

# From genes to geography: a genetic similarity rule for arthropod community structure at multiple geographic scales

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## Abstract

**We tested the hypothesis that leaf modifying arthropod communities are correlated with cottonwood host plant genetic variation from local to regional scales. Although recent studies found that host plant genetic composition can structure local dependent herbivore communities, the abiotic environment is a stronger factor than the genetic effect at increasingly larger spatial scales. In contrast to these studies we found that dependent arthropod community structure is correlated with both the cross type composition of cottonwoods and individual genotypes within local rivers up to the regional scale of 720 000 km<sup>2</sup> (Four Corner States region in the southwestern USA). Across this geographical extent comprising two naturally hybridizing cottonwood systems, the arthropod community follows a simple genetic similarity rule: genetically similar trees support more similar arthropod communities than trees that are genetically dissimilar. This relationship can be quantified with or without genetic data in *Populus*.**

*Keywords:* AFLP composition, alpha-beta-gamma diversity, arthropod community structure, genes vs environment, local-regional gradient, *Populus* spp., spatial scale

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## Introduction

How ecological communities form and diversify is a topic of long-standing interest among ecologists and has been identified as a frontier in ecology (Thompson *et al.* 2001). It has been shown that a positive relationship exists between plant species richness (number of species) and arthropod richness (Murdoch *et al.* 1972; Root 1973; Naeem *et al.* 1994; Siemann *et al.* 1998), and a negative relationship between plant species richness and plant species invasion or fungal infection (Knops *et al.* 1999). In other words, species richness, or diversity, can have benefits for community members. Moreover, there is concern that a loss of species diversity due to human-caused environmental change will affect

ecosystem function (Tilman & Downing 1994; Daily 1997; Loreau *et al.* 2001). Until recently the effects of within-species genetic diversity have not received much attention in community ecology (e.g. Whitham *et al.* 2003; Johnson *et al.* 2006). Consequently, understanding the effect of plant species diversity and genetic diversity within species on dependent communities is an area of research that warrants additional investigation (Thompson *et al.* 2001).

The effect of intraspecific plant phenotypic and genetic variation on community-level patterns has received little attention compared to the effects of interspecific variation. Most studies have concentrated on how intraspecific plant variation affects populations of single arthropod species (review in Karban 1992) on important agricultural plants (e.g. Ylloja *et al.* 2000) and in natural systems (e.g. Service 1984; Mopper *et al.* 2000). More recently, studies have explicitly concentrated on the effect of intraspecific plant variation on plant community composition (Booth & Grime 2003) and arthropod community structure or diversity (Fritz & Price 1988; Whitham *et al.* 1994; Floate & Whitham 1995; Dickson & Whitham 1996; Dungey *et al.*

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**Table 1** ANOVA table for 2003 AFLP composition by cottonwood cross type

Location	Source of variation	d.f.	SS	MS	F	P
Indian Creek, UT	Cross type	2	83.13	41.57	12.04	0.0002
	Residual	27	93.20	3.45		
	Total	29	176.33			
San Miguel River, CO	Cross type	2	176.69	88.35	8.22	0.0001
	Residual	9	96.73	10.75		
	Total	11	273.42			
Blue River, AZ	Cross type	2	1082.98	541.49	10.99	0.0002
	Residual	26	1281.02	49.27		
	Total	28	2364.00			
Rio Nambé, NM	Cross type	2	487.91	243.95	11.02	0.0002
	Residual	27	531.28	22.14		
	Total	29	1019.19			
Clear Creek, CO	Cross type	2	128.81	64.41	3.61	0.0002
	Residual	10	178.57	17.86		
	Total	12	307.38			
St. Vrain Creek, CO	Cross type	2	817.26	408.63	6.23	0.0002
	Residual	23	1509.43	65.63		
	Total	25	2326.69			

