

**HYBRIDIZATION AMONG DOMINANT TREE SPECIES CORRELATES
 POSITIVELY WITH UNDERSTORY PLANT DIVERSITY¹**

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- *Premise of the study:* Elucidating the factors that determine the abundance and distribution of species remains a central goal of ecology. It is well recognized that genetic differences among individual species can affect the distribution and species interactions of dependent taxa, but the ecological effects of genetic differences on taxa of the same trophic level remain much less understood. Our goal was to test the hypothesis that differences between related overstory tree species and their hybrids can influence the understory plant community in wild settings.
- *Methods:* We conducted vegetation surveys in a riparian community with the overstory dominated by *Populus fremontii*, *P. angustifolia*, and their natural hybrids (referred to as *cross types*) along the Weber River in north central Utah, USA. Understory diversity and community composition, as well as edaphic properties, were compared under individual trees.
- *Key results:* Diversity metrics differ under the three different tree cross types such that a greater species richness, diversity, and cover of understory plants exist under the hybrids compared with either of the parental taxa (30–54%, 40–48%, and 35–74% greater, respectively). The community composition of the understory also varied by cross type, whereby additional understory plant species cluster with hybrids, not with parental species.
- *Conclusions:* Genetic composition dictated by hybridization in the overstory can play a role in structuring the associated understory plants in natural communities—where a hybridized overstory correlates with a species-rich understory—and thus can have cascading effects on community members of the same trophic level. The underlying mechanism requires further investigation.

Key words: canopy–understory interactions; community genetics; cottonwoods; hybridization; plant–plant interactions; *Populus angustifolia*; *Populus fremontii*; species–genetic diversity correlation.

Determining the factors that control the distribution and abundance of species is a central goal of ecology (e.g., Gilbert and Lechowicz, 2004). Understory plant species, particularly the herbaceous and grass communities, often represent a prominent component of the diversity of forests (Dirzo et al., 1992). Environmental characteristics such as light, water, and nutrients can vary at a fine spatial scale (i.e., on the order of meters), and these differing niches are known to influence the species composition of the understory (Tessier, 2007). Long recognized as important causes of these microhabitat differences in forests are not only the presence or absence of canopy trees (e.g., Price and Morgan, 2010) but also the particular species composition of the overstory (e.g., Ratliff et al., 1991; Knight et al., 2008).

For example, Ratliff et al. (1991) found that different overstory species in an oak woodland supported different herbaceous species under their canopies. It is not known, however, whether the manner in which understory plants in natural settings respond to genetic variation within closely related species and their hybrids is similar to how they respond to variation across species.

Hybridization is an important pathway of speciation for plants (Soltis and Soltis, 2009). Thus the ecological conditions that promote hybridization have been explored (e.g., Lepais et al., 2009), as have the effects of hybridization on the genetics of the plants themselves for several well-studied hybrid systems, including *Eucalyptus* (Potts and Dungey, 2004), mulberry (*Morus*; Burgess and Husband, 2006), and oak (*Quercus*; Lepais et al., 2009). However, the ecological effects of plant hybridization on other members of the community besides direct competitors (Vilà et al., 2000; Murrell et al., 2011) are much less understood and have been limited predominately to work on herbivorous insects and parasites (e.g., Whitham et al., 1994; Tovar-Sanchez and Oyama, 2006; Nakamura et al., 2010). In contrast, the *Populus* system has been a particularly fertile area for studying links between the genetic variation that results from hybridization with larger patterns of community structure and ecosystem processes (Whitham et al., 2006, 2008). Here we draw on ongoing work in this forest system to test whether the genetic identities of cottonwood trees influence understory plants in natural communities.

Populus spp. (Salicaceae, commonly known as *cottonwoods*, *aspens*, and *poplars*) are prevalent in riparian communities in the western United States and often function as foundational

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species, defined as “species that structure a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes” (Dayton, 1972). Hybridization has been occurring in the *Populus* genus for at least 12 million years and happens naturally when the ranges of two or more *Populus* species overlap (Eckenwalder, 1984a, b). One such site of hybridization is along the Weber River in north-central Utah, USA, where Fremont cottonwoods (*Populus fremontii*), narrowleaf cottonwoods (*Populus angustifolia*), and their hybrids, which are together referred to as *cross types*, naturally occur.

The ecological effects of intraspecific genetic variation and hybridization in this system are beginning to be appreciated (Whitham et al., 2003). A suite of associated organisms, including terrestrial and aquatic arthropods (Wimp et al., 2004; LeRoy et al., 2006), birds (Martinsen and Whitham, 1994), mammals (Bailey et al., 2004), and soil microbes (Schweitzer et al., 2008), are affected by the identity of the different cross types. Moreover, hybridization in *Populus* can affect ecosystem processes, such as decomposition and nitrogen mineralization rates (Schweitzer et al., 2004, 2008) as well as water-use efficiency (Fischer et al., 2004), and can promote the evolution of new animal species living on these hybrid plants (Evans et al., 2008).

The microsite differences created by genetic variation within the foundational *Populus* spp. mosaic, to which diverse taxa occupying multiple trophic levels respond, also have the potential to influence within-trophic level interactions (e.g., Beatty, 1984). In a common garden study, Lamit et al. (2011) showed that hybridization between *P. angustifolia* and *P. fremontii* significantly affected understory biomass, species richness, and composition. Because common garden studies are designed to reduce environmental variation, it is important to determine whether genetic-based differences in common gardens can still be detected in the “wild,” where environmental effects potentially could “swamp” genetic effects. We tested the prediction that the understory plant community in the wild also would respond to the genetic “footprint” of individual trees and, correspondingly, that the genetic effects would not be overshadowed by environmental effects. Responses from other members of the biotic community offer potential mechanisms by which understory plants also may be affected either directly or indirectly by the canopy tree, including variations in light (canopy architecture), water (water-use dynamics), and soil properties such as nutrient dynamics (decomposition and mineralization). If an effect exists, the nature of the relationship—whether hybrids elicit responses that are identical to, intermediate with, or lower than those of either of the parental species—would offer clues as to the likely mechanisms.

