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Mechanisms underlying plant sexual dimorphism in multi-trophic arthropod communities

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Abstract. A growing body of research documents the importance of plant genetic effects on arthropod community structure. However, the mechanisms underlying these effects are often unclear. Additionally, plant genetic effects have largely been quantified in common gardens, thus inflating the estimates of their importance by minimizing levels of natural variation. Using *Valeriana edulis*, a dioecious plant with genetically based sex determination, we conducted surveys and experiments on wild-grown individuals to document field patterns of arthropod association between the sexes and the mechanisms underlying these plant genetic effects. Three years of surveys revealed strong and consistent sex-biased arthropod association in wild-grown plants: female plants supported 4-fold, 1.5-fold, and 4-fold higher densities of aphids, aphid predators, and aphid-tending ants, respectively, compared to males. There was mixed evidence that the female bias for aphids was due to higher plant quality, while we found no difference between plant sexes in aphid preference or the top-down effects of predators and tending ants. Female bias for ants was due to both the greater attractiveness of female plants (direct effect mediated by floral nectar) and an independent, weaker effect of higher aphid abundance on females (density-mediated indirect effect). Conversely, the female bias for predators was driven solely by the greater attractiveness of female plants. We did not find interaction modification, i.e., ant–aphid and predator–aphid interactions were equivalent between plant sexes. Plant sex explained 0.24%, 2.28%, and 4.42% of the variance in aphids, predators, and ants, respectively, values comparable to but slightly weaker than those previously reported from common-garden studies. In contrast to the prediction of diminished plant genetic effects with increasing trophic level, we show how weak indirect effects on predators and parasitoids (via herbivores) can be complemented by strong direct effects via common plant traits (floral resources). In summary, we document direct and indirect effects of genetically based sex on a multi-trophic arthropod community that were expressed in wild-grown plants across multiple years.

Key words: *Aphis valerianae;* community genetics; dioecy; herbivory; indirect effects; interaction modification; mutualism; predation; sex-biased herbivory; tri-trophic interactions; *Valeriana edulis*.

Introduction

There is rapidly accumulating evidence that genetic variation in one species can have far-reaching effects on the structure and dynamics of communities and ecosystems (Whitham et al. 2003, 2006, Johnson and Stinchcombe 2007). Particularly well studied are the consequences of genetic variation within plant species for the structure of associated arthropod communities (Wimp and Whitham 2001, Johnson and Agrawal 2005, Whitham et al. 2006). This body of literature shows that plant genotype identity can explain a large proportion of the variation in metrics of multi-trophic arthropod community structure, including total arthropod abundance, abundance of herbivores and predators, species richness, and the stability of community composition over time (Wimp and Whitham 2001, Johnson and Agrawal 2005, Keith et al. 2010). While making notable contributions, the studies investigating such effects have also suffered from two shortcomings. First, they are based upon experimental common gardens (with the exception of three systems: *Populus* spp. [Wimp et al. 2004, Bangert et al. 2006*a*, *b*, Wimp et al. 2007, Meneses et al. 2012], a tropical tree [Zytynska et al. 2011], and a bromeliad [Zytynska et al. 2012]) that by design minimize natural variation and thus overestimate the contribution of plant genetics to variance in arthropod community structure (Tack et al. 2012). And second, few have explored the mechanisms by which genetic variation in plant traits propagates through arthropod food webs to produce these community-level patterns

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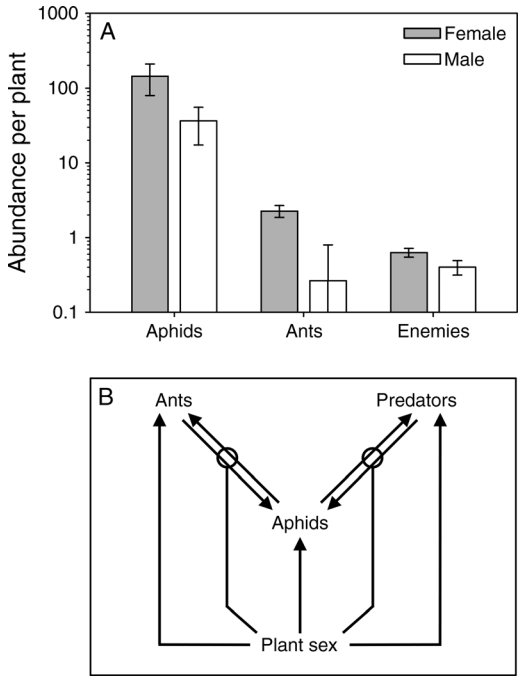


FIG. 1. (A) Abundance (mean ± SE) of aphids, ants, and predatory arthropods on male and female *Valeriana edulis* from three years of surveys. There was significant plant sexual dimorphism in the abundance of aphids ($P = 0.007$) and ants ($P = 0.001$), and marginally significant sexual dimorphism in predators ($P = 0.067$). (B) The hypotheses for mechanisms underlying these patterns. Arrows indicate direct effects; lines with circles indicate interaction modification.

(but see Wimp and Whitham 2001, Mooney and Agrawal 2008, Johnson 2008).

