



# Relative effects of genetic variation *sensu lato* and sexual dimorphism on plant traits and associated arthropod communities

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## Abstract

Intraspecific plant trait variation can have cascading effects on plant-associated biotic communities. Sexual dimorphism is an important axis of genetic variation in dioecious plants, but the strength of such effects and the underlying mechanisms relative to genetic variation are unknown. We established a common garden with 39 genotypes of *Baccharis salicifolia* sampled from a single population that included male and female genotypes and measured plant traits and quantified associated arthropod communities. Genetic variation *sensu lato* (genotypic variation) had strong effects on most plant traits (flower number, relative growth rate, specific leaf area, percent water content, carbon–nitrogen ratio, monoterpene but not sesquiterpene concentrations) and on herbivore and predator density, and on arthropod community composition (relative abundance of 14 orders). In contrast, sexual dimorphism had weaker effects on only a few plant traits (flower number and relative growth rate), on predator density, and on arthropod community composition, but had no effect on herbivore density. Variation in flower number drove genetic variation *sensu lato* and sex dimorphism in predator density and arthropod community composition. There was unique genetic variation *sensu lato* in herbivore density (positively) associated with monoterpene concentration and in arthropod community composition associated with specific leaf area and carbon–nitrogen ratio. There was unique sexual dimorphism in arthropod community composition associated with plant relative growth rate. Together, these results demonstrate that genetic variation *sensu lato* and sexual dimorphism can shape plant-associated arthropod communities via both parallel and unique mechanisms, with greater overall effects of the former.

**Keywords** Dioecy · Tritrophic · Herbivores · Predators · Plant resistance

## Introduction

Intraspecific genetic variation in plant traits can influence plant-associated above- and below-ground communities (Johnson and Agrawal 2005; Whitham et al. 2006; Pratt et al. 2017). These effects on multitrophic above-ground communities are well documented, where genetic differences in plant traits among individual plants have been shown to alter the abundance, composition, and diversity

of herbivorous and predaceous arthropod species (Dungey et al. 2000; Wimp et al. 2004; Johnson and Agrawal 2005; Crutsinger 2016).

Several lines of inquiry have sought to determine the factors underlying the strength of plant genetic influence over associated arthropod communities. Intraspecific genetic variation in plant traits and their effects on associated communities increases with geographic scale at which genotypes are compared (Tack et al. 2012), such that geographic distance between genotypes is proportional to the differences in genetically based variation in associated communities (Zytnyska et al. 2011). Intraspecific genetic variation in plant traits can arise from genetic drift or spatially varying selection and local adaptation over larger geographic distances. Such geographic-based genetic variation in plant traits can be clinal, as in the case of latitudinal and elevational clines in plant traits and associated arthropod communities (Anstett et al. 2015; Pratt et al. 2017). There are

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also non-spatial mechanisms that can lead to increased variation in plant genetics that affect plant traits and associated communities. For example, plant hybridization can lead to high levels of genetic variation within a small geographic context, as has been shown for willows (Wimp and Whitham 2001). Although less frequently studied, plant ploidy level is another axis of genetic variation that may have consequent effects on plant–arthropod interactions (Roccaforte et al. 2015).

Sexual dimorphism is another important axis of genetic variation that underlies variation in ecologically important traits and may thus have consequences for plant-associated arthropod communities (Petry et al. 2013). In particular, the separation of reproductive roles in dioecious plants (separate males and females) has been hypothesized to drive divergence in resource allocation between males and females (Lloyd and Webb 1977; Delph 1999). Such sex-based trait variation can alter interactions between plants and their associates (Ågren et al. 1999; Cornelissen and Stiling 2005). In particular, it is hypothesized that female plants invest more in reproduction and therefore grow more slowly than male plants (Ågren et al. 1999; Cornelissen and Stiling 2005). According to the resource availability hypothesis (Coley et al. 1985), slow-growing female plants should exhibit higher fitness cost of losing tissue to herbivores, thus favoring the evolution of increased defense against herbivores in females. For example, Abdala-Roberts et al. (2016) found that aphid density was higher on *Baccharis salicifolia* males compared to females, consistent with predictions that males invest fewer resources in defenses. Similarly, Boecklen et al. (1990) found that male willows supported higher densities of five species of tenthredinid sawflies than do female willows. However, plant sex might also determine the structure of associated multitrophic communities (Petry et al. 2013; Kabir et al. 2014; Abdala-Roberts et al. 2016). For example, Petry et al. (2013) found higher predator to herbivore ratios on *Valeriana edulis* females relative to males. Such examples demonstrate that sexual dimorphism can strongly influence plant–arthropod interactions, but less is known about the effects of sexual dimorphism on diverse multitrophic communities. Moreover, the relative magnitude of the effect of sexual dimorphism on plant-associated arthropod communities compared to other axes of plant genetic variation is unknown.

Recent work has unveiled the ubiquity of genetic variation effects on associated arthropod communities, but linking plant trait genetic variation to arthropod community composition remains a challenge. To predict the effects of genetic variation on plant traits and on associated communities, the sources of plant trait variation and the specific traits that influence associated communities need to be identified. In some cases, a single trait can drive variation in plant-associated communities (Bailey et al. 2006) but in

many cases plant traits interact with each other (i.e., trait syndromes) to influence associated communities (Agrawal and Fishbein 2006). Additionally, research often focuses on identifying plant traits that directly affect herbivores but focuses less on identifying plant traits that affect predators (Marquis and Whelan 1996) and could indirectly affect herbivores, such as volatiles (Kessler and Baldwin 2001). Together, these findings indicate the importance of assessing suites of plant traits to understand plant trait genetic variation underlying variation in associated communities (Agrawal 2011).