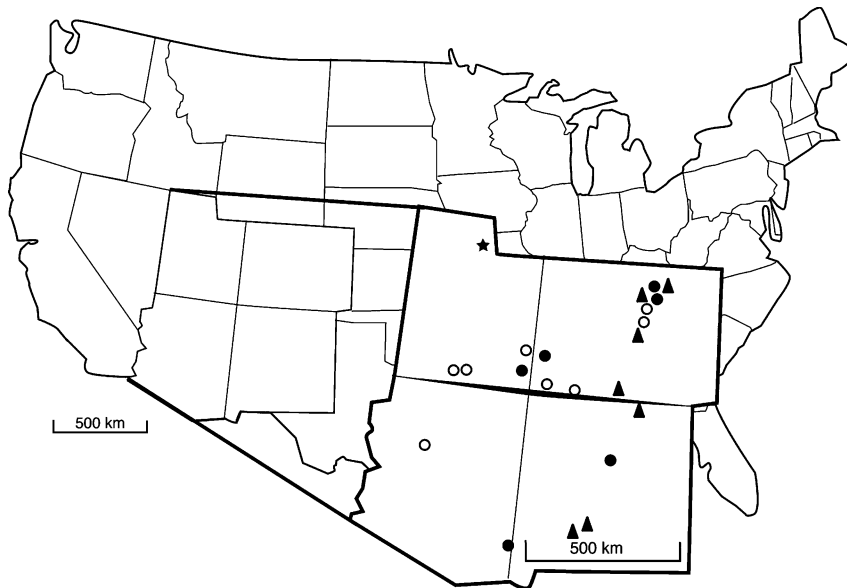
*P*-values are limited by the number of permutations for the test, e.g. 9999. All pairwise comparisons among the cross types were significant with a Bonferroni correction for the family wise  $\alpha = 0.05$ . The pairwise comparison between the  $F_1$  and backcross types was not different ( $P = 0.036$ ) in Clear Creek because of a small sample size in one group.

2000; Hochwender & Fritz 2004; Wimp *et al.* 2004, 2005; Johnson & Agrawal 2005; LeRoy *et al.* 2006) at small spatial scales. The lack of a genetic-based perspective for understanding community structure may have arisen from the perception that there is insufficient genetic variation at lower taxonomic levels in plants to have ecological consequences or because community-level studies are unpredictable and often result in equivocal results (Lawton 1999). Perhaps most importantly, a genetically based perspective of community structure allows us to place these disciplines within a predictive evolutionary framework, where selective pressures acting on the plant may indirectly act on the associated community members (Thompson *et al.* 2001; Whitham *et al.* 2003).

Recent studies suggest that the effects of intraspecific plant genetic variation on dependent communities will be detectable only at local scales. At the regional scale, abiotic factors, such as climate and geology, become more important (Menge & Olson 1990). In a survey of common garden studies, Johnson & Agrawal (2005) found that genotype was important at small scales and environment more important at large scales (but it is not clear if any single study addressed this question at multiple scales). In their study of communities associated with *Oenothera biennis* planted in common gardens in different environments, they found a significant genotype effect on arthropod richness ( $P = 0.03$ ), but the environment and gene-by-environment interactions (G $\times$ E) were highly significant

(all  $P \leq 0.001$ ) for all the community metrics that were measured (Table 1 in Johnson & Agrawal 2005). This suggests that arthropod communities respond more strongly to different host plant genotypes based on the environmental context at the spatial scale of this study (m to 2.8 km; Johnson & Agrawal 2005). Several other studies have concluded that the host plant genotype effect was weak and that the environment was most responsible for arthropod population and community structure (Maddox & Cappuccino 1986; Stiling & Rossi 1996; Stiling & Bowdish 2000). Other work suggests that stressful environments will overcome genetic effects (Stiling & Rossi 1996) or conversely, genetic effects will be detectable only under low environmental variation (Huston 1999).

Given the contrasting results from previous studies, under what circumstances would host plant genetic composition become a significant factor in structuring dependent arthropod communities at multiple scales? As geographical scale increases, it is reasonable to assume that environmental variability increases. If genetic variation in one or more of the interacting species also increases at a similar rate, then community genetic effects should be maintained, and we are most likely to find that genetic differences among individuals predict differences in communities regardless of geographical scale. Conversely, if the variability of genetic effects does not increase as fast as environmental variation, then the environment becomes a stronger organizing factor on dependent communities



**Fig. 1** Tree locations in the Four Corner States, USA. Arthropod data at the river scale were collected from 14 sites in 2002 = ○ & ●. Arthropod and genetic data were collected from six of those sites in 2003 = ●. The Weber River, UT stand data = ★. Supplementary arthropod data = ▲.

and the genetic effects on the community decline (Bangert *et al.*, in review).

