habitat. *C. sparsiflora* selfs readily, with no decrease in fruit set compared to open-pollinated individuals (Wright and Stanton 2007).

Source populations were randomly assigned to locations within each plot. Because of differences in germination, the number of plants per plot ranged from 0 to 19 (mean 11.52 plants per plot). Plants were scored for emergence (weekly observations from 14 December 2003 to 19 January 2004) and survival to flowering (censused weekly from 4 March to 21 April 2004). Herbivory was measured qualitatively (damaged or undamaged) and quantitatively (visual estimates of the proportion of leaf material removed) weekly between 21 December and 20 January 2004. A plant was considered damaged if any leaf material had been removed. Quantitative measures of herbivory were estimated by assessing the proportion of total leaf material damaged by herbivores and assigning each plant to a damage category (0.05 intervals). Because plants typically had only 4–8 leaves, all leaves and cotyledons were examined. For example, if a plant had 10 leaves, and one half of a single leaf was damaged, we would assign that plant a damage level of 0.05. By 20 January, a substantial amount of herbivory had been received but little mortality had occurred, thus maximizing sample sizes; accordingly, the damage level observed on 20 January was used as the herbivory measure in all analyses. After flowering had ceased and fruits had matured, all experimental plants were harvested, and then the aboveground biomass of all other plants occurring in the plot (excluding the planted *C. sparsiflora*) was harvested, dried, and weighed to determine plot biomass.

Data analysis

All analyses were performed using SAS version 8.1 (SAS Institute 2001). Because the niche model effectively predicted only the survival of serpentine ecotypes, only results for serpentine genotypes are presented in the main text. Additional analyses were performed on the full data set, which included data on the non-serpentine ecotypes, however, and these results are reported in Appendices A and B.

Herbivory across the C. sparsiflora *distribution.*—To determine whether plants growing in sites predicted to be less suitable for the persistence of *C. sparsiflora* serpentine ecotypes receive more herbivory than plants in more suitable sites, we calculated the correlation between the proportion of plants in each plot with herbivore damage and predicted occurrence (from the niche model described in Wright et al. 2006*a*), using PROC CORR. We also used ANOVA (PROC MIXED) to test whether experimental plants outside the natural distribution (i.e., plots where *C. sparsiflora* does not naturally occur) receive more herbivory than plants in plots where *C. sparsiflora* naturally occurs. The proportion of serpentine ecotype plants with evidence of herbivore damage was our response variable, and the presence or absence of naturally occurring *C. sparsiflora,* source population, and the source population × *C. sparsiflora* presence interaction were included as predictor variables. The experiment included 25 plots where *C. sparsiflora* was naturally present and 75 plots where *C. sparsiflora* was naturally absent. Plot nested within *C. sparsiflora* presence was included as a random factor. We also performed similar analyses using the arcsine-transformed mean proportion of leaf area damaged as our response variable.

Fitness effects of herbivory across the C. sparsiflora *distribution*.—To determine if the fitness effects of herbivory on serpentine ecotypes (i.e., tolerance) vary across sites that differ in predicted quality, we performed a logistic regression (PROC GENMOD) with survival to flowering as a binomial response variable and predicted occurrence (from the niche model), herbivory (proportion of leaf area damaged), and the interaction as predictor variables. A significant herbivory × predicted occurrence interaction indicates that the fitness effects of herbivory vary with predicted site quality. Similar analyses were also performed where *C. sparsiflora* natural presence/absence, source population, herbivory, and all interactions were included as predictor variables. If herbivory interacts with environmental variables to limit the distribution of *C. sparsiflora* serpentine ecotypes, we expect to detect an interaction between *C. sparsiflora* presence and herbivory, where herbivory decreases fitness more where *C. sparsiflora* is naturally absent.

