

Unique arthropod communities on different host-plant genotypes results in greater arthropod diversity

Sharon M. Ferrier · Randy K. Bangert ·
Erika I. Hersch-Green · Joseph K. Bailey ·
Gery J. Allan · Thomas G. Whitham

Received: 13 March 2011 / Accepted: 26 December 2011 / Published online: 23 March 2012
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Abstract Studies on the effect of plant-species diversity on various ecological processes has led to the study of the effects of plant-genetic diversity in the context of community genetics. Arthropod diversity can increase with plant-species or plant-genetic diversity (Wimp et al. in *Ecol Lett* 7:776–780, 2004). Plant diversity effects can be difficult to separate from other ecological processes, for example, complementarity. We asked three basic questions: (1) Are arthropod communities unique on different host-plant genotypes? (2) Is arthropod diversity greater when associated with greater plant-genetic diversity? (3) Are arthropod communities more closely associated with host-plant genetics than the plant neighborhood? We

studied canopy arthropods on *Populus fremontii* trees randomly planted in a common garden. All trees were planted in a homogeneous matrix, which helped to reduce *P. fremontii* neighborhood effects. One sample was comprised of few *P. fremontii* genotypes with many clones. A second sample was comprised of many *P. fremontii* genotypes with few clones. A second data set was used to examine the relationships between the arthropod community with *P. fremontii* genetic composition and the neighborhood composition of the focal host plant. Unique arthropod communities were associated with different *P. fremontii* genotypes, and arthropod community diversity was greater in the sample with greater *P. fremontii* genotypic diversity. Arthropod community similarity was negatively correlated with *P. fremontii* genetic distance, but arthropod community similarity was not related to the neighborhood of the *P. fremontii* host plant.

First authorship shared by Sharon M. Ferrier and Randy K. Bangert.

Handling Editor: Gary Felton.

S. M. Ferrier (✉) · R. K. Bangert (✉) ·
G. J. Allan · T. G. Whitham
Department of Biological Sciences and the Merriam-Powell
Center for Environmental Research, Northern Arizona
University, P.O. Box 5640, Flagstaff, AZ 86011, USA
e-mail: Sharon.Ferrier@nau.edu

R. K. Bangert
e-mail: bangrand@isu.edu

Present Address:
R. K. Bangert
Trinidad State Junior College, Trinidad, CO 81082, USA

E. I. Hersch-Green
Department of Biological Sciences, Michigan Technological
University, Houghton, MI 49931, USA

J. K. Bailey
Ecology and Evolutionary Biology, University of Tennessee,
569 Dabney Hall, Knoxville, TN 37917, USA

Keywords Arthropod diversity · Common garden ·
Community genetics · Genotypic diversity · *Populus
fremontii* · Microsatellite markers

Introduction

The effect of plant-species diversity on various ecological processes has received much attention for several decades (e.g., Huston 1997; Knops et al. 1999; Murdoch et al. 1972; Naeem et al. 1994; Schulze and Mooney 1993; Siemann 1998; Siemann et al. 1998; Tilman et al. 1997). Attention began to focus on the effect of intraspecific plant-genetic diversity on ecological communities in the 1990s, in the context of community genetics (e.g., Antonovics 1992, 2003; Booth and Grime 2003; Johnson and Agrawal 2005; Morin 2003; Neuhauser et al. 2003; Wade 2003; Whitham

et al. 1999, 2003, 2006, 2008; Wimp et al. 2004). Many studies focused on the effect of plant-genetic diversity on arthropod communities (e.g., Bangert et al. 2005, 2006; Crutsinger et al. 2006; Dungey et al. 2000; Fritz and Price 1988; Johnson and Agrawal 2005; Hughes et al. 2008; Johnson et al. 2006; Keith et al. 2010; Wimp et al. 2004), microbial communities (Schweitzer et al. 2007), and ecosystem processes (Crutsinger et al. 2006; Schweitzer et al. 2004, 2005, 2007, 2008). Many studies have manipulated plant-species and genotypic diversity at the plot-level and identified diversity effects on arthropods and ecosystem processes (e.g., Crutsinger et al. 2006; Johnson and Agrawal 2005; Tilman et al. 1997). However, plant apparency (Feeny 1976), associational resistance (Tahvanainen and Root 1972), associational susceptibility (Atsatt and O'Dowd 1976; White and Whitham 2000), complementarity (e.g., Hughes et al. 2008; Naeem 2002), and neighborhood effects (sensu Addicott et al. 1987) may be difficult to separate from diversity effects in plot-level experiments, because arthropods may respond to the plot rather than individual plants.

