Ecology, 95(2), 2014, pp. 387–398

Genetic variation within a dominant shrub structures green and brown community assemblages

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Abstract. Two rising challenges in ecology are understanding the linkages between above- and belowground components of terrestrial ecosystems and connecting genes to their ecological consequences. Here, we blend these emerging perspectives using a long-term common-garden experiment in a coastal dune ecosystem, whose dominant shrub species, *Baccharis pilularis*, exists as erect or prostrate architectural morphotypes. We explored variation in green (foliage-based) and brown (detritus-based) community assemblages, local ecosystem processes, and understory microclimate between the two morphs. Prostrate morphs supported more individuals, species, and different compositions of foliage arthropods, litter microarthropods, and soil bacteria than erect morphs. The magnitude of community compositional differences was maintained from crown to litter to soil. Despite showing strikingly similar responses, green and brown assemblages were associated with different underlying mechanisms. Differences in estimated shrub biomass best explained variation in the green assemblage, while understory abiotic conditions accounted for variation in the brown assemblage. Prostrate morphs produced more biomass and litter, which corresponded with their strong lateral growth in a windy environment. Compared to erect morphs, the denser canopy and thicker litter layer of prostrate morphs helped create more humid understory conditions. As a result, decomposition rates were higher under prostrate shrubs, despite prostrate litter being of poorer quality. Together, our results support the hypothesis that intraspecific genetic variation in primary producers is a key mediator of above- and belowground linkages, and that integrating the two perspectives can lead to new insights into how terrestrial communities are linked with ecosystem pools and processes.

Key words: *aboveground-belowground linkages; architecture;* Baccharis pilularis; *community genetics; decomposition; dunes; leaf litter; microarthropods; primary production; soil microbes.*

Introduction

A rapidly growing area of ecology seeks to understand the links between above- and belowground components of terrestrial ecosystems (Wardle et al. 2004, Bardgett and Wardle 2010). Goals of this research include detecting interactions between the two subsystems, understanding how these interactions structure above- and belowground communities (Fukami et al. 2006, Peay et al. 2012, Van der Putten 2012), and elucidating their consequences for pools and fluxes of resources (Bardgett and Wardle 2010). In terrestrial ecosystems, plants provide the majority of resources (Chapin and Eviner 2012) and support at least two distinct communities. First, numerous animals depend on the aboveground or "green" components of plants, such as leaves, shoots, and flowers. These species are often referred to as part of the "green food web" (referred to hereafter as the "green assemblage") and have been the primary focus of ecological studies. Most carbon fixed by plants is not consumed by this community, but instead returns to the litter and soil where it is consumed by detritivores, such as microarthropods and microbes (Moore et al. 2004). This detritus-based community is often referred to as the "brown food web" (referred to hereafter as the "brown assemblage"; e.g., Allison 2006, Kaspari and Yanoviak 2009). As plants provide critical resources for both green and brown assemblages, intra- and interspecific variation in amount and quality of plant resources can be important structuring agents of these communities (Hooper et al. 2000, Scherber et al. 2010).

Manuscript received 15 February 2013; revised 5 July 2013; accepted 11 July 2013; final version received 3 August 2013. Corresponding Editor: M. C. Rillig.
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The study of above- and belowground linkages during the past decade has coincided with a "genes-to-ecosystems" approach seeking to understand the importance of genetic variation in community assembly and ecosystem processes (Whitham et al. 2006, Johnson and Stinchcombe 2008, Bailey et al. 2009). For example, intraspecific variation in host-plant chemistry is known to affect herbivores and various other members of green assemblages (Whitham et al. 2012). The few studies that have tested the effects of genetic variation on brown assemblages, however, have observed weak and variable responses (Crutsinger et al. 2008, Schweitzer et al. 2008, Sthultz et al. 2009, Madritch and Lindroth 2011). Furthermore, the ability to link above- and belowground communities requires studies that examine both assemblages within the same ecosystem. Consequently, data are lacking to achieve consensus on the relative importance of host-plant intraspecific genetic variation for green vs. brown assemblages or on the degree to which above- and belowground responses to intraspecific genetic variation may be coupled. In addition, the underlying mechanisms, i.e., the plant traits or associated microenvironments driving interactions with consumers and detritivores, remain unresolved for nearly all systems (but see Whitham et al. 2006).

In this study, we examined the role of intraspecific genetic variation within a dominant shrub, *Baccharis pilularis*, in shaping green and brown assemblages and associated ecosystem processes measured at the scale of individual shrubs. We focused on variation in plant morphology, as *B. pilularis* occurs as two distinct, genetically based architectural forms (erect and prostrate) in the coastal dunes of northern California, USA. Using a decade-old common-garden experiment, we addressed the following questions: (1) How does intraspecific variation within a dominant plant influence the diversity and composition of green (foliar arthropods) vs. brown (litter microarthropods, soil nematodes, soil microbes) assemblages? (2) How does intraspecific variation influence above- vs. belowground processes, including biomass productivity, litter quality and inputs, decomposition, and microclimate? (3) Are there similar responses of green and brown assemblages to intraspecific variation, and are these two groups responding to the same underlying mechanisms?

Methods

Study system

Baccharis pilularis De Candolle (Asteraceae, coyote brush) is a dioecious shrub that dominates coastal sage and chaparral, as well as coastal dunes of California. In the dunes, *B. pilularis* occurs as two distinct architectural types that co-occur: 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 morphs differ in a variety of traits, including height, leaf size, branch number, and susceptibility to insect herbivores. Erect morphs are also taller than prostrate morphs, with larger leaves, fewer branches, and a shallower litter layer (Rudgers and Whitney 2006, Crutsinger et al. 2010). As a consequence of this architectural variation, there are corresponding differences in the understory abiotic environment. For example, understory light availability and soil surface temperature are higher under erect morphs (Crutsinger et al. 2010).

