

# EFFECT OF LOCAL COMMUNITY PHYLOGENETIC STRUCTURE ON POLLEN LIMITATION IN AN OBLIGATELY INSECT-POLLINATED PLANT<sup>1</sup>

RISA D. SARGENT<sup>2</sup>, STEVEN W. KEMBEL<sup>3</sup>, NANCY C. EMERY<sup>4</sup>, ELISABETH J. FORRESTEL<sup>5</sup>,  
AND DAVID D. ACKERLY<sup>6</sup>

Department of Integrative Biology, University of California, Berkeley, CA

- *Premise of the study:* Pollination is a key aspect of ecosystem function in the majority of land plant communities. It is well established that many animal-pollinated plants suffer lower seed set than they are capable of, likely because of competition for pollinators. Previously, competition for pollinator services has been shown to be most intense in communities with the greatest plant diversity. In spite of the fact that community evolutionary relations have a demonstrated impact on many ecological processes, their role in competition for pollinator services has rarely been examined.
- *Methods:* In this study, we explore relations among several aspects of the surrounding plant community, including species richness, phylodiversity, evolutionary distance from a focal species, and pollen limitation in an annual insect-pollinated plant.
- *Key results:* We did not find a significant effect of species richness on competition for pollination. However, consistent with a greater role for facilitation than competition, we found that a focal species occurring in communities composed of species of close relatives, especially other members of the Asteraceae, was less pollen limited than when it occurred in communities composed of more distant relatives.
- *Conclusions:* Our results demonstrate that community phylodiversity is an important correlate of pollen limitation in this system and that it has greater explanatory power than species richness alone.

**Key words:** competition; facilitation; phylogenetic community structure; pollen limitation; pollination; ecosystem services.

Pollinator services are essential to the survival of the vast majority of wild plant communities (Winfree et al., 2008). Moreover, a large proportion of the world's food crops depend critically on animal pollination (Corbet et al., 1991). As evidence mounts that global pollinator populations are in decline (Goulson et al., 2005) and that pollinator-dependent plant species are declining in parallel (Biesmeijer et al., 2006), improving our understanding of the factors affecting pollen limitation—the failure to set a full complement of seeds because of

inadequate pollination (Ashman et al., 2004)—is becoming increasingly urgent.

One challenge to our ability to make general predictions about how plant–pollinator communities function is that they are incredibly complex, typically involving multiple interactions among numerous species. Indeed, because of the difficulties associated with designing experiments or developing theory that can encompass a vast assortment of interspecific interactions, much of our understanding of plant–pollinator communities is based on studies involving a single plant and its pollinator, or interactions among a single plant species and several of its pollinators (Geber and Moeller, 2006). Recent work has built on this foundation of pairwise studies by using network theory to describe the connections and interactions among multiple plant and pollinator species (reviewed by Bascompte, 2009). To date, only a handful of studies have attempted to connect properties of the community with pollen limitation (Schemske et al., 1978; Motten, 1986; Hegland and Totland, 2008).

Interactions among plants that are mediated by pollinators can range from competitive, in which plant species interfere with one another's ability to attract sufficient pollinators, to facilitative, in which plant species enhance one another's ability to attract pollinators (Geber and Moeller, 2006). Competitive interactions among close relatives, because they share similar resource requirements, are typically thought to be the norm. On the other hand, interactions among close relatives may be facilitative, especially those mediated by pollinators, because low plant population densities may fail to attract sufficient pollinators (Moeller, 2004). Moreover, the specific pollinator species attracted to communities composed of close relatives may tend to be more suitable because of similar pollinator requirements (Sargent and Ackerly, 2008).

<sup>1</sup> Manuscript received 1 September 2010; revision accepted 13 December 2010.

The authors thank T. Nelson for her advice on performing the spatial autocorrelation analysis and M. Park for providing the relations among *Lasthenia*. The University of California Reserve System kindly facilitated the authors' use of the Jepson Prairie Reserve. We owe special thanks to S. Waddell for his assistance with setting up and helping to keep sheep out of our plots in the spring of 2007 and 2008. This research was funded by NSF DEB #0621377 to D.D.A. and Bruce Baldwin and Natural Sciences and Engineering Research Council of Canada (NSERC) postdoctoral fellowships to R.D.S. and S.W.K.

<sup>2</sup> Author for correspondence (e-mail: rsargent@uottawa.ca), current address: Department of Biology, University of Ottawa, Ottawa, Ontario K1N 6N5 Canada

<sup>3</sup> Current address: Center for Ecology and Evolutionary Biology, University of Oregon, Eugene, Oregon, USA, e-mail: skembel@uoregon.edu

<sup>4</sup> Current address: Departments of Biological Sciences and Botany and Plant Pathology, 915 West State Street, Purdue University, West Lafayette, Indiana 47907-2054 USA, e-mail: nemery@purdue.edu

<sup>5</sup> Current address: Department of Ecology and Evolution, Yale University, New Haven, Connecticut, USA, e-mail: elisabeth.forrestel@yale.edu

<sup>6</sup> E-mail: dackerly@berkeley.edu

Recent meta-analyses have demonstrated that pollen limitation is positively correlated with plant species diversity on a very large scale (Vamوسي et al., 2006), indicating that species in diverse communities face increased competition for pollinators. On the other hand, studies conducted at local scales have found that an increase in community diversity also can lead to a reduction in pollen limitation due to facilitation (e.g., Moeller and Geber, 2005; Da Silva et al., in preparation, University of Ottawa), which indicates that both types of interactions can occur, and opens up the possibility that different processes dominate at different scales.