Previous studies in the cottonwood system suggest that cottonwood genetic variation is large; therefore we predict that plant genetic effects should be detectable at multiple geographical scales and the genetic effects will not necessarily be swamped out at larger scales. To address these two predictions, we test whether plant genetic variation is correlated with arthropod communities at both local and regional scales from a few m<sup>2</sup> to approximately 720 000 km<sup>2</sup>. Specifically, we ask the following questions. First, are arthropod communities and host plant genetic compositions each different with respect to host plant cross type within individual rivers? Second, are arthropod communities different among the different cross types at the larger regional scale and is the genetic factor (i.e. cross type) as strong as the environmental factor (i.e. individual rivers)? Third, do individual plants with similar genetic compositions also host similar arthropod communities within a river and does this pattern hold at multiple spatial scales? Finally, we discuss our findings in the context of the genetic similarity rule, which argues that hosts that are similar genetically will support similar arthropod communities (Bangert *et al.* 2006).

## Methods

### Study system

**Cottonwoods.** Cottonwood trees (*Populus* spp.) are found in most river systems in the western USA and many of these rivers have two species, in different sections of the genus, that hybridize in a contact zone. One species typically occurs

in the lower, and another species in the upper reaches of a river system, respectively (Eckenwalder 1984). To test whether patterns at local sites scale to a regional level, we chose 14 different hybrid zones that vary considerably with respect to cross type composition and environmental conditions across the intermountain west, USA. Additionally, we sampled trees from random locations for a regional scale analysis (Fig. 1). *Populus angustifolia* James (narrowleaf cottonwood in sect. *Tacamahaca*) hybridizes with *P. fremontii* Watson (Fremont cottonwood in sect. *Aigeiros*) in rivers west of the Continental Divide resulting in a hybrid swarm. The rivers east of the Continental Divide exhibit a similar pattern of hybridization between *P. angustifolia* and *P. deltoides* Marshall (plains cottonwood in sect. *Aigeiros*; Floate *et al.* 1997; J. Mitton, personal communication). The two *Aigeiros* species are sister taxa based on phenetic and genetic analyses (Eckenwalder 1996; Ford 2004).

In the *Tacamahaca* × *Aigeiros* hybridizing system, the first hybridizing event results in F<sub>1</sub> progeny that are intersterile. Subsequently, introgression is unidirectional whereby the F<sub>1</sub> generation backcrosses only with the narrowleaf parent resulting in backcross to narrowleaf progeny. Further backcrossing only occurs with the narrowleaf parent resulting in a backcross complex (Keim *et al.* 1989). The backcross complex becomes more narrowleaf-like with each backcross event to the narrowleaf parent resulting in morphologies that are indistinguishable from the narrowleaf parental type (G. D. Martinsen, unpublished data). In the plains by narrowleaf cottonwood system introgression has not been directly characterized using genetic methods, but morphological data suggest that introgression is also unidirectional (Floate 2004; J. Mitton, personal communication). Although molecular analysis is required to distinguish

between the backcross and narrowleaf cross types, the arthropod community does not discriminate between the two, and chemical compositions are highly similar (Wimp *et al.* 2005; Bangert *et al.* 2006). Moreover, pure narrowleaf cottonwoods are rare in the hybrid zone (Wimp *et al.* 2005); therefore, our backcross classification represents backcrosses and the rare narrowleaf trees in hybrid zones and will be collectively referred to as backcrosses. Thus, we identify three morphological cross types based on the visual assessment of leaf shape in cottonwood hybrid zones: broadleaf-type (Fremont or plains), F<sub>1</sub> hybrids and the backcross hybrid-type (Wimp *et al.* 2005).

*Arthropod community.* In this study we analysed host plant cross type and river system as factors related to the structure of an arthropod community. We also quantified variability in the arthropod community at a finer scale along a genetic continuum that includes multiple cottonwood genotypes. We defined our community as one that interacts directly with leaf tissue and is therefore sensitive to the underlying genetic structure of the host plant (Strong *et al.* 1984; Dreger-Jauffret & Shorthouse 1992; Mani 1992). This group is composed of arthropods that are leafgallers, leaf tiers, leafrollers, leaf folders and leafminers (Bangert *et al.* 2006). Many members of this assemblage are considered to be keystone engineers (e.g. Dickson & Whitham 1996; Martinsen *et al.* 2000; Lill & Marquis 2003) and therefore they may affect other trophic levels from arthropods to vertebrates. These animals leave distinctive species-specific structures that allowed us to quantify them in the field, whether or not the individual was present (Price *et al.* 1987; Floate & Whitham 1993). Species were classified as morphospecies or recognizable taxonomic units (RTU; Oliver & Beattie 1996; Siemann *et al.* 1998), based on their characteristic structures (Price *et al.* 1998). This allowed us to control for temporal turnover of the community and to survey many trees across many rivers. Finally, 23 of the 25 morphospecies were found throughout the geographical extent of this study, indicating that we were working with a single species pool (Bangert *et al.* 2005).