MATERIALS AND METHODS

Study system—*Populus fremontii* S. Wats (hereafter referred to as *Fremont*) dominates lower elevation riparian habitat in the western United States, and *P. angustifolia* James (hereafter *narrowleaf*) dominates higher-elevation habitat. Near Ogden, Utah (elevation 1300 m), the boundaries overlap, and both parental taxa are found along with their hybrids. We surveyed trees occurring within a 13-km stretch of the Weber River that is situated within the hybrid zone. The overstory canopy is dominated by *Populus* spp., representing nearly 70% of the individuals and over 90% of the biomass (Appendix 1). The understory, however, is more varied, composed of grasses, herbs, vines, saplings, and young trees, some of which are nonnative to the region.

Genetic analyses—All raw genetic data used in this study come from a study examining the effect of hybrid diversity on foliar arthropods (Wimp et al., 2004). For that study, Wimp et al. (2004) delimited 10 semidiscrete cottonwood

stands that are nearly identical in tree density, climate, and soil characteristics and are separated from each other by natural or human-made barriers (Schweitzer et al., 2011). Approximately 20 trees in each stand (each tree selected to be at least 30 m from another sampled tree) were genotyped at 48 amplified fragment length polymorphism (AFLP) loci (Wimp et al., 2004). For the current study, we calculated a hybrid index for each tree using those AFLP markers. The hybrid index defined the cross type of each tree and represents admixture coefficients generated under the admixture model in the program Structure (Pritchard et al., 2000). The number of subpopulations was limited to two because this study system contains two parental cottonwood species that readily hybridize. On the basis of this analysis, each tree received a hybrid index that represents the percentage of each individual composed of the two parental taxa. Hybrid index thus could be used to classify trees into discrete cross types (Fremont, narrowleaf, or hybrid) with 10% genetic admixture as the cut-off to delimit pure parental or hybrid status (Vähä and Primmer, 2006). That is, those trees with a hybrid index of <10% were classified as Fremonts, >90% as narrowleafs, and intermediate values as hybrids. We performed hybrid index calculations 10 times using an initial burn-in of 10^4 and 10^6 iterations. All runs then were combined with the CLUMPP program (Jakobsson and Rosenberg, 2007). Thus, although the raw data come from an earlier study (Wimp et al., 2004), the genetic analyses used to characterize parental taxa and their hybrids in the current study were generated for the current study.

Plant surveys and edaphic sampling—We surveyed under approximately 25 of each of the three cross types (Fremont, narrowleaf, and hybrids) across the 13-km stretch of the Weber River in July 2009. A 0.5 m × 0.5 m quadrat containing 25 intersection points was laid down 0.5 m from the base of the tree trunk at both the north and south cardinal directions. We recorded all vegetation touching a pin dropped at each intersection. Plants were identified by using *A Utah Flora* (Welsh, 2003), and the United States Department of Agriculture Natural Resources Conservation Service Plants Database (plants.usda.gov) was used as the final authority for nomenclature. Additionally, the depth of the leaf litter layer was measured at five points in the quadrat (the four corners plus the center), which was averaged per quadrat, and soil samples were collected by using a 15-cm-deep soil corer over a 2-day period. Botanical surveys and soil sampling were done in July 2009, and additional soil sampling occurred in August 2009.

Soil samples were frozen after collection and remained so until used for analysis. First, moisture was measured by drying 5 g of sieved (2 mm) soil in a 60°C drying oven for 48 hours. Soil moisture was calculated at two times during the growing season, and the mean was used for analysis. Second, total soil carbon and nitrogen were measured using a Carlo-Erba (Milan, Italy) 1500 CN Elemental Analyzer. Third, we determined soil pH by mixing soil with deionized water into a slurry and measuring it with a pH meter (Model 301, Orion Research Inc, Beverly, Massachusetts, USA.).

Statistical analysis—To test for spatial clustering of tree cross types, we performed an analysis of similarity (ANOSIM) on the Euclidean distances between trees by cross type within each stand. This was done using the “anosim” function of the vegan package (Oksanen et al., 2009) in the R programming language (R Development Core Team, 2009). A significant result indicates that within a stand, the trees of a particular cross type tend to be closer to each other than to trees of the other cross types.

Response variables of the understory plant community included species richness, Shannon diversity index, and cover. Shannon and Simpson diversity indices were correlated and show the same patterns; thus, for simplicity we use Shannon throughout. Cover was allowed to exceed 100% for a given species to avoid any spurious correlation between richness and cover. Understory diversity metrics were compared across cross types with ANOVA (after testing for assumptions of normality and homoscedasticity), and the location of tree (i.e., stand) was included as a block factor to account for any unmeasured variation across stands. The Weber River is a heavily invaded ecosystem, like many riparian communities in the United States (Stohlgren et al., 1998), and therefore vegetation was partitioned into native and exotic classes (Appendix 2). Furthermore, vegetation also was divided into the two dominant plant life forms, grasses and forbs (Appendix 2). Data were partitioned because, depending on the mechanism by which overstory interacts with understory, it is possible that origin status and growth form of the plant affect its response.

To test for differences in community composition among tree cross types, we used a permutation of multivariate analysis of variance test (PERMANOVA), which uses permutations to calculate significance of partitioning distance matrices among sources of variation (Anderson, 2001). This method was executed by using the “adonis” function of the vegan package in R with 1000 permutations

and was implemented on both understory plant abundance and incidence (i.e., presence/absence) data. To get a representation of understory community composition, we used the nonmetric multidimensional scaling (NMDS) ordination technique with a matrix containing abundances of each understory species for each tree sampled. To graphically depict community structure as a 2-dimensional ordination, we used the “metaMDS” function with the Bray–Curtis dissimilarity coefficient in the R vegan package. Furthermore, indicator species analysis was used to assess whether individual species were associated with certain cross types. We used the method of Dufrene and Legendre (1997) as implemented in the “duleg” function of the labdsv R package (Roberts, 2007), also with 1000 iterations.

Lastly, to relate understory composition with genetic similarity, we followed the method of Bangert et al. (2006b), who found that genetic differences among individual cottonwoods affect the structure of arthropod communities. The genetic similarity rule asserts that the genetic identity of the plant influences the community structure of the dependent organisms, such that plants with a more similar genetic composition will support a more similar associated community (Bangert et al., 2006b). First, we calculated the Euclidean genetic distance between individual trees in the program GenALEX (Peakall and Smouse, 2006) using the AFLP data generated by Wimp et al. (2004). This calculation produced a matrix of distances in which trees that are genetically similar have low values of distance. Secondly, we calculated a dissimilarity matrix of understory community using the Bray–Curtis distance metric, as implemented in the “vegdist” function of the vegan package in R. As with the genetic distance matrix, low values indicate compositional similarity. We then conducted a Mantel test on the two matrices to see whether any correlation existed between genetic distance of trees and compositional differences of the understory. The understory composition matrix was log-transformed before analysis.