Arthropod and microbial communities have been shown to be unique on different host-plant genotypes (Bailey et al. 2009; Bangert et al. 2006; Keith et al. 2010; Schweitzer et al. 2004, 2007, 2008; Shuster et al. 2006; Whitham et al. 2006). We hypothesized that arthropod community metrics (i.e., species richness, evenness, and Shannon's diversity) would be greater in a random sample of plants with higher-genotypic diversity. To test this hypothesis, we collected samples to represent low- and high-host-plant genotypic diversity in the riparian tree, *Populus fremontii*. There was no expectation that individual *P. fremontii* genotypes would be more, or less, genetically diverse in either sample, rather the accumulated ecological effect would be greater in the high-genotypic diversity sample. We tested three predictions: (1) arthropod communities are different on different host-plant genotypes and (2) arthropod diversity [species richness, Pielou's evenness (J), and Shannon's diversity (H')] would be lower in the sample with lower-host-plant genotypic diversity. We framed these two predictions in the context of biodiversity loss for consistency with much of the literature (e.g., Knops et al. 1999; Hughes and Stachowicz 2004; Naeem 2002; Naeem et al. 1994; Reusch et al. 2005). The second prediction was derived from the first prediction coupled with the expectation that when fewer host-plant genotypes are sampled, fewer unique arthropod communities would be sampled; therefore, arthropod diversity would be lower. Additionally, fewer alleles should be associated with fewer host-plant genotypes, potentially decreasing host-plant trait variation, that is, niche space for arthropods to respond to resulting in a decrease in arthropod diversity. We tested a third prediction that the genetic effect would be stronger than the neighborhood effect, in order to begin to

reduce the neighborhood effect as a competing hypothesis. Specifically, the a priori prediction was that arthropod similarity would be negatively correlated with genetic distance (i.e., similar arthropod communities would be associated with closely related trees), and only weakly correlated with the composition of the plant neighborhood. We studied canopy arthropods on Fremont cottonwood (*P. fremontii*) individuals that were planted within a large (8.1 ha, Fig. 2) homogeneous matrix of the woody shrub, *Salix exigua* (coyote willow), thus the sample units in this study were spatially independent, and the influence of plot-level or neighborhood diversity effects of other *P. fremontii* were assumed to be small.

Methods

Common garden

A common garden was planted along the Lower Colorado River near Blythe, CA, USA in 2007 (latitude: 33.71523°N, longitude: 114.499235°W). The garden was comprised of one shrub species (coyote willow, *Salix exigua*) and two tree species (Goodding's willow, *S. gooddingii*; Fremont cottonwood, *P. fremontii*) for southwestern willow flycatcher (*Empidonax traillii extimus*) habitat restoration and community genetics studies. The garden contained 16,896 plants, planted in a grid on 2-m centers, composed of 74% *Salix exigua* (12,503 plants) and 13% each of *S. gooddingii* and *P. fremontii* (2,196 plants each). The two tree species were randomly placed in the garden with *S. exigua* filling in the remaining matrix. *P. fremontii* was the focal tree for this study, representing 23 populations and 207 genotypes across the garden. All planted trees were originally collected from and planted within the USGS Basin and Range hydrographic province. The proportions of these three species span the range reported for natural densities in southwestern willow flycatcher habitat (McLeod et al. 2005).

Microsatellite DNA

Total genomic DNA was extracted from Drierite[®] dried leaf material using DNeasy Plant Mini Kits (Qiagen; Hilden, Germany) and then standardized to roughly 12.5 ng/μl. Reference information for the 15 microsatellite markers used in this study is in Tuskan et al. (2006) and at the International *Populus* Genome Consortium website (<http://www.ornl.gov>http://www.ornl.gov/sci/ipgc/ssr_resource.htm). Genotyping for the microsatellite markers was performed by electrophoretic separation of fluorescently labeled polymerase chain reaction (PCR) products on an ABI 3730 automated sequencer (Applied Biosystems[™]) using

GENESCAN-600 LIZ (Applied Biosystems™) as an internal size standard. Microsatellite loci were scored using Genotyper v. 3.7 NT software (Applied Biosystems™), and data from these 15 microsatellite markers were combined for each individual to obtain multilocus individual genotypes. To ensure marker repeatability, the whole procedure, including DNA extractions, was repeated for four individuals at each step in the process. Any markers that were not repeatable were not included in the final analyses.

