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The Proportion of Three Foundation Plant Species and Their Genotypes Influence an Arthropod Community: Restoration Implications for the Endangered Southwestern Willow Flycatcher

Randy Bangert,[1,2,3] Sharon M. Ferrier,[1] Luke Evans,[1,4] Karla Kennedy,[1] Kevin C. Grady,[5] Erika Hersch-Green,[1,6] Gerard J. Allan,[1] and Thomas G. Whitham[1]

Abstract

As part of a restoration project, multiple genotypes of two tree species, Fremont cottonwood (*Populus fremontii*) and Goodding's willow (*Salix gooddingii*), and one shrub species, Coyote willow (*S. exigua*), were experimentally planted in different proportions at the Palo Verde Ecological Reserve near Blythe, California, U.S.A. These common woody plant species are important to the endangered southwestern willow flycatcher, providing perch, nesting, and foraging habitat. We conducted this study to evaluate plant species proportion and plant genotype effects on the arthropod community, the prey base for the endangered southwestern willow flycatcher. Three patterns emerged. First, plant species proportions were important; the arthropod community had the greatest richness and diversity (*H′*) when Goodding's willow proportion was high and Fremont cottonwood proportion was lower; that is, fewer Fremont cottonwoods are required to positively affect overall arthropod diversity. Second, we found significant genotypic effects, for all three plant species, on arthropod species accumulation. Third, while both planting proportion and genotype effects were significant, we found that the effect of planting proportion on arthropod richness was about twice as large as the effect of plant genotype. This shows that both plant species proportions and genotype should be utilized in restoration projects to maximize habitat heterogeneity and arthropod richness. Similar studies can determine which planting proportion and specific genotypes may result in a more favorable arthropod prey base for the southwestern willow flycatcher and other species of concern. Greater attention to planting design and genotype can result in significant gains in diversity at little or no additional project cost.

Key words: Lower Colorado River, *Populus fremontii*, *Salix exigua*, *Salix gooddingii*.

Introduction

Native riparian habitat along the Lower Colorado River (LCR) has been in a state of steady decline since the mid-1800s (Lower Colorado River Multi-Species Conservation Program: LCR-MSCP 2004). Cottonwood and willow have historically represented the dominant riparian plant species along the LCR (Durst et al. 2008). The existence of many other species is closely tied to the health and long-term success of these foundation plant species (LCR-MSCP 2004; Table S1, Supporting Information). A foundation species is defined as a species that structures its ecosystem by creating locally stable conditions and provides specific resources for a diverse community of organisms (Dayton 1972; Ellison et al. 2005). With the decline in cottonwood and willow habitat in the American Southwest to less than 3% of its historic extent (Noss et al. 1995), many species of flora and fauna that colonize riparian areas in the American Southwest have suffered decreased habitat quality and reductions in population size (e.g. Nelson 2003; LCR-MSCP 2004).

The southwestern willow flycatcher (*Empidonax traillii extimus*) has been especially impacted, and was federally listed as rare and endangered by the United States Fish and Wildlife Service in 1995 (LCR-MSCP 2004; McLeod et al. 2005; Durst et al. 2008). Southwestern willow flycatchers are generalist insectivores (Wiesenborn & Heydon 2007; Durst et al. 2008); the arthropods in the diet of the southwestern willow flycatcher are correlated with the native plants in this

study: Fremont cottonwood (*Populus fremontii* S. Watson), Goodding's willow (*Salix gooddingii* C. R. Ball), and Coyote willow (*S. exigua* Nutt.) (Wiesenborn & Heydon 2007). Studying and monitoring the effects of riparian habitat restoration on the diversity of arthropods (Williams 1997) could be important to the long-term survival of *E. traillii extimus*. Arthropods are vital components of most ecosystems (Wilson 1987) but poorly documented. Studies that quantify the factors that affect arthropod diversity are important to promote regional biodiversity and may play a role in the management of species of concern that depend on arthropods.

It is not currently known how the proportion of plant species and plant genotypes influence the diversity and abundance of arthropods and how this affects the southwestern willow flycatcher. In collaboration with the Bureau of Reclamation, under the LCR-MSCP (2004), we planted an experimental garden to explore techniques to promote the recovery of the southwestern willow flycatcher. With this experimental garden, we tested the effects of varying plant proportion and genotype of three foundation plant species: *P. fremontii*, *S. gooddingii*, and *S. exigua*, on an arthropod community in the context of riparian habitat restoration. This garden is part of a 50-year program that was initiated in 2005 to conserve habitat, work toward the recovery of threatened and endangered species, and reduce the likelihood of additional species being federally listed as endangered (LCR-MSCP 2004).

Populus fremontii and *S. gooddingii* are native tree species that are often components of southwestern willow flycatcher habitat, whereas *S. exigua* is a native shrub of the understory matrix along the LCR. In this study, we addressed two hypotheses: (1) varying proportions of these foundation plant species would affect the arthropod community. Many studies have shown an effect of varying plant composition on arthropod communities (Murdoch et al. 1972; Siemann 1998; Siemann et al. 1998; Knops et al. 1999); (2) the genotype of a foundation plant species would affect the arthropod community, based on previous studies of *Populus* and *Salix* (Fritz & Price 1988; Wimp et al. 2004; Whitham et al. 2006; Bangert et al. 2008), although this is the first study to manipulate species and genetic composition simultaneously.