We conducted this study at the University of California-Davis Bodega Marine Reserve (BMR) in Bodega Bay, California, USA (38°19′ N, 123°04′ W). The two morphs of *B. pilularis* (hereafter *Baccharis*) co-occur here, often growing adjacent to each other in the dunes. There is substantial evidence that the architectural variation in *Baccharis* is heritable, although the underlying genes or quantitative trait loci (QTL) have not yet been described. First, clones of the two forms have been growing in a common garden for over a decade and have retained architectural differences. Second, the prostrate morph is widely used in landscaping along the coastline of California and retains its short stature across a range of environments (Ehler 1982). Third, and most important, crosses between the two morphs result in progeny that segregate into both forms (Thompson et al. 1995; J. A. Rudgers, *unpublished data*).

In 1998, one of us (J. A. Rudgers) established a common-garden experiment at BMR to control for effects of environmental variation on the erect and prostrate architectures of *Baccharis*. The common garden occupied a 60×60 m area, originally consisting of 250 plants (125 erect, 125 prostrate) in 1-m^2 plots spaced 3 m apart and arranged along 15 60-m transects. Plants were grown from cuttings of adult *Baccharis* plants of both genders of the two morphs from randomly chosen locations throughout the 147-ha BMR reserve. Cuttings were started in the greenhouse prior to planting in the garden, and each individual was assigned at random to a plot location (for further details on the common garden, see Rudgers and Whitney [2006]). At the initiation of this study, 134 shrubs (74 prostrate, 60 erect) had survived with identifiable tags to ensure they were original shrubs.

Community-level responses

Foliar arthropods.—In July 2009, we used a combination of techniques to sample the foliar-based arthropod community on randomly chosen individuals of both prostrate ($n = 42$ individuals) and erect ($n = 29$ individuals) morphs in the common garden (Table 1). We first visually surveyed each shrub for sessile arthropod species, specifically leaf and stem galls created by the midge, *Rhopalomyia californica* (Diptera) and the microlepidopteran, *Gnorimoschema baccharisella* (Lepidoptera). We then vacuum-sampled the entire crown of each shrub using a modified leaf blower/vacuum (Craftsman 25cc 2-cycle; Sears Holding Corporation, Hoffman Estates, Illinois, USA) with a fine insect net attached. Vacuum samples were taken to the laboratory

TABLE 1. Schematic of community-level variables and sampling methods, along with ecosystem-level and microclimatic variables, measured in responses to *Baccharis pilularis* architectural variation in a coastal dune ecosystem in Bodega Bay, California, USA.

Community level	No. shrubs	Sampling methods	Ecosystem level	Microclimate
Foliar arthropods	42, 29	vacuuming, visual counting	shrub biomass	light
Litter microarthropods	20	Berlese funnel	litter production	moisture/humidity
Soil nematodes	20	Baermann funnel	leaf, litter, soil C:N	temperature
Soil microbes	10	454 pyrosequencing	decomposition	throughfall

and identified to species or morphospecies. In total, we collected 5720 individuals of 180 species.

Litter microarthropods.—In July of 2009, we collected litter from 20 randomly chosen replicates of each morph, placed it in paper bags and brought the bags immediately into the lab. We extracted litter microarthropods for 72 h using modified Berlese-Tullgren funnels (Merchant and Crossley 1970) made from 25 cm diameter plastic funnels with 0.5 cm diameter hardware cloth in the bottom on which litter was placed. A 25 W light bulb was hung 10 cm above the litterbags and microarthropods were collected in plastic cups filled with 70% ethanol. Microarthropods were counted and identified to species or morphospecies. In total, we extracted 2697 individuals of 81 species.

Nematodes.—To assess soil nematode abundance, we collected 10 cm soil cores from beneath 20 individuals (10 per morph) in July of 2009. Soil was weighed and placed into a Baermann funnel. Nematodes were collected from the funnels after 48 h at 22°C, and total abundance was estimated under a dissecting scope.

Soil microbes.—To characterize soil microbial communities, we collected soil cores (3 cm diameter × 15 cm deep) from beneath 20 individual plants (10 per morph) in July 2010. Microbial sampling occurred a year after foliar and litter communities. However, all communities were sampled at similar time points during the summer dry season and we feel are comparable within the framework of the common-garden experiment. When we have repeatedly measured, communities have shown consistent patterns across years (Rudgers and Whitney 2006; G. M. Crutsinger, *unpublished data*). Soils were taken to the lab, manually homogenized, and a 0.25-g subsample was stored in 2 mL of Lifeguard preservation solution (MoBio, Carlsbad, California, USA) at −20°C until DNA extraction and 454 pyrosequencing (see Appendix A for methods). In the soil, we observed a total of 2767 operational taxonomic units (OTUs) for bacteria/archaea and 1015 OTUs for fungi.

To analyze foliar arthropod and litter microarthropod community responses, we used separate one-way ANOVAs to test for differences in total richness, rarefied richness (using individual-based rarefaction [Gotelli and Colwell 2001]), and abundance between erect and prostrate morphs. Next, we used the Bray-Curtis dissimilarity index and separate one-way ANOSIMs (1000 permutations) to test for significant differences in community composition between morphs. ANOSIM is analogous to an ANOVA on community dissimilarity values. The R statistic generated by ANOSIM is a measure of separation of between groups relative to within group variability. A value of 0 indicates there is complete overlap in the community composition between groups, while a value of 1 indicates that there is no overlap (Clarke and Gorley 2006). We visualized these results using nonparametric multidimensional scaling analysis (NMDS) on Bray-Curtis dissimilarity values in PRIMER v.6 (Clarke and Gorley 2006) using 100 restarts.

In the soil, we analyzed differences in nematodes per gram dry mass of soil using one-way ANOVA. For bacterial and fungal sequence data, we account for differences in sequencing depth by rarefying to 1700 and 3500 sequences, respectively, for fungi and bacteria before we estimated richness (Chao1 richness estimator [Chao 1984]) and calculated the Bray-Curtis dissimilarity index. These rarefaction cutoffs were chosen to maximize the number of usable samples while still maintaining a reasonable sequencing depth for each sample. As not all samples sequenced well, we ended up with a final sample size of 18 for fungi ($n = 9$ erect shrubs, $n = 9$ prostrate shrubs) and 19 for bacteria ($n = 10$ erect shrubs, $n = 9$ prostrate shrubs). We tested for differences between morphs in microbial community richness using ANOVA and in microbial community structure using ANOSIM. 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 figures.

