Notes

Genetic variation within a dominant shrub species determines plant species colonization in a coastal dune ecosystem

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Abstract. The diversity and structure of plant communities is often determined by the presence and identity of competitively dominant species. Recent studies suggest that intraspecific variation within dominants may also have important community-level consequences. In a coastal dunes ecosystem of northern California, we use a decade-old common garden experiment to test the effects of a genetically based architectural dimorphism within a dominant native shrub, *Baccharis pilularis*, on plant colonization success and understory plant diversity. We found that erect *Baccharis* morphs had higher richness and cover of colonizing plant species (both native and exotic species) compared to prostrate morphs, as well as higher biomass of a dominant exotic dune grass (*Ammophila arenaria*). Trait differences between architectural morphs influenced the abiotic understory environment (light availability, soil surface temperature, and litter depth) and were associated with species colonization success. Taken together, our results demonstrate that incorporating within-species variation, particularly within dominant species, into community ecological research can increase the ability to predict patterns of species diversity and assembly within communities.

Key words: Ammophila arenaria; Baccharis pilularis; *community genetics; dioecy; dunes ecosystem; invasion resistance; plant architecture.*

INTRODUCTION

In plant communities, the presence and identity of competitively dominant native species can influence community-level resistance to the establishment of new species (Smith et al. 2004, Emery and Gross 2007). Furthermore, a growing number of studies have found that the presence of particular genotypes within dominant plant species may also be an important structuring agent of communities (Whitham et al. 2006). For example, intraspecific genetic variation within plants can affect the distribution of associated invertebrates (Crutsinger et al. 2006, Johnson et al. 2006), other plant species (Booth and Grime 2003, Lankau and Strauss 2007), and microbes (Schweitzer et al. 2007). Several studies have addressed the role of genetic variation within the colonizing species themselves in determining whether these species are successful

in establishing in new environments (Ellstrand and Schierenbeck 2000, Dlugosch and Parker 2008). For example, the introduction of a nonnative genotype of a common reed (*Phragmites australis*) has displaced native genotypes and led to rapid range expansion of the species (Saltonstall 2002). However, only a few studies to date have asked whether genetic variation within native dominant species alters community-level resistance to species establishment (Rudgers and Maron 2003, Crutsinger et al. 2008, Johnson et al. 2008).

In a recent review, Hughes et al. (2008) discuss the ecological consequences of intraspecific genetic variation and diversity and call for a greater research focus on identifying the underlying mechanisms driving genetic effects. Several plant traits may underlie the effects of genetic variation on species assembly in communities. For example, variation in plant architecture has been shown to be a key factor determining to the abundance of consumer species (Marquis et al. 2002, Wise and Abrahamson 2008). Architectural differences within dominant overstory plants can also determine understo-

ry light and soil moisture availability (Classen et al. 2007), which, in turn, may affect habitat suitability for colonizing plant species. In this study, we focus on the effects of a genetically based architectural dimorphism within a dominant coastal dune shrub on the richness, cover, and biomass of plant species (both native and exotic) colonizing a common garden experiment.

Study System

The dominant dioecious shrub, *Baccharis pilularis* De Candolle (Asteraceae, coyote brush), grows perennially as two distinct architectural forms that co-occur in coastal California: an erect morph (~1–4 m tall, formerly classified as subspecies *B. p. consanguinea*) and a prostrate morph (~0.1–0.2 m tall, formerly *B. p. pilularis* [Munz and Keck 1973]). The two architectural morphs differ in many traits that could influence the colonization of other plant species. For example, erect plants are ~50% taller, possess ~60% larger leaves, have ~70% fewer branches, and have ~50% longer branches than prostrate plants (Rudgers and Whitney 2006). There is substantial evidence that this architectural variation in *B. pilularis* has a genetic basis. First, hybridization of the prostrate morph of *B. pilularis* with the strictly erect species, *B. sarothroides*, produced both upright and prostrate F1 progeny (Thompson et al. 1995). Second, the prostrate morph of *B. pilularis* (hereafter *Baccharis*) is widely used in landscaping and retains its short stature across diverse environments (Ehler 1982). Finally, clones of the two forms planted in a common garden retained architectural differences for over a decade, and the progeny of single-architectural parents segregated into both erect and prostrate offspring (J. A. Rudgers, *unpublished data*).