#### *Data collection and analysis*

*Arthropods.* We surveyed trees during the months of July and August 2002 and 2003 after leaf structures were initiated and before leaf abscission occurred (Floate & Whitham 1993). We constructed species abundance by tree data matrices from surveys of ~45 shoots per tree (average 320 leaves) from ~6–8 m high in the canopy resulting in four different data sets. First, in 2002 we randomly sampled ~20 trees each in 14 hybrid zones, which resulted in different proportions of the tree classes in each hybrid zone. We also conducted surveys to quantify cross type proportions along the length of each hybrid zone and we evaluated

whether the arthropod community differed in hybrid zones having different proportions of the cross type hosts. Second, we collected data from 217 trees at random locations across the region to address the geographical scale questions. In comparisons between the two systems, we analysed these data as presence/absence in order to separate individual population responses from species-specific responses. This controls for differences due to different fluctuating population dynamics within species across the region and allows us to analyse the specific responses by species. Third, in 2003 we sampled ~10 trees each from the broadleaf, F<sub>1</sub> and backcross cross types within each of six hybrid zones for community and AFLP (amplified fragment length polymorphism) data: three in the Fremont and three in the plains cottonwood systems. This resulted in a sample size of 165 trees. We used these data to address the 'cross type' effect (genetic), the 'river' effect (environment), and the interaction between these two factors. The 2002 regional analysis indicated that there are large differences in arthropod abundance between the two hybridizing systems, so we analysed the 2003 regional data separately by hybridizing system. Finally, we collected community and AFLP data from eight trees in each of 10 cottonwood stands along the Weber River, UT (Wimp *et al.* 2004). Overall, the arthropod community was quantified on 742 trees spanning 7° latitude (~900 km), 8° longitude (~800 km), with genetic data for 245 trees. This resulted in an arthropod assemblage of 8755 individual structures representing 25 morphospecies, or RTUs.

*Cottonwood AFLP.* For the genetic compositional analyses we collected leaf material to address the relationship between arthropod community composition and host plant genetic composition. Five leaves were collected and dried in anhydrous calcium sulphate desiccant (CaSO<sub>4</sub>). DNA was extracted with the DNeasy plant extraction kit according to manufacturer protocol (QIAGEN). Genetic composition was quantified using fluorescent amplified fragment length polymorphism (fAFLP) (modified from Vos *et al.* 1995). Pre-selective amplification was done with *EcoRI*-A and *MseI*-C followed by selective amplification with *EcoRI*-ACG, *EcoRI*-ACT, *EcoRI*-AGC, *MseI*-CAG and *MseI*-CCA, resulting in six primer combinations: ACGCCA, ACGCAG, ACTCCA, AGCCCA, ACTCAG and AGCCAG. Genetic composition was assayed using these six primer combinations for each of the rivers and were chosen based on the identification of unambiguous, reliably scored polymorphic markers. For the regional analysis, the primer AGCCAG was used because it provided a large number of polymorphic markers (78 total) for 137 of the trees across all six rivers. Fragments resulting from the final selective amplification step were separated on an ABI 3100 Genetic Analyser and visualized with GENOTYPER 3.7 software (Applied Biosystems). A table of presence/absence of the AFLP

markers was created and re-scored manually with only polymorphic markers retained for analysis (Kjølner *et al.* 2004).