RESULTS

Overstory tree genetics—The vast majority of trees were readily classified as parentals or showed a near 50/50 split between the parental species and therefore most likely represented F₁ hybrids. Although backcrossing of F₁ hybrids to pure narrowleaf does occur (Martinsen et al., 2001), only one tree surveyed for understory vegetation showed an indication of backcrossing. Thus, the hybrid cross type class used in these analyses predominately represented F₁ hybrids, though for clarity we refer to the “hybrid” cross type. The 48 AFLP markers showed all but two genotypes trees across the stands were unique individuals: two sampled F₁ hybrid trees in one stand exhibited the same genetic profile. The composition of the *Populus* taxa had not changed appreciably: only one tree that had been sampled for the 2004 study (Wimp et al., 2004) was found to be dead at the time of our understory sampling (2009), and this tree was not included in the analysis. Spatial analysis showed that within each stand, the tree cross types were not clustered (analysis of similarity for all stands, $P \geq 0.09$).

Understory plant community—Vegetation surveys detected a rich understory of 67 species, composed of grasses, herbs, vines, and trees (Appendix 2). The Poaceae, Asteraceae, and Fabaceae were the most represented of the 30 families encountered. Approximately 40% of the identified species encountered are nonnative to the region (Appendix 2). Most of the species encountered were graminoid and forb species (83%), and the remainder were trees and shrubs. Over 80% of the identified species were perennial, and over 65% were dicots (Appendix 2).

Effects of hybridization on understory plant diversity metrics and edaphic properties—Cross type had a significant signal on the understory plant community (Table 1). Species richness, Shannon index, and cover were significantly higher under hybrids than under either parental species (Fig. 1). Under hybrids, plant species richness was 30–53% greater, plant diversity 40–48% greater, and plant cover 35–74% greater. A similar pattern was found when either exotic or native species in isolation were considered and when the two predominant growth forms (grasses and forbs) were considered in isolation (Fig. 1). The magnitude of the effect was greater on native than exotic plants (native: richness 46–69%, diversity 87–106%, and cover 117–151%; exotic: richness 27–49%, diversity 66–86%, and cover 0–32%) and on forbs compared with grasses (forbs: richness 43–98%, diversity 96–158%, cover 122%; grasses: richness: 30%, diversity: 48–58%, cover: 22–63%). Post hoc analyses revealed that in most cases, narrowleaf and Fremont understory diversity metrics were not significantly different from each other but were different from hybrids (Tukey–Kramer, $P < 0.05$, Fig. 1). For example, native vegetation does not differ under narrowleaf and Fremont cottonwoods for both diversity and cover, and both are significantly lower than hybrids. Stand location also had significant effects on understory diversity patterns (Table 1). This indicates that while the identity of the stand played a role in structuring understory plants communities, the differences across cross type generally emerged independent of the stand in which the tree was surveyed.

Depth of leaf litter (ANOVA, $F_{2,60} = 0.770$, $P = 0.467$), soil moisture (ANOVA, $F_{2,60} = 1.147$, $P = 0.324$), and soil C:N (ANOVA, $F_{2,37} = 1.899$, $P = 0.164$) did not vary by cross type. However, soil pH differed by cross type, with mean values 2–3% lower under hybrids than under parental species (ANOVA, $F_{2,37} = 3.767$, $P = 0.032$).

Effects of hybridization on understory plant community composition—Graphical representation of understory community

TABLE 1. Results of understory diversity metrics compared across *Populus* cross type (*P. fremontii*, *P. angustifolia*, and their hybrids) along the Weber River, Utah, USA, using ANOVA, with stand as a block factor. Significant values ($\alpha < 0.5$) are in bold. Stand df = 9; cross type df = 2.

Diversity metric	All plants		Native plants		Non-native plants		Forbs		Grasses	
	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value
Richness										
Stand	3.725	<0.001	2.788	0.009	2.632	0.012	3.914	<0.001	1.676	0.115
Cross type	4.971	0.010	2.586	0.084	2.805	0.069	1.408	0.253	2.983	0.058
Diversity										
Stand	4.024	<0.001	1.929	0.065	3.753	<0.001	4.483	<0.001	2.811	0.008
Cross type	7.713	0.001	5.708	0.005	7.341	0.001	4.639	0.014	3.577	0.034
Cover										
Stand	3.447	0.002	2.809	0.008	2.155	0.038	3.781	<0.001	3.346	0.002
Cross type	6.643	0.002	7.137	0.002	0.904	0.411	7.438	0.001	1.927	0.154