Direct and herbivore-mediated indirect effects of edaphic variables on C. sparsiflora *serpentine ecotype survival*.—We used path analysis to examine how the edaphic variables found to be important in the initial niche model influence the survival of serpentine ecotypes of *C. sparsiflora* both directly and indirectly, by altering herbivory. The path analysis included the five variables in the initial niche model (slope, aspect, Ca:Mg ratio, organic matter, and phosphorus; see Wright et al. 2006*a*) as exogenous predictor variables. Aboveground biomass of all surrounding competitors in the plot was also included as an exogenous variable because of the strong impacts that vegetation heterogeneity has on herbivory in other systems (Karban 1997, Agrawal et al. 2006). Herbivory (proportion of plants damaged per plot) and survival (proportion of cells with plants surviving to flower) were included as endogenous response variables. Each plot was one replicate ($n = 100$); however, at eight plots, all serpentine genotypes died before herbivory was censused, yielding a final sample size of $n = 92$. Because the path model included the serpentine niche model predictors and because the niche model only successfully predicted occurrence and survival of serpentine plants, only serpentine data were used to test the path model.

We initially tested a full model that included both direct and herbivore-mediated indirect effects of all exogenous variables on survival using maximum likelihood techniques as implemented by PROC CALIS. Because early analyses revealed that phosphorus had minimal effects on herbivory and survival (regression of phosphorus on herbivory $t_{98} = -1.41$, $P = 0.16$; survival $t_{98} = -1.54$, $P = 0.13$), it was dropped from the model to avoid over-parameterization. We performed all analyses on the variance–covariance matrix, and all predictor variables were standardized by their variance, so that each variable had a mean of 0 and a variance of 1.

Path analysis assumes that (1) residuals are normally distributed, (2) correlations between predictor variables are not excessively high (low multicollinearity), and (3) relationships among variables are linear (Hatcher 1994). Preliminary multiple regression analyses, with survival and herbivory as response variables and all habitat characters included as predictor variables, indicated that residuals were normally distributed and that collinearity was negligible (all variation inflation factors <10; VIF option, PROC REG). Furthermore, all Pearson's correlations between predictor variables had $r < 0.60$. We tested for nonlinear relationships between predictor and response variables by including quadratic terms in simple regressions between each predictor variable and each response variable. Although we detected significant quadratic terms in three of 11 cases (in regressions of survival on aspect, survival on Ca:Mg, and herbivory on slope), the quadratic terms were small relative to the linear coefficients, suggesting that the relationship was linear over most of the distribution. Furthermore, in the most extreme case (survival on aspect), linearity was obtained when aspect was log-transformed. Model fits were not qualitatively different when transformed vs. nontransformed data were used; therefore, we only present results from analyses using the nontransformed data.

The results of the CALIS procedure can be evaluated with several goodness-of-fit indices, including χ^2 statistics that test whether the path model fits the data. We also report values for the normed-fit index (NFI; Bentler and Bonett 1980), the non-normed-fit index (NNFI), and the comparative-fit index (CFI; Bentler 1989). NFI, NNFI, and CFI values that exceed 0.9 indicate an acceptable fit between the proposed model and the data (Hatcher 1994). The initial analysis revealed that the full model fit the data well (Table 1); however, examination of the path coefficients and the normalized residual matrix of the full model revealed that model fit could be improved by deleting several paths. Thus, we deleted any paths where the path coefficients did not differ significantly from zero ($P > 0.1$) and where deletion would not influence the χ^2 statistic (Wald test obtained from PROC CALIS output). We also examined the normalized residuals to delete (or add) any paths with

TABLE 1. Goodness-of-fit indices for the full model (all direct and indirect effects included) vs. a reduced model, where nonsignificant paths were removed.

Model	χ^2	df	P	NFI	NNFI	CFI
Full	2.04	2	0.36	0.99	1.00	1.00
Reduced	7.18	5	0.21	0.96	0.93	0.99
Null	203.15	28				

Notes: The data fit both models, and the two models do not differ significantly ($\chi^2 = 5.14$, df = 3, $P = 0.16$). Therefore, the reduced model is preferable because it contains fewer paths and is more parsimonious. Abbreviations: NFI, normed fit index; NNFI, non-normed fit index; CFI, comparative fit index.

large residuals. To determine whether the deletion of these paths significantly reduced model fit, we performed a χ^2 difference test by comparing the χ^2 goodness-of-fit indices for the revised model vs. the full model. If removing paths does not significantly affect model fit, the reduced model is preferred because it contains fewer paths and is more parsimonious (Hatcher 1994). We calculated the relative magnitude of direct vs. herbivore-mediated indirect effects of the edaphic soil variables on *C. sparsiflora* survival by using the path coefficients from the full model to calculate the relative strengths of all potential pathways (Mitchell 1992).