Local ecosystem-level responses

Biomass production and litter inputs.—We measured crown circumference of each individual shrub as a nondestructive estimate of differences in aboveground biomass production between erect and prostrate *Baccharis* morphs. We also placed 30 × 30 cm litter traps under shrubs to estimate litter production. Litter was collected at approximately eight-week intervals or five times from May of 2010 to July of 2011, oven dried at 60°C for 72 h, and weighed to the nearest 0.01 g. We used separate one-way ANOVAs to compare the differences in crown size and annual (cumulative) litter production between morphs. We used a repeated-measures ANOVA to examine differences in litter production over the five collection dates.

Litter quality.—To compare litter quality between *Baccharis* morphs, we examined the nutrient content of leaves, litter, and soil. In May of 2010, we collected

green leaves directly from the shrubs (24 prostrate, 19 erect), litter from the litter traps (15 prostrate, 14 erect), and soil by scraping away the litter layer and using a 1.5 cm diameter core to collect the top 10 cm of soil (11 prostrate, 7 erect). Green leaf and litter samples were ground to a fine powder using a ball mill; soil samples were ground by hand using a mortar and pestle. Subsamples of each material were then analyzed for total carbon (C) and nitrogen (N) on a soil elemental analyzer (NC 2500; Carlo-Erba, Milan, Italy) at the University of California, Berkeley, using acetanilide (10.36% N and 71.09% C) as a reference standard. We used separate one-way ANOVAs to compare the differences in C and N between morphs.

Decomposition.—We evaluated several potential mechanisms that could influence decomposition rates between the two *Baccharis* morphs. First, we explored the effects of litter quality differences using a standard laboratory incubation assay, as described by Wardle et al. (2009). As part of this assay, we performed a reciprocal transplant of litter (collected from litter traps) of the two *Baccharis* morphs placed on soil (collected with soil cores) from underneath the two morphs. The assay consisted of 100 mm diameter Petri plates that were filled two-thirds with the field-collected soil and amended to 250% moisture (dry mass basis) content. On the soil surface, we placed a disc of fiberglass window screen (1.5 mm diameter screening) and placed leaf litter (2 g, oven dried) on top of the mesh. We sealed the Petri plates with parafilm and placed them in a standard greenhouse environment (15°–25°C). We had 12 replicates each for the 2×2 design (prostrate vs. erect litter on prostrate vs. erect soil; 48 Petri plates total). After 16 weeks, we collected the litter, oven dried it at 60°C for 72 h, and weighed it to the nearest 0.001 g to obtain the percentage of mass loss. We used a full factorial, fixed-effect ANOVA to test whether mass loss varied with litter and/or soil origin.

Additionally, we explored whether the understory abiotic environment could influence decomposition in the common garden. We placed 5 cm diameter filter paper in litterbags underneath different individuals of the two *Baccharis* morphs, as well as in the open in the common garden. We collected litterbags after 12 months in the field ($n = 14$ open, $n = 23$ prostrate, $n = 18$ erect; sample size differences are due to loss of bags from high winds at BMR). We oven-dried and weighed the filter paper to determine percent mass remaining. We used one-way ANOVA to test whether final mass loss varied under the two morphs or in the open. We performed Tukey HSD post-hoc pairwise comparisons to identify differences ($P < 0.05$) between groups.

Understory microclimate

In our prior work, erect morphs had, on average, double the light availability and 16% warmer soil surface temperatures than prostrate morphs, but there was no difference in soil moisture (Crutsinger et al. 2010). Yet, these findings were based on a single measurement in July (dry season) when soils under both morphs was likely to be equally dry. Here, we focused in greater detail on water dynamics towards the end of the spring rains by estimating canopy interception of rainwater (i.e., throughfall), understory temperature and relative humidity to characterize vapor pressure deficit (VPD), and litter moisture content under erect and prostrate morphs (see Table 1 for a list of responses measured and Appendix A for methods).

Coupled green and brown assemblage responses and plant traits

To determine whether green and brown community responses to *Baccharis* genetic variation were coupled, we examined pairwise correlations among community variables. Next, we examined correlations between community variables, plant traits, and understory abiotic conditions to evaluate potential mechanisms driving community-level responses. We applied sequential Bonferroni correction to P values from Spearman rank correlations, testing only those relationships with greater than or equal to seven replicates per architectural morph ($n = 14$). From this analysis, we identified a subset of relationships to explore further.

It was not always possible to measure all community, ecosystem, and trait variables on the same subset of shrubs because of the limitations of destructive sampling. Consequently, we lacked sufficient samples sizes across the entire dataset to apply robust multiple regression analysis or path analysis. Therefore, we tested for an effect of architectural morph while including each correlated plant trait or abiotic variable (identified from correlation analysis, described above) as a covariate in a general linear model (Proc GLIMMIX using restricted maximum likelihood, SAS v. 9.3, [SAS Institute 2011]), following methods in Rudgers and Clay (2008). This analysis tested whether a given trait remained a significant predictor of a community response after accounting for the overall effect of architectural morph. If the covariate rendered the main effect of morph nonsignificant because it explained substantial variation in the response, this would indicate it was an important driver of the community response. On the other hand, if inclusion of architectural morph rendered the covariate nonsignificant, this would indicate that the trait was not a strong predictor (statistical power is reduced by addition of factors to the model) and/or that other trait differences between morphs were stronger drivers of the community response.

