

Factors influencing floral traits in Rocky Mountain meadows: competition, environmental filtering, and phylogeny

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ABSTRACT

There is an incredible diversity of floral morphologies and colors within plant communities of the southwestern, Rocky Mountains. However, little research has been done to quantify exactly how diverse these communities are, and to assess which ecological and phylogenetic processes are structuring this diversity. In an observational study, I measured floral traits within five distinct plant communities near the Rocky Mountain Biological Laboratory, Gothic CO. Traits relevant to pollinator interaction with flowers (i.e. display size, corolla depth, etc.) were measured for all biotically-pollinated flowering plants. For all species observed at each site on five sampling days, seven structural traits (height of inflorescence above the ground, flower length, width and height, and floral display length, width and height) and sixty color traits (three color spectra from 300-700nm binned at 20nm intervals) were measured. By considering species traits in a multidimensional trait space, I compared the degree of clustering or overdispersion of species within communities to null communities constructed from the total species pool. At each of the five sites, species traits were significantly phenotypically overdispersed ($p < 0.05$) with respect to the null expectations. This suggests that competition for pollinators or ecological sorting mechanisms may be driving the diversity of floral morphologies within Rocky Mountain meadow communities. Future work will identify the specific traits driving the overdispersion pattern, and will explore the role of phylogeny in structuring these communities.

Keywords: Floral traits, plant community, competition, environmental filtering, community phylogenetics

INTRODUCTION

Though there is a long precedent suggesting the non-independent assembly of species traits within communities, biologists have yet to resolve the processes underlying this non-independence. Recent studies classify these processes into three groups: (1) competition/facilitation, (2) environmental filtering, and (3) phylogenetic influences (Sargent & Ackerly 2008). Under competitive interactions we expect species traits in a community to diverge. Studying the morphology and feeding behavior of stickleback fish, Schluter (1994) was one of the first to empirically show that interspecific competition can drive divergence, a phenomenon known as character displacement. Under some types facilitative interactions, however, we expect the opposite, that species traits will converge (Freestone, 2006). Environmental filtering, or ecological sorting, is the process by which the environment (abiotic and/or biotic) excludes species lacking specific adaptations to that environment while allowing those species with said adaptations to persist (Sargent & Ackerly 2008). Therefore, under an environmental filter we expect species traits to converge upon those best suited for that habitat (Williamson & Harrison 2002). Finally, the role of phylogeny in community assembly has the capacity to increase the co-occurrence of closely related species (phylogenetic clustering) or decrease the co-occurrence of closely related species (phylogenetic overdispersion). For example, in Floridian oak communities it was found that species are phylogenetically overdispersed (Cavender-Bares et al. 2004).

Communities of co-flowering species are excellent systems in which to observe the aforementioned processes, but no studies have tried to address all of them in a single system (Sargent & Ackerly 2008). Existing evidence and theoretical considerations, however, do

support the importance of some of the processes. For example, sympatric plant species are subject to conspecific pollen loss (CPL) and heterospecific pollen deposition (HPD) due to pollinator infidelity, and each has been shown to negatively affect plant fitness (Morales & Traveset 2008). To improve pollinator constancy, competing species tend to diverge morphologically, thereby reducing the amount of interspecific pollen transfer (Whitney 2009, and references cited therein). Gumbert et al. (1999) demonstrated that flower colors in five German plant communities cannot be explained by random assembly. While the distribution of color distances for commonly occurring plants was no different from random, colors of rare species were overdispersed in two communities and clustered in one other community with respect to randomly assembled communities. Armbruster et al. (1994) demonstrated that the divergence of traits, such as style length and position, among closely related, sympatric plant species, i.e. character displacement, is a function of competition for pollinators. Pollination syndromes may *also* act as environmental filters. With increasing elevation there is a decrease in rate of hymenopteran pollination and increase in dipteran and lepidopteran pollination (Arroyo et al. 1982). This suggests that a species may need specific traits to exist at a given elevation, e.g. color cues specialized to a particular pollinator's spectral sensitivities (Arnold et al. 2009). The effects of phylogeny on floral communities have only been tested once, but no effect was found (Arnold et al. 2009).

In this study, I examine evidence for the role of competition/facilitation, environmental filtering, and phylogeny in structuring floral traits in Rocky Mountain meadow communities. Specifically, I ask: (i) Is there evidence of clustering or overdispersion of floral morphologies within communities? and if so, what traits are driving the clustering or overdispersion of floral morphologies? The first of these two questions is approached by determining nearest neighbor distances in a multidimensional trait space (Whitney 2009). The second will be addressed by correlating the value of pairwise species trait distances to pairwise species co-occurrence (Cavender-Bares et al. 2004). (ii) Does phylogeny influence species and traits in the community? This will be tested by examining the correlation of phylogenetic distance between pairs of taxa on their degree of co-occurrence within plots, as well as the examining the correlation of phylogenetic distance between taxa on the distance between traits in trait space (Cavender-Bares et al. 2004). And (iii) Does elevation act as a habitat filter in Rocky Mountain meadow plant communities? Using online elevation range data from Rocky Mountain Herbarium, the Rocky Mountain Biological Laboratory herbarium, and other herbaria, I will correlate the species trait values with elevation using phylogenetically independent contrasts (Cavender-Bares et al. 2004).