RESULTS

Does the amount or fitness impact of herbivory differ across sites differing in predicted suitability or natural occurrence of C. sparsiflora*?*

We predicted that if herbivores limit the local distribution of serpentine ecotypes of *C. sparsiflora*, herbivory should be reduced on *C. sparsiflora* serpentine ecotypes transplanted into locations where the niche model predicted that they would survive and persist compared to locations where they were not predicted to persist. Similarly, we predicted that individuals planted where *C. sparsiflora* does not naturally occur would receive more herbivory than individuals planted where *C. sparsiflora* is naturally present. As expected, predicted occurrence of serpentine ecotypes based on the niche model (described in Wright et al. 2006*a*) was negatively correlated with the proportion of serpentine ecotypes that experienced herbivory ($r = -0.17$, $P = 0.005$; Fig. 1A). This relationship occurred in spite of the fact that herbivory was not included in the construction of the initial niche model, and it suggests that many of the edaphic variables included in the niche model may indirectly influence survival by altering levels of herbivory. Furthermore, a greater proportion of serpentine plants in plots where *C. sparsiflora* is naturally absent received herbivore damage compared to experimental plants where *C. sparsiflora* is naturally present (Fig. 1B), although this difference was not significant ($F_{1,96} = 1.0$, $P > 0.32$). The proportion of leaf area removed also tended to be higher where *C. sparsiflora* does not naturally occur (least squares mean ± SE proportion of leaf material damaged: where *C. sparsiflora* is naturally absent, 0.61 ± 0.03; where *C. sparsiflora* is naturally present, 0.56 ± 0.05), although this difference also was not significant ($F_{1,88} = 0.56$, $P > 0.45$).

Herbivory was negatively associated with survival of *C. sparsiflora* serpentine ecotypes ($\chi^2 = 55.21$, $P < 0.0001$). These negative effects tended to be greater in plots where *C. sparsiflora* was naturally absent than in plots where *C. sparsiflora* was naturally present (logistic regression coefficient = −0.030 ± 0.005 and −0.022 ± 0.005 where *C. sparsiflora* is naturally absent vs. present, respectively); however, we did not detect a significant interaction between herbivory and predicted probability of occurrence (based on the niche model) on the survival of serpentine ecotypes ($\chi^2 = 1.36$, $P < 0.24$).

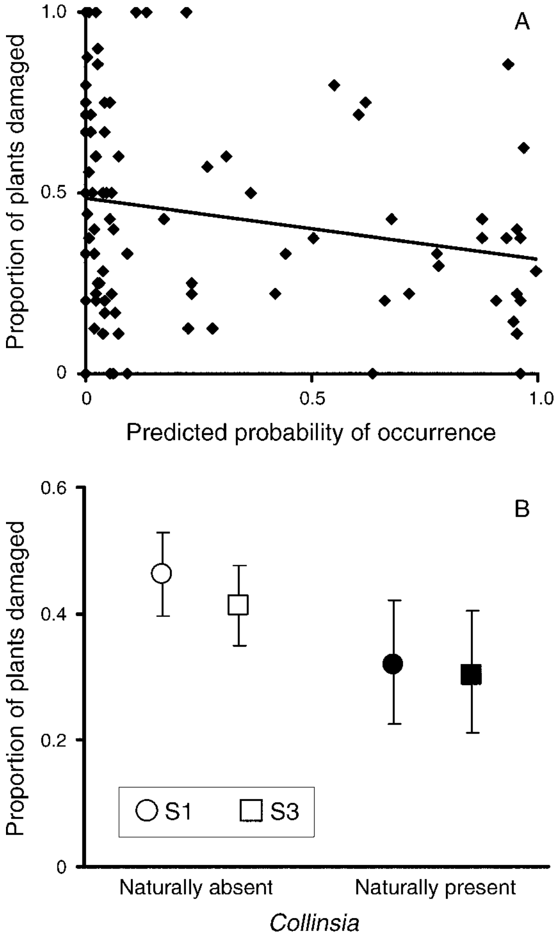

FIG. 1. (A) Herbivore damage to serpentine ecotypes decreased linearly with predicted probability of occurrence, and (B) herbivores tended to damage a greater proportion of *Collinsia sparsiflora* plants in plots where *C. sparsiflora* is naturally absent (open symbols) compared to plots where *C. sparsiflora* is naturally present (solid symbols). In (A), predicted probability of occurrence (i.e., probability of *C. sparsiflora* survival) was estimated from the niche model described in Wright et al. (2006*a*). Values shown in (B) are back-transformed least-squares means ± SE for each serpentine source population (S1 and S3).