Arthropod sampling

Canopy arthropods were sampled on 181 trees in a common garden, representing 36 unique genotypes from 10 source populations, from March 20 to 31, 2009 (Ferrier et al. in prep). Arthropods were visually quantified following the methods of Wimp et al. (2004) and Keith et al. (2010). Biomass and time were standardized among trees. Based on species accumulation curves by Wimp et al. (2004), approximately 200 shoots per tree were surveyed for a minimum of 20 min. Branch diameter was standardized across individuals to control for leaf area. Trees were sampled randomly across the garden to minimize any spatial effects. Unknown arthropods were collected for identification. All arthropods were classified as morpho-species based on previous observations of life cycle, mating individuals, and large morphological differences among individuals within a family or genera. All specimens collected were archived in the Colorado Plateau Arthropod Museum at Northern Arizona University.

Sample selection

Common garden canopy arthropods were sampled on 181 sample units (trees), in 2009, representing 36 genotypes from 10 populations for a study of the effect of *P. fremontii* population differentiation on arthropods. For the first two predictions, we first selected seven genotypes with adequate clonal replication (≥ 7) from the 181 sample units to represent low-genotypic diversity. Each genotype came from a different population. We randomly selected seven clones to represent each of the seven genotypes resulting in a sample size of 49. We then randomly selected 49 trees from the 181 sample units to represent high-genotypic diversity. The high-diversity sample was composed of 31 genotypes from seven populations. The high-diversity sample represents a null model because *P. fremontii* does not readily clone (Schweitzer et al. 2002) and more closely represents a natural population with many genotypes, while the low-diversity sample represents a genetically impoverished population. The two samples had four populations, four genotypes, and eight clones in common.

For the third prediction, we randomly selected one *P. fremontii* clone from each of the 36 genotypes in the 181-sample pool. Since the garden was planted in a Euclidean grid, we classified each of the eight neighbor “cells” as *S. exigua*, *S. gooddingii*, or *P. fremontii* for neighborhood composition. If a focal plant was on an edge of the garden, or a neighboring “cell” contained a dead plant, it was classified as vacant. For each focal genotype, we quantified neighborhood composition based on the surrounding eight “cells.” Two genotypes shared one cell of the same neighborhood.

Data analysis

First, we verified that genotypic diversity also represented genetic diversity by assessing the difference between the samples for total allelic richness, mean allelic richness, and percent polymorphic loci, with the microsatellite data. We quantified mean effective allelic richness (N_e) and total allelic richness because these are useful for hypervariable markers (Petit et al. 1998 and references therein). Allelic richness is an analogue to species richness in the ecological literature, thus allowing a better comparison between genetic and ecological diversity (Petit et al. 1998). Gen Al Ex software was used to calculate N_e , percent polymorphic loci, and genetic distances (Peakall and Smouse 2006).

For the first prediction, we quantified differences in arthropod community composition among *P. fremontii* genotypes. Differences in community composition were quantified on the low-diversity trees because there was better replication for each genotype (7 clones each) within this sample. Differences in arthropod community composition were quantified with the Bray–Curtis similarity coefficient that was calculated on the square root-transformed species by sample abundance data matrix. Differences were assessed with the Canonical Analysis of Principal Coordinates (CAP) procedure using the trace statistic (Anderson and Willis 2003). *P* values were determined from 9,999 permutations with a randomization test. Arthropod community structure on the seven genotypes is graphically displayed as community centroids (Anderson 2001) associated with each cottonwood genotype with 95% confidence-interval error bars. CAP axes are unitless and the relative positions of the community centroids that are closer in ordination space are more similar in arthropod composition than the centroids that are more distant. Non-overlapping error bars represent different arthropod communities.