Plant genetic variation may affect arthropod abundance directly and indirectly. Direct effects result from differences in traits among genotypes that affect plant–arthropod pairwise interactions. Indirect effects are downstream effects of plant traits and may be further subdivided into density-mediated indirect effects (interaction chains, sensu Wootton [1994]) and trait-mediated indirect effects (interaction modification, sensu Wootton [1994], Peacor and Werner [1997]). In the first case, plant traits that directly affect the density of one arthropod species in turn propagate to indirectly affect additional arthropod species. Here the parameter(s) of the functional response (linear or nonlinear) of one arthropod to another arthropod remain constant among plant genotypes. In the second case, plant traits modify the functional response parameters. Distinguishing among these non-mutually exclusive effects of plant genotype provides the mechanistic framework needed to predict the ecological and evolutionary consequences of plant genetic variation for multi-trophic arthropod communities (Mooney and Singer 2012, Strauss et al. 2005). Furthermore, this mechanistic approach allows for comparisons of the relative strengths of these community-organizing interactions and for a test of the hypothesis that plant genetic effects diminish with increasing trophic level due to the primacy of indirect effects at these levels (Johnson and Agrawal 2005, Mooney and Agrawal 2008).

One form of genetic variation in plants with important ecological and evolutionary consequences is that of plant sex in dioecious species (Ågren et al. 1999, Cornelissen and Stiling 2005). Dioecy is a sexual system that occurs in 37 of 51 plant orders and 10% of all angiosperm species (Geber et al. 1999, Cornelissen and Stiling 2005). Because plant sex is by in large genetically determined (Ming et al. 2011) and easily identified in the field, dioecy (and other polymorphic sexual systems) allows for rapid in situ genotyping of wild-growing plants with respect to the sex determination loci. Despite the relatively few genes that typically underlie sex determination (Ming et al. 2011), plant sex is associated with a substantial degree of ecological dimorphism. Female plants typically invest more in reproduction than males (Lloyd and Webb 1977, Delph 1999), grow more slowly, have higher levels of defenses against herbivores, support lower herbivore densities, and receive less herbivore damage (Ågren et al. 1999, Cornelissen and Stiling 2005). In contrast to these well-documented effects of plant sex on herbivores, far less is known about effects on higher trophic levels (but see Ashman and King 2005, Mooney et al. 2012).

This study investigates the mechanisms by which genetically based plant sex influences the tripartite interactions among ants, ant-tended herbivores, and herbivore predators. These food web vignettes (sensu Polis and Strong 1996) are experimentally tractable, consisting of as few as four species (plant, herbivore, ant, and predator), yet still encompass the ecological complexity of tri-trophic interactions, herbivory, predation, and mutualism. Surveys of naturally occurring male and female *Valeriana edulis* over three consecutive years demonstrated strong and consistent plant genetic effects over arthropod community structure, with females supporting aphid, predator, and ant abundances that were 4-fold, 1.5-fold, and 4-fold greater than those of males (Fig. 1A; see Plate 1). These surveys were accompanied by a series of manipulative studies to determine which of the direct effects and density- and trait-mediated indirect effects of plant sex (Fig. 1B) underlie these field patterns. Uniquely, this study identifies the mechanisms of plant genetic control over a multi-trophic arthropod community, and juxtaposes the strength of these effects against realistic levels of natural variation by studying wild-growing plants across multiple years.

METHODS

Study sites

This study was conducted in montane meadows (described by Langenheim [1962]) in Gunnison County, Colorado, USA at 2918 m (38.967° N, 106.995° W) near

the Judd Falls Trailhead parking area (hereafter JF) and at 2780 m elevation and 12 km distant from JF, referred to as Brush Creek (hereafter BC; 38.895° N, 106.890° W). Where experiments were replicated at both sites, the timing was staggered (JF initiated approximately 7 days later) such that both experiments began at a similar phase with respect to plant and arthropod phenology.

Natural history

The plant *Valeriana edulis* Nutt. ex Torr. and A. Gray subsp. *edulis*, is a dioecious perennial herb distributed throughout western North America (Meyer 1951). Plants grow for several years as a basal rosette of leaves before flowering via one to many inflorescences of small (3–5 mm diameter) white flowers (Soule 1981). Inflorescences bolt during the second half of June and consist of a stalk supporting one to several compound cymes. Like its dioecious congener *V. dioica* L. (Meurman 1925), sex determination in this species appears to be genetically controlled by an XY sex chromosome system given that monitoring of 776 plants for three consecutive years never found changes in individual sex expression (Soule 1981). After bolting following snowmelt, *V. edulis* is fed upon by the ant-tended aphid *Aphis valerianae* Cowen (Aphididae, Heteroptera), which then persists into early September. This aphid feeds on the upper portions of the main inflorescence stalk and within compound cymes on the stalks supporting individual cymes. Ants that frequently collect aphid honeydew and *V. edulis* floral nectar include *Tapinoma sessile* (Say), *Formica podzolica* Francoeur, *F. neogagates* group, *Camponotus modoc* (Wheeler), and *Myrmica incompleta* Provancher. None of the ant species have been observed to prey on or move aphids among feeding sites (Petry et al. 2012, Mooney et al. 2012; W. K. Petry, *personal observation*). The community of predators observed to feed on *A. valerianae* includes Araneae, Coccinellidae (Coleoptera), Syrphidae (Diptera), Miridae and Reduviidae (Heteroptera), Braconidae, Ichneumonidae and Vespidae (Hymenoptera), and Chrysopidae (Neuroptera).

Surveys of plant traits and arthropods

In the summer of 2009, plant traits and arthropod abundance were measured on 97 randomly selected flowering plants (67 female and 30 male). In the summers of 2010 and 2011, similar surveys of 13 male and 16 female permanently marked plants were conducted, again measuring plant traits and arthropod abundance. Plant traits measured included several metrics of plant size and reproduction (fully described in Appendix A). Though some plant traits varied among years, there was no difference between the sexes in plant traits except flower number and inflorescence volume (Appendix A). Nectar was difficult to quantify due to its small quantity and high viscosity, but female nectar was frequently visible while male nectar was rarely so. Aphids, ants, and predators were surveyed in all three years through an exhaustive search of each plant. All individuals of taxa commonly reported to be predatory (see *Natural history*) were counted regardless of their observed activity. For each taxon actual predation events were observed on one or more occasions. Survey data for predators and ants were supplemented with observations from plants used in several experiments (see *Mechanistic studies*) to which aphids were added, but no other manipulations were imposed. Consequently, survey sample size for aphids, predators, and ants was 166 (2009, $n = 97$; 2010, $n = 29$; 2011, $n = 40$), 162 (2009, $n = 30$; 2010, $n = 100$; 2011, $n = 32$), and 156 (2009, $n = 97$; 2010, $n = 29$; 2011, $n = 30$) observations, respectively. Mean abundances for each plant were derived by standardizing the number of arthropods observed to the number of times that individual plant was surveyed to avoid pseudoreplication.