Experimental work was conducted at the University of California-Davis Bodega Marine Reserve (BMR) in Bodega Bay, California, USA (38°19′ N, 123°04′ W). In addition to *Baccharis, Ammophila arenaria* (Poaceae) and *Lupinus arboreus* (Fabaceae) dominate the plant assemblage in this coastal dune community (Rudgers and Maron 2003). The two architectural morphs of *Baccharis* account for similar percentage cover of the dunes at BMR (prostrate = 13% cover, erect = 16% cover).

Common Garden Experiment

In 1998, we established a common garden experiment in the dunes at BMR to control for effects of environmental variation on architecture in *Baccharis*. The common garden occupied a 60 m × 60 m area in the dunes and originally consisted of 250 plots (125 erect, 125 prostrate) of 1 m² that were arranged along 13 60-m transects. Plots were spaced a minimum of 3 m apart and cleared of all vegetation. Cuttings were taken from adult *Baccharis* plants of both genders of the two morphs collected from randomly chosen locations throughout the 147-ha BMR reserve. Cuttings were started in the greenhouse prior to planting the garden,

and each individual was assigned at random to plot locations within the common garden (for further details on the common garden, see Rudgers and Whitney 2006). Plots were hand weeded for the first year and then plant species were allowed to colonize from 1999 to 2008. From 1998 to 2001, there were experiment cages on 60% of the *Baccharis* plants in the garden to exclude galling insects. These cages did not prevent the clonal spread of some species (namely *Ammophila*) or the germination of seeds in caged plots (J. A. Rudgers, *personal observation*). However, cages could have prevented seeds entering the plots during this time period, and we account for potential cage effects in our statistical analyses. Out of the ~160 total plant species in these dunes, approximately 25% are exotic (J. Sones, *personal communication*). In this study, we report responses of native and exotic plant species both together and separately. For a full list of species observed in this study and their native status, see Appendix A.

Response Variables

In spring of 2008, we were able to locate with full confidence ~175 of the original plants in the common garden, of which ~40 were dead or nearly dead and excluded from the study. Ultimately, we were able to use 73 individuals (36 female, 37 male) of the prostrate morph and 60 individuals (24 female, 36 male) of the erect morph. Under each plant, we recorded richness and percent cover of all colonizing plant species within a randomly placed 15 × 15 cm quadrat. We then harvested the aboveground biomass of each plant species individually within the quadrat. Plants were oven-dried at 60°C for 72 h and weighed to the nearest 0.01 g. In addition, we measured several factors that might affect colonization success under *Baccharis* plants, including *Baccharis* height, understory light availability (using a LiCor Li1000; LiCor, Lincoln, Nebraska, USA), litter depth, soil surface temperature (using a Raynger MT4 Mini-Temp Infrared Thermometer; Raytek, Inc., Santa Cruz, California, USA), and soil moisture (HydroSense soil water content meter; Campbell Scientific, Logan, Utah, USA). Light, temperature, and moisture measurements were taken at midday on a sunny, relatively wind-free day in June 2008.