Species diversity traditionally has been the metric of choice for exploring the influence of the surrounding community on the various aspects of ecosystem function (Hooper et al., 2005). However, recent studies illustrate that taxonomic diversity may not be the most relevant variable to describe the influence of a community's species composition on its functionality. Rather, attention has shifted toward methods that consider not just species richness and other measures of taxonomic diversity but also the evolutionary relations among species in the community, broadly known as *phylodiversity* (reviewed in Webb et al., 2002). Because closely related species generally share many functional and ecological traits (Wiens et al., 2010), measures of phylodiversity provide an integrated measure of functional diversity that is not captured by taxonomic diversity alone. Phylodiversity therefore may prove a significant explanatory factor for phenomena that result from species interactions, such as pollen limitation. Indeed, several studies have reported that measures of ecosystem function including seedling survival (Webb et al., 2006), conspecific pollen transport (Schuett and Vamوسي, 2010), and community plant biomass (Cadotte et al., 2008) are better explained by the phylogenetic relatedness of the species in the community than by species richness alone.

In this study, we set out to expand our understanding of the influence of various aspects of plant community structure on the availability of adequate pollination services. We performed our study in a California vernal pool wetland habitat. These ephemeral wetlands develop in naturally occurring depressions in a landscape underlain by an impervious layer of soil, preventing the downward percolation of water during the rainy winter months. As the rain subsides and temperatures rise in the spring, resident plant populations produce dense floral displays before setting seed for the summer. Individual pools naturally cluster into vernal pool complexes (Holland and Jain, 1981), creating an archipelago of populations over short spatial scales that facilitates experimental work. Pollinator movements also tend to occur over small spatial scales (Emery, 2009) so that locally conducted experiments represent the appropriate biological scale. Moreover, the pools vary in plant species composition and richness according to various edaphic factors, including pool depth, generating variation in species assemblages over small distances. Because of the patchy distribution of suitable habitat, the diversity and composition of coflowering plants vary widely among pools. This variation in community associations allowed us the unique opportunity to study the influence of community composition, pool species richness, and species density on pollen limitation in the obligately insect-pollinated vernal pool plant *Lasthenia fremontii* (Torr. ex. A. Gray) Greene (Asteraceae).

## MATERIALS AND METHODS

**Study species**—*Lasthenia fremontii* is a self-incompatible, annual plant that is endemic to vernal pools in California's Central Valley. Plants typically produce

a single terminal inflorescence but may produce many more. Each inflorescence contains between 20 and 100 individual disk and 6 to 13 ray flowers (Hickman, 1993). Flowering occurs over approximately 6 to 8 wk between mid March and late April, though this can vary somewhat by location and year. *Lasthenia fremontii* inflorescences are pollinated primarily by solitary specialist bees in the group Andrenidae (Thorp and Leong, 1998). *Lasthenia fremontii* is found almost exclusively in vernal pools, hence its distribution tends to be patchy across the Central Valley landscape.

**Study area**—We studied *L. fremontii* populations and coexisting flowering plant species at the University of California's Jepson Prairie Reserve, just south of Dixon, California (Solano County, +38°18'36.45" N, -121°49'19.66" W). In this area, *L. fremontii* exhibits patchy spatial subdivision, which closely matches the distribution of vernal wetness; whether this spatial segregation translates into population genetic structure in this location and species is currently unknown. The plants we studied were spatially separated into visually distinct subpopulations, or "pools." Among pools, *L. fremontii* density was variable, averaging from 7.4 plants/m<sup>2</sup> to 428.3 plants/m<sup>2</sup>.

**Plots**—In early March 2008, before *L. fremontii*'s flowering period, we identified several potential study plots (pools) on the basis of the distribution of winter ponds. At the start of flowering in late March, we selected 20 pools in which we monitored community richness and species abundance and performed a pollen supplementation experiment during the spring bloom period. At each pool, a 10 m × 10 m study plot was permanently marked with the use of rebar stakes. The plots were centered around the deepest part of the pool. For most pools, the majority of flowering plants fell within this 10 m × 10 m plot. Using randomly generated coordinates, we then identified and marked 10 "focal plants" of *L. fremontii* in each pool for the pollen supplementation experiment (described later). Community species richness was quantified by identifying species in 0.25-m<sup>2</sup> subplots centered around the 10 randomly chosen focal plants. Species lists from all subplots then were pooled and used to create a plot-level species list, from which taxonomic and phylodiversity measures were derived, as described later. One pool was subsequently dropped from the study because the number of *L. fremontii* plants was insufficient for the pollen supplementation experiment, leaving us with a final sample size of 19 plots.

