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Genetically based latitudinal clines in *Artemisia californica* drive parallel clines in arthropod communities

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Abstract. Intraspecific variation in plant traits has been clearly shown to drive the structure of associated arthropod communities at the spatial scale of individual plant populations. Nevertheless, it is largely unknown whether plant trait variation among populations drives landscape-scale variation in arthropod communities, and how the strength of such plant genetic effects compares to, and interacts with, those of environmental variation. We documented the structure of arthropod communities on *Artemisia californica* for two consecutive years in a common garden of plants sourced from five populations along a 5° latitudinal gradient and grown under precipitation treatments approximating the four-fold difference between the north and south range margins for this species. Previous study of plant traits from this garden documented clinal genetic variation, suggesting local adaptation to this environmental gradient, as well as effects of precipitation manipulation that were consistent among populations (i.e., no genotype-by-environment interaction). Within the common garden, arthropod density, evenness, and diversity increased clinally with population source latitude, and arthropod community composition (i.e., species relative abundance) showed a north-south divide. The 2.6-fold cline of northward increase in arthropod density in the common garden was mirrored by a 6.4-fold increase in arthropod density on wild plants sampled along the species range. In contrast to the strong influence of plant genotype, the precipitation manipulation only influenced arthropod community composition, and plant genetic effects on arthropods operated independently of precipitation regime (no genotype-by-environment interaction). Accordingly, we conclude that the strongest driver of landscape-level variation in arthropod communities in this foundational plant species is not variation in the abiotic environment itself, but rather variation in plant traits underlain by the evolutionary process of plant local adaptation.

Key words: Artemisia californica; *arthropod community; California sagebrush; clinal adaptation; common garden experiment; foundation species; latitudinal gradient; precipitation manipulation.*

Introduction

Arthropods depend on plants for both food and refuge and, as a result, are sensitive to variation in plant functional traits. This fact is exemplified by the numerous studies documenting how intraspecific variation in plant traits scales up to drive associated arthropod communities (Johnson and Agrawal 2005, Wimp et al. 2007, Robinson et al. 2012). Through such effects, different plant genotypes systematically differ in the density, richness, evenness, and composition (i.e., relative species abundance) of associated arthropod communities. These community-wide effects of plant genotypes may be particularly strong for foundation plant species (Whitham et al. 2003), which create consistent physical structure throughout an ecosystem and provide resources for a wide range of associated species (Ellison et al. 2005).

Although genetically based plant traits likely influence arthropod community structure at small spatial scales, it is essentially unknown whether landscape-scale variation in plant traits drives parallel patterns of landscape-scale variation in arthropod community structure, including β-diversity. The response of arthropods to plant genetic variation among populations has been documented, but such studies are typically conducted within a common garden in a single site and environment (but see Pennings et al. 2009, Robinson et al. 2012, Johnson and Agrawal 2005). Accordingly, it is unknown whether the observed effects scale up to drive patterns of variation in arthropod community structure across landscapes (Tack et al. 2012). Perhaps the best evidence for landscape-scale dynamics comes from the few studies of wild-grown plants demonstrating positive correlations between genetic similarity (e.g., shared genetic markers) and arthropod community structure across a range of spatial scales (Bangert et al. 2008). Such studies, in combination with the assumption of a declining genetic similarity with distance, are suggestive that landscape-scale variation in plant genetics may underlie parallel patterns in arthropod communities.

Predicting landscape-scale effects of plant genetics on arthropod communities is especially challenging because such dynamics are driven not by plant genetics alone, but

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also by environmental variation and plant genotype-by-environment interactions (Johnson and Agrawal 2005). The biotic and abiotic environments affect arthropod communities not only directly, but also indirectly via the plastic responses of plants (Trotter et al. 2008, Netherer and Schopf 2010, Gornish and Tylianakis 2013). Such plant responses include environmental effects on plant functional traits such as growth, plant nutritional quality, and resistance to herbivory (Lindroth et al. 1993). Similarly, plant genotype-by-environment interactions affect arthropod communities when plant genotypes differ in their plastic responses to the environment (Johnson and Agrawal 2005, Mooney and Agrawal 2008, Abdala-Roberts et al. 2012). Consequently, while landscape-level variation in plant genetics may underlie parallel patterns in arthropod communities, the strength of such effects relative to environment and genotype-by-environment interaction is unclear.

Precipitation regime is a central feature of any environment and may shape arthropod community structure. Such effects may be direct, as water availability and loss are fundamental physiological challenges for arthropods. Yet precipitation regime may have equally strong indirect effects due to changes in plant phenotypes. Water availability is perhaps the key selective force shaping the evolution of plants in arid environments (Niklas 1997) and influencing traits related to primary production (Larcher 2003, Grant et al. 2005, Nicotra et al. 2007), reproductive output (Sultan and Bazzaz 1993, Thompson 2005), phenology (Woods et al. 2012), as well as trophic interactions (e.g., plant defenses; Cunningham et al. 1999, Stamp 2003). Similarly, the plastic responses of plants to altered precipitation regime can indirectly alter arthropod community composition (Trotter et al. 2008). Through such direct and indirect effects, precipitation regime may thus be a fundamental driver of landscape-scale variation in arthropod community structure.

In this study, we examine the consequences of landscape-scale plant genetic variation, precipitation regime, and their interactive effects for arthropod community composition. We studied *Artemisia californica*, a foundation species in California's coastal sage scrub community, with respect to its distribution along a 5° latitudinal gradient (700 km) characterized (from south to north) by a decrease in temperature and interannual precipitation variability, and an increase in precipitation (Pratt and Mooney 2013). We grew plants sourced from five populations in a single common garden, under contrasting treatments approximating the northern and southern precipitation regimes. Our previous work (Pratt and Mooney 2013, Pratt et al. 2014; summarized in Table 1) shows that *A. californica* functional traits varied based upon clinal genetic effects, indicative of plant local adaptation, as well as the effects of manipulated precipitation regime. These genetic and environmental effects were of approximately equal magnitude and, for most traits, there were no detectable genotype-by-environment interactions. Here we conduct parallel analyses for arthropod community structure, and present results from the sampling of arthropods from wild plants along the species distribution. In so doing, we address four questions based upon our past findings: (1) Is there clinal population-level variation in *A. californica* arthropod community structure as has previously been documented for plant traits? (2) Are there effects of precipitation regime on arthropod community structure as has previously been documented for plant traits? (3) How does the magnitude of plant genetic effects compare to those of precipitation regime on arthropod community structure, and do plant genetic effects depend upon precipitation regime, acknowledging this may be unlikely because genotype-by-environment interactions were undetectable for plant traits? Finally, (4) are patterns of genetic variation in arthropod community structure observed in the garden manifest in sampling of wild-grown plants from the population source sites? Overall, this study significantly advances our understanding of the mechanisms by which landscape-scale genetic variation in plant traits drives parallel patterns of variation in arthropod community structure.