The abundance of each arthropod group was analyzed using ANOVA, with plant sex and observation year as independent factors. When residuals were not normally distributed or variances were heteroscedastic, resampling analyses (following Manly 2007) were conducted. Briefly, arthropod abundances were modeled as dependent upon plant sex and year using an ANOVA to generate observed F statistics for each model term. P values were estimated by comparing observed F statistics to null F distributions based on 10^3 permutations of the dependent variable and the result is P_{perm}. In addition, the presence/absence of each arthropod group was analyzed using logistic regression, with plant sex and observation year as independent factors. In these surveys and in all experiments, statistical analyses were conducted using R 2.15.0 (R Development Core Team 2012).

Mechanistic studies

The plant surveys just described revealed a consistent female bias for aphid, predator, and ant abundance across three years (*Results*, Fig. 1A). Accordingly, manipulative experiments and additional analyses of survey data were conducted to elucidate the mechanisms underlying these patterns (Fig. 1B).

Plant effects on aphids.—We used two methods to test for direct plant effects on aphids. First, to test for sexual dimorphism in plant quality to aphids, the growth rate of experimentally established aphid populations was compared between male and female plants in both 2009 and 2010 at JF. This study was based on 60 plants in 2009 (30 male, 30 female) and 100 plants in 2010 (49 male, 51 female). Aphid populations were established at mean initial densities of 8 ± 0.6 (mean $\pm$ SE) and 11 ± 0.2 wingless adults per plant (in 2009 and 2010, respectively) within mesh bags that excluded both predators and ants. Population growth was monitored for 18 days (beginning on 5 July) and 8–12 days (beginning 14 July) for 2009 and 2010, respectively. Population growth rate was calculated according to the following equation:

$$r = \frac{\ln(N_{t1}) - \ln(N_{t0})}{t_1 - t_0} \quad (1)$$

where N_{t0} and N_{t1} are population densities at time t_0 and t_1, respectively. For extinct populations at t_1, r was set to zero. Because analysis residuals for population growth rate did not follow normal or Poisson distributions, resampling analyses were used (as above for survey data).

Second, the relative preference of dispersing aphids for male and female plants was assessed to test whether differences in aphid abundance were due to host plant selection. In 2011, 18 male and 13 female aphid-free plants were selected at JF on 29 June, while 18 male and 24 female aphid-free plants were selected for observation at BC on 11 July. Each plant was then inspected at intervals of 3 to 7 days for the occurrence of newly arrived, individual, winged aphids. While this survey interval may have missed early predation events, it is likely adequate to detect effects of plant sex on aphid establishment and initial reproduction. When ~70% of monitored plants were colonized (after 34 and 14 days for JF and BC, respectively) the occurrence of colonization was modeled using a logistic regression with plant sex, site, and their interaction as independent factors.

Predator effects on aphids.—To compare the effects of predators on aphids between male and female plants, pairs of similarly sized inflorescence stalks were selected at JF in 2009 on 15 male and 15 female plants ($n = 30$ paired inflorescences). Ants were excluded from all inflorescences using tape coated with a sticky paste barrier (Tanglefoot Company, Grand Rapids, Michigan, USA) around the base of the stem. None of the most abundant predators in this system—winged predators (e.g., adult coccinellids, wasps, adult hemipterans) or apterous predators deposited as eggs by winged adults (e.g., larval coccinellids and syrphids)—are affected by these barriers. Both inflorescences were enclosed in breathable mesh bags, and for half of the bags several vertical slits were cut into bags to allow predator access. Although this design may have allowed emigration of aphids in the treatment open to predators, the goal of this experiment was to test for sexual dimorphism in predator effects rather than to quantify the effect of predators absolutely. Moreover, substantial emigration is unlikely because (1) the production of winged dispersal morphs was rare and (2) this specialist species does not appear to disperse among hosts by walking, as we have never observed individuals ascending or descending the plant stems subtending inflorescences (W. K. Petry, *personal observation*). On 3 August, aphid populations were established at a mean initial density of 37 ± 2 aphids per plant and monitored for 10 days. Aphid population growth rate (Eq. 1) was then modeled as a dependent variable on predator exclusion, plant sex, and their interaction, with initial aphid population as a covariate. Here the main effects test the hypothesis that predators and plant sex influence aphid performance while their interaction tests the hypothesis that plant sex modifies the top-down effect of predators on aphid performance.

Ant effects on aphids.—To compare the effects of ants on aphids between male and female plants, experiments were conducted at both JF and BC in 2011. Eight blocks of plants were selected per site with two male and two female plants each, and two experimental inflorescences per plant for a total of 128 experimental inflorescences. Within each block, one male and one female plant were assigned to receive a single unwinged aphid on each inflorescence, representing colony establishment. The other male and female plant received aphids at initial densities of 34 ± 2 aphids, simulating an established colony. Within each plant, ants were then excluded from one inflorescence, with the second inflorescence serving as a control. Aphid populations were monitored for 14 days (beginning on 26 July) and 15 days (beginning on 20 July) for JF and BC, respectively. Aphid population growth rate (Eq. 1) was modeled as dependent on plant sex, initial aphid density, site, and their two- and three-way interactions with block as a random effect. This model tests for effects of ant exclusion, aphid density, and plant sex on aphid population growth (all main effects) as well as sex modification of both ant effects on aphids (plant sex × ant exclusion) and aphid density effects (plant sex × aphid density) and the density-dependent effects of ants (plant sex × density × ant exclusion interaction).