In this study, we investigated how sexual dimorphism and other axes of genetic variation in ecologically important plant traits influenced associated arthropod communities. To do so, we established a common garden with male ( $N = 19$ ) and female ( $N = 20$ ) genotypes from a single population of the dioecious shrub *Baccharis salicifolia* (Ruiz and Pav.). While sexual dimorphism in *Baccharis* sp. is likely genetically determined (Ming et al. 2011), we use the term “genetic variation sensu lato” to refer to additional axes of variation among genotypes other than that associated with plant sex. Across 3 years, we measured a suite of plant traits and arthropod communities associated with each plant. By replicating genotypes within each sex, we sought to answer the following questions: (1) How do the effects of sexual dimorphism (male vs. females) compare to genetic variation sensu lato (genotypic variation within sex) influence plant traits? (2) How does arthropod community composition vary between sexes and across genotypes? And (3) what are the underlying plant traits that drive variation in associated arthropod communities and are these mechanisms parallel across genetic variation sensu lato and sexual dimorphism? By addressing these questions, this study provides a mechanistic insight into the relative importance and mechanisms by which sexual dimorphism and genetic variation sensu lato shape associated multitrophic communities.

## Methods and materials

### Study system

*Baccharis salicifolia* is a perennial, evergreen, woody, dioecious shrub native to the southwestern United States and northern Mexico. It grows in riparian areas and other mesic microhabitats in high-density monospecific stands, where multiple genotypes frequently co-occur at small spatial scales. In coastal southern California, *Baccharis salicifolia* grows and flowers predominantly during the annual winter rains, but can also flower at low levels during the spring and fall.

## Genotype selection and propagation

In February 2008, we collected cuttings from 20 male and 20 female source plants from a naturally occurring population of *Baccharis salicifolia* of ca. 35 ha in the University of California San Joaquin Marsh Reserve (33°39'47"N, 117°51'7"W; CA, USA), the same field site where our past studies of this plant have been conducted (Mooney et al. 2012b; Moreira and Mooney 2013; Abdala-Roberts et al. 2016; Moreira et al. 2016; Abdala-Roberts et al. 2017). To get distinct genotypes, we collected cuttings from wild-grown plants that were separated by approximately 900 m. Cuttings were dipped in a 20% solution of Dip 'N Grow Root Inducing Concentrate (Dip 'N Grow Inc., Clackamas, OR) and planted in perlite for 6 weeks in a greenhouse. We then planted all cuttings in 1 L pots of soil (equal parts silica sand, redwood compost, peat moss, and pumice) where they continued to grow for 2 months, with the exception of one male genotype that did not propagate successfully.

## Common garden

In May 2008, we established a common garden of *B. salicifolia* adjacent to the Marsh Reserve. We planted 39 genotypes with a total of 459 plants, replicating each genotype 8–13 times (mean  $11.5 \pm 0.2$ ). Plants were distributed randomly throughout the common garden in rows and columns with 1 m spacing between them. The garden was divided into 12 spatial blocks to account for soil heterogeneity in statistical analyses. Half of the replicates for each genotype were watered with city water using drip irrigation emitters applied in a checkerboard design to reduce plant mortality during the hot and dry summer. Plants assigned to an emitter grew only slightly faster (6.8% increase in RGR) than those without an emitter, likely due to the spread of water from emitters to adjacent plants and the spread of roots from adjacent plants to emitters. As a result, we de-emphasize this aspect (drought—different water levels) of the experiment design in our analysis.

We use these replicate copies of *B. salicifolia* genotypes to infer genetic variation *sensu lato* in plant traits and associated arthropod communities. However, this variation among genotypes is due not only to heritable (i.e., additive) genetic variation, but also to non-heritable variation (i.e., dominance, epistasis, maternal and paternal effects). We sought to minimize maternal effects by growing all plants for a relatively long period prior to measuring plant traits (Rausher 1992) and *B. salicifolia* experiments subsequent to the one described here found no maternal effects due to multiple cuttings coming from the same source plant (Abdala-Roberts et al. 2016, 2017). Nevertheless, our use of the term “genetic variation” must be recognized to include a non-heritable component.

## Data collection

### Plant traits

To document genetic variation *sensu lato* and sexual dimorphism in plant phenotypes, we measured a suite of plant traits for each genotype including flower number, relative growth rate (RGR), specific leaf area (SLA), percent water content (PWC), leaf toughness, carbon–nitrogen ratio (C:N), and leaf terpene concentration (mono- and sesquiterpenes). Total flower number was counted once each in March 2009 and 2010 (during peak flowering), but also once each during fall (October) and spring (May) 2009. In November 2011, we estimated plant size by measuring and combining the length of all shoots longer than 10 cm. Because all plants were of similar size when planted, variation in subsequent plant size measures reflects variation in growth rate. Using this estimated plant size, we quantified RGR as the log of average growth per year (total length in 2011 divided by 4 years). We estimated SLA, PWC, leaf toughness from all plants, and leaf C:N ratio from approximately half of the plants ( $N = 234$ ) stratified among genotypes ( $N = 6$  per genotype) and between the two watering treatments. We collected 10 fully expanded leaves from each plant during the peak growing season (April and May 2011). Leaves were immediately placed on ice and kept cool until they were scanned and weighed (wet weight) later that same day. Leaf area (cm<sup>2</sup>) was measured from scanned leaf images using ImageJ software (Rasband 2008). Leaves were then dried at 60 °C for 72 h and weighed again (dry weight) to calculate SLA as cm<sup>2</sup> g<sup>-1</sup> dry weight and PWC as ([wet weight-dry weight]/wet weight). For each plant, we used a force gauge penetrometer (Pesola 500 g, Switzerland) to measure toughness as the mass (g) needed to penetrate a surface. We measured toughness on both sides of the mid-rib at the widest point of a leaf and averaged these two values. To assess leaf C:N ratio, 10 dried leaves were ground to a fine, homogenized powder using a Wig-L-bug grinding mill (International Crystal Laboratories, Garfield, NJ). Approximately 1 mg of this powder was packed into a 5 × 9 mm tin to perform elemental analysis (Fisons Instruments 1500) and mass spectrometry (Delta plus XL, Thermo Finnigan, Asheville, NC) at the UC Irvine Stable Isotope Ratio and Mass Spectrometry Facility.