Germination of serpentine ecotypes also was higher in plots where *C. sparsiflora* was naturally present than in plots where *C. sparsiflora* did not naturally occur (proportion of cells with seedlings = 0.97 ± 0.01 vs. 0.87 ± 0.02; $F_{1,98} = 20.62$, $P < 0.0001$), indicating that abiotic factors and safe site limitation may be important factors influencing the observed distribution of *C. sparsiflora* serpentine ecotypes. Altogether, our experiment suggests a large role of abiotic factors influencing recruitment, followed by an interaction of biotic and abiotic factors influencing survival.

Do habitat variables known to predict C. sparsiflora *serpentine ecotype occurrence affect survival directly or indirectly via herbivory?*

Path analysis revealed that habitat variables influenced the survival of serpentine ecotypes of *C. sparsiflora* plants directly, as well as indirectly, via effects on herbivory (Table 2). The final model, which included a subset of direct and indirect effects of the habitat variables, explained 48% of the variation in survival of *C. sparsiflora* serpentine ecotypes and 22% of variation in herbivory. As expected, herbivory decreased the proportion of *C. sparsiflora* serpentine ecotype seeds that survived to flower (standardized path coefficient = –0.21) and resulted in several indirect effects on survival (Fig. 2). Although the net direct effect was much stronger than the net indirect effect (1.02 vs. 0.24), including these herbivore-mediated indirect effects in the path model predicting the survival of *C. sparsiflora* serpentine ecotypes dramatically improved model fit ($\chi^2 = 22.36$, df = 3, $P < 0.0001$).

Higher calcium : magnesium ratios directly decreased survival of *C. sparsiflora* serpentine ecotypes. Slope, biomass, and organic matter influenced survival through both direct and indirect pathways. For biomass, the negative indirect effect exacerbated the negative relationship between biomass and survival. For organic matter and slope, the indirect effect was in the opposite direction of the direct effect: organic matter had a negative direct effect on survival, but a positive indirect effect because plots with more organic matter received less herbivory; slope had a positive direct impact on survival, but a negative indirect effect because plants on steeper slopes experienced more herbivory.

DISCUSSION

Although the role of herbivory in limiting plant distributions and restricting niches has been debated (Harper 1969, Crawley 1989*a*, *b*, Louda 1989), several studies have convincingly demonstrated that herbivores restrict plant distributions to a narrower region than that allowed by their physiological tolerances (Parker and Root 1981, Louda and Rodman 1996, Harley 2003, DeWalt et al. 2004, Fine et al. 2004). For this to occur, the effects of herbivory must be spatially variable (either because herbivory intensities vary or because the fitness effects of herbivory vary), and herbivory must impact plant population growth rates (Louda and Rodman 1996). Spatial variation in edaphic factors is one mechanism that could produce the necessary variation in herbivory. A prior study documented that fine-scale variation in edaphic variables could predict the patchy distribution of the serpentine ecotype of the native annual plant *Collinsia sparsiflora* (Wright et al. 2006*a*). These habitat variables influence survival directly, but as we report here, they also alter herbivory and influence *C. sparsiflora* serpentine ecotype demography through indirect pathways.

TABLE 2. Magnitude of the effect of herbivory and direct and herbivore-mediated indirect effects of each habitat variable on the survival of serpentine ecotypes of *Collinsia sparsiflora*.