Results

Community level

Foliar arthropods.—Within the green assemblage, both the richness ($F_{1,69} = 19.77$, $P < 0.0001$, Fig. 1A) and abundance ($F_{1,69} = 11.07$, $P = 0.0014$, Fig. 1C) of foliar arthropods was approximately two times higher on prostrate morphs than on erect morphs. Rarefied

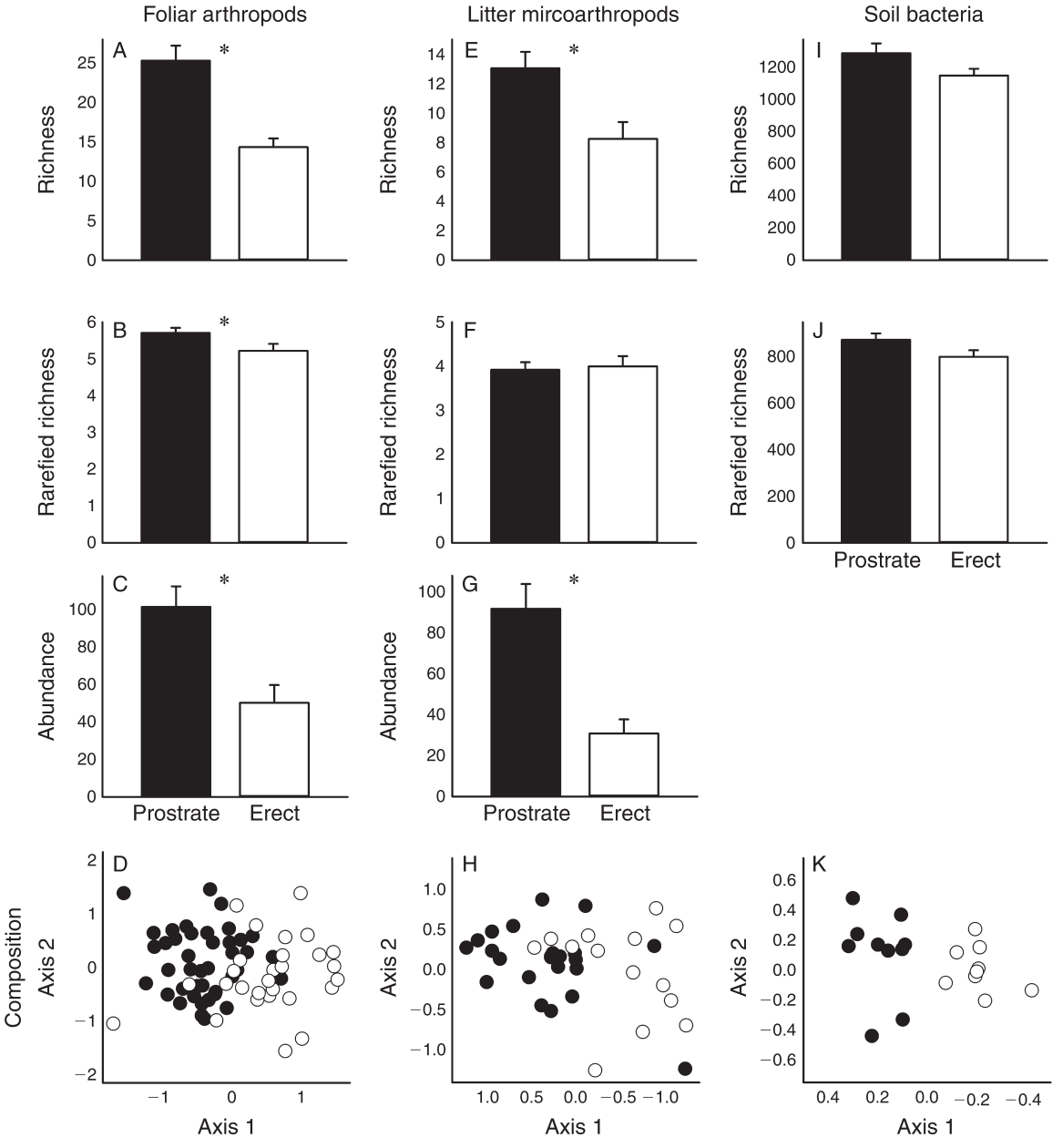

FIG. 1. Above- and belowground responses to *Baccharis pilularis* architectural morph (erect [open] vs. prostrate [solid]) in a decade-long common-garden experiment. Community-level variables for the green (i.e., aboveground) assemblage include (A) foliar arthropods richness, (B) rarefied richness, (C) abundance, and (D) an NMDS ordination of community composition based on Bray-Curtis dissimilarity. (E–H) The same variables are represented for litter microarthropods in the brown (i.e., belowground) assemblage. In the soil, the responses of Chao-estimated (I) bacteria richness, (J) rarefied richness, and (K) an NMDS ordination of bacterial community composition based on Bray-Curtis dissimilarity are depicted. Bars represent means and SE; open circles show prostrate morph, and solid circles show erect morph. Asterisks denote statistically significant differences ($P < 0.05$)

richness was also higher for prostrate morphs ($F_{1,69} = 4.75$, $P = 0.03$, Fig. 1B), although the differences between shrubs were weaker (~9% more rarefied species) than for observed richness. Weaker rarefied richness patterns indicate that the difference in richness between morphs was driven primarily by the greater abundances associated with prostrate morphs, and the increased likelihood of detecting more species when more individuals are sampled. Foliar community composition also varied, with erect and prostrate morphs having an average Bray-Curtis dissimilarity of 77.6% (global $R = 0.31$, $P = 0.001$; Fig. 1D). Compositional differences could be explained by individual species' preferences. For example, leaf gall-forming midges (*Rhopalomyia californica*) were 2.8 times more abundant on prostrate shrubs ($F_{1,69} = 9.31$, $P = 0.003$), whereas