Concurrent with the above leaf trait measurements, we also assessed leaf terpene concentration from the same subset of plants following Pratt et al. (2014). Two leaves were collected and placed into 2 ml n-hexane (99.9% purity), which was sonicated for 10 min and allowed to soak at room temperature for 7 days. Extracts were then poured off and stored at -80 °C. For the terpene analysis, 10 µl of an internal standard solution (0.13 µl ml<sup>-1</sup> m-xylene in n-hexane) was added to 90 µl of each sample extract. Samples were

injected (4  $\mu$ l) onto a gas chromatography (GC) and mass spectrometry fitted with a 30 m  $\times$  0.25 mm  $\times$  0.25  $\mu$  film thickness DB-5 fused silica column. The GC was operated in splitless mode with helium as the carrier gas (flow rate 1 ml min<sup>-1</sup>). The GC oven temperature program was: 1 min hold at 50, 5 °C min<sup>-1</sup> ramp to 180, 20 °C min<sup>-1</sup> ramp to 290 °C, and 1 min hold at 290 °C. The mass spectrometer was operated in electron ionization mode at 70.0 eV, and data were collected between 50 and 650 m/z. We identified terpenes using Kovats retention index from published work (Loayza et al. 1995; Zunino et al. 1997). Terpene concentrations were quantified with standard calibration curves (monoterpenes with  $\beta$ -pinene and sesquiterpenes with  $\beta$ -carophyllene) and reported as  $\mu$ g mg<sup>-1</sup> dry weight. All measured plant traits were continuous variables.

### Plant associated arthropod community

In both 2010 and 2011, we surveyed arthropod communities from the same subset of plants from which leaf traits were measured ( $N = 234$ , 6 plants per genotype). Arthropod sampling was timed to correspond with peak plant growth, flower production, and data collection on plant traits (April and May). We vacuumed each plant for 3 min with an electric vacuum (3.5 HP Rigid model #WD0970) fitted with a fine mesh bag in the vacuum nozzle to collect arthropods. Mesh bags were placed on ice immediately after arthropod samples were collected and transferred to a -20 °C freezer later that same day. Arthropods were subsequently separated from plant matter, stored in 70% ethanol, and identified to morphospecies within family. Because different trophic levels might respond differently to plant traits, we assigned each arthropod to a feeding guild (herbivore and predators comprising 96% of all arthropods) based on ordinal and the familial-level taxonomy as needed. In total, 14 orders were observed (Acarina, Araneae, Coleoptera, Dermaptera, Diptera, Entomobryomorpha, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Orthoptera, Pseudoscorpiones, Psocoptera, and Thysanoptera). Because arthropod sampling effort was constant among plants, arthropod counts are equivalent to arthropod density (i.e., numbers per 3-min vacuum sample) for each plant.

### Statistical analysis

#### Genetic variation sensu lato

We tested for genetic variation sensu lato in plant traits (RGR, SLA, C:N ratio, PWC, flower number, leaf toughness, and mono- and sesquiterpenes concentration using linear mixed models, with flower number and terpenes log-transformed to improve normality of residuals. To

analyze arthropod density (herbivores and predators separately and total arthropods), we used generalized linear mixed models with Poisson distributions because transformations did not provide normally distributed residuals. Block and watering treatment was treated as random effects, while plant genotype was treated as a fixed effect to obtain least-square genotypic means. All mixed models were run using the ‘lme4’ package in R (Bates et al. 2014; R Core Team 2015). We generated  $P$  values for the fixed effect from 10,000 parametric bootstrap simulations, while least-square means were obtained with the ‘afex’ package (Singmann et al. 2015). To quantify the strength of genetic variation sensu lato in plant traits and arthropod density, we calculated the % difference between the highest and lowest genotypes within each sex and then averaged those two values.

For all arthropod community analyses, we pooled data across 2010 and 2011 for each plant as we were not interested in year-by-genotype or year-by-sex variation. We used a permutational multivariate analysis of variance (PERMANOVA) to test for genetic variation sensu lato in community composition based upon the relative densities of arthropod orders, constrained by plant sex to control for any effects of sexual dimorphism. All PERMANOVA analyses were based on 10,000 permutations using the ‘vegan’ package in R (Oksanen et al. 2016). To visualize the results of this analysis, we used pairwise Bray–Curtis dissimilarities as input to a principal coordinates analysis. The result of this analysis was then visualized in two dimensions, where each point reflected the genotype centroid. Influential arthropod orders were selected based upon both statistical significance ( $P < 0.05$ ) and an  $R^2 > 0.10$  for associations with the ordination (using ‘envfit’ in vegan) and displayed using biplot arrows with length scaled to  $R^2$  value.