*Compositional analysis.* To analyse arthropod community structure we used a compositional approach that quantifies community composition among cross types (beta diversity) rather than species richness or abundance within a cross type (alpha diversity). This approach complements previous studies that are generally concerned with alpha diversity (e.g. Fritz *et al.* 1998; Martinsen *et al.* 2000). A compositional approach incorporates multiple factors (i.e. genes, gene products and species). This is important because these factors do not interact in a vacuum (Thompson 2005). Moreover, even when there are no differences in species richness (alpha diversity) among treatments at the local scale, compositional differences can be large (beta diversity; e.g. Wimp *et al.* 2004, 2005), which can result in an increase in regional, i.e. total species richness (gamma diversity; Crist *et al.* 2003; Bangert *et al.* 2005). Most studies quantify various diversity indices (e.g. Simpson's or Shannon's diversity), richness and abundance (Boecklen & Spellenberg 1990; Johnson & Agrawal 2005), but these are not always sufficient to quantify important differences in composition; thus composition can be a highly informative measure of community differences (Wimp *et al.* 2005). This approach precludes the need to conduct allele-by-allele, species-by-species (e.g. Maddox & Root 1990; Fritz *et al.* 1998) and allele-by-species analyses, which can often be logistically unmanageable and not always meaningful (Peakall *et al.* 2003).

Euclidean distance (ED) is a common metric used to calculate genetic composition and measures the genetic distance between two individuals with the familiar distance formula

$$ED = \sqrt{\sum (y_{1j} - y_{2j})^2}$$

where,  $y_{1j}$  represents individual 1 and marker  $j$  (where  $y_{ij} = 1$  or 0), and  $y_{2j}$  represents individual 2 and marker  $j$  summed over all markers (Excoffier *et al.* 1992; Peakall *et al.* 2003). The more related the two individuals, the smaller the Euclidean distance between them. A community similarity matrix is calculated between each pair of the same trees utilizing the Bray-Curtis (BC) similarity coefficient

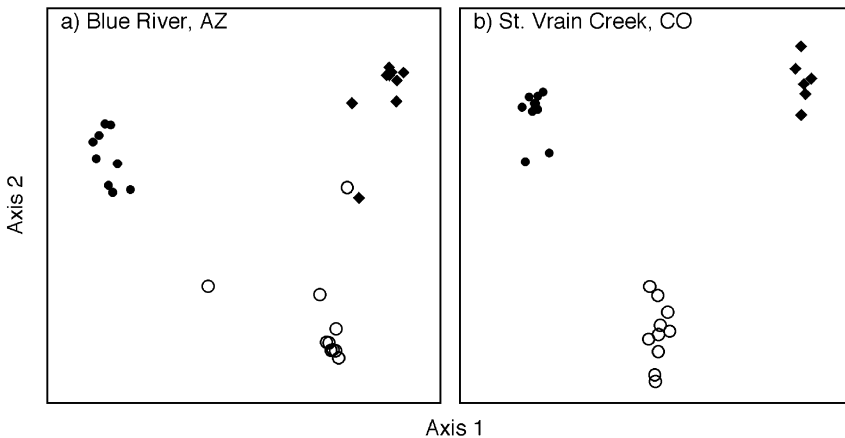
$$BC = \frac{2W}{(A + B)}$$

where,  $W$  is the sum of the minimum abundances between sample  $A$  and  $B$ , divided by the total abundance of species on the two trees and scales between 0 and 1. This measures the proportional similarity between two samples. Similarity is a concept complementary to distance where units that are more similar have a high similarity value. We used a

new ANOVA procedure for the compositional analyses of the distance and similarity metrics of composition. This technique calculates the mean pairwise similarities or distances in an ANOVA framework with  $P$ -values determined through a randomization procedure (Anderson 2001). This allows us to evaluate community structure by factors and their interaction terms. We employed this procedure to address hypotheses that arthropod community structure and genetic compositions were different between the different cottonwood cross types, and to analyse the cross type and river factors along with the interaction terms. We used analysis of similarity (ANOSIM; Legendre & Legendre 1998), which is analogous to an  $F$ -test with  $P$ -values determined through a randomization procedure, for pairwise comparisons among cross types in situations where the ANOVA software could not handle tests due to differences in sample size.

We used two analytical approaches in this study. First, communities were analysed by cross type in the absence of genetic data. Second, communities were analysed along a genetic continuum (i.e. by genotype) with genetic data. Community composition was graphically analysed by cross type with nonmetric multidimensional scaling (NMDS; Legendre & Legendre 1998). Genetic AFLP composition of host plant cross types was graphically analysed using canonical analysis of principal coordinates (CAP, Anderson & Willis 2003), which is a metric multidimensional scaling procedure appropriate for genetic data (Whitehead *et al.* 2003). The two dimensional solutions of the multivariate data were plotted, where each point in the ordination represents the composition associated with a single tree. Points in the ordination that are close together have more similar compositions than points that are far apart, resulting in Euclidean axes that are unit-less. For the regional analyses, community centroids with 95% confidence ellipses were presented for clarity due to the large number of points. To examine the hypothesis that community similarity was related to genetic distance, we used Mantel tests to test this relationship at the tree, stand, river, and regional scales. Results of the Mantel tests were graphically displayed as mean community similarity vs mean genetic distance (e.g. Velend 2001).