Materials and Methods

Study system

California sagebrush (*Artemisia californica* Less., Asteraceae) is a foundation species (sensu Dayton 1972) in coastal sage scrub (CSS) habitats, ranging approximately 1000 km along a five-fold precipitation gradient from Northern Baja, Mexico (average annual precipitation: 20 cm) to Mendocino County, California (average annual precipitation: 103 cm). This plant is host to an abundant and diverse community of arthropods (Burger et al. 2003, Wolkovich 2010). The present work, based upon five populations of *A. californica* distributed over 700 km in southern and central California (32°52′ N to 37°50′ N latitude), represents 70% of its range and includes 85% of the precipitation gradient across which it occurs (Pratt and Mooney 2013). This gradient is characterized (from south to north) by ~3°C decrease in temperature, a fourfold increase in precipitation, a 61% decrease in interannual precipitation variability, and no detectable pattern for temperature variability (Pratt and Mooney 2013). *Artemisia californica* provides important foraging habitat for several vertebrate insectivore species of concern (e.g., coastal Cactus Wren, *Campylorhynchus brunneicapillus*; California gnatcatcher, *Polioptila californica*) and it is therefore a target of conservation and restoration efforts (Pratt and Mooney 2013).

Our previous work (Table 1) shows clinal genetic variation in flowering date, water use efficiency, leaf %N, C:N ratio, and terpene concentration. In addition, leaf terpene composition (i.e., compound relative abundance) varied clinally, i.e., pairwise similarity in leaf terpene composition between populations decreased with geographic distance (Pratt et al. 2014). There were effects of precipitation

TABLE 1. Summary of results from Pratt and Mooney (2013) and Pratt et al. (2014) describing plant traits of *Artemisia californica* in a common garden of plants sourced from five populations along the California coast and grown in southern (low) and northern (high) precipitation regimes.

Trait	Site effects, statistical		South vs. north effects, genetic (G)		G vs. E	Low vs. high precipitation effects, environmental (E)	
	Precipitation	Clinal					
Performance							
Plant volume (m^3)	S, P, S × P	S > N	**1.24 (0.208)**	**0.741 (0.161)**	<	**1.27 (0.156)**	**0.666 (0.165)**
Thousands of flowers	P, S × P		310 (94)	364 (78)	<	**223 (79)**	**425 (75)**
Leaf-level traits							
Water content (%)	P		70.2 (1.29)	72.8 (1.19)	<	**67.7 (0.975)**	**73.2 (0.950)**
SLA (cm^2/g)	P		117 (4.82)	128 (4.19)	<	**114 (2.82)**	**131 (2.63)**
Midday water potential (Mpa)			−1.80 (0.156)	−1.79 (0.157)	–	−1.73 (0.167)	−1.70 (0.166)
WUE (Delta)	S	S > N	**21.9 (0.211)**	**20.9 (0.175)**	>	21.1 (0.119)	21.6 (0.109)
$\delta^{15}N$			3.17 (0.490)	3.37 (0.480)		2.83 (0.475)	3.58 (0.473)
Percent N	S, P	S < N	**2.10 (0.103)**	**2.62 (0.086)**	>	**2.12 (0.058)**	**2.58 (0.053)**
Carbon:Nitrogen	S, P	S > N	**21.7 (0.792)**	**17.9 (0.667)**	>	**21.5 (0.477)**	**17.8 (0.443)**
Terpenes (μg/mg)	S	S > N	**183 (31.1)**	**98.5 (14.7)**	>	139 (17.7)	122 (15.4)
Phenology							
Flower date (day of year)	S, S × P	S > N	**294 (4.76)**	**262 (3.74)**	>	**274 (3.82)**	**272 (3.57)**

Notes: Mean (SE) trait values are shown for the northernmost and southernmost populations and for the two precipitation regimes. Site effects results indicate when effects of site (S), precipitation (P), and their interaction (S × P) were significant ($P < 0.05$; cell is blank if no significant effects). Where there were significant site effects, the significance ($P < 0.05$) of clinal regressions (population means regressed on latitude) are shown by indicating whether the cline was a southward increase (S > N) or northward increase (S < N) in the trait value, and the trait values for northern and southern populations are indicated in boldface type. Where there were significant precipitation effects the trait values are indicated in boldface type. The relative magnitude of genetic effects (southern vs. northern populations) and environmental effects (low vs. high precipitation) are indicated in the column titled G vs. E. SLA, specific leaf area; WUE, water use efficiency.

regime on flowering date, leaf water content, specific leaf area, %N, and C:N ratio. Overall, the magnitude of genetic and precipitation regime effects were approximately equal. Except for flowering date, there were no detectable plant genotype-by-precipitation regime interactions for any functional trait. Nevertheless, these interactions were significant with respect to two measures of plant performance, growth rate and flower production; in both cases, the magnitude of a population's plastic response to precipitation increased southward and closely tracked the interannual variability of the precipitation regime from which the population was sourced ($R^2 = 0.86$ and 0.99, respectively; Pratt and Mooney 2013). However, these aspects of plant performance are unlikely to affect arthropods directly; arthropods are quantified as a density, thus accounting for differences in growth; flowering occurs in the fall while we assess arthropods in the spring.