For the second prediction, we quantified mean arthropod species richness, mean Shannon’s diversity (H'), and mean Pielou’s evenness (J) as measures of arthropod diversity for each sample. Additionally, we were interested in the cumulative contribution of *P. fremontii* genotypes to arthropod species richness so we quantified total allelic- and

total-species richness for each sample. We feel that the samples were adequate for this study because the sample sizes were relatively large ($n = 49$ each) and have good interspersions (Hurlbert 1984; Fig. 2) in a homogeneous matrix across the garden. We tested for a difference in garden spatial location, that is, sample centroids (Anderson 2001), with the Canonical Analysis of Principal Coordinates procedure using the trace statistic (Anderson and Willis 2003), and a difference in sample dispersion was quantified with a multivariate equivalent to Levene's test (Anderson 2004). P values were determined from 9,999 permutations with a randomization test.

Both mean species richness and H' were evaluated with F tests. Mean species richness was \ln transformed to achieve normality, but graphically presented as untransformed. A Wilcoxon test was used for the difference in J because normality was not achieved. Difference between samples for total accumulated alleles and accumulated arthropod species richness were each quantified with a two-sample Kolmogorov–Smirnov test for a difference in distribution (Siegal and Castellan Jr. 1988, p. 148; Sokal and Rohlf 1995, p. 439) between the randomized accumulation curves for each sample. The accumulation curves were generated with 100 randomizations with Estimate S software (Colwell 2006).

For the third prediction, we performed Mantel tests, that is, matrix correlations (Legendre and Legendre 1998; Mantel 1967), between the arthropod community similarity matrix with both the genetic distance and the neighborhood distance matrices. Arthropod similarities were quantified with the Bray–Curtis similarity coefficient (Bray and Curtis 1957; Legendre and Legendre 1998) that was calculated on the square root-transformed species by sample abundance data matrix. The Bray–Curtis similarity coefficient scales from 0 to 1, where 0 = perfect dissimilarity and 1 = perfect similarity. Genetic distances (Excoffier et al. 1992) were quantified from the microsatellite data with GenAlix software (Peakall and Smouse 2006). The neighborhood composition distance matrix was multivariate Euclidean distances because each neighborhood was known (Legendre and Legendre 1998). Genetic and Euclidean distances

scale from 0 to ∞ , where 0 = perfect similarity. Each similarity and distance data matrix was composed of all pairwise comparisons between each of the 36 sample units, where there are $(n \cdot n - 1)/2$ pairs (Legendre and Legendre 1998). Matrix correlations were performed with R-package software (Casgrain and Legendre 2001) and evaluated with the Mantel r statistic (r_M), which is related to Pearson's r (Legendre and Legendre 1998). Because these matrices contain non-independent data, exact P values were derived from a randomization procedure with 9,999 permutations of the data (Manly 1997).

Result

Genotypic diversity was 4.4 times greater for the high-diversity sample (low = 7; high = 31; $\chi^2 = 15.16$, $df = 1$, $P < 0.001$) and was a good surrogate for genetic diversity where the high-diversity sample accumulated 1.4 times as many alleles as the low-diversity sample (low = 49, high = 71). Mean N_e was lower for the low-diversity sample ($F_{1,96} = 7.65$, $P = 0.007$; Fig. 1a) as was total allelic richness, where new alleles accumulated at a slower rate (Kolmogorov–Smirnov $\chi^2 = 23.65$, $df = 2$, $P < 0.001$; Fig. 1b). Percent polymorphic loci was also lower, overall, for the low-diversity sample (low = 66.67%, high = 73.33%; Fig. 1c).

The 98 sample units were well distributed across the garden with good interspersions between the low- and high-diversity samples (centroid location: trace = 0.006, $P = 0.46$; dispersion: $F = 0.677$, $P = 0.68$; Fig. 2). One hundred and sixteen arthropod species representing 1402 individuals were distributed across the 98 sample units. There were 61 species with an abundance of 673 individuals in the low-diversity sample, and 79 species with an abundance of 729 individuals in the high-diversity sample. Differences in arthropod abundance were not significant ($\chi^2 = 2.24$, $df = 1$, $P = 0.13$).