Plant and aphid effects on predators.—Further analysis of survey data were used to identify the pathways (direct, aphid density-mediated, or interaction modification) underlying the higher abundance of predators on female plants. Predator abundance ($n = 162$ replicate plants) was modeled as dependent upon plant sex, aphids, and their interaction while controlling for year using ANCOVA. This model simultaneously tests for direct, aphid density-mediated and interaction modification effects of plant sex on predators. A significant effect of plant sex, while controlling for variation in aphid abundance, is indicative of a direct effect. Similarly, a significant effect of aphid abundance while controlling for plant sex, in combination with the greater abundance of aphids naturally occurring on female plants, is evidence for a density-mediated indirect effect. Finally, a significant plant sex × aphid abundance interaction indicates an interaction modification, as the slope of the relationship between aphid and predator abundance, representing the per capita effect of aphids on predators, would differ between the sexes.

Plant and aphid effects on ants.—Further analysis of survey data were used to identify the pathways underlying the higher abundance of ants on female plants using an ANCOVA in a fashion parallel to that for predators (see *Plant and aphid effects on predators*). Ant abundance (n = 156 replicate plants) was modeled as dependent upon the main effects of plant sex (direct effect) and aphid abundance (aphid-mediated indirect

effect) and their interaction (interaction modification effect) while controlling for year.

We also used a manipulative experiment to specifically test whether sexual dimorphism in the effect of floral nectar influenced ants and ant–aphid interactions. In 2011, 10 pairs of male and female plants were selected at both JF and BC, with two experimental inflorescences per plant (total $n = 80$ inflorescences). For each plant, one inflorescence was randomly selected to receive a nectary-blocking treatment (Rudgers 2004). Glue (Aleene's OK to Wash-It fabric glue; Duncan Enterprises, Fresno, California, USA) was applied to each flower on nectary exclusion plants, while a similar amount of glue was applied to the stems immediately subtending those flowers on control plants. Plants were then stocked with aphids at a mean initial density of 12 $\pm$ 1 aphids per plant. Counts of both ants and aphids were made across 19 days (beginning on 19 July) and 11 days (beginning on 10 July) at JF and BC, respectively. Ants were counted separately with respect to whether they were tending aphids or foraging on inflorescences.

This experiment tested three sets of hypotheses regarding the role of nectar in plant-aphid-ant interactions. First, ant abundance at floral nectaries (averaged across all repeated surveys) was modeled as dependent upon plant sex, exclusion of nectaries, and their interaction, with field site and block included as random effects and aphid abundance as a covariate. Second, the abundance of ants tending aphids (averaged across all repeated surveys) was analyzed with the same independent variables as the model used to analyze flower visitation. In these analyses of ant visitation to flowers or aphids, the main effect of plant sex tests for sexual dimorphism in ant abundance, the main effect of nectar exclusion tests whether floral resources influence ant abundance, while the nectar exclusion $\times$ plant sex interaction tests whether differences in the attractiveness of floral resources between sexes underlie any direct influence of plant sex on ant abundance.

A complementary analysis tested for aphid performance responses to plant sex and floral nectar exclusion (mediated through ant or predator recruitment to nectar). Aphid population growth rate was modeled as dependent upon plant sex, nectary blocking, and their interaction, with field site included as a random effect. In this analysis, the main effect of plant sex tests for sexual dimorphism in plant quality (thus complementing the test of direct effects of plant sex on aphids described in *Plant effects on aphids*), and the main effect of nectary blocking tests whether floral resources (indirectly) influence aphid performance. Because glue did not directly affect aphid performance (experiment described in Appendix B), a significant main effect of nectary blocking is likely mediated through higher trophic levels. Finally, the nectary blocking $\times$ plant sex interaction tests whether any difference in aphid performance between male and female plants is underlain by sexual dimorphism in the higher-trophic-level-mediated effects of floral nectar.

Partitioning variance in arthropod abundance.—The magnitude of plant sex effects on arthropods can be assessed not only by comparing mean abundances between males and females as above, but also by quantifying the proportion of overall variance explained (R^2_{sex}). When these R^2 calculations are made with respect to variance among plant genotypes (e.g., clonal replicates, half- or whole-sib families), such values are similar to broad-sense heritabilities (H^2) for arthropod abundance as an extended plant phenotype (Shuster et al. 2006). In the present case, R^2_{sex} assesses the subset of H^2 that can be ascribed to plant sex determination genes.

The approach for estimating R^2_{sex} for each arthropod group's abundance (survey data) was first to use a sequential sum of squares (type I) ANOVA model to estimate the sum of squares for plant sex (SS_{sex}) and year (SS_{year}) terms as well as the model's total sum of squares (SS_{total}). Here the total proportion of variance in arthropod abundance explained by plant sex (direct + indirect effects) was calculated as SS_{sex} divided by SS_{total} with interannual variation in abundance removed ($SS_{\text{total}} - SS_{\text{year}}$). Because plant sex affected aphid presence (vs. absence) but not abundance when aphids were present (analysis not shown), we used aphid presence in partitioning analyses. For aphids and predators, this value was assumed to be solely due to the direct effect of plant sex based upon our analyses of survey and experimental data (see Results). For ants, however, the total effect of plant sex on ant abundance could be partitioned into direct and aphid-mediated indirect pathways by directly calculating the R^2_{sex} for the direct pathway and subtracting it from the total R^2_{sex} (i.e., from direct + indirect) to yield the indirect R^2_{sex}. Here the direct R^2_{sex} is calculated from a similar model and using the same sum-of-square terms as above, except that a term for aphids is fit before plant sex.