Methods

Common Garden Study Site

The experimental garden was planted in 2007 within the LCR floodplain on 8 ha of agricultural land taken out of production. The garden was located at the Palo Verde Ecological Reserve (PVER), 14 km NE of Blythe, California, U.S.A., within 0.6 km of the LCR (N 33.71391, W −114.49600, elevation 87 m; Fig. 1). Plant collections consisted of one cottonwood species (*Populus fremontii*) and two willow species (*Salix gooddingii* and *S. exigua*), all in the family Salicaceae. Collection sites were within the watershed of the LCR in the USGS Basin and Range hydrogeographic province (Table S2; Fig. 1); the genetic basis for the plant collections was relevant for this restoration project.
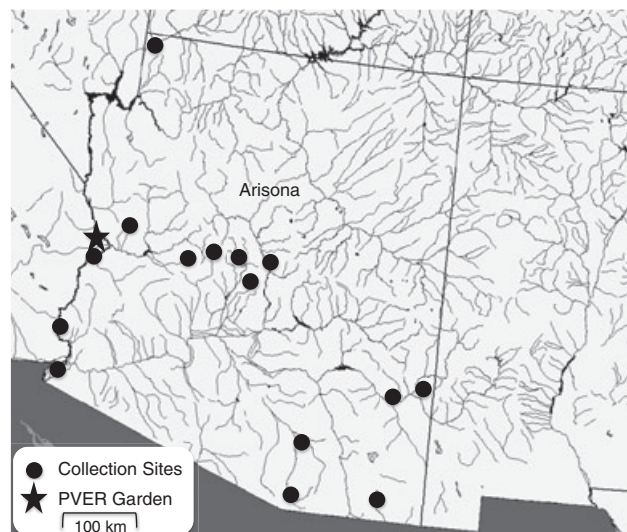

Figure 1. Plant collection locations and the location of the PVER common garden within the USGS Basin and Range hydrogeographic province.

Table 1. Treatment proportions applied simultaneously to the tree species, *Populus fremontii* and *Salix gooddingii*, with the shrub *S. exigua* filling the remaining matrix.

Proportion Treatment	P. fremontii	S. gooddingii	S. exigua	Total
#1	0.09/23	0.09/23	0.82/210	1.0/256
#2	0.09/23	0.17/44	0.74/189	1.0/256
#3	0.17/44	0.09/23	0.74/189	1.0/256
#4	0.17/44	0.17/44	0.66/168	1.0/256

Numbers above the slash are the species proportion and the numbers below the slash are the number of plants per block for each treatment.

Sixty-six blocks of four different plant proportions (Table 1) of the three foundation species were planted in a completely randomized design and flood irrigated. Each block consisted of 256 randomly selected and located, greenhouse propagated stecklings planted on 2 m centers (i.e. vegetative propagated plants that are genetically identical to their parents). The garden contained 2,196 *P. fremontii*, 2,196 *S. gooddingii*, and 12,503 *S. exigua*, for a total of 16,895 plants. A subset of 104 plants was used in this study. The arthropod sample for this study came from the three plant species, comprised of 14 unique genotypes, and their clonal replicates for a total of 104 plants; all clonal replicates were genetically identical. At the time of data collection (2008), the trees had grown from approximately 20 cm to 3 m in height, the shrub had grown from approximately 10 cm to 1 m in height, and all sample units were growing vigorously.

Plant Propagation

Dormant hardwood cuttings were collected for propagation between 5 December 2006 and 19 January 2007 from 15 populations. Field identification of genotypes was based on spatial discreteness of genets and a minimum

distance of 10 m between individuals. Genotypes were fingerprinted to verify uniqueness with simple sequence repeat (SSR) loci derived from the *Populus* SSR Resource database (Tuskan et al. 2004, 2006; http://www.ornl.gov/sci/ipgc/ssr_resource.htm) and from SSRs developed for *Salix* (Hersch-Green unpublished data).

Stecklings were grown in Tinus Rootrainers (Nanodrop Technologies, Wilmington, DE, U.S.A.) in sterilized soil media consisting of equal parts peat moss, perlite, and vermiculite, in greenhouses at Northern Arizona University in Flagstaff, Arizona. Stecklings were treated with rooting hormone, sterilized with an anti-fungal, and grown at ambient air temperature to maintain bud dormancy with bottom heat to stimulate root initiation and development. Bud and leaf flush were delayed as long as possible, and the stecklings were planted in the garden on 26–30 March 2007.