The abundance (i.e., number of flowering stems) and identity of all non-graminoid flowering plant species in every pool was recorded every 3 to 4 d during the 2-mo flowering period of *L. fremontii*. Grasses were excluded because they are not insect-pollinated and were not expected to influence pollinator attraction to the pools. Although detailed pollinator visitation observations are not available for all species in the pools, many are facultatively or obligately insect pollinated (Thorp, 1990).

**Pollen supplementation experiment**—We conducted a pollen supplementation experiment during the flowering period of *L. fremontii* during the spring of 2008. In each subplot, two *L. fremontii* plants were chosen that were similar in size and were within a few centimeters of one another. Before flowering, one plant per pair was randomly assigned as the plant to receive supplemental pollen. Once flowering began, inflorescences with pollen-producing flowers from at least 10 m outside the experimental plots were used as pollen donors. Pollen was transferred to the plants by gently brushing the donor inflorescence over the recipient inflorescence on the experimental plant. If the plant produced more than one inflorescence, we repeated the supplementation on all inflorescences. Entire plants were collected once fruits were visibly mature (but before dispersal). The number of inflorescences per plant was recorded on collection. We counted seeds and unfertilized ovules for each inflorescence under a magnifying lens. Unfertilized ovules have a pale, withered appearance that is easily distinguished from the dark, full cypselae of fertilized ovules (Emery, 2009). Pollen limitation was quantified as the difference in seed set between the hand-pollinated and the open-pollinated plant in each pair in each subplot (i.e.,  $PL = Seed\ Set_{hand-pollinated} - Seed\ Set_{open-pollinated}$ ). Standardization of the difference in seed set by the average seed set of the supplemented plants in each plot (as in Moeller and Geber, 2005) was performed but did not significantly alter the results, so the results associated with unstandardized differences are reported here.

Previous work in vernal pool plant communities suggests that pollinator foraging likely occurs at the spatial scale of the pool (Emery, 2009). Thus, we used our plots as the unit of replication for estimates of phylogenetic and taxonomic diversity, and we calculated a single estimate of the average degree of pollen limitation observed in each pool. We tested for experiment-wide pollen limitation in *L. fremontii* using a paired *t* test that compared the mean seed set of supplemented plants and unsupplemented plants for each pool. Because some information about

variation in pollen limitation below the pool level could have been lost through averaging, we performed weighted regression for all the analyses by weighting the mean pollen limitation calculated at the pool level by the inverse of the variance. This allowed us to put more statistical weight on data points that represented pools with lower variance in pollen limitation—those for which the estimate was likely more accurate. In all cases, this either strengthened or had no discernible effect on the relation between pollen limitation and the trait.

**Phylogeny**—We used Phylomatic (Webb et al., 2006) to generate a phylogeny that included all plant species that coflowered with *L. fremontii* in our sample plots. Taxa were grafted onto the angiosperm supertree published in Davies et al. (2004), which includes branch lengths based on estimated divergence times among taxa (Fig. 1). Relations among *Lasthenia* species were resolved on the basis of a genus-level phylogeny that was produced by reanalyzing the sequence data generated by Chan et al. (2001) (M. Park, unpublished data, University of California, Berkeley). Relations among *Downingia* were resolved on the basis of Schultheis (2001), and branch lengths for this genus were spaced evenly between the present and the estimated age of the genus.

**Community descriptors**—Descriptors of community diversity were calculated with the software Phylocom 3.41 (Webb et al., 2008) and the *picante* library in R (Kembel et al., 2010). We quantified the following indices for the 19 pools:

1) Species richness—The total number of nongraminoid flowering plant taxa in a pool (summed over the season) that coflowered with focal *L. fremontii* individuals.

2) Faith's phylogenetic diversity (PD)—A measure of the amount of phylogenetic diversity of plants that coflowered with *L. fremontii* in each plot, calculated as the sum of the branch lengths for taxa in a community (Faith, 1994).

3) Nearest taxon index (NTI)—A standardized measure of the phylogenetic distance to the nearest taxon (closest relative) for each taxon in the sample, which quantifies the extent of terminal clustering on the phylogeny (Webb et al., 2002).

4) Mean phylogenetic distance from the focal species (MPDF)—An index that quantifies the average phylogenetic distance between each species in the coflowering community and the focal species, *L. fremontii* (larger values indicate that individual species are on average more distantly related to *L. fremontii*; smaller values indicate that individual species are on average relatively closely related to *L. fremontii*).