Experimental protocols

Common garden design.—The design of the common garden used for this experiment is described in detail elsewhere (Pratt and Mooney 2013, Pratt et al. 2014). Briefly, in spring 2008, we collected 20 cuttings from each of 20 *A. californica* plants in each of five source populations distributed along the environmental gradient described above; from south to north the source population sites were Scripps Coastal Reserve, San Diego, California, USA (32°52′ N, 117°14′ W; 95 m above sea level; 25 cm average annual precipitation [avg. precip.]; hereafter, "SD33"), Santa Monica Mountains National Recreation Area, Santa Monica, California (34°03′ N, 118°59′ W; 80 m above sea level; 32 cm avg. precip.; hereafter, "SM34"), Kenneth S. Norris Rancho Marino Reserve, Cambria, California (35°31′ N, 121°04′ W; 20 m above sea level; 50 cm avg. precip.; hereafter, "CAM35"), Wilder Ranch State Park, Santa Cruz, California (36°58′ N, 122°07′ W; 20 m above sea level.; 74 cm avg. precip.; hereafter, "SC37"), and Rodeo Beach, Golden Gate National Recreation Area, San Francisco, California (37°50′ N, 122°32′ W; 57 m above sea level; 95 cm avg. precip.; hereafter, "GG38"). To minimize non-genetic (maternal) effects associated with plants cloned from cuttings (Roach and Wulff 1987), rooted cuttings were grown in a greenhouse and common garden for 24 months before the onset of data collection. Approximately 80% of cuttings died due to fungal attack. In December 2008, surviving plants ($n = 152$; SD33 = 17, SM34 = 43, CAM35 = 33, SC37 = 31, GG38 = 28) were transferred into common garden plots at a site in Newport Beach, California (33°39′ N, 117°53′ W; 16 m above sea level.; 28 cm avg. precip.) that is approximately 100 m from Newport Bay, 6 km inland from the ocean coastline and within 10 m of CSS habitat including *A. californica*.

The common garden consisted of three blocks, each containing a pair of 5 × 6 m plots, with 2 m between plots

and 4 m between blocks. The total sample size for each source population was evenly distributed among plots and randomized within each plot. In December 2009, we implemented a precipitation manipulation at the plot level using overhead sprinklers to supply supplemental water to one plot within a block (hereafter high precipitation plots); the remaining plot received ambient precipitation (low precipitation plots). We applied water equivalent to the precipitation difference between the southern and northern extremes of the species range (70 cm annually), mimicking the seasonal cycles of precipitation in our Mediterranean climate with 56% applied in winter (December–February, 13 cm/month), 22% applied in spring (March–May, 5 cm/month), 1.5% applied in summer (June–August, 0.75 cm/month), and 20.5% applied in fall (September–November, 4.5 cm/month; data from Western Regional Climate Center, *available online*[2]).

Arthropod sampling and identification.—We sampled arthropods on 2–8 May 2010 and 2–6 May 2011 from all surviving plants (96.7% for 2010, $n = 147$; 96.0% for 2011, $n = 146$), a sampling period that corresponds with our collection of data on plant performance (growth and flowering), functional traits, and phenology as previously reported by Pratt and colleagues (Pratt and Mooney 2013, Pratt et al. 2014). To collect arthropods, we vacuumed each shrub exhaustively, up to 3 min for the largest plants (range: 49–180 s), with an electric shop vacuum (3.5 HP Ridgid model #WD0970). A fine mesh bag was inserted into the vacuum nozzle to collect arthropods and plant chaff. Bags were placed on ice immediately after sample collection and transferred to a −20° freezer later that same day. Arthropods were subsequently separated from plant chaff and stored in 70% ethanol and identified to morphospecies within family (Oliver and Beattie 1996) and, for the most abundant arthropods, to the genus or species level.

Each morphospecies was assigned to one of nine guilds based on published accounts for the taxonomic groups. Predatory guilds consisted of: (1) web-spinning spiders (Araneae, 17 species from five families); (2) hunting spiders (Araneae, 28 species from six families); (3) parasitoids (Hymenoptera, 35 species from 11 families) and other predators (e.g., larval and adult Coccinellidae beetles). Herbivorous guilds consisted of (1) phloem-feeding herbivores (Hemiptera, 38 species from nine families); (2) chewing herbivores (e.g., Orthoptera, juvenile Lepidoptera); and (3) other herbivores (i.e., pollen and nectar feeders, and adult individuals of galling species sampled by vacuum). The remaining guilds included (1) omnivores (mostly Hemiptera, Miridae); (2) detritivores (e.g., Entomobryidae); and (3) incidentals (e.g., non-feeding, adult Diptera and Hymenoptera; Appendix S1). Although mirids (Hemiptera, Miridae) are sometimes omnivorous (Wheeler 2001), we categorized the four most abundant mirid species as herbivores based upon the assumption that herbivorous taxa should be substantially more abundant than predators; these four taxa were cryptic and all among the 10 most abundant in each year. Because we could not always assign juvenile morphospecies to an adult form, we only include juveniles in our measures of arthropod density and not other community traits (i.e., species richness, evenness, diversity, and community composition).

Wild arthropod sampling.—We sampled the arthropod communities of wild-grown *A. californica* from plants at five natural CSS sites distributed along the California coast in May 2014. The four southernmost sites were the same as described in *Common garden design*, while the northernmost site was located at Devils Slide, Pacifica, California (37°36′ N, 122°31′ W; 51 m above sea level.; 78 cm avg. precip.; hereafter, "DS37"), 30 km south of the northernmost site from the common garden (GG38, see *Common garden design*). At each site, 15 plants were chosen haphazardly within an area of approximately 1 ha, their sizes ranging from 0.5 m^3 to 1.5 m^3 to correspond to the range of plant volumes in the common garden. Arthropods were collected and samples assessed as described in *Arthropod sampling and identification*, with the exceptions that we used a battery-powered backpack aspirator (Bioquip Products, Rancho Dominguez, California, USA) and only total arthropod density was assessed.

Statistical analyses

Arthropod density, richness, evenness, and diversity.—We tested for the main and interactive effects of source population and precipitation regime over time (2010, 2011) on the density (individuals/m^3 plant volume) of total herbivores (three guilds; phloem-feeding, chewing, and other herbivores), total predators (four guilds; web-spinning spiders, hunting spiders, parasitoids, and other predator), and total arthropods (all nine guilds) using repeated-measures ANOVA in SAS (PROC MIXED; SAS Institute 2010). We did not analyze the density of other guilds (omnivore, detritivore, and incidentals) because their abundance was low (~10% of individuals, combined) compared to predators and herbivores (~90% of individuals, combined). The model included all two- and three-way interactions between source population, precipitation regime, and year, with individual plant, block, and the precipitation-by-plot interaction as random effects. Including the precipitation-by-plot interaction is necessary because the precipitation regime was applied at the whole plot level to one of each pair of plots and thus gives the appropriate degrees of freedom for testing the effect of the precipitation manipulation. To meet ANOVA assumptions of normally distributed residuals and homogeneity of variances, all density measurements were log-transformed. A significant source population effect indicates genetic differences among populations, a significant precipitation effect indicates trait plasticity, and a significant source

[2] http://www.wrcc.dri.edu/

population-by-precipitation interaction indicates differences among populations in the degree of plasticity. A significant two- or three-way interaction with year indicates that the main and interactive effects of source population and precipitation regime were dependent upon sampling year. Species richness, Shannon-Weiner diversity (H') and Pielou's evenness (J') were calculated in Primer 6 (Anderson et al. 2008), using data on the abundance of all adult morphospecies summed across both sampling years. We pooled data for these community descriptors across guilds and years as these measures are more sensitive to sampling effort, whereas estimates of arthropod density can more accurately be assessed in a single year. We tested for main and interactive effects of source population and precipitation regime on species richness, diversity and evenness with two-way ANOVAs identical to those above, but not including year or interactions with year.