Results

Surveys of plant traits and arthropods

Preliminary analyses showed patterns of sexual dimorphism in arthropod associations to be consistent across years (i.e., no sex $\times$ year interaction, $P \geq 0.12$), and this interaction term was excluded from all models. There was strong sexual dimorphism in the abundance of aphids, ants, and predators (Fig. 1). Female plants hosted fourfold more aphids compared to males (Table 1). Aphids were also more likely to be present (vs. absent) on females than males, occurring on 43% and 24% of plants, respectively (Table 1). Aphid presence appeared to drive the significant difference in aphid abundance: on those plants with one or more aphids, there was no difference in aphid abundance ($F_{1,59} = 2.50$, $P = 0.12$), though the trend was for a greater abundance (back-transformed mean $\pm$ asymmetric SE: lower, upper) on females (50.6 $\pm$ 11.0, 19.0) than males (22.8 $\pm$ 6.7, 15.0). There was a trend ($F_{1,158} = 3.48$, $P = 0.067$)

TABLE 1. Analysis of variance tables of tests for arthropod community dimorphism between female and male *Valeriana edulis* plants and least-square mean arthropod frequencies and abundances.

Arthropod and source	*F*	df	*P*
Aphid abundance			
Sex	7.44	1, 162	**0.007**
Year	30.83	2, 162	**<0.001**
Aphid presence/absence			
Sex	4.94	1, 162	**0.028**
Year	21.80	2, 162	**<0.001**
Ant abundance			
Sex	9.13	1, 152	**0.001**
Year	4.97	2, 152	**0.007**
Ant presence/absence			
Sex	17.73	1, 152	**<0.001**
Year	5.08	2, 152	**0.007**
Predator abundance			
Sex	3.48	1, 158	**0.067**
Year	14.02	2, 158	**<0.001**
Predator presence/absence			
Sex	<0.01	1, 158	0.999
Year	3.56	2, 158	**0.031**

Notes: Significant ($P < 0.05$) and marginally significant ($P < 0.10$) model terms and their *P* values are shown in bold. No sex × year interactions were significant ($P > 0.12$).

for female plants to host more predators compared to males (1.5×; Table 1). Predators were equally likely to be present (vs. absent) on female than male plants (46% of plants; Table 1). On those plants with one or more predators during any survey visit, females again hosted marginally more predators ($F_{1,71} = 3.59$, $P = 0.06$), with means (±SE) of 1.08 ± 0.11 and 0.81 ± 0.11 predators per survey visit, respectively. Female plants hosted fourfold more ants compared to males (Table 1). Ants were more likely to be present (vs. absent) on females than males, occurring on 51% and 16% of plants, respectively (Table 1). On those plants with one or more ants during any survey visit, there was a trend for ant abundance to be higher on females than on males ($F_{1,55} = 3.93$, $P = 0.05$), with means of 2.91 ± 0.23 and 1.37 ± 0.57 ants per survey visit, respectively.

Mechanistic studies

Plant effects on aphids.—When aphids were reared within mesh bags in the absence of ants and predators, population growth rate (*r*) was not significantly different between male and female plants (Fig. 2A; $F_{1,156} = 0.12$, $P_{perm} = 0.72$) when controlling for a significant year effect ($F_{1,156} = 9.96$, $P_{perm} = 0.001$). Similarly, dispersing aphids also did not show an overall preference for female or male plants (Fig. 2B; $F_{1,69} = 0.77$, $P = 0.38$) and this pattern was consistent across both sites (i.e., no site effect, $F_{1,69} = 0.266$, $P = 0.61$, or sex × site interaction, $F_{1,69} = 0.005$, $P = 0.94$).

Predator effects on aphids.—Comparing aphid population growth between predator exclusion and control treatments on male and female plants, predators had a negative effect on aphid performance ($F_{1,55} = 6.22$, $P_{perm} = 0.014$) when controlling for initial aphid abundance ($F_{1,55} = 10.75$, $P_{perm} = 0.001$), reducing population growth rate by 19% (predator exclusion, 0.074 ± 0.007; control, 0.060 ± 0.007). Although there was a trend toward greater predator abundance on female plants (see *Results: Surveys of plant traits and arthropods*), there was no evidence that plant sex mediated the effect of predators on aphid performance (i.e., no trait-mediated indirect effect indicated by an insignificant sex × predator treatment interaction; $F_{1,55} = 0.42$, $P_{perm} = 0.53$).

Ant effects on aphids.—The exclusion of ants (Fig. 3) increased aphid population growth rate by 46% ($F_{1,119} = 20.83$, $P_{perm} < 0.001$) and did so to an equal extent on male and female plants, i.e., no ant × plant sex interaction ($F_{1,119} = 0.03$, $P_{perm} = 0.87$). Furthermore, aphid performance was 41% higher on females than males ($F_{1,119} = 6.84$, $P_{perm} = 0.011$), contrasting the assessment of host plant quality to aphids within mesh bags (see *Plant effects on aphids*). Neither aphid density ($F_{1,119} = 0.14$, $P_{perm} = 0.24$), study site ($F_{1,119} = 0.98$, $P_{perm} = 0.32$), nor any two- and three-way interactions between the four main effects were significant ($P_{perm} > 0.60$).