At the smallest scale, we quantified community and genetic composition on individual trees within each of six rivers. At the stand and river scales, we characterized each scale by pooling the data at that scale. For example, we pooled the community and genetic data from eight trees within each of 10 stands: the community was quantified at the stand level and the occurrences of individual AFLP markers present in each stand were individually summed resulting in a unique genetic composition for each stand. At the river scale we conducted two analyses on two separate data sets. First, the arthropod and AFLP variables were quantified in each of six rivers surveyed in 2003 in the same



**Fig. 2** 2003 ordinations of cottonwood genetic (AFLP) composition by host plant cross type from two representative rivers. Ordinations represent genetic distance between individual trees. Axes are unit-less and only serve to put points into Euclidean space relative to all other points. Points that are close are more similar than points that are further apart. 2a) is representative of rivers from the Fremont  $\times$  narrowleaf hybridizing system, and 2b) is representative of rivers from the plains  $\times$  narrowleaf hybridizing system. ● = Fremont or plains cottonwood; ○ =  $F_1$  hybrids; and ◆ = backcross type cottonwoods. All groups are significantly different.

manner as at the stand level. At the regional scale, we analysed 137 individual trees from across the region in a single analysis because pooling data at the regional scale resulted in a sample size of one. Second, we used host plant cross type composition as a surrogate for genetic composition. Fourteen hybrid zones were surveyed in 2002. We pooled the arthropod communities from 20 trees into a single river-level community. We conducted surveys and calculated the proportions (i.e. composition) of the three cottonwood cross types in each river. A chi-square test for heterogeneity was used to test for differences in cross type proportions among rivers; thus, rivers with different proportions of the cross types were predicted to differ in arthropod community structure. Finally, Euclidean geographical distance matrices were used to test for spatial autocorrelation. When there was spatial autocorrelation it was factored out with partial Mantel tests (Legendre 1993; Peakall *et al.* 2003). Where necessary, data were natural log transformed to improve variance structure and linearity.

For the cross type analysis at the regional scale, we combined trees from the 2002 data into a geographical community by cross type and hybridizing system. Because this data set was unbalanced across rivers in 2002, we assessed the river effect by randomizing out that component in this analysis while maintaining host plant cross type integrity. Five trees were randomly selected from the 2002 geographical community from within a cross type and combined into a single community. Each random community had a minimum of one tree from each hybridizing system and all five trees were from different rivers. This procedure was applied to all trees across each of the three cross types. If the environment was a strong component we would expect composition by cross type to be weak. In 2002, we found a strong system effect, so we analysed the hybridizing systems separately for the 2003 data. We evaluated these geographical scale data (cross type, system and river) of the arthropod community with the ANOVA procedure.

## Results

### *River scale patterns: arthropod and genetic compositions by cross type*

In 2003, genetic compositions were different among the cross types within each river (all pair-wise  $P \leq 0.001$  are significant with a Bonferroni correction; Table 1; Fig. 2). These findings support a genetic basis to these morphological classes.

Likewise, the arthropod community discriminated among the same cottonwood cross types, but not as discretely (Table 2; Fig. 3). For example, in some river systems, community composition was significantly different among the three cross types (e.g. Figure 3). In other rivers, the  $F_1$  class was not different from the broadleaf class (Indian Creek,  $P = 0.04$ ; Rio Nambe,  $P = 0.48$ ) and the  $F_1$  class was not different from the backcross class (Clear Creek,  $P = 0.03$ ), but the broadleaf and backcross communities were always different.