Where ANOVAs showed a significant main effect of population for an arthropod community attribute, we in turn evaluated whether this pattern of population variation was clinal. In addition to qualitatively inspecting the pattern of variation among populations for clinal patterning (e.g., monotonic increase or decrease with latitude), we also statistically tested for a clinal pattern, regressing population means for each dependent variable (across both precipitation regimes) against latitude using PROC REG (SAS Institute 2010). Nevertheless, these statistical tests must be interpreted cautiously; the small sample size of five populations results in relatively low statistical power (high Type II error). Accordingly, nonsignificant regressions do not rigorously demonstrate a lack of clinal pattern, and in such cases it is difficult to reach a definitive conclusion.

Because two species of herbivore were numerically dominant in our arthropod community samples (see below), we repeated analyses of herbivore density, total arthropod density, species richness, evenness and diversity with these two taxa removed using the same ANOVA and regression models described above.

Arthropod community composition.—Differences in arthropod community composition (i.e., species relative abundance), independent of differences in overall abundance, were assessed with data on the relative abundance of individual adult morphospecies summed across years. We pooled data for this analysis of community composition across years as these measures are more sensitive to sampling effort, whereas estimates of arthropod density can more accurately be assessed in a single year. To examine the main and interactive effects of source population and precipitation regime on community composition, we conducted a permutational multivariate ANOVA (PERMANOVA) on the Bray-Curtis dissimilarity matrix for the total adult arthropod community (231 morphospecies) and for the arthropod community summarized by feeding guilds (nine guilds, see *Arthropod sampling and identification*). The PERMANOVA model incorporated the same random effects as the ANOVA model. The species-level approach, while incorporating important variation among individual taxa within guilds, can make it difficult to determine the functional basis for how plant source populations vary. Looking at the contribution of aggregate patterns across morphospecies with similar life-history strategies (guilds) in driving source population differences in community composition provides a more mechanistic understanding of what drives such differences. Analyses were performed using PRIMER 6+ PERMANOVA (Anderson et al. 2008). We conducted the PERMDISP procedure on the Bray-Curtis dissimilarity matrices to test the assumption of equal dispersion/variance among groups (Anderson and Walsh 2013). Source populations differed significantly in their dispersion/variance ($F_{4,143} = 12.104$, $P = 0.0001$). With unbalanced designs, PERMANOVA can suffer from inflated Type-I or Type-II error, depending on whether unequal variance is in the group with the largest or smallest sample size (Anderson and Walsh 2013). Our design was unbalanced (sample size varying from 17 to 43 among populations), and the two populations with the highest variance had the smallest and largest sample size. Accordingly, it is difficult to judge whether these analyses suffered from inflated Type-I or Type-II error. Precipitation regimes did not differ in dispersion/variance ($F_{1,146} = 1.15$, $P = 0.34$). All PERMANOVA tests were based upon 9999 permutations of raw data (relative abundances of morphospecies or guilds). When we found significant differences among source populations in arthropod community composition, we then conducted a pairwise PERMANOVA, which uses permutation tests with t-statistics, to determine which pairs of populations differed from each another.

To examine which morphospecies or guilds contributed to differences observed among source populations and between precipitation regimes, we used the similarity percentages (SIMPER) routine in PRIMER (Anderson et al. 2008). SIMPER analysis calculates the average contribution of individual components to the average dissimilarity between samples or groups (i.e., source populations and precipitation regimes) that are known to differ based upon PERMANOVA results.

Our analyses (see *Results*) suggested that differences among source populations and between precipitation regimes were driven by the two numerically dominant species of phloem-feeding herbivores (species-level analysis) and the phloem-feeding herbivore guild (guild-level analysis). To explore these results, we calculated the proportion of total arthropods these two taxa (species-level analysis) and the phloem-feeding herbivores (guild-level analysis) represented for each sample, and tested how these proportions varied among source populations and between precipitation regimes using the same ANOVA models previously described.

To test for clinal patterns in arthropod community composition, we tested whether community dissimilarity between pairs of populations was positively correlated with the geographic distance separating populations. A

Mantel statistic (r) was calculated to measure the relationship between the matrices for arthropod community composition (Bray-Curtis dissimilarities of relative abundance for both guilds and morphospecies) and geographic distance (decimal degrees in latitude), and Monte Carlo randomization (9,999 permutations) using the ade4 package in R (R Core Team 2013). The small sample size for this analysis (i.e., $n = 5$ populations) makes this a weak test (high Type II error), and thus requires caution in interpreting nonsignificant results.

Latitudinal clines in wild arthropod density.—We first tested for population variation in total arthropod density using an ANOVA with PROC GLM (SAS Institute 2010). We then tested for a clinal pattern in the density of total arthropods (individuals/m^3 plant volume) in wild plants across the latitudinal gradient by conducting linear regressions between the population means and latitude using PROC REG (SAS Institute 2010).

Results

Overall, we identified 38,515 individual arthropods belonging to 231 morphospecies from 16 different orders and 84 families on *Artemisia californica* grown within a common garden (Appendix S1). Across both years, herbivores represented an average of 81.2% ± 0.7% (mean ± SE; range 26–100%) of total arthropod abundance with predators comprising 7.9% ± 0.4% (range 0–40%). Phloem-feeding herbivores were by far the most abundant guild, comprising 79.8% ± 0.7% (range 25–100%) of the total arthropod community. Thirteen morphospecies, all individually >1% of arthropod abundance, represented 80% of total arthropods across both years; the remaining 20% was comprised of morphospecies that individually represented <1% of total abundance. In both 2010 and 2011, the two most abundant morphospecies were *Empoasca decora* Delong and Davidson (Hemiptera, Cicadellidae) and *Proba* sp. 1 (Hemiptera, Miridae) making up 41.1% ± 0.9% (range 0–74%) and 14.2% ± 0.5% (range 0–51%) of total arthropod abundance, respectively.