Data Analyses

While the original *Baccharis* plants were assigned randomly to a location in the common garden, the plants used in this study were a subset (those that were alive and could be positively identified as the original shrubs). To account for some loss of random placement, we used transect location within the common garden as a random blocking effect in our statistical analyses. We first included all plant colonization variables (nine responses: richness, cover, and biomass of total, native, and exotic plant species) in a MANOVA that tested the independent factors of *Baccharis* architecture and
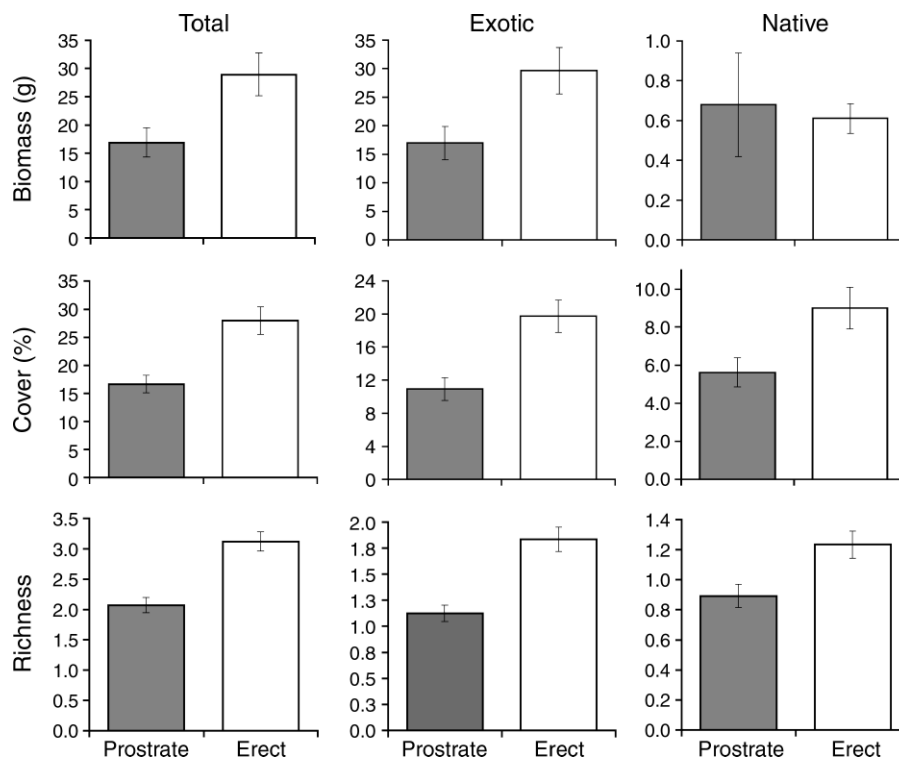
FIG. 1. The relationship between colonization success (richness, percent cover, and aboveground biomass) of plant species (total, exotic, and native) and plant architectural morphology of coyote bush (*Baccharis pilularis*) in a common garden experiment in a coastal dunes ecosystem. Error bars indicate ±SE.

gender and the blocking effect of transect (13 transects). If the independent effects were significant in the multivariate model, we then used separate analysis of variance (ANOVA) models to examine each individual response, including *Baccharis* architecture, gender, and transect location as main effects. We also present *P*-values for univariate models corrected for inflated Type I error using Holm's (1979) method for multiple response variables. Similarly, we used separate ANOVA models to examine the effects of architecture, gender, and transect location on the biomass of the six most abundant colonizing species, which included *Ammophila arenaria* (European beachgrass; exotic), *Daucus pusillus* (American wild carrot; native), *Vulpia bromoides* (squirreltail fescue; exotic), *Pterostegia drymarioides* (native), *Lotus heermannii* (Wooly lotus; native), and *Rumex acetosella* (sheep's sorrel; exotic). Originally, we included the initial cage treatments that were terminated in 2001 (Rudgers and Whitney 2006) as another main effect in the models. Since we detected no effect of caging on plant colonizers or most of the understory variables, we excluded the caging treatments from all the analyses. The single exception was a significant cage effect on leaf litter depth. In this case, caging was kept in the model and is presented in the results (Table 2). Moreover, in our initial analyses, we also included the interaction

term (architecture × gender). Since no interactions were detected, and the results were not affected by the inclusion of this term for any analyses, we present only the reduced models without the interaction term.

To determine whether understory environmental conditions varied between architectural morphs, genders, and transect location, we included litter depth, light availability, and soil moisture as response variables in an understory environment MANOVA. If the independent effects were significant in the multivariate model, we then used separate ANOVA models with *Baccharis* height, litter depth, light availability, and soil moisture as response variables, and we corrected *P* values using Holm's method (1979). We used separate forward stepwise multiple regressions (with $P = 0.10$ used as the threshold for variables to be included or excluded) to examine the variables that best accounted for total colonization success. For all analyses, data were log- or square-root transformed as needed to improve normality and reduce heteroscedasticity. For clarity, we show the untransformed values in all figures.

RESULTS

In total we observed 16 species colonizing the common garden (nine native, seven exotic) (Appendix A). We found that *Baccharis* morphs varied consider-

TABLE 1. Results from ANOVA analyses examining the main effects of *Baccharis pilularis* architectural morphology (morph: erect or prostrate), gender, and transect location on plant species colonization success (richness, cover, and biomass) in a decade-old common garden.