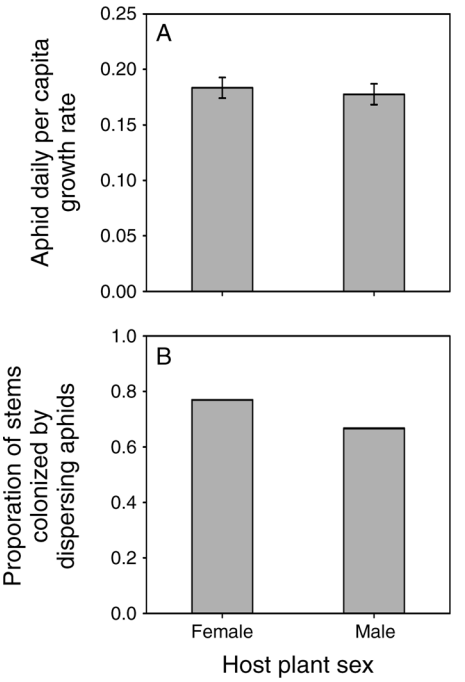


FIG. 2. (A) Daily per capita daily growth rate (mean ± SE) of the aphid *Aphis valerianae* on female and male *Valeriana edulis*, controlling for year. Plant sex did not influence aphid growth rate ($P_{perm} = 0.72$; see *Methods: Surveys of plant traits and arthropods* for definition of P_{perm}). (B) The proportion of female and male plants colonized by winged aphids did not differ ($P = 0.38$) at both study sites, BC and JF.

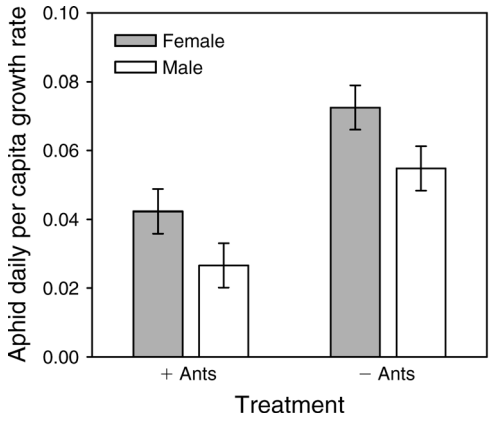


FIG. 3. Daily per capita daily growth rate (mean ± SE) of aphids on female (dark bars) and male (light bars) plants, with ants allowed (+) or excluded (–) controlling for field site. Aphids performed better on females ($P_{perm} = 0.011$), and ants strongly reduced aphid performance ($P_{perm} < 0.001$).

Plant and aphid effects on predators.—We further analyzed survey data to assess the association between predators and aphids on male and female plants. Plant sex affected predators directly, but not through aphid density-mediated indirect effects or modification of aphid–predator interactions. Predator abundance was higher on female plants ($F_{1,157} = 3.86$, $P_{perm} = 0.050$), and there was no evidence for an influence of aphid abundance ($F_{1,157} = 0.476$, $P_{perm} = 0.49$), nor that the attractiveness of aphids to predators differed between plant sexes, i.e., there was no plant sex × aphid abundance interaction ($F_{1,156} = 0.683$, $P_{perm} = 0.41$). Following this unusual lack of association between aphids and their predators, we performed a Fisher's exact test of association between plants hosting aphids and those hosting their predators but found no significant association ($n = 162$ observed plants; $P = 0.68$). An analysis (not shown) of predator abundance on plants without aphids ($n = 29$ observed plants) revealed a similar but nonsignificant ($P = 0.35$) pattern of higher abundance on females.

Plant and aphid effects on ants.—We further analyzed survey data to assess the association between ants and aphids on male and female plants. Plant sex affected ants directly and indirectly through aphids, but did not modify aphid effects on ants. Ant abundance was higher on female plants ($F_{1,298} = 8.85$, $P = 0.003$) and was positively associated with aphid abundance ($F_{1,298} = 6.39$, $P = 0.012$), supporting a direct and aphid-density-mediated attraction of ants to female plants. The attractiveness of aphids to ants did not differ between plant sexes, i.e., there was no plant sex × aphid abundance interaction ($F_{1,297} = 0.05$, $P = 0.82$). Thus ants were attracted to female plants additively and independently by direct and aphid-mediated indirect pathways. An analysis (not shown) of those plants without aphids ($n = 97$ plants) revealed 3.3× higher ant abundance on females than males ($P = 0.011$).

We compared ant abundance between experimentally blocked and control floral nectaries on male and female plants with aphids. This manipulative experiment showed that floral nectar drives the direct effect of plant sex on ants and that nectar- and aphid-mediated ant recruitment operated independently. Although there was biased ant visitation toward female flowers across both nectary blocking and control treatments ($F_{1,67} = 4.91$, $P_{perm} = 0.016$), this effect of plant sex depended upon nectar blocking ($F_{1,67} = 5.48$, $P_{perm} = 0.01$); there was strong female bias in ant visitation to flowers when nectaries were open, but visitation was lower and no longer sexually dimorphic when nectaries were blocked (Fig. 4A). In addition, the abundance of aphids did not influence ant visitation to flowers ($F_{1,67} = 0.193$, $P_{perm} = 0.66$). Despite this greater recruitment of ants to female nectar, the abundance of aphid-tending ants was influenced by aphid abundance alone ($F_{1,67} = 19.04$, $P_{perm} < 0.001$), and not by plant sex ($F_{1,67} = 0.70$, $P_{perm} = 0.41$), the blocking of floral nectar ($F_{1,67} = 0.04$, P_{perm}