Following our specific research questions, we describe the response of this arthropod community to the effects of (1) clinal population variation, (2) precipitation regime, (3) their interactive effects. We did not find significant three-way interactive effects of source population, precipitation regime, and year on any measure of arthropod density and therefore only describe main and two-way interactive effects below (Table 2). Except where otherwise noted, population-by-year or precipitation-by-year interactions were also non-significant (Table 2). Finally, we then describe (4) patterns of variation among wild-sampled plants.

Clinal source population effects.—Source populations varied in total, herbivore, and predator density (Table 2, Fig. 1a–c). Density increased clinally from south to north based on regressions between source population means and latitude (total arthropods $F_{1,4} = 80.65$, $P = 0.003$, $R^2 = 0.95$; herbivores only $F_{1,4} = 46.28$, $P = 0.0\ 07$, $R^2 = 0.92$; predators only $F_{1,4} = 35.08$, $P = 0.01$, $R^2 = 0.89$), with the mean of total arthropod density from the northernmost populations (GG38) being more than 2.6-fold greater than the southernmost populations (SD33; Fig. 1). We observed a significant two-way interaction between source population and year for total arthropod density and herbivore density (Table 2). All source populations had lower arthropod densities in 2011 than 2010, and in both years arthropod densities increased monotonically from south to north, but populations differed in the magnitude by which densities decreased between the two years. Repeating arthropod density analyses with the two most abundant species (*Empoasca decora* and *Proba* sp. 1) removed showed qualitatively identical results to those including these taxa (Appendix S2).

Arthropod species richness did not differ among source populations (Table 2; Fig. 1d). Arthropod species evenness (Pielou's J') and diversity (Shannon-Weiner H') differed among source populations (Table 2, Fig. 1e, f), with southern populations (SD33 and SM34) having lower evenness and diversity than northern populations (CAM35, SC37, GG38; according to post hoc Tukey

Table 2. F ratios from ANOVAs testing for the main and interactive effects of source population (S; $n = 5$), precipitation regime (P; $n = 2$), and year (Y; $n = 2$) on *Artemisia californica* arthropod density.

Category	df	Total density	Herbivore density	Predator density	Richness	J'	H'
Source population (S)	4, 130	**12.00*****	**10.86*****	**13.77*****	1.11	**6.11*****	**5.81*****
Precipitation (P)	1, 2	0.40	0.03	0.00	8.80†	1.11	0.35
S × P	4, 130	0.75	0.51	0.66	0.34	0.48	0.27
Year (Y)	1, 130	**29.68*****	**51.51*****	0.03			
S × Y	4, 130	**2.91***	**3.80****	1.37			
P × Y	1, 130	1.89	2.00	0.22			
S × P × Y	4, 130	0.52	1.29	1.78			

Notes: Arthropods were pooled across years for community measures including richness, evenness (J'), and Shannon-Weiner diversity (H') and we therefore report statistics from a reduced model. Values in boldface type are statistically significant.

†$P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

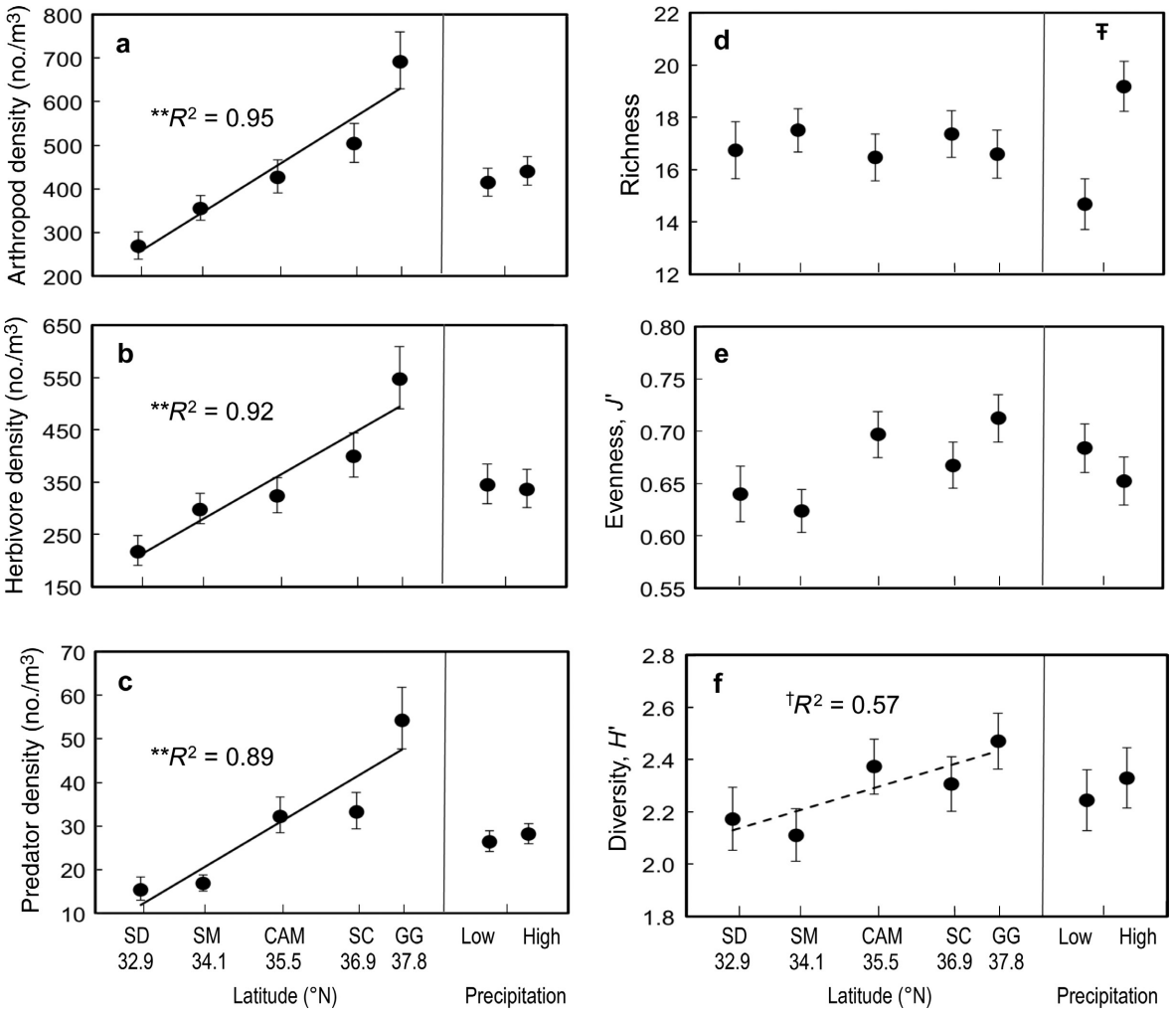

FIG. 1. Source population (n = 5) and precipitation regime (n = 2) means (± SE) for arthropod community responses from *Artemisia californica* grown within a common garden. Richness, the total number of morphospecies; J', Pielou's evenness; H', Shannon-Weiner diversity. For all traits where ANOVA results indicated significant differentiation among source populations and for which that variation was clinal, it is indicated with regression lines using the five population means and latitude. A dashed line indicates a marginally significant regression. Symbols next to R^2 values indicate the level of significance of the regressions and the main effect of precipitation: †$0.05 < P < 0.10$, *$P < 0.05$, **$P < 0.01$. We did not find a significant source population-by-precipitation interaction for any traits shown in Fig. 1.