Confirmation of Unique Genotypes With SSR Markers

For each genotype, total genomic DNA was extracted from dried leaf material using DNeasy Plant Mini Kits (Qiagen, Hilden, Germany), spectrophotometrically quantified, and standardized to 12.5 ng/μL (NanoDrop® ND-1000, Nanodrop Technologies). After screening of various marker loci to insure repeatability, we selected and amplified 15 SSR loci from *P. fremontii* (Tuskan et al. 2004, 2006), 13 SSR loci from *S. gooddingii* (Barker et al. 2003), and14 SSR loci from *S. exigua* (Barker et al. 2003). All loci were amplified using polymerase chain reaction (PCR) and standard touchdown protocols (Don et al. 1991). PCR products were resolved on an ABI 3730xl automated sequencer using GENESCAN-600 LIZ as an internal size standard. Genotypes were scored using GeneMapper v. 4.0 software (all from Applied Biosystems, Inc., Foster City, CA, U.S.A.). We then evaluated the uniqueness of genotypes with the canonical analysis of principal coordinates (CAP) procedure and the trace statistic $Q_m' H Q_m$ on the SSR data; p-values were generated with 9999 permutations of the data (Anderson & Willis 2003; Anderson 2004).

Study Design

We chose genotypes that had clones within all four of the plant-proportion treatments. This resulted in 4–9 clones each of five *P. fremontii* genotypes representing five populations, 7–8 clones each of four *S. gooddingii* genotypes representing four populations, and 7–8 clones each of five *S. exigua* genotypes representing four populations. The proportions of the two tree species, *P. fremontii* and *S. gooddingii*, varied, with the remaining matrix filled with the shrub *S. exigua* (Table 1). The proportions span the range reported for natural densities in southwestern willow flycatcher habitat (McLeod et al. 2005). The same plants were used for both the plant proportion and genotype portions of this study to allow us to contrast the relative importance of the genotype effect versus the plant-proportion effect. Some analyses included all three species, and some analyses were conducted separately for each species.

Arthropod Sampling

Canopy arthropods were sampled from 13 to 23 August 2008. Arthropods were visually quantified following the methods of Wimp et al. (2004, 2005). Biomass and time were standardized among plants. Branch diameter was standardized to control for leaf area. On the basis of the species accumulation curves, approximately 200 shoots were surveyed for a minimum of 20 minutes per plant. All arthropods were classified as recognizable taxonomic units (RTUs; Oliver & Beattie 1993, 1996; Bolger et al. 2000) based on previous observations of life cycle, mating individuals, and large morphological differences. Unknown arthropods were collected for identification and archived in the Colorado Plateau Arthropod Museum at Northern Arizona University (http://www.bugs.nau.edu).

Data Analysis

To evaluate whether plant proportion affects the arthropod community we quantified the difference in the slopes of the species accumulation curves among the plant-proportion treatments with analysis of covariance (ANCOVA) using JMP 5.1.2 software (SAS Institute, Inc., Cary, NC, U.S.A.). The accumulation curves were linearized with an ln transformation. To evaluate the two hypotheses simultaneously, we quantified mean arthropod richness, abundance, Shannon's diversity (H'), and Pielou's evenness (J) with ANCOVA. The model included the factors: PLANT-PROPORTION, PLANT-SPP, GENOTYPE[PLANT-SPP], and PLANT-PROPORTION * PLANT-SPP interaction. Because of inadequate replication of
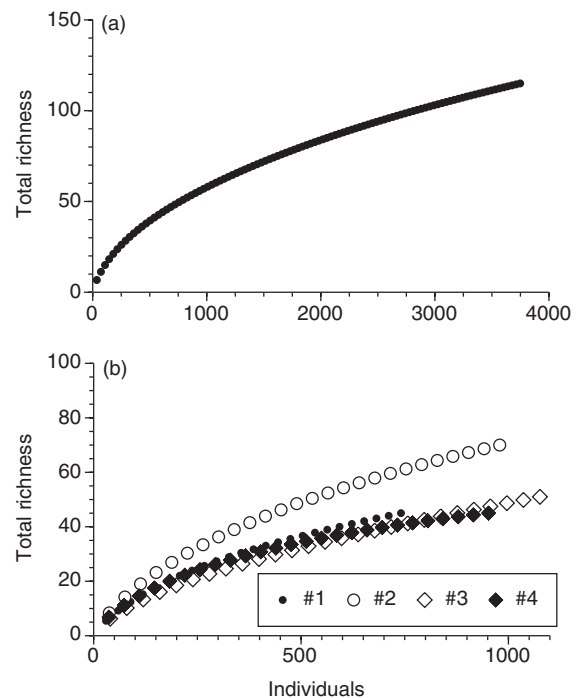

Figure 2. (a) Total arthropod species richness accumulation. (b) Total arthropod species richness accumulation by plant-proportion treatment. Non-linearized curves are presented.

genotypes, we did not include a GENOTYPE[PLANT-SPP] * PLANT-PROPORTION interaction in the model. The model included the *x,y* garden Cartesian coordinate location for each plant as a covariate to control for garden environmental factors not included in the model.

Because mean richness is not additive, it may not always be a sufficient community metric. We quantified the difference in the slopes of the species accumulation curves for total arthropod richness among the plant-proportion treatments and genotypes for each species with ANCOVA in order to evaluate the relative effects of plant proportion and genotype by comparing *F*-values (Table 3). These accumulation curves had not reached an asymptote, were linear, and not transformed. However, it is in the pre-asymptotic portion of species accumulation where differences initially occur (Bangert et al. 2005). All accumulation curves were generated with 999 randomizations (Colwell 2009), analyzed, and presented as richness versus accumulating individuals as recommended by Gotelli and Colwell (2001).