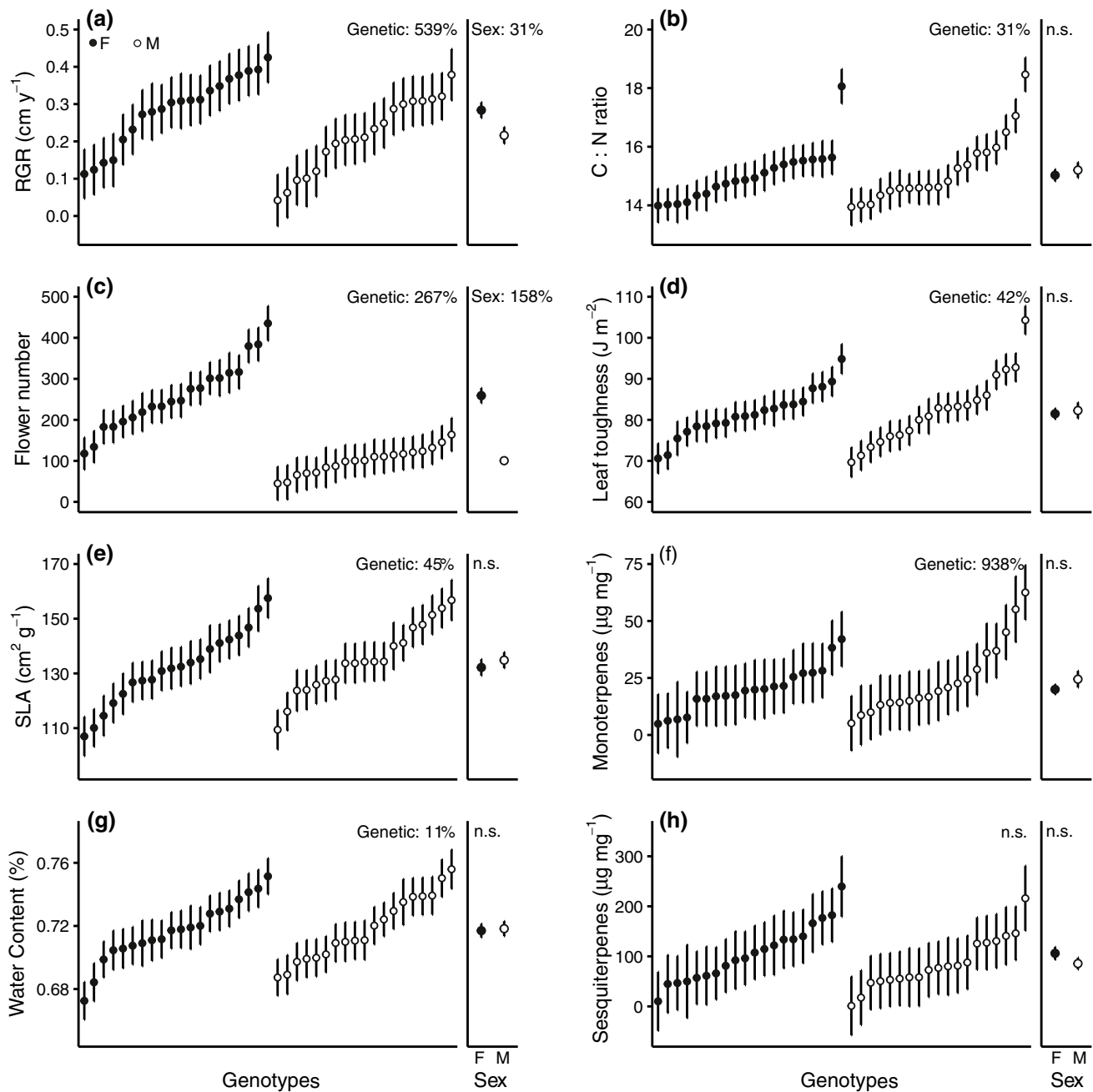
#### Sexual dimorphism

Based upon the genotype analyses, we took trait and arthropod density means for each genotype ( $n = 19$  male,  $n = 20$  female) to test for sexual dimorphism in plant traits and associated arthropod communities using the ‘lsmeans’ package in R (Lenth 2016). Using these genotype means, we tested for differences in plant traits and arthropod density (total arthropods, herbivores, and predators) between male and female plants with ANOVA tests. The same procedures used to test for genetic variation sensu lato were then used to test for sexual dimorphism (with PERMANOVA) and visualized sexual dimorphism (with ordination) in arthropod community composition, with the two sex centroids as well as the mean values for each male and female genotypes displayed on the ordination plot.

**Linking plant trait genetic variation *sensu lato* to associated arthropod communities**

To determine which plant traits were related to arthropod densities, we used multiple regressions with plant traits as predictor variables and log-transformed all measures of arthropod density as the response variables, applying

backward elimination variable selection using Akaike information criterion (‘stepAIC’ in the MASS package in R) (Venables and Ripley 2002). The initial models included all traits except for sesquiterpenes, for which we did not detect genetic variation *sensu lato* (see below; Fig. 1, Table 1). We report results for the final models that predict total arthropod, herbivore, and predator densities.



**Fig. 1** Genetic variation *sensu lato* (left) and sexual dimorphism (right) (mean  $\pm$  SE) in *B. salicifolia* **a** relative growth rate, **b** carbon-to-nitrogen ratio, **c** flower number, **d** leaf toughness, **e** specific leaf area, **f** monoterpene concentration, **g** percent water content, and **h** sesquiterpene concentration. Female genotypes ( $n = 20$ ) are indicated

by filled circles and male genotypes ( $n = 19$ ) as open circles. Genotypes are ranked from low to high within each sex. Genotype and sex percentage effects (see methods for details) are indicated for traits that exhibited significant variation (LMM;  $P < 0.05$ ), and “n.s.” is written where trait means do not differ



**Table 1** Summary of results from linear mixed effects models testing for genetic variation in plant traits and on associated arthropods

| Plant trait       | Chi Sq | Chi df | P value |
|-------------------|--------|--------|---------|
| RGR               | 123.93 | 38     | 0.0001* |
| SLA               | 124.01 | 38     | 0.0001* |
| PWC               | 99.84  | 38     | 0.0001* |
| Leaf toughness    | 157.25 | 38     | 0.0001* |
| C:N ratio         | 115.90 | 38     | 0.0001* |
| Flower number     | 220.68 | 38     | 0.0001* |
| Monoterpenes      | 746.06 | 38     | 0.0022* |
| Sesquiterpenes    | 37.87  | 38     | 0.6700  |
| Arthropod density | 63.19  | 38     | 0.0260* |
| Predator density  | 71.37  | 38     | 0.0060* |
| Herbivore density | 55.00  | 38     | 0.0360* |

RGR relative growth rate, SLA specific leaf area, PWC percent water content, C:N ratio carbon–nitrogen ratio

\*Designate significant statistical difference

Multivariate relationships between plant traits and arthropod community composition were examined with constrained ordinations using distance-based redundancy analysis (db-RDA) in separate analyses for genotypic and sex effects. Db-RDA is a generalization of redundancy analysis (RDA) used to analyze non-Euclidean multivariate dissimilarities (Legendre and Anderson 1999; McArdle and Anderson 2001). Specifically, we used pairwise Bray–Curtis dissimilarities for arthropod community composition (either among genotypes or between sexes) as input to a principal coordinates analysis constrained by rescaled traits (mean = 0, SD = 1) to maximize linear combinations of plant traits that explained variation in arthropod community composition (db-RDA). For the genetic variation *sensu lato* analysis, we used a partial db-RDA of data from individual plants, controlling for plant sex. For the sexual dimorphism analysis, we use genotypic means for arthropod orders and traits. We tested whether there was significant genetic variation *sensu lato* or sexual dimorphism in the constrained portion of variation in arthropod community composition associated with plant traits using permutation tests for the overall significance ( $P < 0.05$ ) of the db-RDAs and for the significance of the first two axes. The results of these analyses were visualized in two dimensions with centroids for each genotype or sex and with the genotypic means displayed for the sexual dimorphism analysis. Influential orders were identified based upon both statistical significance ( $P < 0.05$ ) and an  $R^2$  greater than 0.10 for associations with the ordination (using ‘envfit’ in vegan). For plant traits, we used permutation tests for statistical significance ( $P < 0.05$ ) on db-RDA constraints as the basis for inferring which traits were most important in driving variation in arthropods community structure. Both influential arthropod orders and plant

traits were then displayed using biplot arrows with length scaled to  $R^2$  value.