Variable and source	df	Erect morph/male	Prostrate morph/ female	Mean square	F	P	Holm's corrected P
Total richness							
Morph	1, 132	3.116	2.054	37.161	32.144	**<0.0001**	0.0011
Gender	1, 132	2.452	2.633	1.749	1.513	0.221	
Transect	12, 132			2.613	2.335	**0.010**	0.070
Total cover (%)							
Morph	1, 132	28.708	16.513	4676.874	20.218	**<0.0001**	0.0012
Gender	1, 132	19.150	25.500	1001.471	4.329	**0.039**	0.078
Transect	12, 132			501.027	2.166	**0.017**	0.085
Total biomass (g)							
Morph	1, 128	30.741	18.425	4344.043	5.288	**0.023**	0.092
Gender	1, 128	21.502	27.187	1283.749	1.562	0.213	
Transect	12, 128			530.925	0.6464	0.793	
Exotic richness							
Morph	1, 132	1.833	1.123	14.732	25.370	**<0.0001**	0.0013
Gender	1, 132	1.452	1.433	0.103	0.179	0.672	
Transect	12, 132			0.969	1.668	0.0824	
Exotic cover (%)							
Morph	1, 132	19.708	10.897	2260.421	14.061	**0.0003**	0.003
Gender	1, 132	13.500	16.541	251.800	1.566	0.213	
Transect	12, 132			301.076	1.872	**0.044**	0.044
Exotic biomass (g)							
Morph	1, 132	29.619	16.951	4940.655	6.137	**0.014**	0.084
Gender	1, 132	20.317	25.523	1214.801	1.5091	0.221	
Transect	12, 132			560.978	0.6969	0.7518	
Native richness							
Morph	1, 132	1.233	0.890	4.190	9.312	**0.002**	0.018
Gender	1, 132	0.972	1.133	0.340	0.756	0.386	
Transect	12, 132			0.460	1.022	0.433	
Native cover (%)							
Morph	1, 132	9.000	5.616	434.463	8.540	**0.004**	0.032
Gender	1, 132	5.650	8.958	248.939	4.893	**0.0289**	0.086
Transect	12, 132			835.732	4.893	0.190	
Native biomass (g)							
Morph	1, 132	0.610	0.679	0.023	0.007	0.929	
Gender	1, 132	0.558	0.757	0.520	0.174	0.677	
Transect	12, 132			1.769	0.592	0.8451	

Notes: A conservative Bonferroni-correction would require that $P < 0.006$. Corrected P values have been adjusted using Holm's (1979) method. P values <0.05 are shown in boldface type.

ably in resistance to colonization by both native and exotic plant species, with erect morphs being more susceptible than prostrate morphs (see Appendix B for MANOVA results). Erect morphs had 52% higher total richness (63% higher exotic; 38% higher native), 74% higher total cover (81% higher exotic; 60% higher native cover) and 64% higher total biomass (75% higher exotic, no difference in native biomass) of colonizing plant species than prostrate morphs (Fig. 1). We note that biomass results were driven almost entirely by one exotic species. *Ammophila* made up 95% of the total colonizer biomass (Appendix C). When we removed *Ammophila* biomass from the dataset, we found no difference in total colonizer biomass between the two morphs. However, erect morphs still maintain ~50% higher

plant species richness and cover than prostrate morphs when *Ammophila* was excluded from the analyses.

We also observed gender differences in colonization resistance, but only in total and native cover. Female shrubs had 33% higher total cover compared to male shrubs (driven primarily by 58% higher native cover, Table 1).