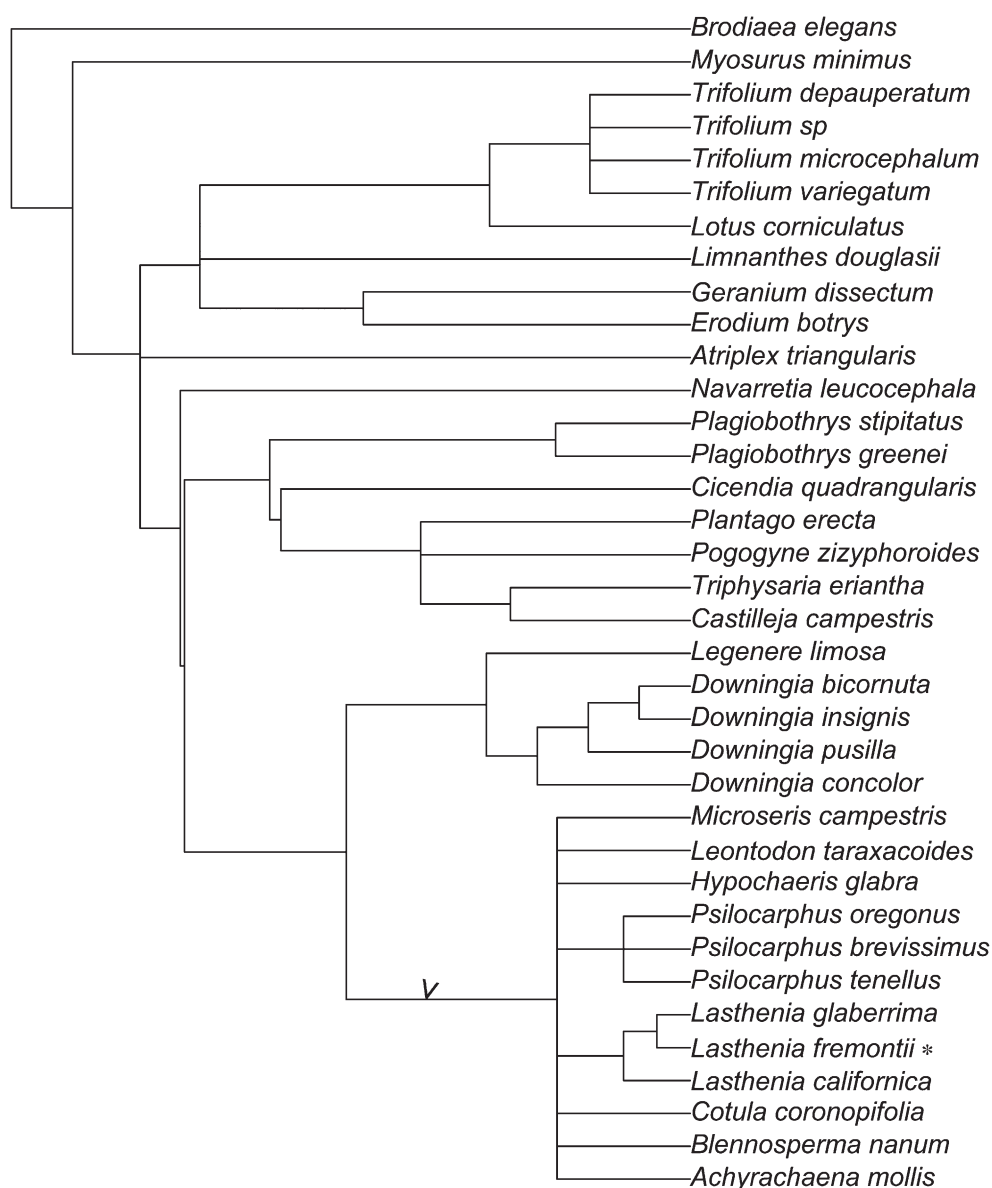


Fig. 1. Phylogenetic relations used to create the phylodiversity statistics in the study. The focal species is indicated by an asterisk, the branch leading to the Asteraceae by a pointer. Relations and branch lengths were pruned from the APG III phylogenetic tree of angiosperms (Bremer et al., 2003) with the Phylomatic software package (<http://www.phylodiversity.net/phylomatic>).



5) Focal species density—The average flowering density of the focal species (*L. fremontii*) for each pool.

**Statistical analyses**—An ANOVA was used to determine whether pollen limitation differed significantly among plots. We used multiple regression to determine the best set of predictor variables for pollen limitation. We determined the best fit model using the stepwise AIC algorithm implemented in the statistical package R (R Development Core Team, 2010). In addition, univariate regression tests were performed. Tests for spatial autocorrelation among plot descriptors (species richness, phylogeny, and pollen limitation) were performed with the spatial statistical package OpenGeoDa 0.9.8.14 (Anselin et al., 2006).

RESULTS

**Pollen limitation**—Basic pool descriptions such as species richness, phylogeny, and density are listed in Table 1. The average degree of pollen limitation of *L. fremontii* in a plot was significantly greater than zero ( $t = 2.24$ ,  $df = 18$ ,  $P = 0.038$ ; hand-pollinated seed set: mean  $\pm$  SD =  $159.1 \pm 62.4$ , open-pollinated mean  $\pm$  SD =  $150.8 \pm 59.6$ ; effect size = 0.17 SD units). An ANOVA confirmed that pollen limitation differed significantly among plots ( $F_{18, 169} = 1.74$ ,  $P = 0.0372$ ). Some correlations were present among the predictor variables (Table 2), indicating redundancy among them. In particular, species richness and phylogenetic diversity were strongly correlated. In multiple regression, this collinearity can cause problems with model fitting if both terms are included, but this problem did not arise, as the best-fit model selected by AIC had neither term.