## Results

### Genetic variation *sensu lato*

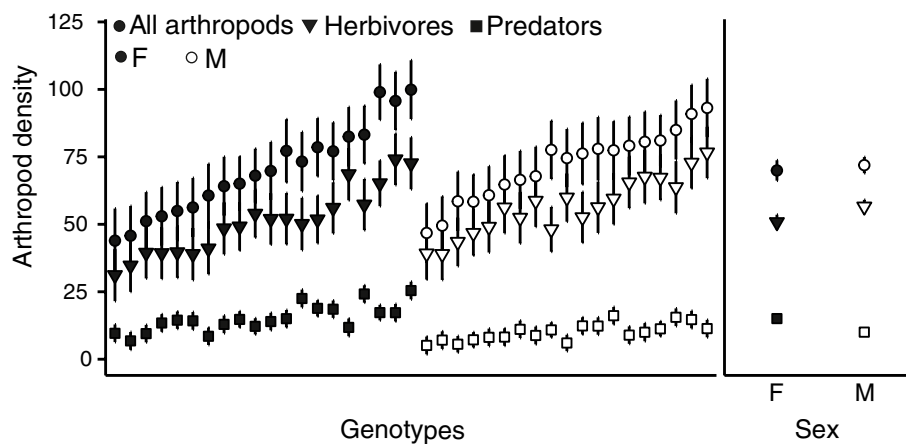
We found significant genetic variation *sensu lato* in all plant traits, including RGR [539% variation (i.e., from the lowest to highest of the 39 genotypes)], flower number (267% variation), SLA (45% variation), PWC (11% variation), C:N ratio (31% variation), leaf toughness (42% variation), and monoterpenes (938% variation), but not for sesquiterpenes (Fig. 1, Table 1). Moreover, there was genetic variation *sensu lato* in the densities of herbivores (146% variation), predators (398% variation), and total arthropods (127% variation) (Fig. 2; Table 1).

Total arthropod community composition varied across genotypes (PERMANOVA,  $P < 0.0001$ ) with permutations constrained to control for any effects of sexual dimorphism. The procedures we used do not produce an  $R^2$  value for constrained PERMANOVAs, but the  $R^2$  for separate male and female analyses were 0.18 and 0.26, respectively, and the value for an unconstrained PERMANOVA across both sexes was 0.21. The ordination to visualize this genetic variation *sensu lato* accounted for 69% of the genetic variation *sensu lato* in arthropod community composition, with the first two axes explaining 32 and 12% of this variation, respectively (Fig. 3a). Genetic variation *sensu lato* in arthropod composition was primarily associated with variation in the relative densities of arthropod order Psocoptera ( $P < 0.001$ ,  $R^2 = 0.93$ ), Hemiptera ( $P < 0.001$ ,  $R^2 = 0.77$ ), Coleoptera ( $P < 0.001$ ,  $R^2 = 0.56$ ), and to a lesser extent Diptera ( $P < 0.001$ ,  $R^2 = 0.27$ ), Acarina ( $P < 0.001$ ,  $R^2 = 0.21$ ), and Hymenoptera ( $P < 0.001$ ,  $R^2 = 0.15$ ). There were negative correlations among three separate axes of variation, consisting of (1) a positive association between Coleoptera and Acarina, (2) a positive association among Hemiptera, Diptera and Hymenoptera, and (3) Psocoptera alone.

### Sexual dimorphism

There was sexual dimorphism in flower number ( $P < 0.0001$ ) and RGR ( $P = 0.034$ ) but not in SLA, C:N ratio, PWC, leaf toughness, or terpene (mono- and sesquiterpenes) concentrations (Table 2; Fig. 1). There were 158% more flowers and a 31% increase in RGR on females compared to males (Fig. 1). Furthermore, there was sexual dimorphism in predator density, with 50% more predators on females than on males, but not in total arthropod or herbivore density (Fig. 2; Table 2).

There was sexual dimorphism in arthropod community composition (PERMANOVA,  $P = 0.0023$ ,  $R^2 = 0.15$ ;



**Fig. 2** Genetic variation *sensu lato* (left) and sexual dimorphism (right) in *B. salicifolia* arthropod densities. Mean densities ( $\pm$  SE) are shown for total arthropods (circles), herbivores (triangles), and predators (squares). Female genotypes ( $n = 20$ ) are indicated by filled circles and male genotypes ( $n = 19$ ) as open circles. Genotype

percentage effects (see methods for details) for the densities of total arthropods, herbivores, and predators were 113, 117, 245%, respectively. Predator density was 50% (higher on females), while total arthropod and herbivore density did not vary

**Fig. 3**). The ordination to visualize this variation accounted for 87% of the variation in arthropod community composition, with the first two axes explaining 46 and 15% of this variation, respectively (Fig. 3b). Sexual dimorphism in arthropod composition was associated mainly with variation in the relative densities of Psocoptera ( $P < 0.001$ ,  $R^2 = 0.97$ ), Hemiptera ( $P < 0.001$ ,  $R^2 = 0.97$ ), Coleoptera ( $P < 0.001$ ,  $R^2 = 0.86$ ), and Acarina ( $P < 0.001$ ,  $R^2 = 0.23$ ). There were negative correlations along three separate axes of variation in arthropod community composition between the sexes, consisting of (1) a positive association between Coleoptera and Acarina, (2) Diptera alone, and (3) Psocoptera alone.