We further evaluated the effects of plant-proportion treatment and genotype of each plant species on arthropod community composition with the ordination procedure, CAP using the trace statistic, $Q_m'HQ_m$; *p*-values were generated with 9999 permutations of the data (Anderson & Willis 2003; Anderson 2004).

Results

Molecular analysis showed that the 14 genotypes used in the study were genetically unique from one another. There were five unique *Populus fremontii* genotypes ($Q_m'HQ_m = 2.0$, $p = 0.0001$), four unique *Salix gooddingii* genotypes ($Q_m'HQ_m = 1.0$, $p = 0.0001$), and five unique *S. exigua* genotypes ($Q_m'HQ_m = 2.0$, $p = 0.0001$). A relatively rich arthropod community quickly colonized the plants in this restoration garden and our findings are based on two growing seasons. Seventeen months after planting, 115 arthropod RTUs were sampled represented by 3,748 individuals on 104 plants (Fig. 2a).

Plant-Proportion Effects

The first hypothesis (that plant proportion would affect the arthropod community) was supported by three analyses. First, there were significant differences among the slopes
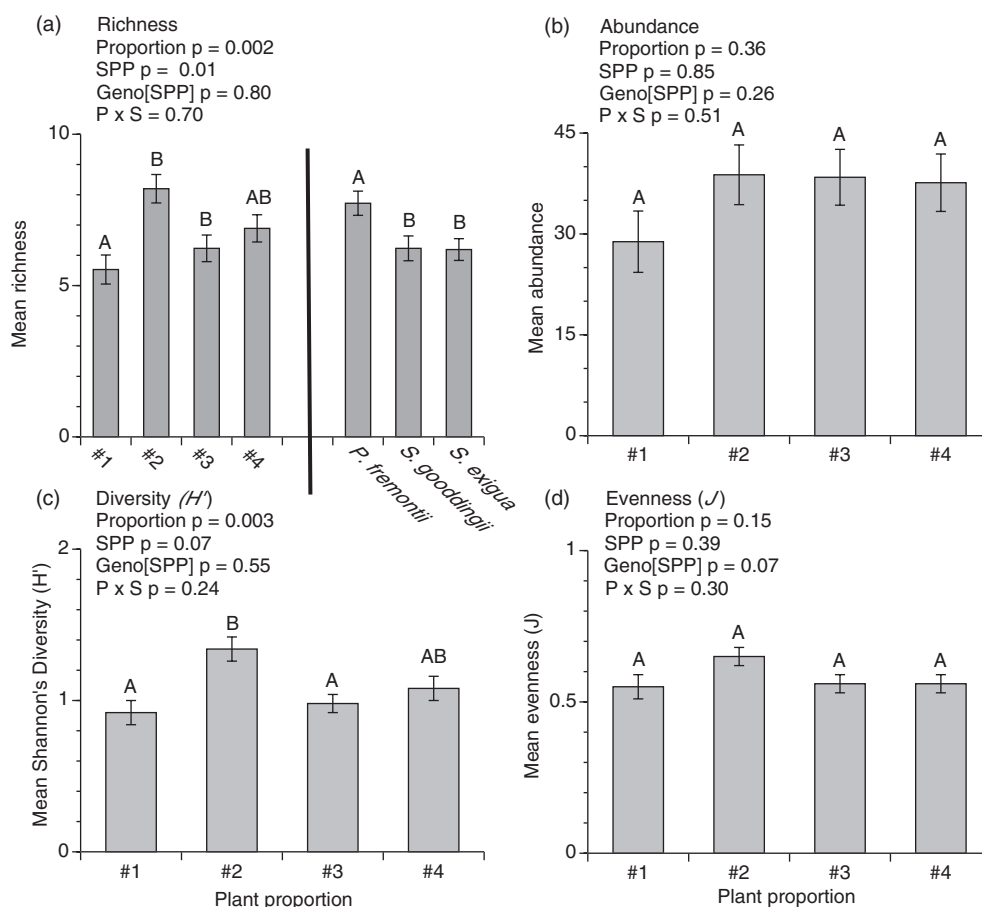

Figure 3. (a) Mean arthropod RTU richness response to plant-proportion treatment and plant species. (b) Mean arthropod abundance. (c) Mean arthropod Shannon's diversity (*H'*). (d) Mean arthropod evenness (*J*). Bars represent means; error bars represent ±1 SE. Different letters represent significant differences within a treatment.

of the species accumulation curves of the plant-proportion treatments ($F_{[100,3]} = 34.25$, $p < 0.0001$; Fig. 2b). When rarified on arthropod individuals, the most species (61) accumulated in treatment #2, with high *S. gooddingii* and low *P. fremontii* proportions, and the fewest species (41) accumulated in treatment #4, with high *S. gooddingii* and high *P. fremontii* proportions. Second, mean RTU richness and H' tended to be highest in plant-proportion treatment #2 (Fig. 3a & 3c). Third, there was strong support for differences in the rates of total RTU richness accumulation among the plant-proportion treatments based on accumulation curves for each plant species (all $p < 0.0001$; Table 3; Fig. 4a, 4c, & 4e).