We had no hypotheses involving interactions among our five variables, and thus our full model did not include interaction terms. The stepwise AIC procedure retained only two of our five predictor variables: the density of the focal species and the mean phylogenetic distance between species in the plot and the focal species (Table 3;  $F_{2, 26} = 6.20$ ,  $P = 0.01$ , adjusted  $R^2 = 0.366$ ). Both terms had positive effects, indicating less pollen limitation in pools with low focal species density and a greater number of close relatives of *L. fremontii* (Fig. 2).

All variables met the assumption of normality according to a Shapiro-Wilk test, except for MPD, which was only mildly nonnormal ( $W = 0.89$ ,  $P = 0.03$ ). Residual tests were performed, and factors included in the final model lack significant curvature. We also performed the tests of the factors influencing pollen limitation in the form of independent univariate regression analyses, weighted by the inverse of the variance in pollen limitation at the plot level (Table 4). We included two independent variables to further investigate the initial multiple regression results. These variables were (1) frequency of congeners: the

TABLE 1. Mean and standard deviation of the taxonomic and phylogenetic descriptors for the 19 plots.

Trait	Mean	Standard Deviation
Species richness*	10.9	3.0
Faith's PD	735.8	192.1
NTI	1.06	0.516
MPD	181.8	15.7
MPDF	115.2	15.2
Density	119.4	20.1

Note: Faith's PD = Faith's phylogeny; NTI = nearest taxon index; MPD = mean phylogenetic distance; MPDF = mean phylogenetic distance from the focal species; Density = focal species density. See text for detailed descriptions.

\*Number of distinct species in the plot.

TABLE 2. Correlation matrix indicating correlation coefficients among the various descriptors of phylogenetic and taxonomic diversity, along with focal species density. See Table 1 for definitions of descriptors.

	SR	PD	NTI	MPD	MPDF
PD	0.933**	—	—	—	—
NTI	−0.209	−0.364*	—	—	—
MPD	0.298	0.571*	0.298	—	—
MPDF	0.0609	0.16*	−0.295	0.327	—
Density	−0.136	−0.0908	−0.222	0.286	0.286

\*  $P < 0.1$ .

\*\*  $P < 0.05$ .

number of *Lasthenia* species (not including the focal species) in a plot, divided by the total number of species observed in the plot over the entire season, and (2) frequency of confamilials: the number of *Asteraceae* species (not including the focal species) in a plot, divided by the total number of species in the plot observed over the entire the season. The results of these analyses were qualitatively similar to those of the multiple regression except for the nearly significant negative correlations between NTI and pollen limitation (Table 4), and mean phylogenetic distance (MPD) and pollen limitation, which were not found to be important predictors of pollen limitation in the multiple regression analysis. We found a nearly significant negative relation between the frequency of confamilials (i.e., other *Asteraceae*) and pollen limitation in a plot, indicating that *L. fremontii* exhibits less pollen limitation in plots that are populated by other *Asteraceae* species.

**Spatial autocorrelation**—An unknown feature of our data set is the degree to which the pools we identified actually represent independent units of study. We used Moran's I to determine whether *L. fremontii* density, pool species richness, MPDF, or pollen limitation were statistically autocorrelated. We based our neighborhood distance (estimated distance at which data exhibit spatial differentiation) of 50 m on explorations of spatial patterns in the data using a variogram analysis in the *spatial* package in R (R Development Core Team, 2010). Except for species richness, all the factors we explored exhibited negative spatial autocorrelation, as opposed to positive autocorrelation, evidenced by the negative value of Moran's I (Table 5; Lichstein et al., 2002). **Species richness exhibited weakly positive spatial autocorrelation**; however, a randomization test indicated that none of the results were significantly different from random. These results indicate that pools can be treated as independent spatial units for the factors examined in our analyses.

DISCUSSION

We found a significant effect of the mean evolutionary distance among species in a community and a focal species on the degree of pollen limitation in the focal species. Specifically, *L. fremontii*

TABLE 3. Best predictors of pollen limitation in a plot based on stepwise regression. See Table 1 for definitions of descriptors. *P* values less than 0.05 are highlighted in bold.

Coefficients	<i>b</i>	SE	<i>t</i>	<i>P</i>
Intercept	−70.2	29.3	−2.39	<b>0.0294</b>
MPDF	0.597	0.263	2.27	<b>0.0373</b>
Density of <i>L. fremontii</i>	0.272	0.140	1.93	0.0717