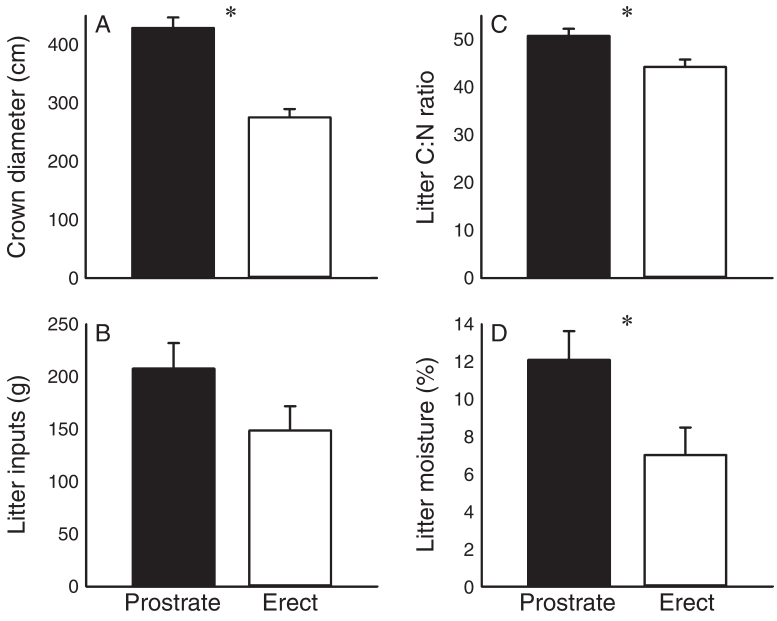

FIG. 2. Ecosystem-level and abiotic responses to intraspecific variation in erect (open bars) vs. prostrate (solid bars) *Baccharis pilularis* architectural morphs, including (A) crown circumference (i.e., aboveground productivity), (B) cumulative litter inputs, (C) C:N ratios of leaf litter, and (D) leaf litter moisture content between erect and prostrate morphs. Bars represent means and SE.

stem gall-forming moths (*Gnorimoschema baccharisella*) were 2.5 times more abundant on erect forms ($F_{1,69} = 9.20$, $P = 0.003$).

Litter microarthropods.—Richness of litter microarthropods was 1.6 times greater in litter under prostrate than erect morphs ($F_{1,39} = 8.36$, $P < 0.006$, Fig. 1E). Similarly, mite ($F_{1,39} = 6.62$, $P < 0.014$) and Collembola ($F_{1,39} = 11.68$, $P < 0.001$) richness were 1.5 times and 3.3 times higher under prostrate morphs. Total abundance ($F_{1,39} = 14.69$, $P = 0.0005$, Fig. 1G), as well as mite ($F_{1,39} = 13.69$, $P = 0.0007$) and Collembola abundance ($F_{1,39} = 4.68$, $P = 0.036$) were 3 times, 3 times, and 8.5 times higher respectively under prostrate morphs. Rarefied arthropod richness was not different between morphs ($F_{1,38} = 0.08$, $P = 0.776$, Fig. 1F), indicating higher richness was due to greater abundances. *Baccharis* morphs supported very different community compositions of microarthropods (global $R = 0.28$, $P = 0.001$, Fig. 1H), with an average Bray-Curtis dissimilarity of 74%.

Soil microbes and nematodes.—*Baccharis* morphs also supported distinct soil bacterial communities (global $R = 0.87$, $P < 0.001$), with an average Bray-Curtis dissimilarity of ~68% between morphs (Fig. 1K). Bacterial richness showed a weak trend, with ~8% higher bacterial rarefied richness under prostrate shrubs than erect ($F_{1,17} = 2.61$, $P = 0.124$, Fig. 1J) and a marginal response of Chao-estimated richness ($F_{1,17} = 3.2$, $P = 0.09$, Fig. 1I). Soil bacterial communities were more sensitive than the soil fungi targeted with ITS primers (mainly saprotrophs). Fungal community composition (global $R = 0.002$, $P = 0.39$), observed species richness ($F_{1,16} = 0.16$, $P = 0.694$) and Chao estimated richness ($F_{1,16} = 0.02$, $P = 0.877$) did not vary between morphs. Total nematode abundances were very low in the dune soils (0–17 individuals/g dry soil) and also did not differ between morphs ($F_{1,28} = 1.57$, $P = 0.219$). Sampling during the dry season and the nutrient-poor dune soils may be responsible for the low nematode abundances in our samples.

Local ecosystem-level responses

Productivity.—Genetic variation in *Baccharis* had a strong influence on estimated aboveground biomass. Cuttings were of equal size at the initiation of the experiment, yet prostrate shrubs had ~1.6 times larger crowns compared to erect morphs ($F_{1,130} = 40.89$, $P < 0.0001$, Fig. 2A) after a decade. Crown size was also positively correlated with leaf litter inputs (Spearman $r = 0.44$, $P < 0.0001$, $n = 132$ shrubs) indicating that crown size offered a good estimation of variation in aboveground primary production between morphs.

Litter inputs.—Prostrate morphs produced 39%, or an average of ~61.1 $g \cdot m^{-2} \cdot yr^{-1}$ (30.9 g $C \cdot m^{-2} \cdot yr^{-1}$), more litter compared to erect morphs, although this statistical difference was marginal ($F_{1,25} = 3.05$, $P = 0.09$, Fig. 2B). This result is consistent with prior observations of a 30% deeper litter layer under prostrate shrubs (Crutsinger et al. 2010). Peak litter production occurred in summer months (May–July; collection date $F_{4,13} = 14.70$, $P < 0.001$), during which prostrate morphs had, on average, 87% more litter mass than erect morphs ($F_{1,23} = 7.48$, $P = 0.012$). Differences in litter inputs between morphs were not as strong during winter and spring months when less litter was produced, as indicated by a significant

TABLE 2. Spearman correlation coefficients (r) between foliar arthropods, litter microarthropods, and soil bacteria in a common-garden experiment of *Baccharis pilularis*.

Metric	Foliar richness	Foliar rarefied rich	Foliar abundance	Litter richness	Litter rarefied richness	Litter abundance	Bacteria richness	Bacteria Chao richness
Foliar richness	1							
Foliar rarefied richness	**0.57**	1						
Foliar abundance	**0.72**	0.04	1					
Litter richness	0.46	**0.55**	**0.55**	1				
Litter rarefied richness	−0.08	0.12	0.12	0.37	1			
Litter abundance	0.57	**0.53**	**0.53**	**0.73**	−0.09	1		
Bacteria richness	0.15	−0.12	−0.12	**0.44**	−0.43	0.52	1	
Bacteria Chao richness	0.20	−0.05	0.15	**0.47**	−0.36	0.52	**0.96**	1

Note: Correlations that are significant after sequential Bonferroni corrections are indicated in boldface type.

collection date × morph interaction ($F_{4,13} = 3.41$, $P = 0.04$), and there was no average morph effect across all five collection dates ($F_{1,16} = 1.26$, $P = 0.27$). Although productivity and litter inputs were greater for prostrate morphs, the leaves and litter were of poorer quality. C:N ratios were, on average, 12% higher for leaves ($F_{1,40} = 15.38$, $P = 0.003$) and 14% higher for litter ($F_{1,27} = 9.33$, $P = 0.005$, Fig. 2C) of prostrate morphs compared to erect morphs. This result was driven by 10% lower N content in the leaves ($F_{1,27} = 10.062$, $P = 0.003$) and 13% lower N in the litter ($F_{1,27} = 6.48$, $P = 0.017$) of prostrate shrubs, as there were no differences between morphs in C content for either leaves ($F_{1,27} = 1.66$, $P = 0.205$) or litter ($F_{1,27} = 1.52$, $P = 0.227$).