tests). Variation in evenness and diversity showed a trend toward being clinal according to regressions between source population means and latitude, (evenness, $P = 0.10$; diversity, $P = 0.06$). Repeating these analyses with the two most abundant species (*Empoasca decora* and *Proba* sp. 1) removed, arthropod species evenness and diversity did not differ among source populations. Accordingly, the clines of decreasing evenness and diversity in the initial analyses were likely driven, at least in part, by changes in these two species.

The analyses of arthropod community composition using either all adult morphospecies or the community summed by guild gave qualitatively similar results (Table 3). Arthropod community composition differed between source populations (Table 3). The two southern populations (SD33 and SM34) hosted different arthropod communities than the three northern populations (CAM35, SC37, and GG38), but within these groupings populations did not differ from one another (according to pairwise PERMANOVA tests; Table 4). A clinal pattern in arthropod community composition was not detectable; Mantel tests found no relationship between population pairwise dissimilarities in arthropod community composition (as revealed from SIMPER analysis) and pairwise differences in source population latitude ($r = 0.13$, $P = 0.39$), but this interpretation requires caution as the small sample makes this an inherently weak test (i.e., a high probability of Type-II error).

SIMPER analyses were used to quantify the contributions of individual morphospecies or guilds to the pairwise

Table 3. PERMANOVA statistics for the main and interactive effects of source population and precipitation regime on *Artemisia californica* arthropod community composition, based on relative abundance.

Category	df	All adults	Guilds
Source population (S)	4,136	**3.34*** **	**2.79** **
Precipitation (P)	1,2	**5.05*** **	**2.43***
S × P	4,136	1.06	1.22

Notes: Boldface type highlights significant values. S, southern population; N, northern population.
*$P \leq 0.05$, **$P < 0.01$, ***$P < 0.001$.

dissimilarity among populations. For the species-level analysis, *Empoasca decora* Delong and Davidson (Hemiptera, Cicadellidae) and *Proba* sp. 1 (Hemiptera, Miridae), the two most abundant herbivore species (both phloem-feeding herbivores), were the primary taxa distinguishing among populations, explaining 16.9% and 9.0% (on average; Appendix S3), respectively, of the pairwise dissimilarity in community composition. For the guild-level analysis, phloem-feeding herbivores was the primary guild distinguishing among populations, explaining 34.8% (on average; Appendix S3) of the pairwise dissimilarity in community composition.

Analyses of the proportion of total arthropods represented by *Empoasca decora* and *Proba* sp. 1 (species-level analysis) and phloem-feeding herbivores (guild-level analysis) showed effects largely consistent with the conclusions from SIMPER analyses that these species and this guild drive a north-south divide in arthropod community structure (Appendix S2); source populations differed in these proportions, with the two southern-most populations having proportions greater than or equal to those of the three northern-most populations, and clinal regressions in turn demonstrated a nonsignificant pattern of southward increase.

Precipitation regime effects

Arthropod density (total, herbivore, and predator), evenness (Pielou's *J′*) and diversity (Shannon-Weiner *H′*) did not differ among precipitation regimes (Table 2, Fig. 1a–c, e, f), though there was a trend for increased species richness under high precipitation ($P = 0.09$; Table 2; Fig. 1d). Repeating these analyses with the two most abundant species (*Empoasca decora* and *Proba* sp. 1) removed, high precipitation increased species richness (marginally significantly), but also decreased evenness.

The analyses of arthropod community composition using either all adult morphospecies or the community summed by guild gave qualitatively similar results (Table 3). Arthropod community composition differed between precipitation regimes (Table 3). The pairwise dissimilarity was approximately equal in magnitude to the mean pairwise dissimilarity among populations, but less than both the maximum pairwise dissimilarity and the dissimilarity between the southern and northernmost populations (SD33 and GG38; Appendix S3).

SIMPER analyses were used to quantify the contributions of individual morphospecies or guilds to the pairwise dissimilarity between precipitation regimes. For the species-level analysis, *Empoasca decora* Delong and Davidson (Hemiptera, Cicadellidae) and *Proba* sp. 1 (Hemiptera, Miridae), the two most abundant herbivore species (both phloem-feeding herbivores), were the primary taxa distinguishing between precipitation regimes, explaining 35.0% and 17.0% (Appendix S2) of dissimilarity in community composition, respectively. For the guild-level analysis, phloem-feeding herbivores was the primary guild distinguishing between

Table 4. PERMANOVA statistics for pairwise tests for differences between source populations.

Groups	Comparison type	All adult morphospecies		Summed by guild	
		t	*P*	*t*	*P*
SD33, SM34	S-S	1.15	0.1905	0.98	0.3759
SD33, CAM35	S-N	1.73	**0.0045**	1.3	0.1468
SD33, SC37	S-N	1.69	**0.0059**	0.66	0.7579
SD33, GG38	S-N	2.01	**0.0004**	1.25	0.1902
SM34, CAM35	S-N	2.34	**0.0001**	2.99	**0.0003**
SM35, SC37	S-N	2.34	**0.0002**	1.9	**0.019**
SM34, GG38	S-N	2.75	**0.0001**	2.58	**0.0011**
CAM35, SC37	N-N	0.89	0.6262	1.35	0.1321
CAM35, GG38	N-N	1.05	0.3305	0.84	0.5487
SC37, GG38	N-N	1.18	0.1644	1.09	0.2944

Notes: Pairwise tests indicate that the arthropod community of *A. californica* shows a south-north divide. For adult morphospecies, populations within region did not differ from one another (S-S and N-N), but every across-region comparison indicated significantly different arthropod communities (S-N). For guilds, all significant differences among populations are across-region comparisons (S-N). Boldface type highlights significant values. S, southern population; N, northern population.