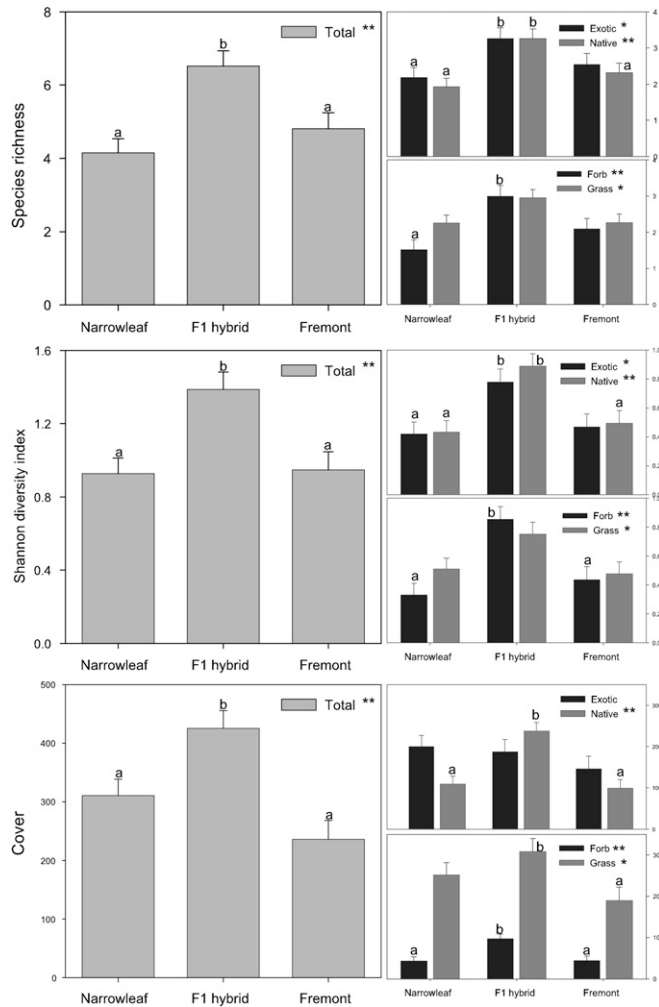


Fig. 1. Comparison of species richness, Shannon diversity index, and cover (%) reveal that hybrids of *Populus fremontii* (Fremont) and *P. angustifolia* (narrowleaf) along the Weber River in Utah, USA, have significantly greater diversity metrics of the understory plant community, compared with parental species. A significant effect of cross type when the factor of stands is blocked in the ANOVA is illustrated with an asterisk. Results are shown for all species pooled (three left panels), for exotic and native species in isolation, and for forbs and grasses in isolation (right panels). Data are means (± 1 SE) grouped by cross type. Significant differences across cross type, as determined by post hoc analysis, are indicated with different letters.

composition demonstrated significant differences among cross type (Fig. 2). Moreover, statistical analysis showed that community composition was different under the broad category of cross types, after factoring out stand location, with both abundance (PERMANOVA $F_{2,58} = 1.952$, $P = 0.016$) and incidence data (PERMANOVA $F_{2,69} = 2.956$, $P = 0.009$). Pairwise comparisons of community composition indicated that the divergence between communities under hybrid and narrowleaf cottonwoods was driving this pattern (narrowleaf vs. hybrid, PERMANOVA $F_{1,38} = 2.942$, $P = 0.004$; Fremont vs. hybrid, PERMANOVA $F_{1,41} = 1.087$, $P = 0.363$; narrowleaf vs. Fremont, PERMANOVA $F_{1,37} = 0.981$, $P = 0.444$; Fig. 2).

Indicator species analysis highlighted five species as clustering under hybrids (4 native, 1 exotic) when all three cross types

are considered as separate classes (Table 2A). Because compositional analysis indicated no difference under narrowleaf and Fremont parental trees, indicator species analysis also was done to compare understory composition under hybrids vs. under the pooled parental species. A further two species emerged as important under the hybrids (total 5 natives, 2 exotic; Table 2B). This contingent of species spanned several growth forms (including forbs, vines, grasses, and tree), life forms (annuals and perennials), and origin (native/exotic) status.

Finally, our findings support the genetic similarity rule (Bangert et al., 2006a, b; Barbour et al., 2009), in which genetically similar trees support more similar understory communities than do genetically dissimilar trees. Across cross types, the understory composition tended to diverge as the genetic distance between individual trees increased (Mantel r value = 0.076, $P = 0.008$). However, testing the genetic similarity rule among trees within each of the cross types showed no correlation (narrowleaf only: Mantel r value = 0.095, $P = 0.090$; hybrid only: Mantel r value = 0.064, $P = 0.298$; Fremont only: Mantel r value = -0.012 , $P = 0.515$).

DISCUSSION

Overstory and understory linkage—We found evidence to support our hypothesis that understory community composition and diversity were influenced by the genetics of the overstory foundation cottonwoods in wild settings. First, richness, diversity, and cover of understory plants were 30–74% higher under the hybrids between *P. fremontii* and *P. angustifolia* than under the parental species. Second, understory plant community composition clustered by overstory cross type, and the community under hybrids represented a unique assemblage rather than a merging of the parental communities. The distribution of understory vegetation in natural settings is obviously complex and dynamic (e.g., Tessier, 2007), and by demonstrating a consistent and significant linkage between canopy tree cross type and the herbaceous community, we show that the genetic differences in the overstory that result from hybridization should be included as an influential factor.

Although unmeasured environmental factors as causative agents cannot be ruled out in this observational study in the wild, we demonstrate a clear link between overstory genetic composition and understory species diversity. Several findings argue that this link is influenced by the genetic make-up of the tree. (1) The environment conditions along the brief stretch of the Weber River where the trees were sampled are remarkably similar (Schweitzer et al., 2011), and thus abiotic differences among stands and trees should be minimal. Indeed, the signal of tree identity on understory appeared independent of stand identity. Moreover, processes known to influence diversity at regional scales, such as dispersal limitation, are unlikely to operate in the fine scale of this geographic area. (2) All trees fall within the recognized hybrid zone and demonstrate no obvious spatial structure. Hybrids are spatially intermixed with Fremont and narrowleaf cottonwoods, appear in the center and periphery of stands, and are situated proximate and farther from the river, etc. Also, this hybrid zone is naturally occurring, formed at mid elevation where ranges overlap and not from an area of high disturbance. (3) Although it is possible that extremely localized patches of disturbance could produce a correlation between overstory genetics and understory species, we find this unlikely given the lack of spatial structure in cross types: the highly localized

(i.e., on the order of meters) disturbance would have to be persistent across years, such that the disturbance that favored the establishment of hybrids in a particular location in the past continues to influence understory plants today. Such parallel effects of disturbance on species diversity of plants and hybridization between plants in one locality would be predicted (Petraitis et al., 1989; McKinnon, 2005) though to our knowledge has never been documented. Experimental manipulation of understory plants in natural stands would explicitly test the hypothesis that it is the tree cross type that shapes the understory plant community.

Plant–plant interactions—A positive association between overstory diversity and the associated organisms lends support for the “diversity begets diversity” hypothesis of Whittaker (1975), and several genetic and demographic processes in tree hybrid zones could affect understory community structure in specific ways. As was hypothesized for the effect of hybridization on phytophagous insects (Whitham et al., 1994), interbreeding could break down genetically determined chemical composition and consequently disrupt any negative interactions with community members. Similarly, because hybrid zones are often on the periphery of the parent species ranges, parental species may be physiologically stressed and thus less effective at enforcing negative or positive interactions. From a genetic perspective, introgression between parental taxa is often asymmetrical because of factors such as differences in species abundances (Burgess et al., 2005) or asynchronous phenology (Belahbib et al., 2001). If one of the parental species structures the understory community in a more dominant manner, then the understory could be “pushed” to match the genetically overriding taxa. Moreover, hybrid zones can support the maintenance and evolution of interacting species that associate specifically

with hybrids (Fritz et al., 1994) and thus represent areas of special concern from a conservation perspective.