When rarified on arthropod individuals, *P. fremontii* and *S. exigua* accumulated the most arthropod RTUs in treatment #2 and accumulated the fewest RTUs in treatment #3 (Fig. 4a & 4e). *Salix gooddingii* accumulated the most RTUs in treatment #3 and the fewest RTUs in treatment #1, with low *S. gooddingii* and low *P. fremontii* proportions (Fig. 4c).

Genotype Effects

The second hypothesis (that the genotype of a foundation plant species affects the arthropod community) was supported for species richness accumulation (Table 3; Fig. 4b, 4d, & 4f).
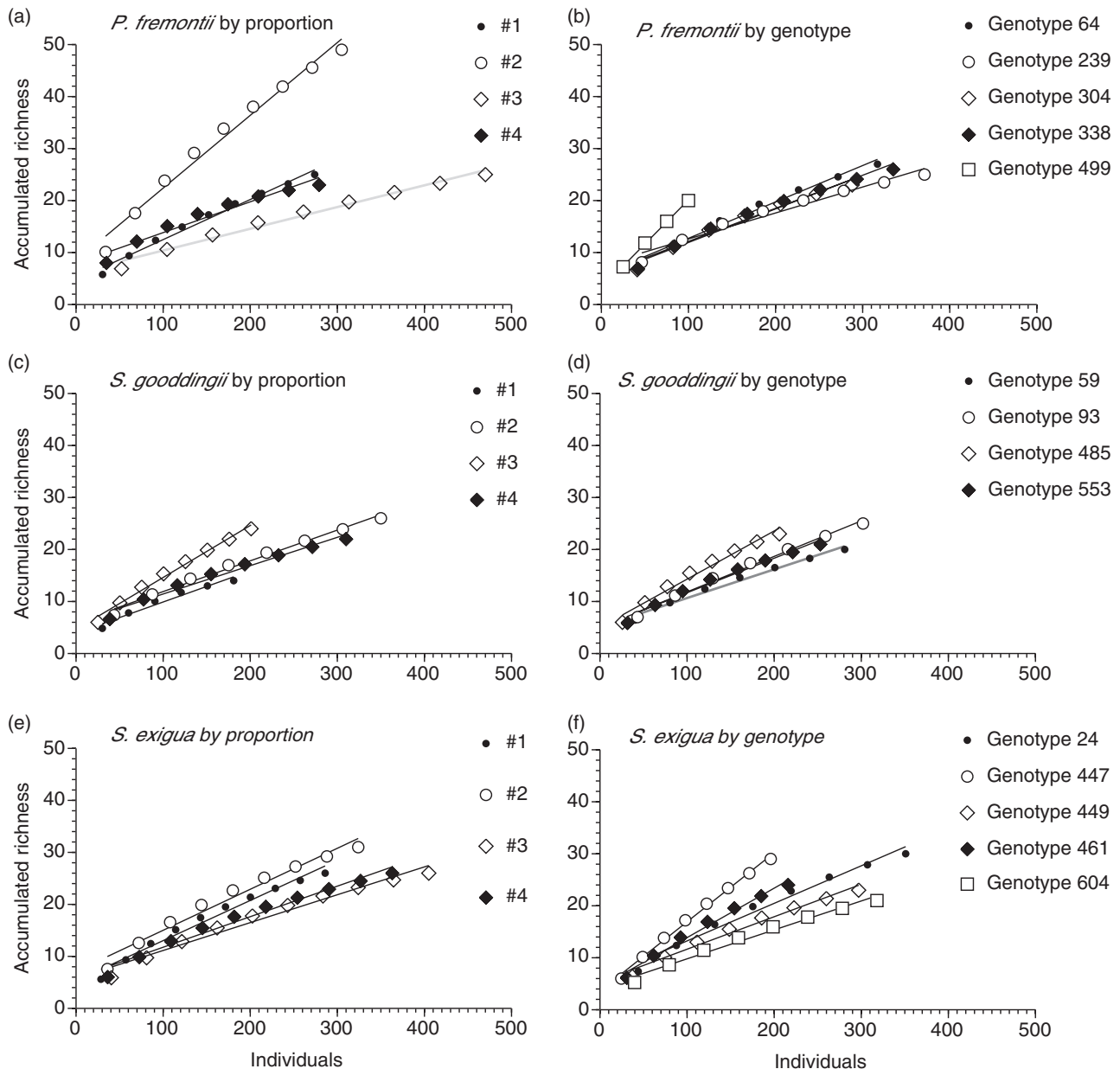

Figure 4. Total arthropod species richness accumulation for each plant species by proportion treatment and genotype. Panels a, c, and e represent plant-proportion treatment for each species. Panels b, d, and f represent genotype for each species.

Table 2. ANCOVA results for PLANT-PROPORTION and GENOTYPE[SPP] effects on arthropods.