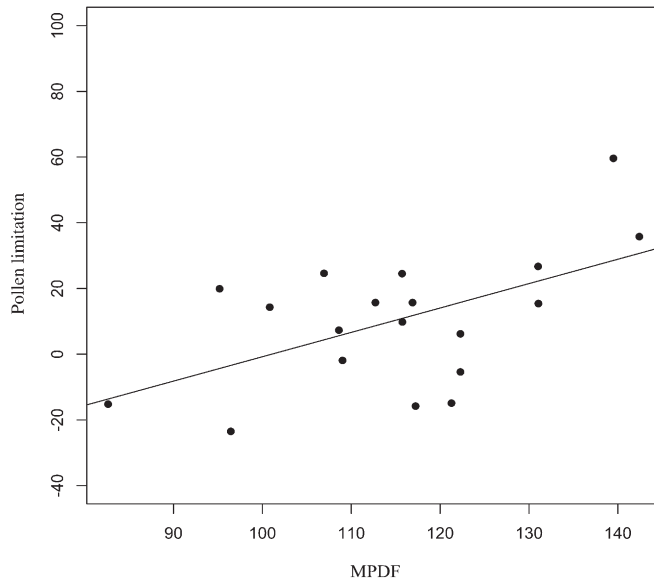


Fig. 2. Relation between mean pollen limitation and mean phylogenetic distance from the focal species (*Lasthenia fremontii*) for 19 vernal pool plots.

showed less pollen limitation in communities that contained, on average, species more closely related to *L. fremontii* than in communities that contained species that tended to be more distantly related to *L. fremontii*. To our knowledge, this is the first study to report an effect of a community's evolutionary distance from a focal species on a key aspect of ecosystem function—pollinator service. Our results echo the findings of other recent studies (Cadotte, Cardinale, and Oakley, 2008; Schuett and Vamasi, 2010) in that our response variable, pollen limitation, is more sensitive to factors that consider evolutionary relations among species than to species richness alone.

Our findings suggest the presence of facilitative pollinator-mediated interactions among close relatives. Many of the plant species in our communities are in the same family as our focal species (Asteraceae) and include several species in the genus *Lasthenia* itself; since *Lasthenia* species have been shown to share pollinators (Thorp and Leong, 1998), we hypothesize that an abundance of close relatives in a pool has a positive impact on pollinator attraction in this system. This seems to be supported by the nearly significant negative relation between pollen limitation and the frequency of other Asteraceae species in

TABLE 4. Results of univariate regression models among pollen limitation and eight potential predictor variables ( $df = 1, 17$  for all tests). The tests are weighted by the inverse variance of pollen limitation in a plot. See Table 1 for definitions of descriptors. *P* values less than 0.05 are highlighted in bold.

Factor	<i>t</i>	<i>P</i>
SR	0.49	0.633
PD	0.93	0.368
NTI	-1.89	0.076
MPD	1.95	0.0677
MPDF	3.73	<b>0.0017</b>
Density	2.92	<b>0.0136</b>
Frequency of congeners	-0.257	0.619
Frequency of confamilials	-4.29	0.0538

TABLE 5. Moran's *I* for pollen limitation and relevant predictor variables. See Table 1 for definitions of descriptors.

Factor	Moran's <i>I</i>	<i>P</i> (999 Randomizations)
Species richness	0.0664	0.14
Pollen limitation	-0.0591	0.55
MPDF	-0.212	0.073
Density	-0.1347	0.287

a plot (Table 4). In addition, vernal pool species outside of the Asteraceae (e.g., in Campanulaceae) tend to have specialized relations with their pollinators (Thorp, 1990). Thus, pollinators that are attracted to pools composed of distant relatives of *L. fremontii* may attract a larger number of unsuitable pollinators.

The dominance of pollen competition in studies of plant communities may be a reflection of the type of communities typically examined. Many studies focus on the influence of an invasive species on native plants in the community (e.g., Brown and Mitchell, 2001; Ghazoul, 2004; Morales and Traveset, 2009). Competition may be more likely in these communities because the interactions are relatively novel. In established communities, however, species are more likely to have co-evolved over multiple generations. Species that faced intense competition would likely evolve strategies to mitigate the effects (e.g., phenological or pollinator shifts), or they would not be competitive enough to coexist long term or establish in the first place (Strauss et al., 2006). Moreover, from a community assembly perspective, established communities where facilitation, not competition, is the dominant interaction may be more commonly observed because facilitation likely enhances species (and therefore community) persistence.

California vernal pools, because of their unique habitat characteristics, act as a strong filter, excluding species that are not adapted to the wet winter and dry summer conditions (Gerhardt and Collinge, 2007). For example, invasive grasses that often dominate the surrounding upland matrix are virtually nonexistent within the pools themselves (Holland and Jain, 1981). This suggests that the species interactions in this system are likely to have been relatively stable over evolutionary time, increasing the likelihood that individual species will evolve adaptations to mitigate the effects of pollinator competition. This could explain why pollen limitation was generally weak in our study, in spite of the fact that as a self-incompatible annual, *L. fremontii* is predicted to be highly susceptible to pollen limitation (Knight et al., 2005).

The association between *L. fremontii* density within a plot and pollen limitation suggests that intraspecific competition is also a factor influencing pollen limitation in these communities. Our findings are congruent with other studies reporting increased pollen limitation with increased population density (e.g., Spigler and Chang, 2009). However, the relationship differs from that reported for experiments with *Trillium grandiflorum* and *Lythrum salicaria*, in which pollen limitation was greatest in small populations (Agren, 1996; Knight, 2003). It's possible we had a wider range of densities and therefore were able to capture the influence of high density that other studies in naturally occurring populations might not have observed: peak *L. fremontii* density in our subplots ranged from 20 plants to over 300.