In support of the first prediction, community composition was different among the genotypes in the low-diversity

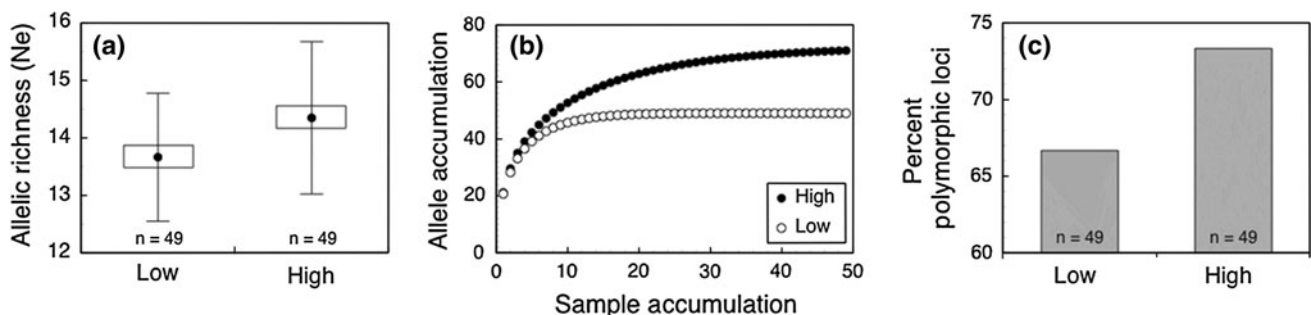


Fig. 1 Microsatellite genetic diversity. **a** Mean effective allelic richness (N_e); filled circle mean, box SE, error bars SD. **b** Total allele accumulation. **c** Percent polymorphic loci

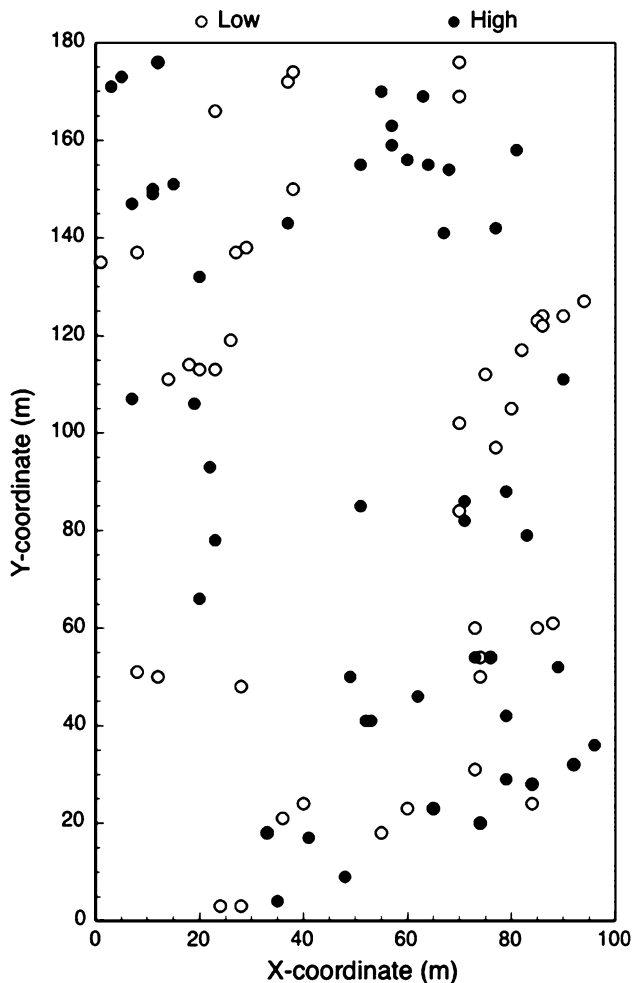


Fig. 2 Tree locations in the common garden. Fremont cottonwood trees were distributed throughout the garden with good interspersion and equal dispersion between the low- and high-diversity samples