Factor		df	ss	ms	F	p
Richness	Model	24	232.90	9.70	1.95	0.01
	Error	79	393.09	4.98		
	Total	103	625.99			
	Proportion	3	80.06		5.36	**0.002**
	SPP	2	47.16		4.74	**0.01**
	Genotype[SPP]	11	34.17		0.62	0.82
	Proportion × SPP	6	18.95		0.63	0.70
Abundance	Model	24	12109.27	504.55	1.14	0.32
	Error	79	34894.57	441.70		
	Total	103	47003.85			
	Proportion	3	1438.68		1.09	0.36
	SPP	2	141.64		0.16	0.85
	Genotype[SPP]	11	6170.94		1.27	0.26
	Proportion × SPP	6	2357.37		0.89	0.51
Shannon's diversity (H')	Model	24	6.81	0.28	1.97	**0.01**
	Error	79	11.39	0.14		
	Total	103	18.20			
	Proportion	3	2.18		5.03	**0.003**
	SPP	2	0.77		2.68	0.07
	Genotype[SPP]	11	1.42		0.90	0.55
	Proportion × SPP	6	1.18		1.37	0.24
Evenness (J)	Model	24	0.97	0.04	1.53	0.08
	Error	79	2.08	0.03		
	Total	103	3.05			
	Proportion	3	0.05		1.80	0.15
	SPP	2	0.09		0.96	0.39
	Genotype[SPP]	11	0.52		1.78	0.07
	Proportion × SPP	6	0.20		1.23	0.30

SPP, plant species; ss, sum of squares; ms, mean square.
Garden coordinates were included as covariates to control for environmental gradients in the garden. Statistics for garden coordinates are not reported. Bold *p*-values denote significance at $\alpha = 0.05$.

Although mean richness was not different among GENO-TYPE[SPP] ($p = 0.80$; Table 2), total richness was significantly different among genotypes for all three species based on the species accumulation curves (all $p < 0.0001$; Fig. 4b, 4d, & 4f. *P. fremontii* range: 12–24 species; *S. gooddingii* range: 17–23 species; *S. exigua* range: 16–29 species).

Relative Effects of Plant Proportion and Genotype

On the basis of the ANCOVA *F*-values, arthropod richness accumulation on *P. fremontii* and *S. gooddingii* both showed stronger responses to the plant-proportion treatment than genotype (*P. fremontii* plant-proportion treatment: $F_{[31,3]} = 100.93$, $p < 0.0001$; *P. fremontii* genotype: $F_{[30,4]} = 55.26$, $p < 0.0001$. *S. gooddingii* plant-proportion treatment: $F_{[26,3]} = 23.67$, $p < 0.0001$; *S. gooddingii* genotype: $F_{[26,3]} = 13.42$, $p < 0.0001$; Table 3). In contrast, arthropod richness accumulation on *S. exigua* showed a stronger response to genotype than plant-proportion treatment (*S. exigua* plant-proportion treatment: $F_{[35,3]} = 10.70$, $p < 0.0001$; *S. exigua* genotype: $F_{[34,4]} = 42.00$, $p < 0.0001$; Table 3). On average, RTUs accumulated twofold faster on the plant-proportion treatments relative to genotype (Fig. 4).

There was a difference in arthropod community composition by plant-proportion treatment ($Q_m'HQ_m = 0.7706$,

$p = 0.0006$; Fig. 5a). There was also a difference in arthropod community composition by genotype for *S. gooddingii* ($Q_m'HQ_m = 1.2912$, $p = 0.0391$; Fig. 5c), with *P. fremontii* and *S. exigua* approaching significance (*P. fremontii*: $Q_m'HQ_m = 1.1445$, $p = 0.1386$; Fig. 5b; *S. exigua*: $Q_m'HQ_m = 0.8613$, $p = 0.0783$; Fig. 5b & 5d).

Discussion

Although many ecological studies have manipulated either plant-species or plant-genetic diversity, we are not aware of any restoration studies that have manipulated both in the same study. Using the same genotypes of three foundation species planted in different proportions, we found that both plant proportion and genotype effects were important.

On the basis of the studies of ecological neighborhoods (Addicott et al. 1987), interspecific competition, and facilitation (Brooker et al. 2008), we expected that plant proportion would have a strong effect on arthropod community metrics (Bangert et al. 2008). For example, it is well known that plant–plant interactions can have strong effects on plant community and ecosystem properties, including diversity, structure, productivity, and stability (e.g. Kéfi et al. 2007; Brooker et al. 2008; Michalet et al. 2011). We show that different

Table 3. ANCOVA results for differences in slopes for total arthropod species accumulation among plant-proportion treatments and genotypes for each plant species.