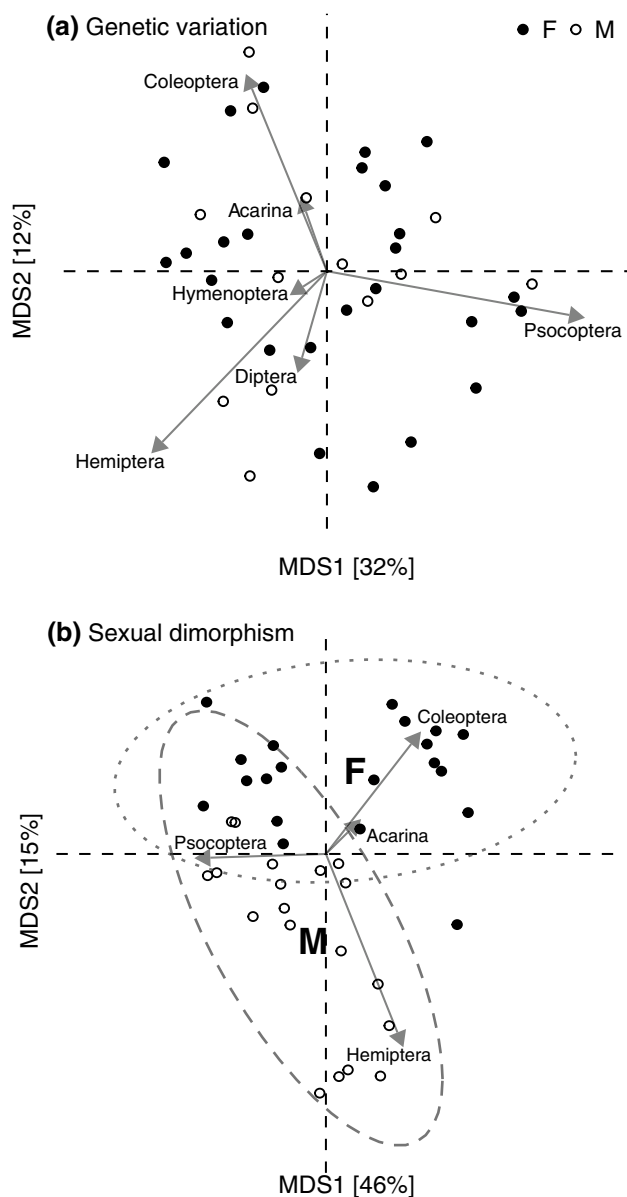
### Linking plant trait genetic variation *sensu lato* to associated arthropod communities

In multiple regressions relating genotypic means for plant traits to total arthropod densities, stepwise variable selection resulted in a model with a positive effect of monoterpene concentration and a negative effect of leaf toughness on arthropod density (Table 3). When arthropod trophic levels were evaluated separately, model selection for herbivores indicated a positive effect of monoterpene concentration, while model selection for predators indicated a positive effect of monoterpene concentration and flower number and a negative effect of leaf toughness (Table 3).

Assessing the relationships between plant traits and arthropod community composition, the overall db-RDA for genetic variation *sensu lato* was significant ( $P < 0.001$ ), with plant traits explaining 18% of the overall variation in arthropod

community composition (as compared to 69% in the unconstrained ordination). Within this constrained ordination, the first two axes were significant ( $P < 0.001$  and  $P = 0.014$ , respectively), accounting for 65 and 18% of the constrained variation (Fig. 4a). Genetic variation *sensu lato* in arthropod composition was driven by variation in flower number ( $P < 0.001$ ), SLA ( $P = 0.019$ ), and C:N ratio ( $P = 0.010$ ), and marginal effects of PWC ( $P = 0.082$ ). Psocoptera and Araneae were negatively correlated with flower number and PWC, while Hemiptera, Hymenoptera, and Diptera were negatively correlated with C:N ratio and SLA (Fig. 4a).

Assessing the relationships between plant traits and arthropod community composition, the overall db-RDA for sexual dimorphism was significant ( $P = 0.0079$ ), with plant traits explaining 33% of the overall variation in arthropod community composition (as compared to 87% in the unconstrained ordination). Within this constrained ordination, the first two axes were significant ( $P < 0.001$  and  $P = 0.019$ , respectively), accounting for 62 and 19% of the constrained variation (Fig. 4b). Sexual dimorphism in arthropod composition was driven by variation in flower number ( $P < 0.001$ ) and RGR ( $P = 0.013$ ), with marginal effects of SLA ( $P = 0.064$ ) and PWC ( $P = 0.066$ ). This analysis showed that Hemiptera and Acarina were negatively correlated with RGR, while Coleoptera, Hymenoptera, and Thysanoptera were associated with higher flower number (Fig. 4b). Both male and female genotypes varied in Psocoptera density, which was associated with SLA and PWC.



**Fig. 3** Unconstrained ordinations of **a** genetic variation *sensu lato* and **b** sexual dimorphism in arthropod community composition. Biplot arrows show associated linear trends with arthropod orders, scaled to reflect relative magnitude of effects based on  $R^2$  values. Females ( $n = 20$ ) and males ( $n = 19$ ) are indicated by closed and open circles, respectively. **a** The genotypic ordination, displays genotypic centroids while controlling for sexual dimorphism. The PERMANOVA (controlling for the effects of sex) indicates that 18 and 21% of total arthropod community variation is explained by male and female genotypic variation, respectively. Overall, the ordination (all axes) explains 69% of the total arthropod community variation, with the first and second axes (displayed) capturing 32 and 12% of this variation, respectively. **b** The sex ordination, displays male and female centroids and 95% ellipses, as well as the means for each genotype. The PERMANOVA indicates that 15% of total arthropod community variation is explained by sex. Overall, the ordination (all axes) explains 87% of the total arthropod community variation, with the first and second axes (displayed) capturing 46 and 15% of this variation, respectively