sample (trace = 1.65 $P = 0.006$; Fig. 3). In support of the second prediction, mean arthropod species richness was lower in the low-diversity sample (ln mean species richness: $F_{1,96} = 7.09$, $P = 0.009$; Fig. 4a). Total-species richness was lower in the low-diversity sample (Kolmogorov–Smirnov $\chi^2 = 11.19$, $df = 2$, $P < 0.01$; Fig. 4b), where species accumulated slower resulting in fewer species (low = 61; high = 79; Fig. 4b). Mean evenness (J) was lower for the low-diversity sample ($\bar{x} \pm SE$: low = 0.750 ± 0.027 , high = 0.817 ± 0.028 , $\chi^2 = 3.97$, $P = 0.047$; Fig. 4c). Mean Shannon's diversity (H') was also lower in the low-diversity sample ($H' \pm SE$: low = 1.20 ± 0.069 ; high = 1.50 ± 0.075 ; $F_{1,96} = 8.50$, $P = 0.004$; Fig. 4d).

In support of prediction three, according to which as genetic distance increased arthropod communities would become less similar, arthropod community similarity was negatively correlated with genetic distance ($r_M = -0.1519$, $P = 0.04$; Fig. 5), but not related to plant neighborhood

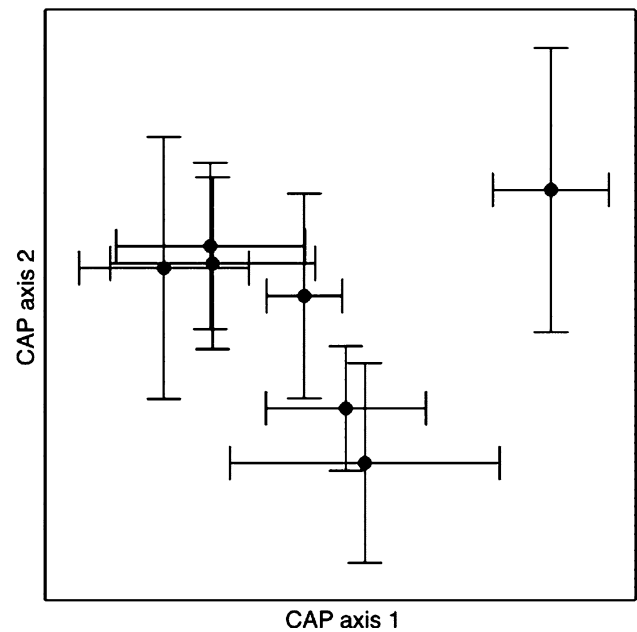


Fig. 3 Arthropod community structure. Arthropod community structure was different among genotypes of the low-diversity trees. Differences in community composition were quantified on the low-diversity trees because there was better replication for each genotype (7 clones each) within this sample. Each symbol represents the community centroid (filled circle) of the seven replicates (clones) of each of seven genotypes, and error bars represent the 95% confidence intervals. CAP axes are unitless and the relative positions of the community centroids that are closer in ordination space are more similar in arthropod composition than in centroids that are more distant. Non-overlapping 95% confidence-interval error bars represent different arthropod communities

composition ($r_M = 0.0733$, $P = 0.24$). Neighborhood composition and genetic composition of the focal host plant were also not related ($r_M = 0.0039$, $P = 0.48$).

Discussion

These results demonstrate three key findings. First, plant genotypic diversity can be a surrogate for genetic diversity when individual genotypes can be identified. In fact, genotypic diversity may be a good measure of genetic diversity because it represents the genetic composition of the entire organism, while genetic markers only quantify a fraction of the genome (Petit et al. 1998). We did not quantify heritable trait variation in the host plant; however, information on heritable trait variation is of interest (e.g., Hughes et al. 2008) and would help to determine the mechanisms responsible for the arthropod patterns we observed (e.g., Bailey et al. 2006; Bangert et al. 2006; Barbour et al. 2009; O'Reilly-Wapstra et al. 2010; Schweitzer et al. 2004; Whitham et al. 2006). Second, arthropod communities are different among host-plant

Fig. 4 Arthropod diversity. **a** Mean arthropod species richness. **b** Arthropod species accumulation. **c** Mean Pielou's evenness (J). **d** Mean Shannon-Weaver diversity (H'). Greater species richness (**a**, **b**), and J (**c**) both contribute to higher diversity (H'). *filled circle* mean, *box* SE, *error bars* SD