Species		df	ss	ms	F	p
Populus fremontii proportion	Model	7	3687.07	526.73	334.93	<0.0001
	Error	27	42.46	7.02		
	Total	34	3729.53			
	Slopes test	3	476.17		100.93	**<0.0001**
P. fremontii genotype	Model	9	2129.91	236.66	231.83	<0.0001
	Error	25	25.52	1.02		
	Total	34	2155.43			
	Slopes test	4	225.64		55.26	**<0.0001**
Salix gooddingii proportion	Model	7	990.15	141.45	238.09	<0.0001
	Error	22	13.07	0.59		
	Total	29	1003.22			
	Slopes test	3	42.18		23.67	**<0.0001**
S. gooddingii genotype	Model	7	838.59	119.80	195.80	<0.0001
	Error	22	13.46	0.61		
	Total	29	852.06			
	Slopes test	3	24.63		13.42	**<0.0001**
S. exigua proportion	Model	7	1746.36	249.48	171.67	<0.0001
	Error	31	45.05	1.45		
	Total	38	1791.41			
	Slopes test	3	46.63		10.70	**<0.0001**
S. exigua genotype	Model	9	1717.73	190.86	247.38	<0.0001
	Error	29	22.37	0.77		
	Total	38	1740.10			
	Slopes test	4	129.61		42.00	**<0.0001**

Bold *p*-values denote significance at $\alpha = 0.05$.

plant-proportion neighborhoods can have strong effects on an arthropod community. Thus, plant–plant interactions may affect arthropods.

In our study, plant proportion represents the neighborhood to which an individual arthropod is exposed. In another study of cottonwoods, White and Whitham (2000) found that a heterospecific plant neighbor (box elder [*Acer negundo*]) influenced the insects on cottonwoods. In agreement with their study, we found that different heterospecific plant proportions affected the arthropod community.

A rich literature has found that plant-species or plant-genetic diversity can affect arthropod communities (e.g. Wimp et al. 2004, 2005, 2007; Johnson & Agrawal 2005; Bailey et al. 2006; Bangert et al. 2006; Crutsinger et al. 2006; Shuster et al. 2006; Barbour et al. 2009; Keith et al. 2010; Zytynska et al. 2011; Ferrier et al. in press2012). In a recent review of the importance of intraspecific genetic variation on dependent communities, Whitham et al. (2012) found that 64/75 communities examined worldwide significantly responded to genetic variation within a single focal plant species. The focal plant species included tropical trees, eucalypts, coastal dune shrubs, boreal conifers, alpine cushions, and old-field forbs. The communities in which a significant genotype response was detected included: arthropods, fungal endophytes, mycorrhizal fungi, epiphytic and terrestrial plants, and soil microbes. We emphasize that the importance of plant genetic composition on individual species can vary widely. At one end of the continuum some species show a weak to no response to plant genetics, whereas, at the other extreme genetic effects

predominate. For example, Evans et al. (2012) found that cottonwood genetics played a key role in affecting the abundance of the mite, *Aceria parapopuli*, and that genotypic effects were 130 times greater than climate variable effects (e.g. winter minimum temperature, growing season temperature, and moisture availability). Ferrier et al. (unpublished data) found that plant genotypes (the same species as in this study) that grow more vigorously support more arthropods than less vigorously growing plants.

We also detected significant genotype effects. Because replicate genotypes were distributed across the plant-proportion treatments, genotype effects were potentially attenuated by the proportion effect. However, Bangert et al. (2008) suggested that when genetic variability is high, plant genotypic effects on a community should be detectable. Because both plant proportion and genetic identity were important factors, they should be given consideration in restoration projects. This study was done on 1-year-old plants; continued monitoring is required to determine these patterns through time.