METHODS

Study Sites

I compared the floral color and morphology of animal-pollinated species within five communities in the Rocky Mountains of western Colorado (Table 1). I visited each site once every two weeks from June 10th to August 23rd and recorded all species in flower. On the initial visit, I measured the floral morphology for two individuals of all flowering species. Measured individuals were then uprooted, bagged and brought back to the lab in Gothic, CO for color analysis and identification. Identification was based on (Weber & Whitman 2001, Darrow 2006,

Kershaw et al. 1998) and comparison to specimens in the RMBL herbarium. On subsequent visits, I collected newly flowering species.

Due to phenological differences among species within a plot, early-flowering species and late-flowering species are expected to interact weakly. I kept track of flowering phenology by recording the species flowering in each plot in each of five temporal periods (one visit per plot per period): June 10th- June 24th, June 26th-July 9th, July 10th-July 24th, July 25th-August 8th, and August 9th-August 23rd.

Measurement of Floral Traits –

For each species, I measured traits relevant to pollinator signaling and reward (Table 2). Overall display size was measured for species in which multiple flowers of the inflorescence are in close proximity, i.e. touching or almost touching. When flowers did not touch, the Overall Flower measurements represented the display (i.e. the same set of measurements was used to describe both the flower and the display). I omitted measuring particular traits when appropriate, e.g. when a species lacked distinct corolla tubes. For composites, petal length was measured for ray flowers, when applicable. For color measurement, the entirety of the floral display was scanned using an Avantes AvaSpec-2048 (Serialnr: 0603016U1) spectrometer with an AvaLight-XE (s/n-LS-0701023) light source at a distance of 8mm. Each species was characterized by three colors (sets of spectra), corresponding to structures exhibiting distinctly different reflectance spectra, e.g. the basal-distal color range on the petals of certain Ranunculaceae. In general, color 1 represented the center of the flower, color 2 represented an intermediate area, and color 3 represented the distal part of the flower (e.g. tips of the petals). For each color, reflectance spectra were binned at 20nm intervals from 300-700nm (the range encompassing the vision of insect and vertebrate pollinators).

Data analysis –

*Is there evidence of clustering or overdispersion of floral morphologies within communities?
What traits are driving the clustering or overdispersion of floral morphologies?*

There were 67 traits used in the analysis reported here (60 color traits, comprising of 20 bins for each of three colors; display length, width and height; flower length width and height; and the height of the inflorescence above the ground). Each trait measured represents an axis in a multidimensional trait space. Using SAS macro language we calculated the average pairwise Euclidian distances between species at each site (Gumbert et al. 1999, Chittka 1997), examining only the pairs of species that overlapped in flowering phenology (flowered together in one or more sampling periods). For each species, the nearest-neighbor (NN) distance was retained. These NN distances were then averaged for each site. Then, to compare this observed mean NN distance to NN distances in random species assemblages, we created 500 artificial plant communities with the same number of plant species as each of the five real ones, again using SAS macro language. This was done by randomly selecting species from the roster of species sampled across all sites in the first three sampling periods (Gumbert et al. 1999). Significance was assessed by examining whether the actual NN value fell within or outside the central 95% of the distribution of NN distances from randomly assembled communities (alpha level 0.05). For each natural community, mean NN distances that are significantly larger than those in the

randomly assembled communities indicate phenotypic overdispersion of morphologies, while significantly smaller mean NN distances indicate phenotypic clustering.

Future analyses:

To determine which specific traits are driving the clustering or overdispersion of floral morphologies, I will correlate pairwise species trait differences with pairwise species co-occurrence (Cavender-Bares et al. 2004). Co-occurrence of two species, i and h , is assessed via an index:

$$CI_{ih} = 1 - 0.5(\sum |p_{ij} - p_{hj}|)$$

where p_{ij} = proportion of occurrences of i^{th} species in j^{th} plot

The correlation coefficient is then compared to a distribution of coefficients from a null model in which co-occurrence indices are shuffled across communities. A strong negative correlation between pairwise trait differences and co-occurrence indicates phenotypic clustering. While, a strong positive correlation between pairwise trait differences and co-occurrence would indicate phenotypic overdispersion. Thus, those traits with the largest correlation coefficients will be those most important in driving the overall phenotype pattern.