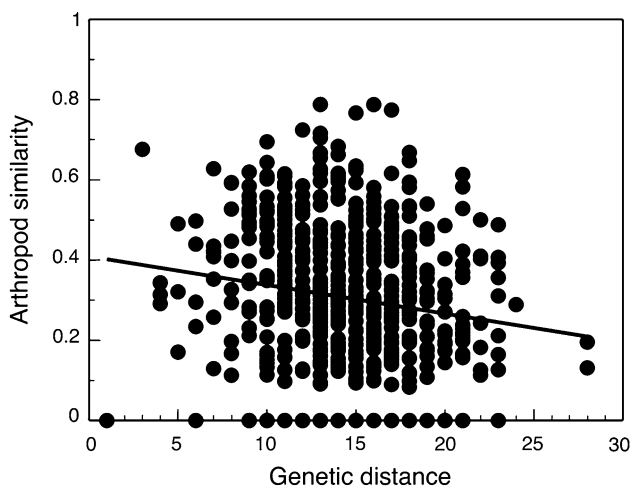
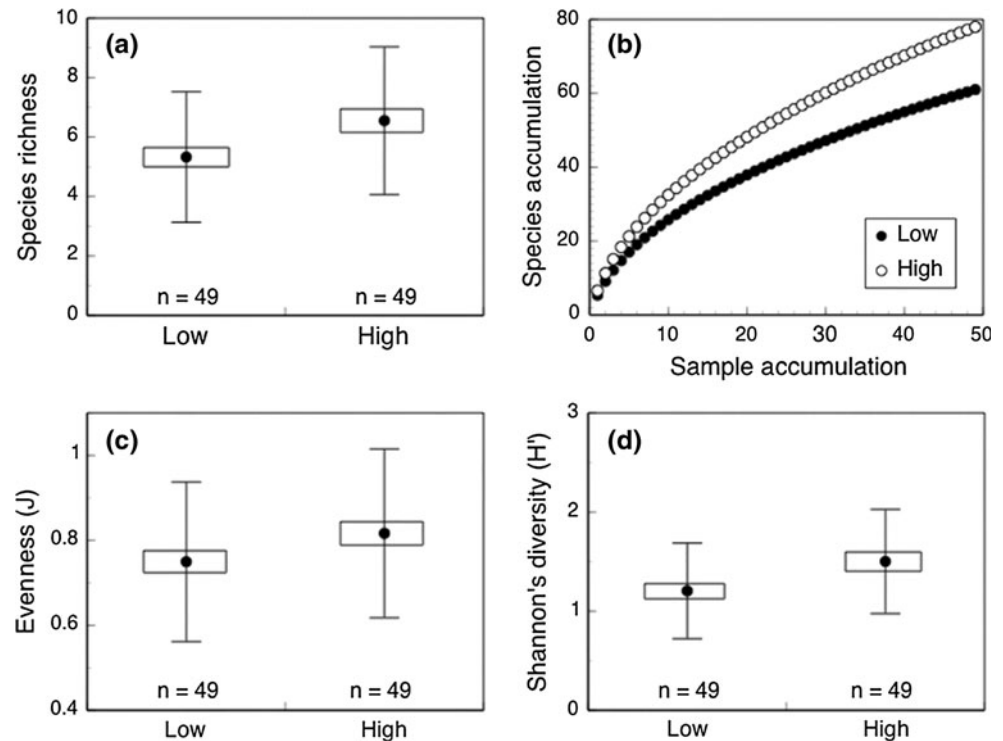


Fig. 5 Arthropod community similarity decreases with genetic distance of the host plant. Each point (x, y) represents the pairwise genetic distance (x) and pairwise arthropod community similarity (y). There are $(n \cdot n - 1)/2$ pairs (i.e., $[36 \cdot 35]/2$ pairs)

genotypes (Keith et al. 2010; Shuster et al. 2006), and the arthropod community is correlated with the genetic composition of the host plant even when genotypes are isolated within a homogeneous matrix. This results in an increase in arthropod diversity as host-plant genotypic diversity increases. Conversely, lower-plant genotypic diversity can result in lower-arthropod diversity (Fig. 4). This is important because plants are the foundation for the diversity of other trophic groups (Hunter and Price 1992), for

example arthropods (Keith et al. 2010; Murdoch et al. 1972; Siemann 1998; Siemann et al. 1998).