The lack of association between plot species richness and pollen limitation in our study is somewhat surprising, given this was a key finding reported by a meta-analysis (Vamasi et al., 2006). However, several important differences exist between our study and that of Vamasi et al. (2006). First, the size of

plots used in that study was several orders of magnitude larger than ours (100 000 m<sup>2</sup> compared with our 10 m<sup>2</sup>). Our study was designed to understand patterns on the scale of pollinator movements among a focal species and its immediate community, whereas that of Vamosi et al. (2006) is more relevant to large-scale processes. Spatial scale is an important consideration in studying plant–pollinator interactions that may influence the ability to detect the effects (e.g., (Cariveau and Norton, 2009)). On the other hand, our study included many fewer data points than the meta-analysis, which could indicate that we had a lack of power to detect the influence of species richness on pollen limitation. If this is the case, the influence of evolutionary relations on plant–pollinator interactions in vernal pools may be even greater than our results indicate.

Phylogenetic data have already proved to be a very powerful tool in untangling the relations between ecological and evolutionary patterns and processes. Our study expands on existing work by exploring the role of evolutionary relations with respect to a focal species and their potential effect on pollen limitation. Our findings highlight the importance of including evolutionary relations among species in studies of community dynamics and ecosystem function.

#### LITERATURE CITED

- AGREN, J. 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology* 77: 1779–1790.
- ANSELIN, L. I. SYABRI AND Y. KHO. 2006. GeoDa: An Introduction to Spatial Data Analysis. *Geographical Analysis* 38: 5–22.
- ASHMAN, T. L., T. M. KNIGHT, J. A. STEETS, P. AMARASEKARE, M. BURD, D. R. CAMPBELL, M. R. DUDASH, ET AL. 2004. Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. *Ecology* 85: 2408–2421.
- BASCOMPTE, J. 2009. Disentangling the web of life. *Science* 325: 416–419.
- BIESMEIJER, J. C., S. P. M. ROBERTS, M. REEMER, R. OHLEMULLER, M. EDWARDS, T. PEETERS, A. P. SCHAFFERS, ET AL. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313: 351–353.
- BREMER, B., K. BREMER, M. W. CHASE, J. L. REVEAL, D. E. SOLTIS, P. S. SOLTIS, P. F. STEVENS, ET AL. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* 141: 399–436.
- BROWN, B. J., AND R. J. MITCHELL. 2001. Competition for pollination: Effects of pollen of an invasive plant on seed set of a native congener. *Oecologia* 129: 43–49.
- CADOTTE, M., B. J. CARDINALE, AND T. H. OAKLEY. 2008. Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences, USA* 105: 17012–17017.
- CARIVEAU, D. P., AND A. P. NORTON. 2009. Spatially contingent interactions between an exotic and native plant mediated through flower visitors. *Oikos* 118: 107–114.
- CHAN, R. B. G. BALDWIN, AND R. ORNDUFF. 2001. Goldfields revisited: A molecular phylogenetic perspective on the evolution of *Lasthenia* (Compositae: Heliantheae sensu lato). *International Journal of Plant Sciences* 162: 1347–1360.
- CORBET, S. A., I. H. WILLIAMS, AND J. L. OSBORNE. 1991. Bees and the pollination of crops and flowers in the European Community. *Bee World* 72: 47–59.
- DAVIES, T. J., T. G. BARRACLOUGH, M. W. CHASE, P. S. SOLTIS, D. E. SOLTIS, AND V. SAVOLAINEN. 2004. Darwin's abominable mystery: Insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences, USA* 101: 1904–1909.
- EMERY, N. C. 2009. Ecological limits and fitness consequences of cross-gradient pollen movement in *Lasthenia fremontii*. *American Naturalist* 174: 221–235.
- FAITH, D. P. 1994. Phylogenetic diversity: A general framework for the prediction of feature diversity. In P. L. Forey, C. J. Humphries, and R. I. Vane-Wright [eds.], *Systematics and conservation education*. Clarendon Press, Oxford, UK.
- GEBER, M. A., AND D. A. MOELLER. 2006. Pollinator responses to plant communities and implications for reproductive character evolution. In L. D. Harder and S. C. H. Barrett [eds.], *Ecology and evolution of flowers*. Oxford University Press, Oxford, UK.
- GERHARDT, F., AND S. K. COLLINGE. 2007. Abiotic constraints eclipse biotic resistance in determining invasibility along experimental vernal pool gradients. *Ecological Applications* 17: 922–933.
- GHAZOUL, J. 2004. Alien abduction: Disruption of native plant–pollinator interactions by invasive species. *Biotropica* 36: 156–164.
- GOULSON, D., M. E. HANLEY, B. DARVILL, AND J. S. ELLIS. 2005. Causes of rarity in bumblebees. *Biological Conservation* 122: 1–8.
- HEGLAND, S. J., AND O. TOTLAND. 2008. Is the magnitude of pollen limitation in a plant community affected by pollinator visitation and plant species specialisation levels? *Oikos* 117: 883–891.
- HICKMAN, J. C. 1993. The Jepson manual: Higher plants of California. University of California Press, Berkeley, California, USA.
- HOLLAND, R. F., AND S. K. JAIN. 1981. Insular biogeography of vernal pools in the Central Valley of California. *American Naturalist* 117: 24–37.
- HOOPER, D. U., F. S. CHAPIN, J. J. EWEL, A. HECTOR, P. INCHAUSTI, S. LAVOREL, J. H. LAWTON, ET AL. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75: 3–35.
- KEMBEL, S. W., P. D. COWAN, M. R. HELMUS, W. K. CORNWELL, H. MORLON, D. D. ACKERLY, S. P. BLOMBERG, AND C. O. WEBB. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics (Oxford, England)* 26: 1463–1464.
- KNIGHT, T. M. 2003. Floral density, pollen limitation, and reproductive success in *Trillium grandiflorum*. *Oecologia* 137: 557–563.
- KNIGHT, T. M., J. A. STEETS, J. C. VAMOSI, S. J. MAZER, M. BURD, D. R. CAMPBELL, M. R. DUDASH, ET AL. 2005. Pollen limitation of plant reproduction: Pattern and process. *Annual Review of Ecology and Systematics* 36: 467–497.
- LICHSTEIN, J. W., T. R. SIMONS, S. A. SHRINER, AND K. E. FRANZREB. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* 72: 445–463.
- MOELLER, D. A. 2004. Facilitative interactions among plants via shared pollinators. *Ecology* 85: 3289–3301.
- MOELLER, D. A., AND M. A. GEGER. 2005. Ecological context of the evolution of self-pollination in *Clarkia xantiana*: Population size, plant communities, and reproductive assurance. *Evolution; International Journal of Organic Evolution* 59: 786–799.
- MORALES, C. L., AND A. TRAVESET. 2009. A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters* 12: 716–728.
- MOTTEN, A. F. 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecological Monographs* 56: 21–42.
- R DEVELOPMENT CORE TEAM. 2010. R: A Language and Environment for Statistical Computing 2.12. <http://www.R-project.org>.
- SARGENT, R. D., AND D. D. ACKERLY. 2008. Plant–pollinator interactions and the assembly of plant communities. *Trends in Ecology & Evolution* 23: 123–130.
- SCHEMSKE, D. W., M. F. WILLSON, M. N. MELAMPY, L. J. MILLER, L. VERNER, K. M. SCHEMSKE, AND L. B. BEST. 1978. Flowering ecology of some spring woodland herbs. *Ecology* 59: 351–366.
- SCHUETT, E. M., AND J. C. VAMOSI. 2010. Phylogenetic community context influences pollen delivery to *Allium cernuum*. *Evolutionary Biology* 37: 19–28.
- SCHULTHEIS, L. M. 2001. Systematics of *Downingia* (Campanulaceae) based on molecular sequence data: Implications for floral and chromosome evolution. *Systematic Botany* 26: 603–621.