Decomposition.—Plant architecture-based differences in the understory environment (see microclimate results), rather than differences in litter quality had a greater influence on decomposition in this system. Despite differences in litter quality, our decomposition incubation assay showed a marginal and weak effect of genetic variation on mass loss ($F_{1,42} = 3.65$, $P = 0.062$). Erect morphs had ~3% higher mass loss than prostrate morphs after 16 weeks, a difference consistent with the higher N content in erect litter. We observed no effect of soil origin (erect vs. prostrate) on litter decomposition ($F_{1,42} = 0.16$, $P = 0.687$), nor did we find an interaction between litter and soil origin ($F_{1,42} = 0.09$, $P = 0.761$). Furthermore, we observed no differences in the nutrient content of soils between the two morphs (carbon $F_{1,16} = 0.007$, $P = 0.931$; nitrogen $F_{1,16} = 0.673$, $P = 0.798$; C:N $F_{1,16} = 0.043$, $P = 0.838$), though soils of these dunes were very nutrient poor. However, field decomposition results contrasted sharply with the lab incubation assay. A standard carbon substrate (filter paper) placed beneath shrubs in the common garden for 12 months decomposed much faster under prostrate than erect morphs, or an average of ~30% vs. 2% mass loss ($F_{1,37} = 11.06$, $P = 0.002$). Filter paper placed away from shrubs in the open dunes had an intermediate rate of decomposition (16% mass loss). Greater decomposition in the open compared to under erect morphs may result from greater photo-degradation from sunlight exposure (Wolkovich et al. 2010).

Understory microclimate

Prostrate morphs created a more humid environment than erect morphs, likely driven by denser canopies, buffering of coastal winds by a prostrate crown, and thicker litter layers that help to retain soil moisture. Higher moisture and humidity may account for the faster decomposition rates of filter paper placed under prostrate morphs. Canopies of erect and prostrate morphs both intercepted approximately 20% of precipitation, but there was no difference in throughfall ($F_{1,9} = 256.32$, $P = 0.105$). We observed substantial day-to-day variation in midday maximum sub-canopy VPD across days, ranging from less than 0.5 kPa to over 3.0 kPa ($F_{1,13} = 57.29$, $P < 0001$). Erect morphs had 40% higher (marginally significant) midday mean VPD (i.e., less humid) than did prostrate morphs ($F_{1,13} = 4.766$, $P = 0.079$) but there was no difference between morphs as VPD approached nightly dewpoint. Prostrate morphs also appeared to retain litter moisture longer following rain events: one week after a rain, prostrate litter was 72% wetter than erect litter (12% moisture vs. 7%; $F_{1,23} = 5.754$, $P = 0.024$, Fig. 2D).

Coupled responses of green and brown assemblages and links to plant traits

Green and brown assemblages showed parallel responses to morphological variation within *Baccharis* shrubs (Fig. 1). Prostrate morphs had higher richness and abundances of both foliar and litter arthropods, with a similar trend for soil bacteria, but no effect on soil fungi. The average community dissimilarity for foliar arthropods, litter microarthropods, and soil bacteria was >68% between morphs. Furthermore, the abundance of litter arthropods was positively correlated with the abundance of foliar arthropods (Table 2, Appendix B).

Detailed analyses suggested different underlying mechanisms driving green vs. brown assemblage responses to plant morphotype. Overall, correlations of litter and foliar arthropod abundances with plant traits were in the same direction (either positive or negative) for 12 of 13 relationships, with the single exception of leaf N (Table 3). Although the correlations were nonsignificant following sequential Bonfer-

TABLE 3. Spearman correlation coefficients (r) between foliar arthropods, litter, and plant traits in a common-garden experiment on *Baccharis pilularis*.

Trait	Foliar arthropod abundance	Foliar rarefied richness	Litter arthropod abundance	Litter rarefied richness	Bacteria Chao richness
Plant height	−0.212 (70)	−0.116 (70)	−0.364 (40)	0.243 (39)	−0.035 (19)
Crown circumference	**0.732***** (70)	0.237 (70)	**0.570***** (40)	−0.207 (39)	0.446 (19)
Stem diameter	−0.018 (70)	−0.163 (70)	−0.192 (40)	0.306 (39)	0.096 (19)
Light	**−0.532***** (54)	−0.185 (54)	**−0.529**** (37)	0.309 (36)	−0.604 (14)
Soil temperature	**−0.501***** (69)	−0.240 (69)	**−0.657***** (39)	0.127 (38)	−0.589 (19)
Leaf N	0.008 (33)	−0.276 (33)	−0.285 (22)	0.320 (22)	
Leaf C:N	0.066 (33)	0.366 (33)	0.352 (22)	−0.294 (22)	
Litter N	−0.408 (18)	−0.468 (18)	−0.612 (14)	0.178 (14)	−0.443 (15)
Litter C:N	0.494 (18)	0.445 (18)	**0.742**** (14)	−0.319 (14)	0.418 (15)
Litter moisture	0.418 (19)	**0.635**** (19)	0.401 (14)		
Litter depth	**0.504***** (70)	0.156 (70)	0.405 (40)	−0.032 (39)	0.542 (19)
Soil N	0.066 (16)	0.179 (16)	0.037 (18)	−0.101 (17)	
Soil C:N	0.088 (16)	0.032 (16)	0.083 (18)	0.005 (17)	

Notes: Correlations that are significant after sequential Bonferroni corrections are indicated in boldface type. The number in parenthesis indicates sample size (number of shrubs) for each correlation. Correlations were not performed for empty cells, due to low sample size.