Considering beyond the diversity that results from hybridization specifically, the field of community genetics (Agrawal, 2003) has increasingly highlighted the importance that genetic identity and genetic diversity within species and species complexes have for within-trophic interactions in a community ecology context. For instance, phenotypic differences within an overstory tree and a shrub affect understory plants (Pakeman et al., 2006; Crutsinger et al., 2010), as does variation within dominant herbaceous plants (Lankau and Strauss, 2007; Crutsinger et al., 2008; Michalet et al., 2011). The causes of this influence differ by system and include variation in the chemical diversity of monoterpenes (Jason et al., 2005; Pakeman et al., 2006) and canopy architecture (Crutsinger et al., 2010). Thus, differences between plant taxa—ranging from different species, to closely related species and their hybrids, and even within individuals at the population level—are associated with microsite differences to which the understory species demonstrate a niche-based response.

Potential mechanisms—Light, water, and soil properties are the predominant factors generally considered to determine understory plant community diversity metrics (e.g., Dirzo et al., 1992) and to limit understory plant growth (e.g., Shirley, 1945), and here we discuss each of these in turn for the *Populus* system. Architecture does vary among the cross types, where narrowleaf canopies are tapered and Fremont canopies wide (Martinsen and Whitham, 1994). In a common garden, it was shown that photosynthetically active radiation levels decrease with hybrid index (i.e., lower light under Fremont); however, this variation in light did not correlate with understory plant richness or composition (Lamit et al., 2011). Indeed, if light is

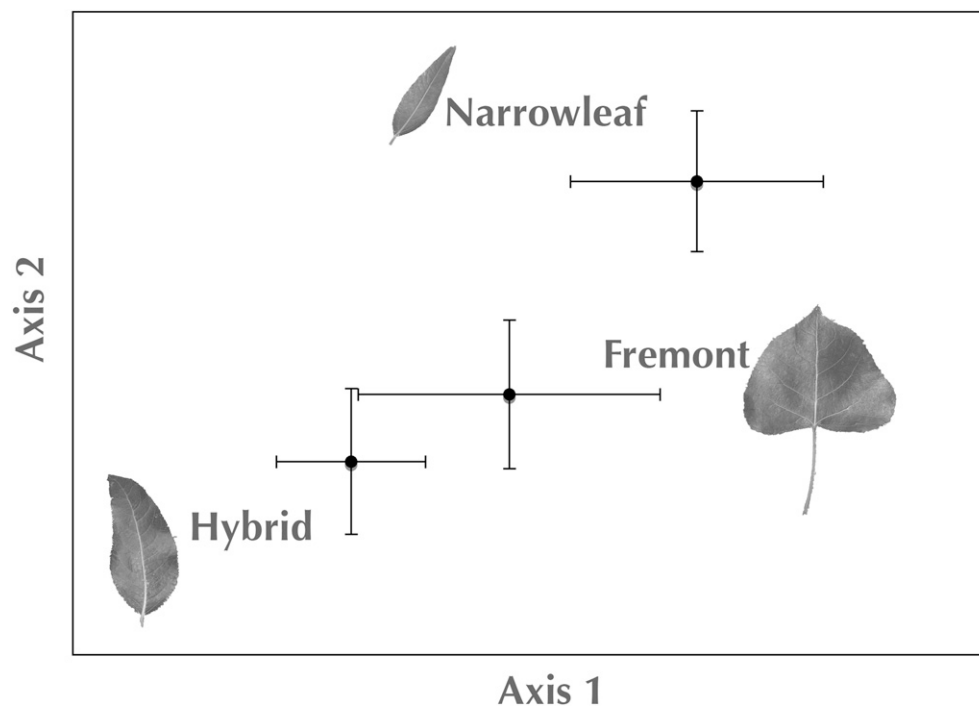


Fig. 2. Plot of understory plant community composition under *Populus fremontii* (Fremont), *P. angustifolia* (narrowleaf), and their hybrids along the Weber River in Utah, USA, based on nonmetric multidimensional scaling. Represented are the mean and standard errors of the ordination axis scores for the three categories, showing differences in the understory plant community composition under each tree cross type.

the dominant factor in determining understory plants in natural *Populus* stands, then tree-level surveys would have shown narrowleaf to have the highest understory species diversity. The absence of this pattern in the wild strongly suggests that light is not the prominent mechanism, possibly because individual tree canopies may not consistently vary or because larger canopy dynamics supersede the influence.

Second, belowground processes also are important to consider. Plant secondary compound concentrations, particularly condensed tannins, are lower in the leaves of Fremont than narrowleaf cottonwoods, and condensed tannins are strongly tied to litter decomposition and nitrogen mineralization rates (Schweitzer et al., 2004). Furthermore, in apparent response to these effects of litter quality on decomposition and nutrient cycling, Fischer et al. (2006) found that fine root production varied greatly among cross types in which narrowleaf cottonwoods invested the most, Fremont the least, and hybrids were intermediate. Thus, one could predict that genotype-determined moderation of the nutrient pool available to plants and competition with fine roots via condensed tannins could alter understory communities. In this case, the pattern observed would again be linear, with hybrids intermediate between the parents. This linear pattern is the observation made in a common garden study, in which the authors demonstrate a correlative link between foliar condensed tannins in *Populus* and the understory (Lamit et al., 2011). However, we did not observe a linear pattern in the natural stands, and the discrepancy in the response of understory plants to overstory genetic identity by location—either a common garden or natural stands—indicates that although understory species and tree genetic diversity correspond in nonrandom ways, the particular mechanism for the correlation may be context dependent. For instance, in the common garden, *Populus* trees are spaced at regular intervals, and it is possible that under uniform conditions, hybrids can modulate belowground processes via leaf litter; in the wild, however, variable spacing of trees could respond to or, more likely, contribute to a highly patchy environment that overwhelms differences due to variation in condensed tannin production. In addition to differences in plant secondary compounds, soil pH levels can be associated with different tree species (Crozier and Boerner, 1984), and here we find that soils underneath hybrids are more acidic. Plant-induced changes in soil pH can occur through a variety of mechanisms, including changes in nitrification rate

and cation redistribution (Ehrenfeld et al., 2001). The mechanistic link between cross type and soil pH in this particular system remains unclear.