Does phylogeny influence species and traits in the community?

Future analyses:

For all species across the five plots, I will construct a family-level phylogeny using Phylomatic (Webb & Donoghue 2005), which implements the angiosperm supertree of Davies et al. 2004. Resolution at the genus and species levels will be added where possible with phylogenies from the literature. Two tests will then be run:

A) Test for phylogenetic overdispersion (Cavender-Bares et al. 2004). This test examines the correlation between phylogenetic distance between pairs of taxa (i.e., the sum of the branch lengths connecting them) and the degree of co-occurrence (see above) within plots. The correlation coefficient is then compared to a distribution of coefficients from a null model in which phylogenetic distances are shuffled across taxa. A significant positive correlation indicates that taxa are phylogenetically overdispersed (i.e., close relatives do not usually co-occur in a plot), while a significant negative correlation indicates that taxa are phylogenetically clustered.

B) Test for convergence/conservatism of traits (Cavender-Bares et al. 2004). This test examines the correlation between trait differences and phylogenetic distance, again using pairs of species as replicates. Again, the correlation coefficient is then compared to a distribution of coefficients from a null model in which phylogenetic distances are shuffled across taxa. A significant positive correlation indicates trait conservatism (closely related species have similar traits); while a significant negative correlation indicates trait convergence.

Does elevation act as a habitat filter Rocky Mountain meadow plant communities?

Future analyses:

Test for environmental filtering (Cavender-Bares et al. 2004). I will use the online records from the Rocky Mountain Herbarium, the Rocky Mountain Biological Laboratory herbarium and other herbaria to find elevation range data for all species present in my communities. For each specimen listed I will record the elevation (when present). Then using phylogenetically

independent contrasts, I will test for a correlation between species traits (e.g. petal reflectance in the ultraviolet) and their mean recorded elevation.

RESULTS

The first three sampling periods yielded 104 species across all plots. Errors encountered while exporting color spectra lead to 6 species being temporarily excluded from the analysis. Therefore 98 species were used in null model construction and subsequent analyses (Table 3).

Is there evidence of clustering or overdispersion of floral morphologies within communities?

The distributions of randomly assembled null communities were unimodal and symmetric for all sample sizes (Figure 1). For Site 1, the null distribution was centered at a mean of 5.26 with a standard deviation of 0.38. The natural community had a significantly greater average nearest neighbor (NN) distance of 8.96 ($p < 0.05$). For Site 2, the null distribution was centered at a mean of 5.06 with a standard deviation of 0.35, and the natural community had a significantly greater average NN distance of 10.9 ($p < 0.05$). For Site 3, the null distribution was centered at a mean of 5.12 with a standard deviation of 0.34, and the natural community had a significantly greater average NN distance of 10.5 ($p < 0.05$). For Site 4, the null distribution was centered at a mean of 5.48 with a standard deviation of 0.47, and the natural community had a significantly greater average NN distance of 9.77 ($p < 0.05$). Finally for Site 5, the null distribution was centered at a mean of 5.26 with a standard deviation of 0.31. The natural community again had a significantly greater average NN distance of 11.6 ($p < 0.05$).

DISCUSSION

The significantly greater average NN distances observed across each of the natural communities show strong evidence for phenotypic overdispersion of floral traits in Rocky Mountain meadows. This suggests that competition for pollinators and/or ecological sorting may be affecting the diversity of floral traits. Furthermore, with strong evidence for the overdispersion of floral traits, we may also suggest that the abiotic environment is not filtering out species based on their floral traits. As mentioned earlier, in the presence of strong abiotic stressors we would expect the species pool to be constrained to species with higher stress tolerances. More tolerant species would most likely have more similar traits, thereby decreasing the average NN distances observed in community trait space, i.e. phenotypic clustering.

However, even though we observe a strong pattern of overdispersion, it will remain unclear what traits are driving the overdispersion of morphologies in these communities until subsequent analyses are conducted. Once specific driving traits are identified we can generate hypotheses about what specific mechanisms within plant-pollinator interactions may be most important in determining the structure of floral communities. Future analyses will additionally investigate the phylogenetic structure of these five communities.