** $P < 0.001$; *** $P < 0.0001$.

roni correction, trends for bacteria richness were similar to those for arthropod abundances, showing negative associations with both understory light and soil temperature (Table 4). Foliar arthropods, litter arthropods, and soil bacteria also showed positive trends with litter depth (Table 3). We note that with higher sample sizes and increased power, these trends may become statistically significant. However, refined analyses of the strongest correlations detected in Table 3 showed that the key drivers differed between community assemblages.

For foliar arthropod abundance, crown circumference ($F_{1,67} = 26.9$, $P < 0.0001$; morph $F_{1,67} = 2.5$, $P = 0.119$), soil temperature ($F_{1,66} = 4.5$, $P = 0.039$; morph $F_{1,66} = 10.2$, $P = 0.002$), and litter depth ($F_{1,67} = 13.0$, $P = 0.0006$; morph $F_{1,67} = 19.3$, $P < 0.0001$) remained significant predictors after architectural morph was included in statistical models. Of these three plant traits, crown circumference appeared to be the strongest driver of foliar arthropod abundance, as it was the only trait to render the effect of architectural morph nonsignificant when morph was included in the model (Table 3), and had the highest correlation coefficient with foliar arthropod abundance (Table 2). Interestingly, light level under the canopy was the only trait that appeared to affect foliar arthropods differently under the two morphs, as evidenced by a significant interaction between light and morph (Table 4); erect forms showed no significant relationship between foliar arthropod numbers and light (Pearson $r = 0.20$, $P = 0.36$, $n = 24$), whereas prostrate forms had a negative correlation (Pearson $r = -0.39$, $P = 0.03$, $n = 30$). In contrast to results for foliar arthropods, litter arthropod abundances appeared to be affected mainly by soil temperature, which was the only trait that remained a significant predictor once architectural morph was added to the analysis (soil temperature $F_{1,36} = 7.9$, $P = 0.008$; morph $F_{1,36} = 1.1$, $P = 0.305$) and which had the largest correlation coefficient of the traits examined (Table 3).

TABLE 4. Results from general linear models exploring relationships between plant architectural-related traits and responses of green and brown assemblages (Proc GLIMMIX using restricted maximum likelihood in SAS v. 9.3 [SAS Institute 2011]), following Rudgers and Clay (2008).

	log(foliar arthropod abundance)			log(litter arthropod abundance)		
	df	χ^2	P	df	χ^2	P
Crown circum.	1, 67	26.9	<0.0001	1, 37	1.3	0.261
Morph	1, 67	2.5	0.115	1, 37	2.9	0.089
Light under canopy	1, 50	1.6	0.201	1, 34	0.1	0.722
Morph	1, 50	18.5	<0.0001	1, 34	7.1	0.008
Light × morph	1, 50	4.2	0.040		not tested	
Soil temperature	1, 66	4.5	0.039	1, 36	7.9	0.005
Morph	1, 66	10.2	0.002	1, 36	1.1	0.298
Litter depth	1, 67	13.0	<0.001		not tested	
Morph	1, 67	19.3	<0.0001		not tested	
Litter C:N		not tested		1, 11	1.2	0.274
Morph		not tested		1, 11	1.7	0.193

Note: Only models cases in which the interaction was statistically significant are presented.

PLATE 1. (Left) Erect and (right) prostrate morphotypes of *Baccharis pilularis* growing in a common garden in Bodega Bay, California, USA. Photo credit: G. M. Crutsinger.

DISCUSSION

1. *How does intraspecific variation within a dominant plant influence the diversity and composition of green vs. brown assemblages?*—Genetically based variation in morphology within *Baccharis* had a strong influence on the diversity and composition above- and belowground communities in coastal California dunes. Variation in susceptibility to galling insects between erect and prostrate morphs was consistent with prior results (Rudgers and Whitney 2006), demonstrating that community responses to genetic variation can persist on the timescale of decades. While foliar arthropod responses to genetic variation have now been observed in variety of host-plant study systems (see Whitham et al. 2012 for a review), litter microarthropod responses were surprisingly strong in our study relative to prior reports from other systems. For example, microarthropods did not respond to variation in litter of either turkey oak (*Quercus laevis*; Madritch and Hunter 2005) or goldenrod (*Solidago altissima*; Crutsinger et al. 2008), but did respond to genetic relatedness within the tropical tree, *Brosimum alicastrum* (Zytynska et al. 2011). Past studies have typically placed the same amount of litter in a common environment for relatively short time periods (e.g., Crutsinger et al. 2008) and often focus on litter quality differences (Madritch and Hunter 2005, Crutsinger et al. 2008, Schweitzer et al. 2011). Here, erect and prostrate *Baccharis* morphs varied in litter production, depth, and quality and the effects have accumulated for more than a decade in our experiment. These differences between morphs, combined with the considerable differences in the understory microclimate (darker moister conditions under prostrate morphs) likely accounted for the strong litter microarthropod responses, and suggest that short-term studies may be insufficient for understanding how brown assemblages respond to intraspecific genetic variation in plants.

Similarly, very different soil bacterial communities developed beneath erect vs. prostrate *Baccharis* morphs. Soil microbial responses to plant genetic variation have also been observed within cottonwoods (*Populus* hybrid zone; Schweitzer et al. 2005, 2011) and aspen (*Populus tremuloides*; Madritch and Lindroth 2011). While we found no difference in the soil fungal community, other studies have observed that ectomycorrhizal fungi can respond to intraspecific variation in trees such as spruce (*Picea abies*; Korkama et al. 2006) and pinyon pine (*Pinus edulis*; Gehring and Whitham 1994). Because our fungal sequencing captured primarily saprotrophs, it is possible that obligate biotrophs, such as mycorrhizal fungi, respond more strongly to genetic variation in host plants than do other fungal groups.