Third, water remains an intriguing possibility, as hybrids are known to exhibit higher water use than either parental types (Fischer et al., 2004). Greater water use is expected to be associated with a greater hydraulic lift (also known as *hydraulic redistribution*), the process by which deep-rooted plants bring water from lower soil layers to upper soil layers (Horton and Hart, 1998). It is possible that hydraulic lift may still be occurring—and producing the observed outcome by increasing soil moisture under hybrids relative to parental taxa—but the increased water availability to neighboring plants was undetectable with our sampling methodology. Hydraulic lift, too, is a potential mechanism that could differ between wild and common garden settings: in the common garden, the regular and relatively closely situated trees (5–7 m; Lamit et al., 2011) could negate the possible influence of soil moisture on understory plants; whereas in the wild, differences in hydraulic lift among patchily distributed trees could demonstrate a marked influence on understory plants.

Several facets of the analysis do offer support for potential mechanisms behind the link between overstory and understory in natural settings. First, the effect of hybridization on understory is not linear (where hybrids are intermediate between parental species). Instead, this signal for heterosis could imply a breakdown of process that otherwise limits understory growth, such as that which occurred for the generation of allelopathic compounds in Scots pine trees (Iason et al., 2005), or the strengthening of process that fosters understory growth, such as hydraulic lift. Second, the fact that the pattern is consistently followed for both native and exotic plants, as well as for variable life forms (e.g., forbs, grasses), is evidence that the effect is rather general. Therefore, we would expect the mechanism to draw on a common, non-specific strategy for plant growth. Third, indicator species analysis revealed that many understory species are associated with the hybrids specifically, indicating that the species that define composition under the hybrids are not a random sample of the environment under the parentals but rather contain a unique assemblage of additional plant species. Moreover, it is not simply that community composition differs by cross type but also by richness, diversity, and cover (unlike foliar arthropods; Wimp et al., 2004, 2005). This indicates that the area under hybrids is overall more hospitable to plant growth. Fourth, little indication exists for a role

TABLE 2. Indicator species analysis comparing community composition (A) among the three *Populus* cross types and (B) between hybrids and the parental species. IV = indicator value (corresponding *P* value is shown); cluster = the group with which the understory species is associated.

Understory Species	IV	<i>P</i>	Cluster	Status	Growth form	Duration
(A) Three groupings: Narrowleaf–hybrid–Fremont						
<i>Ambrosia artemisiifolia</i>	0.506	0.001	Hybrid	Native	Forb, herb	Annual
<i>Clematis ligusticifolia</i>	0.158	0.025	Hybrid	Native	Vine	Perennial
<i>Elymus glaucus</i>	0.462	0.002	Hybrid	Native	Grass	Perennial
<i>Lactuca serriola</i>	0.242	0.026	Hybrid	Exotic	Forb, herb	Annual, biennial
<i>Pseudoroegneria spicata</i>	0.182	0.014	Hybrid	Native	Grass	Perennial
(B) Two groupings: Hybrid–parental taxa						
<i>Ambrosia artemisiifolia</i>	0.527	0.001	Hybrid	Native	Forb/Herb	Annual
<i>Clematis ligusticifolia</i>	0.171	0.008	Hybrid	Native	Vine	Perennial
<i>Elymus glaucus</i>	0.537	0.001	Hybrid	Native	Grass	Perennial
<i>Lactuca serriola</i>	0.258	0.018	Hybrid	Exotic	Forb, herb	Annual, biennial
<i>Melilotus officinalis</i>	0.134	0.134	Hybrid	Exotic	Forb, herb	Annual, biennial, perennial
<i>Pseudoroegneria spicata</i>	0.182	0.014	Hybrid	Native	Grass	Perennial
<i>Rosa woodsii</i>	0.131	0.131	Hybrid	Native	Subshrub	Perennial

of other biotic factors influencing particular understory species. Although more bird nests appear in hybrids (Martinsen and Whitham, 1994), few of the indicator species associated with hybrids are bird dispersed. In total, these factors indicate that the trees seem to alter the microenvironment in a broad way to which understory plants in general respond, and soil-based properties, particularly increased water availability brought about through hydraulic lift or changes in soil pH, remain promising hypotheses to test.

Conclusions—We have surveyed understory vegetation in a natural riparian community to show an association between tree cross type within hybridizing *Populus* and the associated understory plant community. Hybrid trees are characterized by a more diverse understory and a unique assemblage of understory plants compared with either of the parental tree species. We show that understory plant communities can consistently respond to micro-site habitat differences associated with particular tree cross types, and the precise underlying mechanism represents a promising line of further study.

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APPENDIX 1. At 10 cottonwood stands in the *Populus fremontii* × *angustifolia* hybrid zone, woody vegetation encountered along six 40-m transects was recorded to assess overstory composition. *Populus* is uniformly dominant in number and biomass.