Effect	Pathway	Magnitude
Herbivory	ρ(survival, herbivory)	**−0.2132**
Slope		
Direct	ρ(survival, slope)	**0.1503**
Indirect	ρ(herbivory, slope) × ρ(survival, herbivory)	**−0.0803**
Aspect		
Direct	ρ(survival, aspect)	0.1435
Indirect	ρ(herbivory, aspect) × ρ(survival, herbivory)	0.0283
Ca:Mg		
Direct	ρ(survival, Ca:Mg)	**−0.2017**
Indirect	ρ(herbivory, Ca:Mg) × ρ(survival, herbivory)	−0.0185
Biomass		
Direct	ρ(survival, biomass)	**−0.3104**
Indirect	ρ(herbivory, biomass) × ρ(survival, herbivory)	**−0.0604**
Organic matter		
Direct	ρ(survival, organic matter)	**−0.2098**
Indirect	ρ(herbivory, organic matter) × ρ(survival, herbivory)	**0.0505**

Notes: Values shown are standardized path coefficients estimated from the full model, which included all potential direct and indirect paths. Effects shown in boldface are statistically significant ($P < 0.05$).

We used experiments in which we planted *C. sparsiflora* into well-characterized environments, combined with path analysis, to separate the direct effects of habitat attributes known to restrict the distribution of *C. sparsiflora* serpentine ecotypes from indirect effects that occur when habitat properties alter interactions with insect herbivores. Although experimental manipulations of environmental variables (such as employed by Louda and Rodman 1996) are particularly convincing, this manipulative approach becomes unfeasible when several intrinsically correlated environmental variables are known to influence plant distributions, i.e., the "*n*-dimensional niche" (Hutchinson 1959, Pulliam 2000). Path analysis was especially useful in this study because it allowed us to link variation in several continuous habitat characteristics with variation in herbivory and, in turn, to explore how these factors both directly and indirectly impact the survival of serpentine ecotypes of

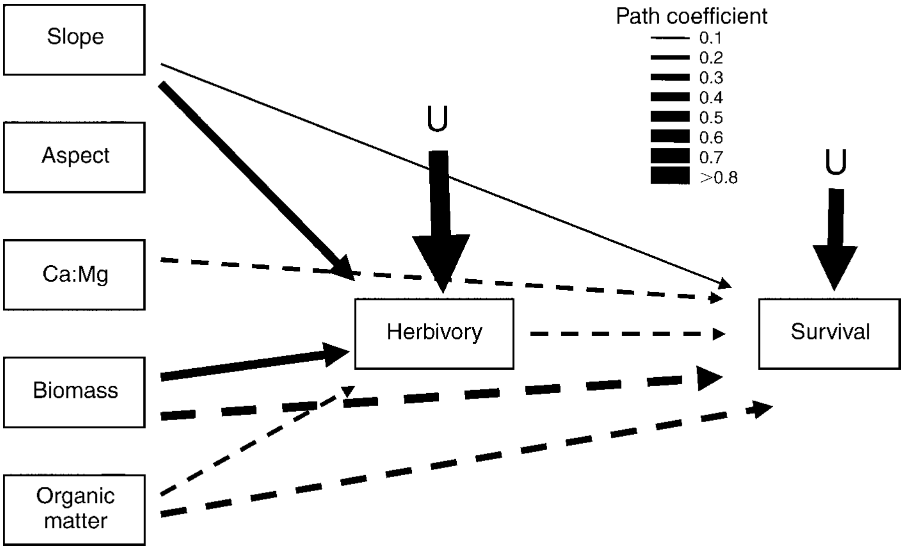

FIG. 2. Revised path diagram showing the direct and herbivore-mediated indirect effects of habitat attributes on the survival of *C. sparsiflora* serpentine ecotypes. Dashed lines indicate negative path coefficients; solid lines indicate positive path coefficients. Line thickness indicates the magnitude of effect (i.e., magnitude of the standardized path coefficient). Actual values of path coefficients (calculated from the full model) are presented in Table 2. "U" denotes the variation explained by all other causes. For figure clarity, significant covariances are not shown.

C. sparsiflora. Path analysis was useful for understanding how multiple abiotic environmental characters interacted with biotic selective agents to determine the realized niche, but additional experiments are needed to determine whether the observed impact of herbivores actually restricts the local distribution of *C. sparsiflora* serpentine ecotypes. In particular, experiments demonstrating that population growth rates increase outside the natural distribution or at predicted poor-quality sites when plants are protected from herbivores would provide especially convincing evidence that herbivores restrict the distribution of this ecotype.