**Table 2** Summary of results from ANOVAs testing for sexual dimorphism in plant traits and associated arthropods

| Plant trait       | Sum Sq    | df | F value | Pr (> F) |
|-------------------|-----------|----|---------|----------|
| RGR               | 0.045     | 1  | 4.841   | 0.0340*  |
| SLA               | 69.056    | 1  | 0.399   | 0.5310   |
| PWC               | < 0.001   | 1  | 0.038   | 0.8460   |
| Leaf toughness    | 6.234     | 1  | 0.117   | 0.7330   |
| C:N ratio         | 0.417     | 1  | 0.415   | 0.5230   |
| Flower number     | 8.788     | 1  | 74.729  | 0.0010*  |
| Monoterpenes      | 195.809   | 1  | 1.135   | 0.2940   |
| Sesquiterpenes    | 4,405.335 | 1  | 1.457   | 0.2359   |
| Arthropod density | 0.015     | 1  | 0.306   | 0.5830   |
| Herbivore density | 0.135     | 1  | 2.760   | 0.1050   |
| Predator density  | 1.589     | 1  | 13.638  | 0.0010*  |

RGR relative growth rate, SLA specific leaf area, PWC percent water content, C:N ratio carbon-to-nitrogen ratio

\*Designate significant statistical difference

## Discussion

Our findings are consistent with previous studies that showed that plant intraspecific variation influences associated arthropod communities (e.g., Whitham et al. 2006; Bailey et al. 2009).

Overall, we found strong genetic variation *sensu lato* in both plant traits and arthropod densities. In contrast, plant sexes varied relatively weakly in only a few traits and also varied in predator (but not herbivore) density. Nevertheless, genetic variation *sensu lato* was comparable to, but slightly greater than sexual dimorphism for arthropod community composition, with the former being driven by a relatively greater number of traits than the latter. This study, thus, provides mechanistic insight into the relative importance of plant genetic variation *sensu lato* and sexual dimorphism in multitrophic communities that underlies observed asymmetry between genetic variation *sensu lato* and sexual dimorphism.

Although genetic variation *sensu lato* is expected to scale with the spatial scale at which plants are sampled (Tack et al. 2010, 2012), we nevertheless found strong genetic variation *sensu lato* among *B. salicifolia* genotypes drawn from a single population in a relatively small area (a 35 ha site). Genetic variation increases with spatial scale due to neutral evolutionary processes, spatially varying selection at fine scales, and local adaptation to different environments at larger geographic scales (Pratt and Mooney 2013; Pratt et al. 2017). *Baccharis salicifolia* may, thus, be unusual in the amount of genetic variation within a single population, possibly due to high dispersal ability. This high level of within-population variation may result in arthropod community turnover among co-occurring genotypes, potentially



**Table 3** Summary of results from final regression models relating genetic variation in plant traits to arthropod, herbivore, and predator densities

| Parameter      | Arthropod density<br>$P = 0.0089, R^2 = 0.23$ |       |                | Herbivore density<br>$P = 0.0039, R^2 = 0.20$ |       |                | Predator density<br>$P < 0.0001, R^2 = 0.48$ |       |                |
|----------------|---|-------|----------------|---|-------|----------------|--|-------|----------------|
|                | Est   | SE    | <i>P</i> value | Est   | SE    | <i>P</i> value | Est  | SE    | <i>P</i> value |
| Monoterpenes   | 0.006   | 0.002 | 0.0100*        | 0.007   | 0.003 | 0.0039*        | 0.163  | 0.077 | 0.0640         |
| Leaf toughness | – 0.007                                       | 0.004 | 0.0790         |   |       |                | – 0.019                                      | 0.006 | 0.0038*        |
| Flower number  |   |       |                |   |       |                | 0.387  | 0.082 | < 0.0001*      |

Final model parameters were selected using AIC-based backward elimination from a full model including all traits as predictors

\*Designate significant statistical difference

mitigating herbivore pressure and reinforcing genetic variation through resource dilution effects (Hambäck et al. 2014). Such dynamic is supported by previous work in this system, which demonstrated that the density of a generalist herbivore was reduced on a plant when the generalist herbivore was associated with the opposite plant sex (Abdala-Roberts et al. 2017).

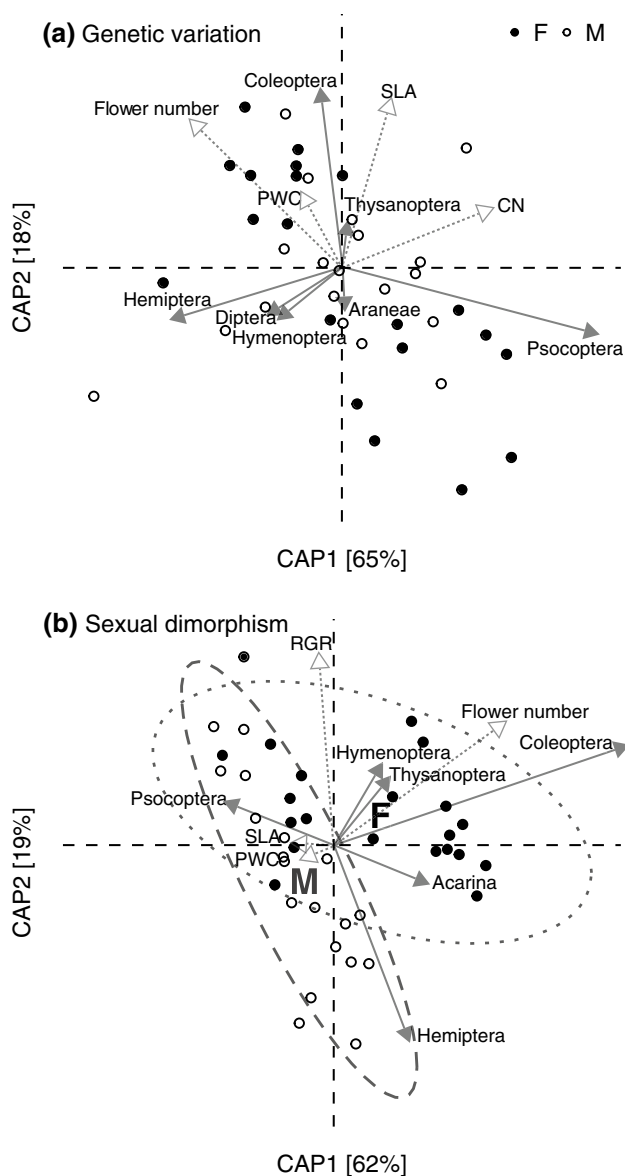
Our results also showed that *B. salicifolia* plants exhibited relatively weak sexual dimorphism compared to genetic variation *sensu lato* in only two plant traits (RGR, flower number). This was particularly surprising given that the whole *Baccharis* genus is dioecious, thus implying there has been ample time for sexual divergence in ecologically important traits to evolve. Our findings partially support previous thinking about dioecy effects on plant traits and arthropod communities. Theory predicts that, due to trade-offs between growth, reproduction, and defense, female plants invest more energy in reproduction and in defensive traits (lower herbivory) and in turn tend to exhibit decreased growth relative to male plants (Cox 1982; Cornelissen and Stiling 2005; Cepeda-Cornejo and Dirzo 2010). Supporting this hypothesis, we found that female *B. salicifolia* plants produced more flowers than male plants. However, in contrast to previous thinking, female plants exhibited higher RGR compared to males and there was no sexual dimorphism terpene concentration or herbivore density. Although it is well known that resource allocation can be different in male and female plants, not all previous studies have supported these premises. For example, Nichols-Orians et al. (1993) found that the concentration of two phenolic glycosides in leaves of *Salix sericea* was not sexually dimorphic.