2. *How does intraspecific variation influence above- vs. belowground processes and microclimate?*—Morphological variation within *Baccharis* was a key driver of local

processes, including estimated aboveground biomass production, litter inputs and quality, and decomposition. Genetic variation in plant productivity is a common (Hughes et al. 2008, Bailey et al. 2009) and fairly well established phenomenon, particularly in agricultural and forestry systems (Tooker and Frank 2012). We suspect that the high winds at BMR limit vertical growth of erect shrubs through wind pruning, as has been shown at a nearby site (Miller and Weis 1999), while predominantly horizontal spread allows prostrate shrubs to escape such limitations. Larger crown sizes were associated with greater annual litter inputs and a deeper litter layer under prostrate shrubs (Crutsinger et al. 2010); crown circumference and litter depth were positively correlated throughout the common garden. Moreover, we lost fewer litterbags to wind beneath prostrate shrubs, suggesting the importance of wind buffering in the understory environment. Prostrate morphs might also trap more of the litter produced, further intensifying differences in understory litter accumulation. Surprisingly few studies present data on genetic variation in litter inputs. We found similar variation from only one other system, a hybrid zone between two *Populus* species, where annual litter inputs varied by >80% depending on the productivity of individual trees (Lojewski et al. 2012).

The effects of *Baccharis* morphotype on decomposition in our lab incubation assay were relatively weak compared to results from other studies (Madritch et al. 2006, Crutsinger et al. 2009). For example, Silfver et al. (2007) found a 28% difference in decomposition among birch (*Betula pendula*) genotypes after a 12-week incubation. Our results suggest that a 14% difference in litter C:N ratio has little effect on litter breakdown in a common environment, and that the microenvironments of *Baccharis* morphotypes are critical to local ecosystem fluxes. Although we did not measure defensive compounds in the leaves or litter, the genus *Baccharis* is reported to have trichothecenes, diterpenes, triterpenes, and flavonoids (Grecco et al. 2010). Chemical analyses have not yet been performed on this species, and more research is needed to identify potential differences in secondary metabolites between erect and prostrate morphs. However, if major chemical differences exist, they do not appear to influence decomposition rates or associated soil C and N pools.

3. *Are there similar responses of green and brown assemblages to intraspecific variation, and are these two webs responding to the same underlying mechanisms?*—Green and brown assemblages showed strikingly similar responses to genetic variation within *Baccharis* (Fig. 1). Yet, an important component of "genes-to-ecosystems" research, along with a trait-based approach to community ecology (Violle et al. 2012), is determining which traits predict community assembly (Hughes et al. 2008). Here, the combination of morph-specific differences in aboveground productivity and the understory abiotic environment accounted for green and brown responses.

Although the two assemblages responded in similar ways to *Baccharis* morphotype, above- and belowground communities were most strongly associated with different underlying traits. Foliar arthropod abundance was greater on prostrate shrubs, which had larger crowns than erect shrubs of the same age and initial size. With more arthropod individuals, prostrate shrubs, in turn, supported more foliar arthropod species (Fig. 1C; Srivastava and Lawton 1998). This result is consistent with other studies showing genetic variation in aboveground primary productivity to be a strong predictor of foliar arthropod richness and abundance (Crutsinger et al. 2006). Responses of litter microarthropods and soil bacteria, on the other hand, correlated with differences in litter depth and the understory microclimate. We did, however, find that the abundance of litter and foliar arthropods were positively correlated (Appendix B), raising the possibility for direct effects of one assemblage on the other. For example, frass deposition from foliar arthropods could influence litter and soil communities (Pringle and Fox-Dobbs 2008), and facilitate faster decomposition rates observed under prostrate morphs. Moreover, plant traits that affect both assemblages are correlated with each other, as well as with abiotic conditions, as part of the general phenotypic differences between the morphs. For example, greater biomass of prostrate shrubs provided more foliage for the green assemblage, more litter for the brown assemblage, and wetter understory conditions for soil bacteria. Taken together, our findings support an important role for intraspecific genetic variation in structuring communities and suggest these effects occur through a suite of different plant-associated traits and microenvironments, rather than through a single "silver bullet" trait.

Conclusions

Our intra-specific results correspond with interspecific work in coastal California dunes revealing that different shrub species can act as ecosystem engineers by shaping the abiotic environment beneath their canopies, thereby altering local communities and processes (Preisser et al. 2006, Cushman et al. 2010). Our system also parallels the pinyon pine (*Pinus edulis*)-dominated-ecosystem in which genetic variation associated with susceptibility to insect attack is correlated with differences in plant architectural morphology (Whitham and Mopper 1985). Architectural differences in pines have been shown to influence a wide diversity of species, including arthropods, birds, and soil microbes (Whitham et al. 2006), as well as rates of nutrient cycling (Chapman et al. 2003) and microclimate (Classen et al. 2005). While most studies have focused on the ecological consequences of genetic variation in phytochemistry, there is growing support that architecture is an important driver of variation in terrestrial communities and ecosystems.

Studies on plants at both the intra- and interspecific levels have typically observed weaker effects on belowground communities (brown assemblage) compared to their aboveground counterparts (green assemblage [Bailey et al. 2009, Sherber et al. 2010]). In contrast, erect and prostrate *Baccharis* shrubs supported unique assemblages of foliar, litter, and soil communities; in addition, the magnitude of community compositional differences was maintained from crown to soil. There are many next steps in understanding the genes involved in shaping plant architecture, the population genetics of the *Baccharis* system, and further elucidating the underlying mechanisms. Nevertheless, our study demonstrates that merging above- and belowground linkages with a "genes-to-ecosystem" perspective through the use of long-term common gardens can yield novel insights into how communities are structured.

Acknowledgments

We thank J. Sones at BMR for valuable research assistance. N. Ask and J. Knisley assisted with litter collections, and the Crutsinger lab provided valuable comments on the manuscript. G. M. Crutsinger was supported by the Miller Institute for Basic Research in Science, as well as an NSERC Discovery grant. J. A. Rudgers was supported by a UC–Davis Matthias Award, BMR travel awards, and the Godwin Assistant Professorship at Rice University.

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Supplemental Material

Appendix A

Extended methods for soil microbial extraction and analyses, along with understory water dynamics (*Ecological Archives* E095-034-A1).

Appendix B

A figure depicting the correlation between foliar arthropod abundance and litter microarthropod abundance (*Ecological Archives* E095-034-A2).