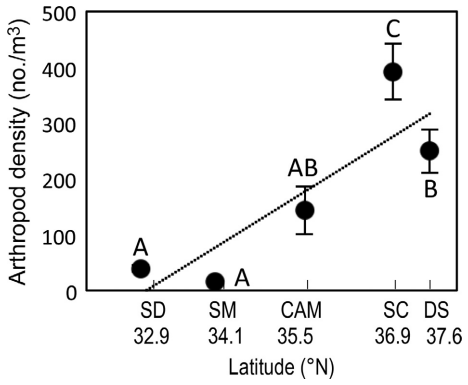

FIG. 2. Variation in mean (± SE) total arthropod density from wild plants sampled in five populations along the California coast (n = 15 plants per population). Clinal variation was marginally significant (P = 0.06, see *Results*) as indicated by the dashed line. Sampled populations are the same as those included in the common garden (Fig. 1), except for the northernmost population. Letters above the data points indicate post-hoc Tukey groupings.

precipitation regimes, explaining 9.1% (Appendix S2) of dissimilarity in community composition.

Analyses of the proportion of total arthropods represented by *Empoasca decora* and *Proba* sp. 1 (species-level analysis) and phloem-feeding herbivores (guild-level analysis) did not show effects consistent with the conclusions from SIMPER analyses that these species and this guild drive the precipitation regime effects on arthropod community structure (Appendix S2). These proportions did not differ between precipitation regimes, although the pattern was for higher proportions in the low than high precipitation regimes.

Interactive effects of clinal source population and precipitation regime

Arthropod density (total, herbivore and predator), richness, evenness (Pielou's J') and diversity (Shannon-Weiner H') were not affected by the source population-by-precipitation regime interaction (Table 2, Fig. 1a–f). Repeating these analyses with the two most abundant species (*Empoasca decora* and *Proba* sp. 1) removed did not alter this result (Appendix S2).

Arthropod community composition was not affected by the source-population-by-precipitation regime interaction whether assessed using all adult morphospecies or the community summed by guild (Table 3).

Latitudinal clines in wild arthropod density

Populations differed significantly in total arthropod density ($F_{4,70}$ = 21.43, P < 0.0001) and there was a significant increase in arthropod density with latitude ($F_{1,4}$ = 8.73, P = 0.04, R^2 = 0.66), with the mean of the northernmost population (DS37) being 6.4-fold greater than the southernmost population (SD33; Fig. 2). While we did not separately identify and analyze wild-collected herbivore and predatory taxa, herbivores and predators were highly correlated within our common garden (r = 0.56, n = 293, P < 0.0001) suggesting that this clinal pattern in total arthropod density is underlain by parallel clines in both herbivores and predators.

DISCUSSION

Overview

We found clinal plant genetic variation in the structure of the diverse arthropod community (231 species) associated with *A. californica* in an experimental common garden (Fig. 1). We demonstrate regional (north vs. south) variation in arthropod community composition (i.e., species and guild relative abundance), as well as northward clines of increasing evenness and diversity. We similarly found a northward cline of increasing arthropod density (2.6-fold increase; Fig. 1a) that was mirrored in our sampling of wild plants along the species range (6.4-fold increase; Fig. 2). In contrast, our four-fold manipulation of precipitation regime only influenced arthropod community composition, and these effects were weaker than, and did not mediate the effects of plant genetics (i.e., no genotype-by-environment interaction). Variation in arthropod community composition among populations and between precipitation regimes was largely attributable to an increase in the relative abundance of phloem-feeding herbivores for southern populations. Accordingly, the strongest driver of arthropod communities in this foundational plant species was not the abiotic environment itself, as indicated by our four-fold manipulation of precipitation regime, but rather the evolutionary process of plant local adaptation to that environment.

Plant genetic effects

Clinal variation in arthropod community structure within our common garden is necessarily driven by parallel clinal variation in plant functional traits (Pratt and Mooney 2013, Pratt et al. 2014; Table 1). Arthropod density and diversity (and marginally so for evenness) increased with population source latitude in the common garden (Fig. 1), and this pattern was mirrored by increasing arthropod density in wild-grown plants (Fig. 2). Similarly, arthropod community composition (i.e., species and guild relative abundance) showed a north-south divide within the common garden. These effects on arthropod diversity, evenness, and community composition were driven by a pattern of decreasing relative abundance of the phloem-feeding herbivores. Because of the relatively small number of populations studied in this experiment (i.e., n = 5), it was not possible to quantitatively assess which of the clinally varying *A. californica* traits drives clinal variation in arthropod community composition. Our previous work demonstrated northward clines of decreasing water use

efficiency, growth rate, plasticity in growth and flowering (in response to increased water availability), leaf monoterpene concentration, and C:N ratio, as well as increases in leaf %N and (a trend for) specific leaf area, and an earlier flowering date (Table 1). We speculate that variation in nitrogen concentration, terpene concentration, and terpene composition may underlie variation in arthropod community composition; the northward clines of increasing nitrogen and decreasing terpene concentration (Table 1) were associated with parallel northward increases in herbivore densities, and past work has demonstrated the importance of these traits to herbivores (reviewed by, e.g., Bryant et al. 1983, Price 1991, Herms and Mattson 1992). In addition, arthropod community composition appears to be more similar on plants from populations with more similar terpene composition; pairwise dissimilarity matrices for terpene composition (SIMPER analysis of terpene relative abundance; Pratt et al. 2014) were significantly correlated with those from arthropod community composition (SIMPER analyses for arthropod species relative abundance; this study) based upon a Mantel test (Mantel $r = 0.50$, $P = 0.04$), although the small sample size (i.e., $n = 5$ populations) makes this conclusion somewhat uncertain.

There are in turn several sources of evidence suggesting that clinal variation in plant traits is driven by local adaptation to the California coastal aridity gradient (Pratt and Mooney 2013, Pratt et al. 2014). Our previous study demonstrates phenotypic selection by water availability on monoterpene concentration, with contrasting patterns of selection under high and low precipitation that are consistent with decreasing monoterpene concentration for populations from relatively wet, northern source sites (Pratt et al. 2014). Similarly, leaf nitrogen content has been shown to increase with aridity (Pratt and Mooney 2013). More generally, genetically based clinal variation in species traits provides strong evidence that such traits either underlie local adaptation, or are correlated with traits that do so. Accordingly, we conclude that the aridity gradient occurring along *A. californica*'s coastal distribution drives clinal adaptation in these resistance-conferring traits, with resultant indirect consequences for the structure of associated arthropod communities.