*Baccharis salicifolia* plants also showed sexual dimorphism in predator density, with 50% more predators on females than on males. Consistent with our results, past studies have shown female plants to recruit more natural enemies (Mooney et al. 2012a; Petry et al. 2013) by increasing the availability of floral resources that provide nutritional benefits (i.e., nectar) to associated arthropod communities (Ashman and King 2005; Wäckers et al. 2005; Pacini and Nepi 2007). Such effects can increase indirect defenses from predators and parasitoids attracted to these floral resources

(Cepeda-Cornejo and Dirzo 2010). Plants commonly use this strategy to mechanistically employ indirect plant defenses, increasing top-down effects (Kessler and Heil 2011). This dynamic is leveraged in agricultural systems, where they intercrop flowering plants as a biological control method (Letourneau et al. 2011; Bickerton and Hamilton 2012). Our findings, thus, lend support to the growing consensus that floral resource for natural enemies are a key trait driving sexual dimorphism in the structure of plant-associated multitrophic communities.

Our current study is novel in that it explicitly compares the magnitude of sexual dimorphism to the better-studied effects of genetic variation *sensu lato*. Plant genotypes were more variable than the sexes in plant traits and, correspondingly, the effects of genetic variation *sensu lato* exceeded those of sexual dimorphism on associated arthropod densities. We found corresponding effects on herbivore, predator, and total arthropod densities with genetic variation *sensu lato* but sexual dimorphism only on predator density that was weaker than genetic variation *sensu lato*. Variation in herbivore density among genotypes was positively associated with monoterpene concentration and negatively associated with leaf toughness. Furthermore, variation in predator density among genotypes and between sexes was positively associated with flower number. Accordingly, our results provide a mechanistic link between plant traits and the densities of multitrophic arthropod communities that underlies the observed asymmetry between genetic variation *sensu lato* and sexual dimorphism.

Genetic variation *sensu lato* effects on arthropod community composition exceeded those of sexual dimorphism, although this contrast was less pronounced than that observed for plant traits and arthropod densities. Accordingly, although sexual dimorphism in plant traits was low, the traits that varied (i.e., flower number) influenced arthropod community composition at levels comparable to the variation observed among plant genotypes. While we found genetic variation *sensu lato* to be stronger than sexual dimorphism in this particular system, more such comparisons are needed to gain a general understanding of this dynamic.



**Fig. 4** Distance-based redundancy analysis (db-RDA) ordinations of **a** genetic variation *sensu lato* and **b** sexual dimorphism in arthropod community composition when constrained by plant traits. Biplot arrows show significant linear trends with arthropod orders (solid lines) and explanatory traits (dotted lines) scaled to reflect their relative magnitude of effect based on  $R^2$  values. Females ( $n = 20$ ) and males ( $n = 19$ ) are depicted as closed and open circles, respectively. **a** The genotypic ordination, displays genotypic centroids while controlling for sexual dimorphism. This constrained ordination explained 18% of the overall variation in arthropod community composition (vs. 69% of the variation in the unconstrained ordination), with the first and second axes (displayed) capturing 65 and 18% of this constrained variation, respectively. **b** The sex ordination displays male and female centroids and 95% ellipses, as well as the means for each genotype. This constrained ordination explained 33% of the overall variation in arthropod community composition (vs. 87% of the variation in the unconstrained ordination) with the first and second axes (displayed) capturing 62 and 19% of this constrained variation, respectively

In conclusion, our study explicitly compares the magnitude of intraspecific genetic variation *sensu lato* in plant traits and arthropod communities attributed to plant genotype and sexual dimorphism, showing the former to exceed the latter. Within genetic variation *sensu lato* and sexual dimorphism, we find both parallel and contrasting mechanisms that structure the associated arthropod communities, contributing to a growing understanding that plants influence higher trophic levels through multiple co-varying traits. The generality of our findings is unknown given the paucity of such studies, perhaps with the exception of the effects of flower number on arthropods, which has been noted to be influential in other systems. Further work is needed to mechanistically link plant trait genetic variation *sensu lato* to the structure of associated arthropod communities to predict how plant responses to abiotic and biotic conditions can in turn affect the broader ecological community. In addition, further work in plant dioecious species should also manipulate biotic (e.g., herbivory) and abiotic (e.g., light, soil nutrients) factors to investigate the potential evolutionary and functional determinants of sexual dimorphism in patterns of resource allocation to reproduction, growth, and defense.

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**Author contribution statement** KM conceived and designed the experiment. KM, XM, and JP performed the experiment. CN analyzed the data. MML, JC, CN, AN, and KM wrote the manuscript.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflicts of interest.

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