Of the six most abundant colonizing species, three species varied in colonization success beneath the two *Baccharis* architectural morphs (nonsignificant species data not presented). *Ammophila* cover was 95% higher, *Pterostegia* cover was 54% higher, and *Daucus* cover was 300% higher beneath erect morphs compared to prostrate morphs (Appendix C). Biomass of these three species also varied between morphs. *Ammophila* biomass
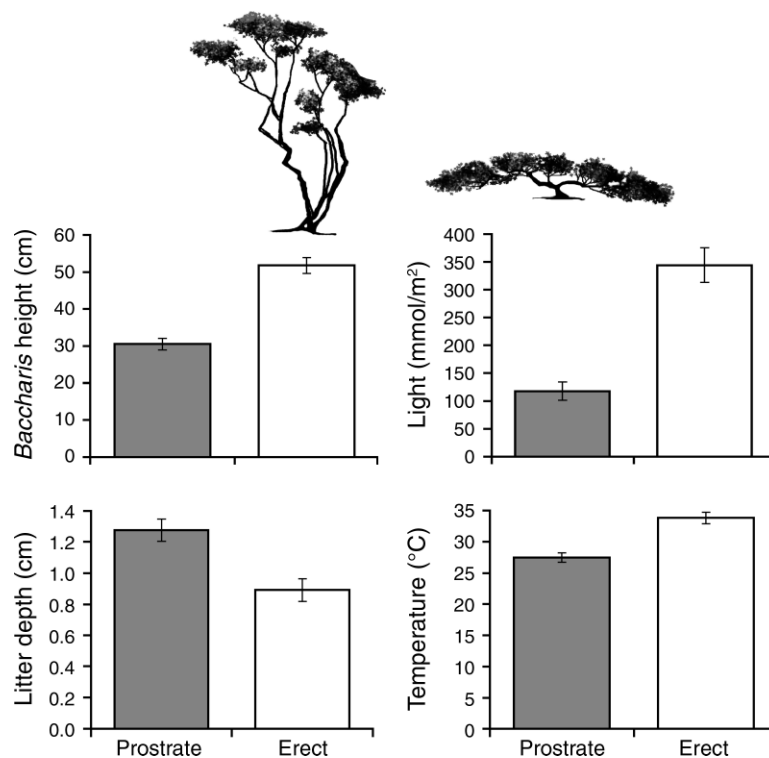
FIG. 2. The relationship between coyote bush (*Baccharis pilularis*) height (cm), understory light availability (mmol/m^2), leaf litter depth (cm), and soil surface temperature (°C) and plant architectural morphology of coyote bush. Error bars indicate ±SE.

was 48% higher, *Pterostegia* biomass was 95% higher, and *Daucus* biomass was 600% higher under erect morphs. When we examined the effects of *Baccharis* gender on the six most abundant colonizers, we observed differences only in *Ammophila* biomass, with 35% higher biomass beneath female plants than male plants.

Potential mechanisms driving patterns of plant colonization include several observed differences in the understory environment between the two architectural morphs. Erect morphs had ~200% higher understory light, ~16% higher soil surface temperatures, and ~30% shallower litter depth than prostrate morphs (Fig. 2, Table 2). Despite this variation, we observed no difference in soil moisture content. Of the characteristics of the understory environment we measured in this study, we found no significant differences between *Baccharis* genders, though female plants showed a trend of having ~20% higher understory light availability ($P =$ 0.10, Table 2). In regression analyses, understory light availability, *Baccharis* height, and soil surface temperature accounted for 32% of the variation in total colonizer richness (Appendix D), whereas, *Baccharis* height, soil surface temperature, and litter depth accounted for ~28% in total colonizer cover (Appendix D). Finally, *Baccharis* height alone accounted for ~13% of the variation in total biomass of colonizers (Appendix D).

DISCUSSION

In this study, we found considerable variation in plant colonization success associated with different *Baccharis pilularis* architectural morphs. Erect morphs had higher total, exotic, and native plant species richness and cover, as well as higher total and exotic biomass than prostrate morphs. Several architectural traits, including height, branch length, branch number, and leaf size, vary between morphs (Rudgers and Whitney 2006) and act as likely mechanisms for variation in colonization success via their effects on the understory environment. Erect morphs had higher understory light availability and warmer soil surface temperatures, both of which might facilitate seed germination and the survival of colonizing species in the dunes. Moreover, erect plants had a shallower litter layer compared to prostrate morphs. We found that litter depth was negatively related to colonizer cover, which supports other studies showing that litter accumulation under dominant plants can suppress plant species establishment (Facelli and Pickett 1991). Deeper litter layers under prostrate morphs could be due to greater litter production, the production of more recalcitrant litter, or simply that prostrate morphs protect the litter from high winds that occur at BMR. Teasing apart these mechanisms requires further investigation.

TABLE 2. Results from ANOVA analyses examining the main effects of *Baccharis pilularis* architectural morphology (morph), gender, and transect location on the understory environment in a common garden experiment.