The high-diversity sample added new plant alleles and arthropod species faster than the low-diversity sample. In a study of two cottonwood species, and their hybrids growing in the wild, researchers found that genetic diversity at the stand level accounted for approximately 60% of the variation in the diversity of an arthropod community, where arthropod H' increased with genetic diversity (Wimp et al. 2004). In studies of *P. angustifolia* planted in a common garden, arthropod communities were different among host-plant genotypes (Shuster et al. 2006) and consistent across three years (Keith et al. 2010). Similarly, we found greater arthropod H' in the sample with greater genotypic diversity, and the arthropod community appeared to be a function of genetic composition of the host plant (Figs. 3 and 5). In a restoration context, the result would be greater arthropod diversity with greater host-plant genotypic diversity.

We cannot rule out the sampling effect (e.g., Huston 1997), where a sample with more genotypes is likely to include a genotype, or genotypes, that host more arthropod species. We feel that the sampling effect may work in conjunction with diversity effects when the diversity effect is strong; that is, the sampling and diversity effects are potentially co-occurring processes and not mutually exclusive (sensu Naeem 2002); the sampling effect may be an important component of the diversity effect. Our results may not be a reflection of the sampling effect, *per se*, but

rather unique communities associated with different genotypes (Fig. 3). First, there appears to be a genetic basis to arthropod community structure, where unique arthropod communities are associated with different host-plant genotypes (Fig. 3), and arthropod community composition is correlated with genetic composition (Fig. 5). Second, as genotypic diversity increases, unique arthropod communities are sampled resulting in greater arthropod richness. Host-plant genotypic diversity affects arthropod communities.

Third, confounding effects, such as plant apparency (Feeny 1976), were reduced because the isolated sample units were planted within a homogeneous matrix, resulting in the sample units being less apparent than if they were planted in plots with conspecifics or clones. Likewise, since the sample units were well dispersed throughout the garden, other effects such as associational resistance (Tahvanainen and Root 1972), associational susceptibility (Atsatt and O'Dowd 1976; White and Whitham 2000), and neighborhood effects (Addicott et al. 1987) were reduced and influence both samples equally. Similarly, complementarity effects (e.g., Hughes et al. 2008) were reduced because the sample units were probably not interacting strongly with each other; additionally, the arthropod community was not correlated with neighborhood plant composition. These results lend support to other community genetics studies, where associated communities can be structured by the genetic composition of the host-plant and community diversity increases with host-plant genotypic diversity (Crutsinger et al. 2006; Keith et al. 2010; Whitham et al. 2006). This helps to put community ecology into a genetic and evolutionary context (Bailey et al. 2006, 2009; Bangert and Whitham 2007; Bangert et al. 2006; Schweitzer et al. 2004; Shuster et al. 2006; Whitham et al. 2006; Wimp et al. 2004), where selection pressure on host-plant traits may affect associated communities (Barbour et al. 2009; Keith et al. 2010; Shuster et al. 2006).

Cottonwoods are considered a foundation species (sensu Ellison et al. 2005; Whitham et al. 2006). The conservation, restoration, and management of whole ecosystems may be more tractable than previously thought when foundation species are the foci of restoration studies (Whitham et al. 2010). Maximizing the genotypic diversity of a foundation species may increase the diversity of associated communities. Expensive techniques required to evaluate genetic diversity might not be necessary initially (e.g., for naturally non-clonal plants) for restoration projects that may benefit many other associated organisms. For example, selecting multiple plant genotypes from multiple populations can increase the diversity of associated communities in restoration projects, as in the garden we studied. For example, although producing clones from a single genotype might be efficient, the long-term result may be lower biodiversity.

Because different genotypes support different community members, this simplifies the dilemma of having to understand the complex interactions of multiple species (Shuster et al. 2006) to make appropriate management decisions (Whitham et al. 2010). Our findings support this idea when considered in a community genetics context (Whitham et al. 2006). One testable question is: Does greater plant-genetic diversity cascade up beyond the arthropod community to affect higher trophic levels (sensu Hunter and Price 1992)?

Acknowledgments We thank Reclamation for grant number CESU-06FC300025 and California Game and Fish for the land to plant the garden. We also thank the Cottonwood Ecology Group and anonymous reviewers for constructive comments.

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