Our study provides one of the few tests for the hypothesis that genetically based variation in plant traits at the landscape scale drives parallel patterns of variation in arthropod community structure. Robinson et al. (2012) found herbivorous arthropod abundance decreased with latitude in parallel with decreasing plant size, and that population differences in arthropod community composition were explained by plant traits that exhibited clinal variation (e.g., stem height, leaf area), but did not explicitly test for a corresponding clinal pattern in arthropod community composition. In addition, Woods et al. (2012) and Anstett et al. (2015) each documented genetically based latitudinal clines in defense traits and resistance, with *Asclepias syriaca* increasing northward (Woods et al. 2012) and *Oenothera biennis* increasing southward (Anstett et al. 2015). Furthermore, recent work shows that plant β-diversity (species turnover) is the major driver of butterfly phylogenetic β-diversity over elevational gradients (Pellissier et al. 2013). Accordingly, a small but growing body of evidence is indicating a key role for plant traits as drivers of landscape-scale variation in arthropod community composition.

Our results are consistent with theoretical predictions of increasing herbivore defense in plants at lower latitudes. Long-standing theory predicts that plant defense increases at lower latitudes based on stronger biotic interactions, including herbivory (Dobzhansky 1950). While evidence for increased defense at lower latitudes is mixed (Pennings et al. 2009, Moles et al. 2011, Rasmann and Agrawal 2011, Woods et al. 2012), our findings are consistent with this prediction, with plant defenses (i.e., high terpene concentration, low percent N) and resistance (herbivore density) increasing at lower (southern) latitudes within our study area. However, our sampling of wild-grown plants found 6.4-fold higher herbivore densities in the north (vs. south; Fig. 2), suggesting that clinal variation in herbivore pressure does not drive investment in plant defense as predicted by this theory. We envision two (non-mutually exclusive) explanations for our findings. Clinal variation in resistance and defense might arise from variation in tolerance to herbivory (Coley et al. 1985, Herms and Mattson 1992), such that southern populations in more resource-limited environments have lower tolerance and thus invest more in defense even though herbivore pressure is relatively low. Alternatively, defense traits may vary as a function of plant adaptation to this abiotic cline in aridity, with variation in resistance being a secondary outcome, and northward clines of increasing herbivore density being driven from the bottom-up.

Environmental effects

The relatively weak effects of precipitation regime on arthropods is surprising given the possibility for precipitation to affect arthropods both directly and indirectly through plant traits. In contrast to the strong influence of plant genetics, our four-fold manipulation of precipitation did not affect arthropod density, richness, evenness, or diversity, although it did affect arthropod community composition. High (vs. low) precipitation had strong effects on plant traits (Table 1), including increases in leaf percent water content, specific leaf area, and leaf percent N content and decreases in C:N ratio, although several other traits were unaffected, including leaf terpene concentration. Accordingly, strong effects of precipitation regime on plant traits did not manifest in the predicted indirect effects on arthropods. The weak responses of arthropod community composition to the plant traits altered by precipitation in turn suggests plant genetic effects on arthropod community composition are

underlain by those traits that did not respond to precipitation, unmeasured plant traits, or both.

Genotype-by-environment interactions

Precipitation regime did not mediate plant genetic effects on arthropod communities, as we found no evidence for genotype-by-environment interactions. These findings for arthropods parallel past findings for plant functional traits (Table 1); plastic changes in plant functional traits in response to precipitation regime were uniform among populations, i.e., we observed weak genotype-by-environment interaction for plant functional traits. Nevertheless, plasticity in growth and flowering in response to precipitation varied clinally, increasing toward the south.

Whereas a large body of literature has documented plant genetic effects on arthropod communities (e.g., Hochwender and Fritz 2004, Bangert et al. 2008, Robinson et al. 2012), far less is known about how such effects interact with environmental effects. Johnson and Agrawal (2005) compared arthropod communities of *Oenothera biennis* genotypes across five habitat types, while Mooney and colleagues (Mooney and Agrawal 2008, Smith et al. 2008, Abdala-Roberts et al. 2012) compared aphid communities of *Asclepias syriaca* genotypes in environments with and without ants and previous damage by leaf-feeding herbivores. In both systems, patterns of variation in arthropods among genotypes depended strongly on environment. In contrast, Keith et al. (2010) compared arthropod communities of *Populus angustifolia* genotypes across three years and found consistent plant genetic effects. Similarly, Tack et al. (2010) found minimal genotype-by-environmental interactions in oak gall communities, although genotype influences were generally weak. Our finding that precipitation regime did not mediate plant genetic effects on arthropods in *A. californica* is not surprising, given that there were no detectable genotype-by-environment interactions with respect to plant traits (Table 1). Based on our findings, and those of past studies (Johnson and Agrawal 2005, Mooney and Agrawal 2008, Keith et al. 2010, Tack et al. 2010, Abdala-Roberts et al. 2012), we speculate that the traits and associated arthropod communities of woody plants (e.g., *P. angustifolia*, *A. californica*) may be relatively consistent across environments as compared to herbaceous species (e.g., *O. biennis*, *A. syriaca*).

Future directions

Additional study will be required to thoroughly understand the consequences of landscape-scale variation in genetically based plant traits for associated arthropod communities. There are at least three approaches, each with its own merits and limitations. First, key aspects of the biotic or abiotic environment can be manipulated within a single common garden of broadly distributed populations to characterize the effects of plant genotype, environment and genotype-by-environment interactions (e.g., as done in the present study). This approach has the advantage of investigating a focal environmental variable and the response of a single pool of arthropod species (i.e., the community local to that garden), but suffers from a lack of ecological realism. A second approach is to conduct common garden studies of broadly distributed populations at multiple locations spanning the environmental variation encompassed by the plant species' distribution (e.g., Pennings et al. 2009, Robinson et al. 2012, Woods et al. 2012). This approach brings in the ecological realism of incorporating multiple axes of environmental variation, but suffers from not identifying the influence of individual environmental factors, and variation in regional arthropod pools (amongst gardens) may make interpretation of findings challenging. Finally, the third approach involves surveys of wild-grown plants and their associated arthropods. This approach is important in relating experimental results to real-world patterns, but does not provide mechanistic insight into the sources of variation in either plant traits or associated arthropod communities. Ultimately, this program of inquiry is likely to be challenging and require a multi-tiered approach. Our findings here thus represent an important step in determining the role of plant genetics as a driver of landscape-scale variation in arthropod community structure.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.1620/suppinfo