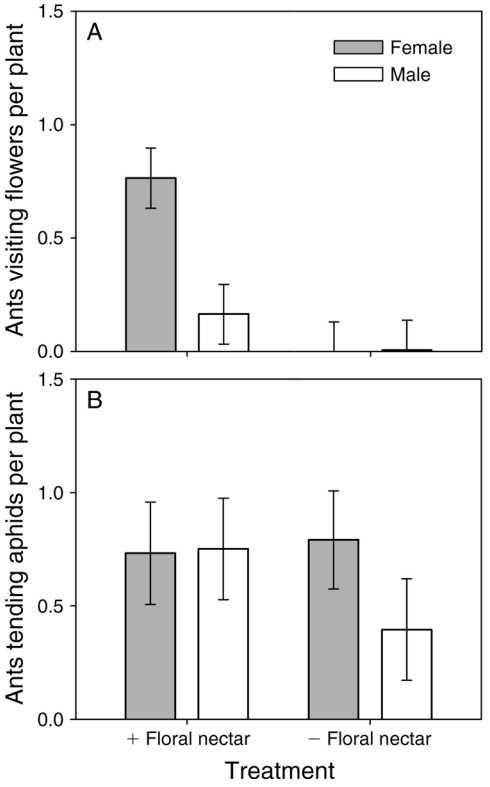
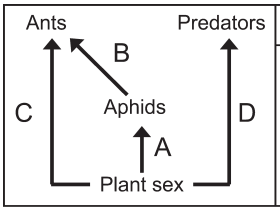


FIG. 4. (A) Number (least-square mean ± SE) of ants visiting flowers on female (dark bars) and male (light bars) *Valeriana edulis* with floral nectaries open (+) or blocked with glue (–). Floral visitation was higher on females on control plants but was negligible on plants with blocked floral nectaries ($P_{perm} = 0.016$). (B) Number (least-square mean ± SE) of total ants tending aphids on female (dark bars) and male (light bars) plants with floral nectaries open (+) or blocked with glue (–). Ant tending of aphids was not affected by plant sex ($P_{perm} = 0.41$) or floral nectar availability ($P_{perm} = 0.49$).



Plant sex effects on:	R^2_{sex}	F vs. M
Aphids, direct (A)	0.24%	4-fold
Ants, direct (C)	3.60%	4-fold
Ants, indirect (AB)	0.81%	
Predators, direct (D)	2.28%	1.5-fold

FIG. 5. The subset of potential mechanisms (Fig. 1B) determined to underlie sexual dimorphism in arthropod abundances (left) and comparisons of mechanism effect sizes (right). Mechanism effect sizes (arrows and values labeled A–D) are quantified as both percentage of variance explained (R^2_{sex}) and difference in abundance between female and male plants (F vs. M).

$= 0.84$), or their interaction ($F_{1,67} = 0.93$, $P_{perm} = 0.34$; Fig. 4B).

Partitioning variance in arthropod abundance.—Sequential fitting of plant sex and aphid model terms to both predator and ant abundance partitioned the variance in arthropod abundance among the significant mechanistic pathways (Fig. 5). Plant sex explained a relatively small amount of variance (R^2_{sex}) in aphid presence (0.24%) and slightly more for the abundances of predators (2.28%) and ants (4.42%). Only ants had statistical support for both direct and indirect effects of plant sex. Decomposing the total effect on ants into direct and indirect pathways showed direct recruitment to females was fourfold stronger than the aphid-mediated pathway (3.61% vs. 0.81%).

DISCUSSION

Plant surveys conducted over three consecutive years demonstrated strong and consistent evidence for plant genetic control over arthropod community structure, with female plants having 4-fold more aphids, 1.5-fold more predators, and 4-fold more ants as compared to male plants. Mechanistic studies demonstrated plant genetic effects directly on aphids, predators, and ants, as well as weaker indirect plant genetic effects on ants (but not predators) mediated by aphid abundance (Fig. 5). These direct and indirect effects on ants operated independently of each other and there was no evidence for interaction modification, i.e., aphid–ant and aphid–predator interactions were not influenced by the sex of the plant upon which they occurred. Plant sex explained somewhat less variance in aphid, predator, and ant abundance (0.24%, 2.28%, and 4.42% respectively) relative to past studies documenting plant-genetic effects on arthropod communities (reviewed in Johnson and Agrawal 2005). This study is unusual among those investigating plant genetic effects on arthropod community structure in its documentation of mechanism across multiple trophic levels, and as only the fourth system demonstrating the strength of plant genetic effects for wild-grown plants under non-experimental conditions.

Despite a consistent female-bias in aphid abundance, our results were ambiguous with respect to the mechanism. There were two experiments in which aphid population growth rate was compared between male and female plants. When aphids were isolated from interactions with predators and ants in mesh bags (Fig. 2A) there was no detectable difference in aphid performance. In contrast, in a separate experiment where aphids were unbagged, their performance was stronger on females (Fig. 3), although such effects did not depend on the presence of ants or predators. While our experiments provide some positive evidence for higher quality of female plants, consistent with the female bias observed in surveys (Fig. 1), there was no corresponding female-bias in aphid host plant selection. In addition, plant sex did not mediate the top-down effects of predators and ants on aphids; we did not detect differences in the rates of association between either tending ants or predators and aphids (density-mediated indirect effects), nor in the strength of their effects on aphid performance (interaction modification). So while there is some evidence superior plant quality underlies greater aphid abundance on females, further studies are required to definitively resolve this.