Stand	Species	Density ^a	Frequency ^b	Dominance ^c	Importance value ^d	Stand	Species	Density ^a	Frequency ^b	Dominance ^c	Importance value ^d
FSH	<i>Acer negundo</i>	4	0.50	1790.23	41.06	H6	<i>Populus</i> spp.	25	1.00	14140.50	204.61
	<i>Crataegus monogyna</i>	1	0.17	41.59	10.94		<i>Rhus trilobata</i>	1	0.17	25.16	9.20
	<i>Populus</i> spp.	17	0.83	30504.92	184.97		<i>Rosa woodsii</i>	2	0.33	25.67	18.23
	<i>Prunus virginiana</i>	1	0.17	41.59	10.94		<i>Salix</i> spp.	3	0.33	124.76	21.69
	<i>Rosa woodsii</i>	3	0.33	38.51	24.88		<i>Elaeagnus angustifolia</i>	3	0.33	124.76	24.36
	<i>Salix</i> spp.	6	0.17	249.51	27.21		<i>Malus</i> spp.	1	0.17	25.16	10.60
H1	<i>Acer negundo</i>	3	0.50	218.20	23.46	<i>Populus</i> spp.	25	1.00	18409.95	210.49	
	<i>Cornus sericea</i>	2	0.33	50.31	14.94	<i>Salix</i> spp.	6	0.50	827.60	44.01	
	<i>Crataegus monogyna</i>	3	0.50	124.76	22.78	<i>Tamarix chinensis</i>	1	0.17	12.84	10.54	
	<i>Elaeagnus angustifolia</i>	1	0.17	41.59	7.59	<i>Acer negundo</i>	1	0.17	51.34	8.00	
	<i>Mahonia repens</i>	1	0.17	25.16	7.47	<i>Elaeagnus angustifolia</i>	1	0.17	10.40	7.75	
	<i>Populus</i> spp.	16	1.00	13082.05	168.42	<i>Juniper chinensis</i>	1	0.17	41.59	7.94	
	<i>Prunus virginiana</i>	1	0.17	25.16	7.47	<i>Populus</i> spp.	33	1.00	15685.20	200.39	
	<i>Rhus trilobata</i>	6	0.83	150.94	40.49	<i>Prunus americana</i>	2	0.33	83.17	15.88	
	<i>Rosa woodsii</i>	1	0.17	12.84	7.38	<i>Rhus trilobata</i>	3	0.33	75.47	17.96	
	<i>Salix</i> spp.	9	0.67	340.90	32.61	<i>Salix</i> spp.	6	0.83	249.51	42.08	
H3	<i>Acer negundo</i>	8	0.67	179.43	30.17	<i>Juniper chinensis</i>	1	0.17	41.59	10.96	
	<i>Cornus sericea</i>	4	0.50	52.88	18.78	<i>Populus</i> spp.	9	0.83	3616.40	146.91	
	<i>Elaeagnus angustifolia</i>	1	0.17	86.76	5.97	<i>Quercus gambelii</i>	2	0.33	166.86	23.86	
	<i>Fraxinus pennsylvanica</i>	2	0.33	66.87	11.48	<i>Rhus trilobata</i>	15	0.83	377.35	92.05	
	<i>Juniper chinensis</i>	1	0.17	37.09	5.76	<i>Rhus trilobata</i>	3	0.33	124.76	26.22	
	<i>Juniperus communis</i>	1	0.17	0.51	5.60	<i>Salix</i> spp.	3	0.33	124.76	26.22	
	<i>Mahonia repens</i>	1	0.17	25.16	5.71	<i>Acer negundo</i>	1	0.17	51.34	7.55	
	<i>Populus</i> spp.	25	1.00	22917.62	163.29	<i>Crataegus monogyna</i>	12	0.33	184.95	30.30	
	<i>Rhus trilobata</i>	2	0.17	37.99	7.51	<i>Elaeagnus angustifolia</i>	3	0.33	786.02	18.91	
	<i>Rosa woodsii</i>	3	0.33	38.51	13.12	<i>Populus</i> spp.	40	1.00	27688.54	189.09	
H4	<i>Salix</i> spp.	9	0.67	340.90	32.61	<i>Rhus trilobata</i>	2	0.33	50.31	14.92	
	<i>Elaeagnus angustifolia</i>	5	0.50	281.86	28.26	<i>Rosa woodsii</i>	2	0.33	25.67	14.84	
	<i>Fraxinus pennsylvanica</i>	2	0.17	83.17	9.71	<i>Salix</i> spp.	6	0.17	249.51	15.69	
	<i>Populus</i> spp.	42	1.00	5020.79	184.48	<i>Ulmus pumila</i>	1	0.17	391.47	8.71	
	<i>Salix</i> spp.	16	1.00	92.80	56.79	<i>Acer negundo</i>	1	0.17	12.84	9.20	
	<i>Tamarix chinensis</i>	3	0.50	30.29	20.75	<i>Crataegus monogyna</i>	1	0.17	41.59	9.32	
	H5	<i>Acer negundo</i>	1	0.17	51.34	9.38	<i>Elaeagnus angustifolia</i>	2	0.33	83.17	18.65
		<i>Cornus sericea</i>	2	0.33	28.24	18.25	<i>Fraxinus pennsylvanica</i>	1	0.17	51.34	9.37
		<i>Elaeagnus angustifolia</i>	1	0.17	41.59	9.31	<i>Populus</i> spp.	41	1.00	22687.88	223.47
		<i>Juniper chinensis</i>	1	0.17	41.59	9.31	<i>Quercus gambelii</i>	1	0.17	4.62	9.16
						<i>Salix</i> spp.	3	0.33	124.76	20.83	

^aNumber of individuals.

^bProportion of transects in which taxon appears.

^cSum of basal area (cm) for all individuals of a taxon.

^dSum of all three relativized values. Relativized values are the percentage of the metric (density, frequency, dominance) that each taxa represents in each stand and thus sums to 300 for each stand.

APPENDIX 2. Table of plant species composing understory community in the *Populus fremontii* and *P. angustifolia* hybrid zone along the Weber River in north-central Utah, USA.

Species	Family	Native or exotic	Growth form	Duration	Group
<i>Acer negundo</i>	Sapindaceae	Native	Tree	Perennial	Dicot
<i>Achillea millefolium</i>	Asteraceae	Native	Forb	Perennial	Dicot
<i>Aegilops cylindrica</i>	Poaceae	Exotic	Grass	Annual	Monocot
<i>Agastache urticifolia</i>	Lamiaceae	Native	Forb	Perennial	Dicot
<i>Agropyron cristatum</i>	Poaceae	Exotic	Grass	Perennial	Monocot
<i>Ambrosia artemisiifolia</i>	Asteraceae	Native	Forb	Annual	Dicot
<i>Apocynum cannabinum</i>	Apocynaceae	Native	Forb	Perennial	Dicot
<i>Artemisia ludoviciana</i>	Asteraceae	Native	Forb	Perennial	Dicot
<i>Artemisia tridentata</i>	Asteraceae	Native	Shrub, tree	Perennial	Dicot
<i>Asclepias speciosa</i>	Asclepiadaceae	Native	Forb	Perennial	Dicot
<i>Astragalus utahensis</i>	Fabaceae	Native	Forb	Perennial	Dicot
<i>Bromus carinatus</i>	Poaceae	Native	Grass	Annual, perennial	Monocot
<i>Bromus diandrus</i>	Poaceae	Exotic	Grass	Annual, perennial	Monocot
<i>Bromus erectus</i>	Poaceae	Exotic	Grass	Perennial	Monocot
<i>Bromus inermis</i>	Poaceae	Exotic	Grass	Perennial	Monocot
<i>Bromus tectorum</i>	Poaceae	Exotic	Grass	Annual	Monocot
<i>Cardaria draba</i>	Brassicaceae	Exotic	Forb	Perennial	Dicot

APPENDIX 2. Continued.