Restoration projects often use a single or a few genotypes (G. Garnett 2006, Bureau of Reclamation, personal communication), possibly resulting in lower arthropod diversity. (Ferrier et al. 2012) found that a sample of *Populus fremontii* with high genetic/genotypic diversity supported higher arthropod diversity than a sample of *P. fremontii* with low genetic/genotypic diversity. We recommend that restoration plantings should avoid monoculture practices. Using many clones from a few genotypes may not maximize arthropod richness because different arthropods, microbes, and other community types are
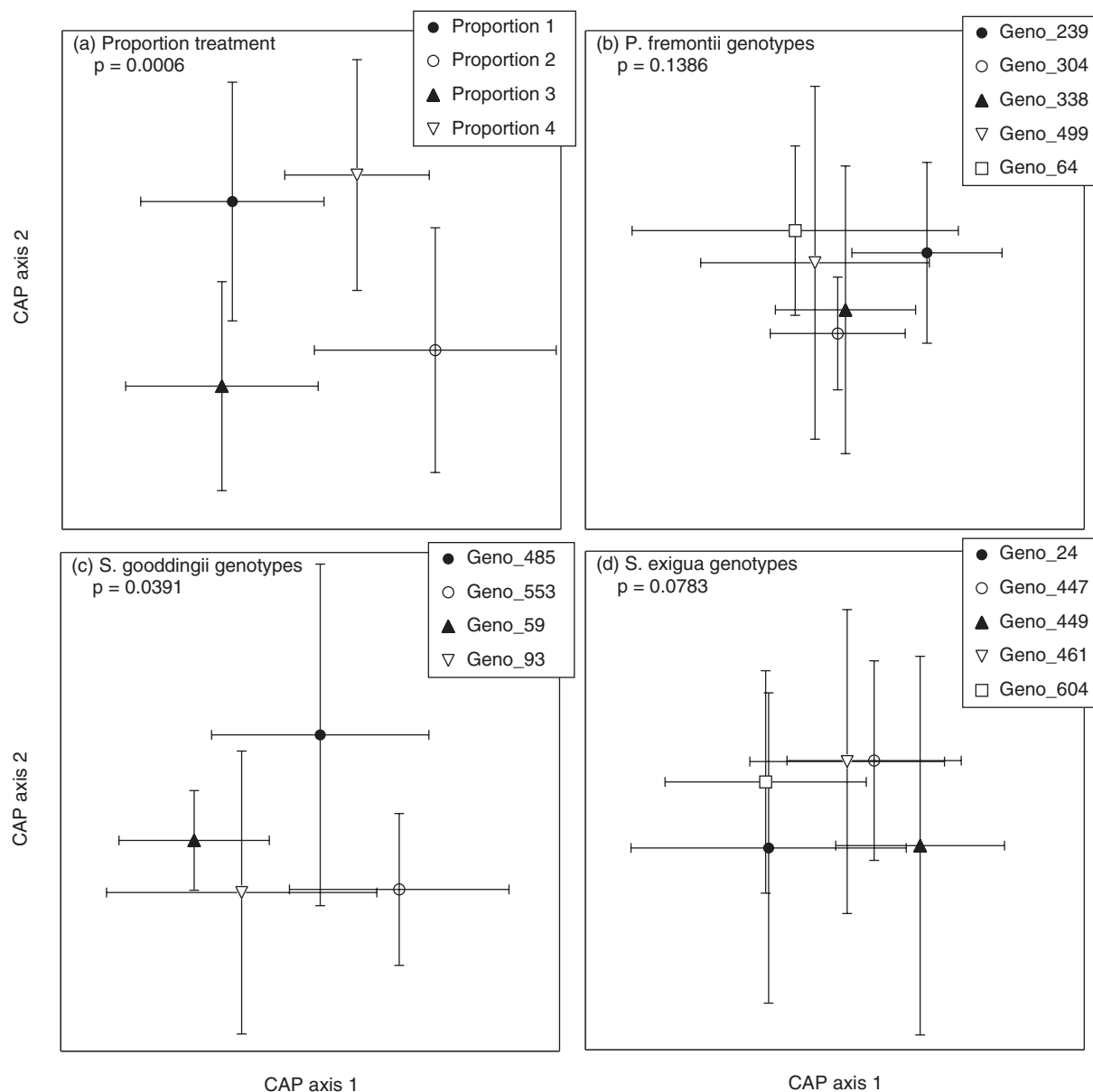
Figure 5. Arthropod community composition by plant-proportion treatment and plant genotype. Symbols represent community centroids; error bars represent 95% confidence intervals. Error bars that do not overlap indicate different communities.

commonly associated with different plant genotypes (Ferrier et al. 2012). Other studies have found that different cottonwood genotypes also support different trophic interactions between arthropods and birds (Bailey et al. 2006; Smith et al. 2011), which may indirectly influence arthropod diversity.

Greater arthropod richness coupled with greater diversity (H') should result in a more broadly available arthropod prey base, such as we found in plant-proportion treatment #2. This indicates that this proportion of *Salix gooddingii* and *P. fremontii* may result in a more optimum prey base for the southwestern willow flycatcher. However, eliminating either species would tend to lower arthropod diversity because each plant species and genotype likely contributes unique arthropod

species to the overall community (MacArthur 1972; Siemann 1998; Whitham et al. 2012; Ferrier et al. 2012).

Increasing both plant proportion and genotypic variability in restoration projects will help to increase habitat heterogeneity (e.g. Ferrier unpublished data), which may benefit species like the southwestern willow flycatcher (Wiesenborn & Heydon 2007; Durst et al. 2008). Future tests of this idea will involve determining which plant-proportion treatments are preferred when southwestern willow flycatchers, and other species, colonize the restoration site. On the basis of the results from this study, we predict that plant-proportion treatment #2, with high *S. gooddingii* and low *P. fremontii* proportions, should be favored. Although we discuss this restoration project in

the context of the southwestern willow flycatcher, there are numerous other terrestrial animal species typically associated with the habitat type along the LCR that may also benefit from this restoration study.

Implications for Practice

- The proportion of commonly associated plant species used in restoration should receive greater attention from managers.
- Genotype effects are important and plant-restoration material should be collected from multiple plant species, populations, and genotypes.
- Plant species and genotype polycultures should be favored over monocultures.
- Once the effort has been expended to collect multiple genotypes from multiple populations, superior genotypes can be identified for future use. Existing plant-restoration projects with clearly identified genotypes can become a seed and cutting orchard for future plant-restoration projects.
- The best plant proportions and genotypes can be identified, based on criteria appropriate to an individual project, through continuous research and monitoring.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Terrestrial animal species that may benefit from the restoration of this site by conversion from agriculture to *Populus/Salix* habitat (LCR-MSCP 2004; Table 5–1).

Table S2. Plant collection locations and elevations within the Lower Colorado River watershed of the USGS Basin and Range hydrogeographic province.

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