We found that biomass of competitors and slope were associated with increased herbivory. Biomass may increase herbivory by providing additional food sources for generalist herbivores. Biomass also could influence herbivores by making the abiotic or biotic environment more suitable (e.g., by altering temperature, protection from predators, and so on). Slope and aspect probably influence herbivory because of their associations with other abiotic and biotic variables. For example, the positive association between slope and herbivory is likely to result more from the fact that steeper slopes tend to be warmer and drier than from any inherent preference of herbivores for steeper areas. Many of the effects of the habitat variables included in our model on herbivores also could be trait-mediated and result from differences in plant phenotypes on different growth environments within this heterogeneous serpentine habitat. The habitat variables included in our model could alter nutrient content, water use, or other plant traits that might influence allocation to defense or general host plant quality. These habitat characteristics also may influence the fitness consequences of herbivory, potentially by altering the amount of resources available for regrowth.

Our data suggest that herbivores may play a role in limiting the distribution of one ecotype of *C. sparsiflora*. Work by Fine and coauthors suggests that, in addition to limiting distributions of particular taxa, herbivores may contribute to habitat specialization and divergence between populations or ecotypes inhabiting different environments (Fine et al. 2004, 2006, Marquis 2004). In particular, Fine and coauthors find that herbivores heighten differences between habitats and that a fundamental growth–defense trade-off is a major mechanism contributing to habitat specialization on different soil types in a suite of tropical tree species. Although we have focused on the serpentine ecotype of *C. sparsiflora*, non-serpentine ecotypes were also included in our experimental planting. Serpentine and non-serpentine populations did not differ in the amount of herbivory received; however, the fitness of non-serpentine genotypes was less affected by herbivore damage than that of serpentine genotypes (Appendices A and B). Little is known about the edaphic and biotic variables associated with the niche of non-serpentine ecotypes of *C. sparsiflora*, but it is clear that the factors describing the niche of the serpentine ecotype do not adequately describe the niche of the non-serpentine ecotype (Wright et al. 2006*a*). Because the serpentine path model includes several strong herbivore-mediated indirect effects, whereas the survival of non-serpentine genotypes is less influenced by herbivory, variation in the ecotypes' responses to herbivory (i.e., tolerance) may contribute to this lack of fit. Since *C. sparsiflora* serpentine and non-serpentine ecotypes did not differ in the amount of herbivory received, but did differ in the fitness effects of herbivory, our results suggest that ecotypic differences in tolerance to herbivory (i.e., the ability to withstand herbivore damage with minimal reductions in fitness), rather than resistance (i.e., differences in the amount of damage received), may contribute to differentiation in habitat use.

Prior work on this system has convincingly demonstrated that serpentine and non-serpentine ecotypes are genetically distinct and locally adapted to their soil environment; however, the selective forces maintaining these ecotypic differences have not been identified. Serpentine and non-serpentine soils favor different *C. sparsiflora* genotypes; however, Wright and Stanton (2007) did not detect differences in patterns of selection between soil environments for any of six phenological, early size, and floral traits measured. Thus, selection on unmeasured traits is probably maintaining these ecotypic differences. Our results suggest that traits involved in interactions with herbivores may be especially relevant and perhaps may be under divergent selection in serpentine vs. non-serpentine habitats.

In conclusion, our data suggest that herbivores play an important role in restricting the realized niche of serpentine ecotypes of *C. sparsiflora*. Several of the abiotic habitat attributes associated with the natural distribution of serpentine ecotypes of *C. sparsiflora* alter herbivory, resulting in strong indirect effects on *C. sparsiflora* survival. Thus, spatial variation in habitat variables, combined with interactions between habitat attributes and herbivory, probably influences the distribution of one ecotype of this native plant. Interestingly, variation in tolerance to herbivory among populations may also promote divergence in habitat use between genetically distinct ecotypes.

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APPENDIX A

Effects of herbivory on the survival of serpentine and non-serpentine ecotypes of *Collinsia sparsiflora* (*Ecological Archives* E089-041-A1).

APPENDIX B

Results from analyses investigating whether herbivory differs across source populations and sites differing in the presence of naturally occurring *Collinsia sparsiflora* (*Ecological Archives* E089-041-A2).