Species	Family	Native or exotic	Growth form	Duration	Group
<i>Cirsium arvense</i>	Asteraceae	Exotic	Forb	Perennial	Dicot
<i>Clematis ligusticifolia</i>	Ranunculaceae	Native	Vine	Perennial	Dicot
<i>Convolvulus arvensis</i>	Convolvulaceae	Exotic	Vine, forb	Perennial	Dicot
<i>Crataegus monogyna</i>	Rosaceae	Exotic	Shrub, tree	Perennial	Dicot
<i>Cynoglossum officinale</i>	Boraginaceae	Exotic	Forb	Biennial	Dicot
<i>Dactylis glomerata</i>	Poaceae	Exotic	Grass	Perennial	Monocot
<i>Digitaria sanguinalis</i>	Poaceae	Native	Grass	Annual	Monocot
<i>Dipsacus fullonum</i>	Dipsacaceae	Exotic	Forb	Biennial	Dicot
<i>Eleocharis palustris</i>	Cyperaceae	Native	Sedge	Perennial	Monocot
<i>Elymus glaucus</i>	Poaceae	Native	Grass	Perennial	Monocot
<i>Elymus spicatus</i>	Poaceae	Native	Grass	Perennial	Monocot
<i>Elymus trachycaulus</i>	Poaceae	Native	Grass	Perennial	Monocot
<i>Erodium cicutarium</i>	Geraniaceae	Exotic	Forb	Annual, biennial	Dicot
<i>Festuca ovina</i>	Poaceae	Exotic	Grass	Perennial	Monocot
<i>Galium aparine</i>	Rubiaceae	Native	Vine, forb	Annual	Dicot
<i>Glycyrrhiza lepidota</i>	Fabaceae	Native	Forb	Perennial	Dicot
<i>Gutierrezia sarothrae</i>	Asteraceae	Native	Forb, shrub	Perennial	Dicot
<i>Heterotheca villosa</i>	Asteraceae	Native	Forb	Perennial	Dicot
<i>Isatis tinctoria</i>	Brassicaceae	Exotic	Forb	Annual, perennial	Dicot
<i>Juncus arcticus</i>	Juncaceae	Native	Rush	Perennial	Monocot
<i>Juniperus communis</i>	Cupressaceae	Native	Shrub, tree	Perennial	Gymnosperm
<i>Lactuca serriola</i>	Asteraceae	Exotic	Forb	Annual, biennial	Dicot
<i>Leymus cinereus</i>	Poaceae	Native	Grass	Perennial	Monocot
<i>Linaria dalmatica</i>	Scrophulariaceae	Exotic	Forb	Perennial	Dicot
<i>Matantherum stellatum</i>	Liliaceae	Native	Forb	Perennial	Monocot
<i>Medicago sativa</i>	Fabaceae	Exotic	Forb	Annual, perennial	Dicot
<i>Melilotus officinalis</i>	Fabaceae	Exotic	Forb	Annual, biennial, perennial	Dicot
<i>Mentha arvensis</i>	Lamiaceae	Native	Forb	Perennial	Dicot
<i>Opuntia polyacantha</i>	Cactaceae	Native	Shrub	Perennial	Dicot
<i>Phalaris arundinacea</i>	Poaceae	Native	Grass	Perennial	Dicot
<i>Plantago major</i>	Plantaginaceae	Exotic	Forb	Perennial	Dicot
<i>Poa bulbosa</i>	Poaceae	Exotic	Grass	Perennial	Monocot
<i>Poa pratensis</i>	Poaceae	Exotic ^a	Grass	Perennial	Monocot
<i>Populus</i> spp.	Salicaceae	Native	Tree	Perennial	Dicot
<i>Pseudoroegneria spicata</i>	Poaceae	Native	Grass	Perennial	Monocot
<i>Rhus trilobata</i>	Anacardiaceae	Native	Shrub	Perennial	Dicot
<i>Ribes aureum</i>	Grossulariaceae	Native	Shrub	Perennial	Dicot
<i>Rosa woodsii</i>	Rosaceae	Native	Subshrub	Perennial	Dicot
<i>Rumex crispus</i>	Polygonaceae	Exotic	Forb	Perennial	Dicot
<i>Salix</i> spp.	Salicaceae	Native	Shrub, tree	Perennial	Dicot
<i>Schoenoplectus acutus</i>	Cyperaceae	Native	Grass	Perennial	Monocot
<i>Senecio riddellii</i>	Asteraceae	Native	Forb	Perennial	Dicot
<i>Smilax</i> spp.	Smilacaceae	–	Shrub	Perennial	Monocot
<i>Solanum dulcamara</i>	Solanaceae	Exotic	Forb, vine	Perennial	Dicot
<i>Solidago velutina</i>	Asteraceae	Native	Forb	Perennial	Dicot
<i>Taraxacum officinale</i>	Asteraceae	Exotic	Forb	Perennial	Dicot
<i>Toxicodendron radicans</i>	Anacardiaceae	Native	Forb, shrub, vine	Perennial	Dicot
<i>Tragopogon dubius</i>	Asteraceae	Exotic	Forb	Annual, biennial	Dicot
<i>Urtica dioica</i>	Urticaceae	Native	Forb	Perennial	Dicot

^aThe USDA lists the native status of *Poa pratensis* (Kentucky bluegrass) as debated; following the *Manual of Grasses for North America* (ed. Barkworth et al., 2007), we classify the species as exotic but naturalized. Barkworth, M. E., L.K. Anderton, K.M. Capels, S. Long, and M. B. Piep [eds.], 2007. *Manual of Grasses for North America*. Intermountain Herbarium and Utah State University Press, Logan, Utah, USA.