- SPIGLER, R. B., AND S. M. CHANG. 2009. Pollen limitation and reproduction varies with population size in experimental populations of *Sabatia angularis* (Gentianaceae). *Botany-Botanique* 87: 330–338.
- STRAUSS, S. Y., C. O. WEBB, AND N. SALAMIN. 2006. Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences, USA* 103: 5841–5845.
- THORP, R. W. 1990. Vernal pool flowers and host-specific bees. In D. H. Ikeda and R. A. Schlising [eds.], *Studies from the herbarium, California State University, Chico*, number 8. The University Foundation, Chico, California, USA.
- THORP, R. W., AND J. M. LEONG. 1998. Specialist bee pollinators of showy vernal pool flowers. In C. W. Whitham, E. T. Bauder, D. Belk, W. R. Ferren Jr., and R. Ornduff [eds.], *Ecology, conservation, and management of vernal pool ecosystems*, 169–179. California Native Plant Society, Sacramento, California, USA.
- VAMOSI, J. C., T. M. KNIGHT, J. A. STEETS, S. J. MAZER, M. BURD, AND T.-L. ASHMAN. 2006. Pollination decays in biodiversity hotspots. *Proceedings of the National Academy of Sciences, USA* 103: 956–961.
- WEBB, C. O., D. D. ACKERLY, AND S. W. KEMBEL. 2008. Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics (Oxford, England)* 24: 2098–2100.
- WEBB, C. O., D. D. ACKERLY, M. A. McPECK, AND M. J. DONOGHUE. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475–505.
- WEBB, C. O., G. S. GILBERT, AND M. J. DONOGHUE. 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology* 87: 123–131.
- WIENS, J. J., D. D. ACKERLY, A. P. ALLEN, B. L. ANACKER, L. B. BUCKLEY, H. V. CORNELL, E. I. DAMSCHEN, ET AL. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13: 1310–1324.
- WINFREE, R., N. M. WILLIAMS, H. GAINES, J. S. ASCHER, AND C. KREMEN. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology* 45: 793–802.