Variable and source	df	Erect morph/male	Prostrate morph/female	Mean square	F	P	Holm's corrected P
Light (mmol/m^2)							
Morph	1, 97	344.183	117.682	1 314 972	47.133	<**0.0001**	0.0008
Gender	1, 97	206.510	249.630	73 384	2.630	0.108	
Transect	12, 97			18 306	0.6561	0.728	
Soil surface temperature (C°)							
Morph	1, 126	33.869	27.457	4742.713	36.505	<**0.0001**	0.0007
Gender	1, 126	30.173	30.416	9.769	0.075	0.784	
Transect	12, 126			251.529	1.936	**0.037**	0.037
Litter (cm)							
Morph	1, 125	0.891	1.275	5.141	16.477	<**0.0001**	0.0006
Gender	1, 125	1.103	1.105	0.183	0.588	0.444	
Caging				0.929	2.954	**0.022**	0.044
Transect	12, 125			0.739	2.370	**0.009**	0.027
Soil moisture (%)							
Morph	1, 128	4.377	4.298	0.244	1.509	0.221	
Gender	1, 128	4.292	4.381	0.000	0.000	0.994	
Transect	12, 128			1.164	7.201	<**0.0001**	0.0005
Baccharis height (cm)							
Morph	1, 129	51.775	30.534	12 993.52	57.475	<**0.0001**	0.0004
Gender	1, 129	41.732	37.940	88.87	0.393	0.531	
Transect	12, 129			262.13	1.159	0.320	

Notes: A conservative Bonferroni correction would require that $P < 0.0125$ for ANOVA on the understory environment responses. Corrected P values have been adjusted using Holm's (1979) method. P values <0.05 are shown in boldface type.

We also compared plant colonization success between *Baccharis* genders, and observed that female plants had higher cover of colonizing species than male plants. While plant dioecy may not be a major influence on community assembly in this system, this result might not hold in other systems. For example, in a meta-analysis of 54 studies of dioecious plants, Cornelissen and Stiling (2005) found that male plants had more leaves, larger leaves, longer stems, and higher growth rates than conspecific female plants. Thus, dioecy may serve as another form of genetic variation within dominant plant species that merits more exploration in its role in community assembly.

European beachgrass (*Ammophila arenaria*) was by far the most prominent plant species establishing in the common garden, both in terms of cover and biomass. Beachgrass is also the most dominant exotic species in the dunes at BMR and is known to have negative impacts on the indigenous coastal flora. For example, in previous work in this system, Rudgers and Maron (2003) found that the performance of a nitrogen-fixing species, *Lupinus arboreus*, was reduced when planted under beachgrass in the dunes. In contrast, *L. arboreus* performance actually increased under the prostrate form of *Baccharis* compared to exposed sand, indicating that the prostrate form of *Baccharis* can facilitate some native plant species in the dunes. Rudgers and Maron (2003) did not include the erect morph in this study and we observed only a single *L. arboreus* individual colonizing the common garden. Yet, together these results indicate that the presence of prostrate morphs within *Baccharis* populations can have dual functions: impeding exotic species while facilitating some natives in the dunes.

To date, most studies have examined how the presence of particular dominant plant species can limit species colonization (Smith et al. 2004, Emery and Gross 2007). Our study adds to a growing body of research showing that the presence and identity of particular genotypes within populations of native dominants can also influence the assembly of plant communities (Fridley et al. 2007, Crutsinger et al. 2008, Johnson et al. 2008). Teasing apart the specific mechanisms through which genetic variation influences the structure of communities can be difficult. Taken together, our results indicate that plant architectural variation is a key trait that shapes the understory environment in a coastal dunes ecosystem and determines the richness, cover, and biomass of understory plant species.

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APPENDIX A

Species list of invaders (*Ecological Archives* E091-087-A1).

APPENDIX B

Results from separate MANOVA analyses examining the main effects of *Baccharis pilularis* architectural morphology, gender, and transect location on plant colonization and the understory environment in a decade-old common garden (*Ecological Archives* E091-087-A2).

APPENDIX C

Results from separate ANOVA analyses examining the main effects of *Baccharis pilularis* architectural morphology, gender, and transect location on individual plant species cover and biomass in a decade-old common garden (*Ecological Archives* E091-087-A3).

APPENDIX D

Results of stepwise multiple regressions examining the effects of *Baccharis pilularis* understory variables on total colonizer richness, cover, and biomass (*Ecological Archives* E091-087-A4).