Plant genetic effects on ants were driven by two mechanisms. First, plant sex directly influenced ants, with female plants being more attractive than male plants due to differences in nectar rewards. Past studies have similarly shown dimorphism in ant recruitment to male and female flowers, although these studies are evenly divided with respect to which is the more attractive sex (Ashman and King 2005, Mooney et al. 2012). Second, the higher abundance of aphids on female plants resulted in an indirect genetic effect on ants, a dynamic that has previously been observed in four other plant–aphid systems (Wimp and Whitham 2001, Mooney and Agrawal 2008, Johnson 2008, Abdala-Roberts et al. 2012). Although these two plant genetic effects on ants operated in parallel, each contributing to greater ant abundance on female plants, they operated independently in that ant recruitment to aphids did not vary between male and female plants, even though there were more ants associated with female flowers. The additive recruitment of ants to these co-occurring resources runs counter to the prediction that plant resources should mediate ant interactions with herbivores (Becerra and Venable 1989, Ness et al. 2009). A better understanding of dual resource effects on arthropods (i.e., synergistic attraction or antagonism) may come from comparing the nutritive composition of honeydew and floral nectar (e.g., Blüthgen et al. 2004).

We observed higher abundances of predators on female plants that was not driven by sexual dimorphism in aphid abundance, and the effects of predators on aphids was equal between plant sexes. That is, unlike ant abundance that was driven by both direct and indirect effects of plant sex, only direct effects influenced

PLATE 1. (Right) Ants (*Camponotus* sp.) tending aphids (*Aphis valerianae*) on host plant *Valeriana edulis*. (Left) Ant (*Formica* sp.) collecting nectar from female flowers of *V. edulis*. Photo credit: K. A. Mooney.

predator abundance. Higher predator abundance on females is consistent with a direct effect of sexual dimorphism in floral rewards (Pacini and Nepi 2007). Because predator effects on aphids were equivalent between male and female plants, we speculate that sexual dimorphism in floral attraction of predators did not mediate predator attack of aphids.

While both ants and predators were more abundant on female plants (Fig. 1A), the strength of the direct plant genetic effect was greater for ants. This finding is consistent with past studies that show plant genetic effects on ant but not predator abundance (Johnson 2008, Mooney and Agrawal 2008, Abdala-Roberts et al. 2012). The emerging generality of this pattern may be due to the social foraging of ants vs. the generally solitary foraging of predators. This provides a pathway to greater recruitment to resources that are underlain by genetically variable plant traits. For these higher trophic levels more broadly, the strength of direct effects of plant sex exceeded indirect (herbivore-density-mediated) effects. This suggests that, although plant genetic effects on higher trophic levels may be diluted through intervening trophic links (e.g., herbivores), plant genetic variation in traits directly attractive to these arthropods may outweigh weak herbivore density-mediated effects. Specifically, consideration of floral nectar may be particularly important for understanding the strength of direct plant genetic effects. Floral nectar is attractive to both predators and ants (Wäckers 2005), and nectar traits can differ among genotypes (Eckhart 1999, Mitchell 2004). Furthermore, there is growing evidence that plant genetic effects on higher trophic levels are more apparent when floral rewards are available (this study; Crutsinger et al. 2008) vs. when they are absent (Johnson 2008, Mooney and Agrawal 2008, Abdala-Roberts et al. 2012).

Plant genetic effects on arthropod communities can be quantified both in terms of difference between genotype means (Fig. 1A) and in terms of the percentage of variance explained by genotype (community-level heritability sensu Goodnight and Craig [1996] and Shuster et al. [2006]). Johnson and Agrawal (2005) reviewed the percentage of variance in arthropod groups attributable to plant genotype from plant collections across multiple spatial scales. In the 26 plant–arthropod interactions measured at a comparable spatial scale to this study, they showed that plant genotype explains an average of 8.5% of the variation in arthropod abundance. Consequently, the variance in aphid, predator, and ant abundance due to plant genotype (sex) in this study (0.24%, 2.28%, and 4.42% respectively) was comparable, although somewhat lower than that generally observed. By using wild-grown plants in situ, this study measured plant genetic effects against levels of environmental variation that are greater, and more realistic, than that occurring in the experimental common gardens used in past studies (see reviews in Tack et al. 2012 and Johnson and Agrawal 2005). Thus our study adds to a small literature showing the importance of plant genetic effects on arthropod communities in natural settings previously known only from two tree systems, *Populus* spp. (Wimp et al. 2004, 2007, Bangert et al. 2006*a*, *b*, Meneses et al. 2012) and *Brosimum alicastrum* (Zytynska et al. 2011), and the bromeliad *Aechmea bracteata* (Zytynska et al.

2012). It is perhaps not surprising to find less variance explained by a small proportion of the genome, the sex-determining genes (Ming et al. 2011), as compared to studies using clones, half or full siblings that measure the influences of whole plant genomes. Our study methodology thus offers a conservative estimate of extended consequences of plant genetics on arthropod community structure.

In summary, our study adds a mechanistic perspective to the growing literature on plant genetic control over arthropod community structure. Genetically based sex affected arthropod abundances though both direct and density-mediated indirect effects, but not through interaction modification, suggesting that the latter interaction type may not always play a role in structuring arthropod communities. Our findings also challenge the perspective that plant genetic effects diminish with increasing trophic level (Johnson and Agrawal 2005, Mooney and Agrawal 2008), observing that strong direct effects overshadowed this prediction. Thus genetic variation in traits both widely known to directly influence higher trophic levels (e.g., extrafloral nectaries, domatia, and volatiles) and those less studied traits like floral traits (this study) and plant morphology (Marquis and Whelan 1996) deserve attention. Furthermore, we measured these effects in wild-grown plants, finding patterns that were consistent across multiple years and comparable in strength to those previously found in more controlled, common garden experiments. This study thus documents the mechanisms underlying plant genetic control of arthropod community structure in a natural setting.

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Supplemental Material

Appendix A

Statistical methods and detailed results of tests for sexual dimorphism in plant traits (*Ecological Archives* E094-187-A1).

Appendix B

Statistical methods and detailed results of tests for direct effects of nectary gluing on aphids (*Ecological Archives* E094-187-A2).