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FIGURES & TABLES

Table 1. Study Site Information

Size	Elevation	Location	Habitat Type
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Site1	900m ²	~2800m	Almont Triangle	Open Sagebrush
Site2	900m ²	~3000m	Kebler Pass Road	Montane meadow
Site3	900m ²	~2900m	Rosy Point	Montane meadow
Site4	900m ²	~3000m	Judd Falls Research Meadow	Montane meadow
Site5	900m ²	~3400m	Virginia Basin	Sub-alpine meadow

Table 2. Morphological traits measured

Floral Trait	Dimensions	Accuracy
Distance of display above soil	Height	0.5 cm
Petal	Length, Width	0.1 mm
Tube	Length	0.1 mm
Bract (if part of display)	Length, Width	0.1 mm
Sepal (if part of display)	Length, Width	0.1 mm
Overall Flower	Length, Width, Height	0.1 mm
Overall Display	Length, Width, Height	0.1 mm

Table 3. The number of species incorporated into the null model species pool for each site as of 7/22/09

	Location	Number of Species
Site1	Northern Almont Triangle	31
Site2	Kebler Pass Road	38
Site3	Rosy Point	36
Site4	Judd Falls Research Meadow	25
Site5	Virginia Basin	41
Total	Across Sites	98

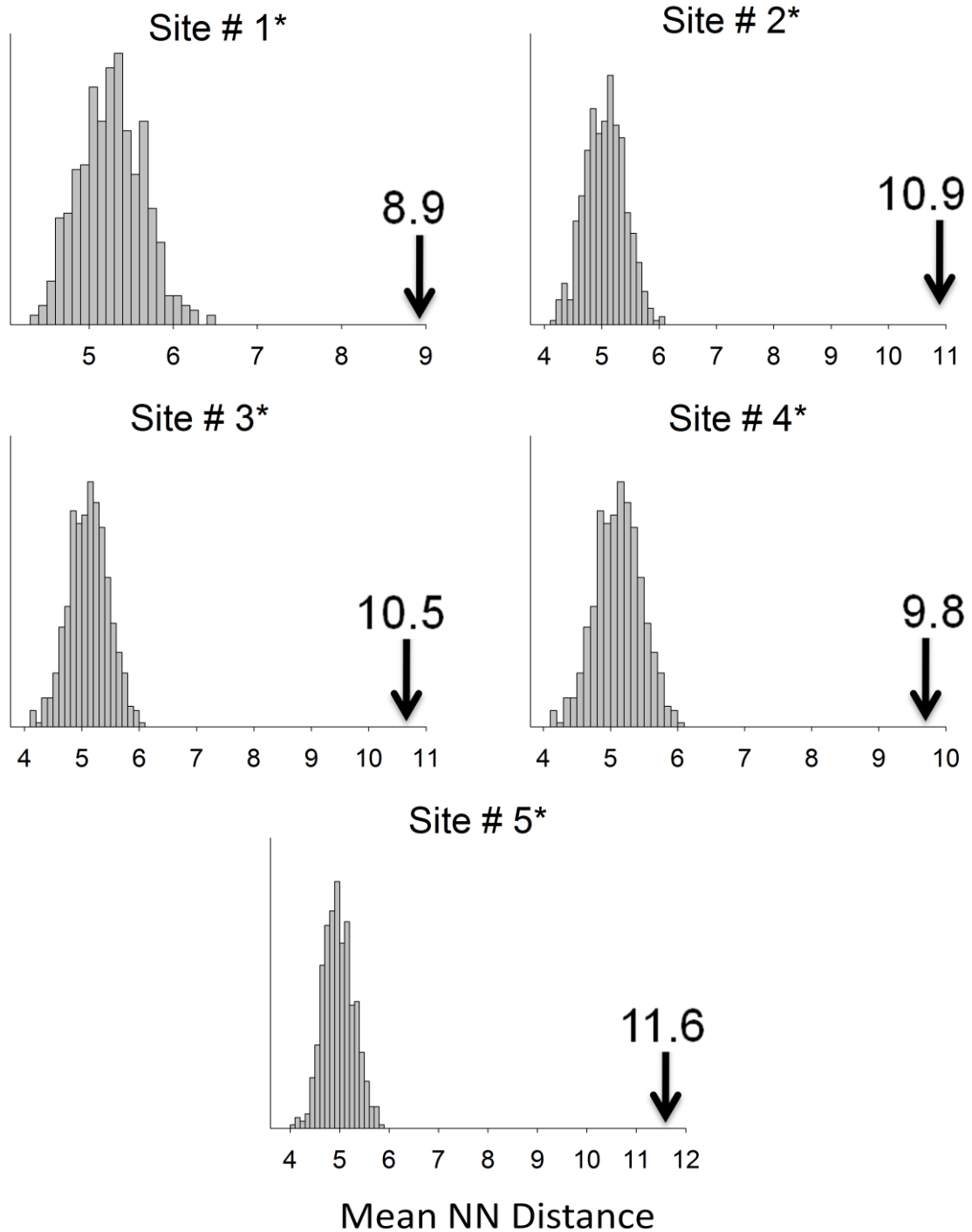


Figure 1. Overdispersion of floral traits in five communities. Mean NN distances for actual natural communities are indicated by the large numerical value and the arrow. In each case they fall outside the distribution of mean NN distances from randomly assembled communities, shown by histogram

* $p < 0.05$