### *Regional scale patterns: arthropod composition by cross type*

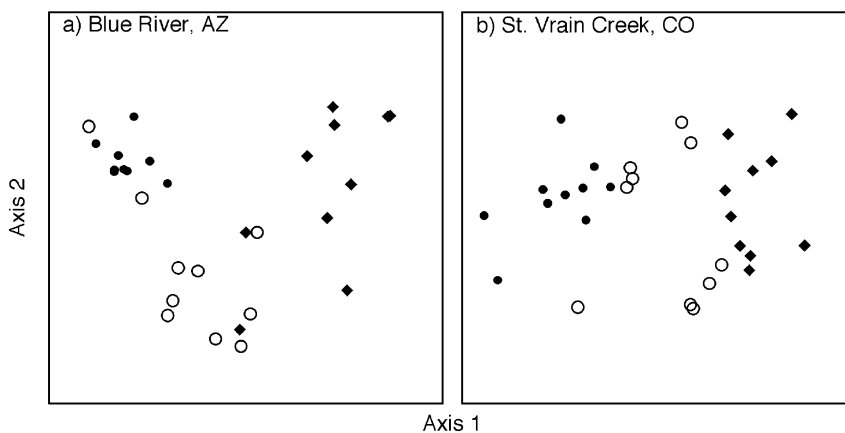
Patterns of arthropod community composition at the regional scale were similar to the individual river scale patterns. We quantified the differences between the hybridizing systems, the cross types, the rivers, and the interaction terms. Quantifiable differences were significant for all factors (Table 3), but the cross type effect was the strongest factor, or nearly so, in all analyses (all pair-wise  $P \leq 0.001$  were significant with a Bonferroni correction). The significant difference between the two hybridizing systems and cross types in the 2002 data suggests a hierarchical structure where the cross types were primarily differentiated along Axis 1 and the systems were secondarily differentiated along Axis 2 (Fig. 4a).

Because the hybridizing system and interaction terms were significant in 2002, but weaker than the cross type

**Table 2** ANOVA table for 2003 arthropod community composition by cottonwood cross type

Location	Source of variation	d.f.	SS	MS	F	P
Indian Creek, UT	Cross type	2	29417.0	14708.5	5.62	0.0002
	Residual	27	70629.2	2615.9		
	Total	29	100046.2			
San Miguel River, CO	Cross type	2	27093.6	13546.8	3.93	0.0002
	Residual	27	93111.1	3448.6		
	Total	29	120204.7			
Blue River, AZ	Cross type	2	26004.3	13002.1	6.30	0.0002
	Residual	27	55747.2	2064.7		
	Total	29	81751.4			
Rio Nambre, NM	Cross type	2	18622.9	9311.5	2.76	0.0008
	Residual	27	91203.5	3377.9		
	Total	29	109826.4			
Clear Creek, CO	Cross type	2	1.5	0.7	2.58	0.0012
	Residual	12	3.4	0.3		
	Total	14	4.8			
St. Vrain Creek, CO	Cross type	2	32415.5	16207.7	6.65	0.0002
	Residual	27	65823.0	2437.9		
	Total	29	98238.5			

*P*-values are limited by the number of permutations for the test, e.g. 9999. Within river pairwise comparisons among cross types were all significantly different with a Bonferroni correction, except between the broadleaf and  $F_1$  types in Indian Creek ( $P = 0.04$ ) and Rio Nambre ( $P = 0.48$ ), or the backcross and  $F_1$  types in Clear Creek ( $P = 0.03$ ).



**Fig. 3** 2003 arthropod ordinations of community composition by host plant cross type. Each point represents the arthropod composition on a single tree. Axes are unit-less and only serve to put points into Euclidean space relative to all other points. Points that are close are more similar than points that are further apart. 3a) is representative of rivers from the Fremont  $\times$  narrowleaf hybridizing system, and 3b) is representative of rivers from the plains  $\times$  narrowleaf hybridizing system. ● = Fremont or plains cottonwoods; ○ =  $F_1$  hybrids; and ◆ = backcross type cottonwoods. Same rivers as in Fig. 2.

factor, we randomized these components out of the analysis to further assess differences among the general cross types. When these components were randomized into five tree communities the cross type effect was still highly significant suggesting that this factor effect holds across a wide range of environments and these two hybridizing systems (all pairwise  $P \leq 0.001$  are significant with a Bonferroni correction; Table 3; Fig. 4b).

To quantify the effects of the genetic and environmental factors on arthropod composition we controlled the confounding factor of the different hybridizing systems by analysing them separately with the 2003 data (Fig. 4c–d). Even though all three terms were significant, the cross type factor

was as strong as the river factor and approximately 2x stronger than the interaction term (Table 3) for both systems.

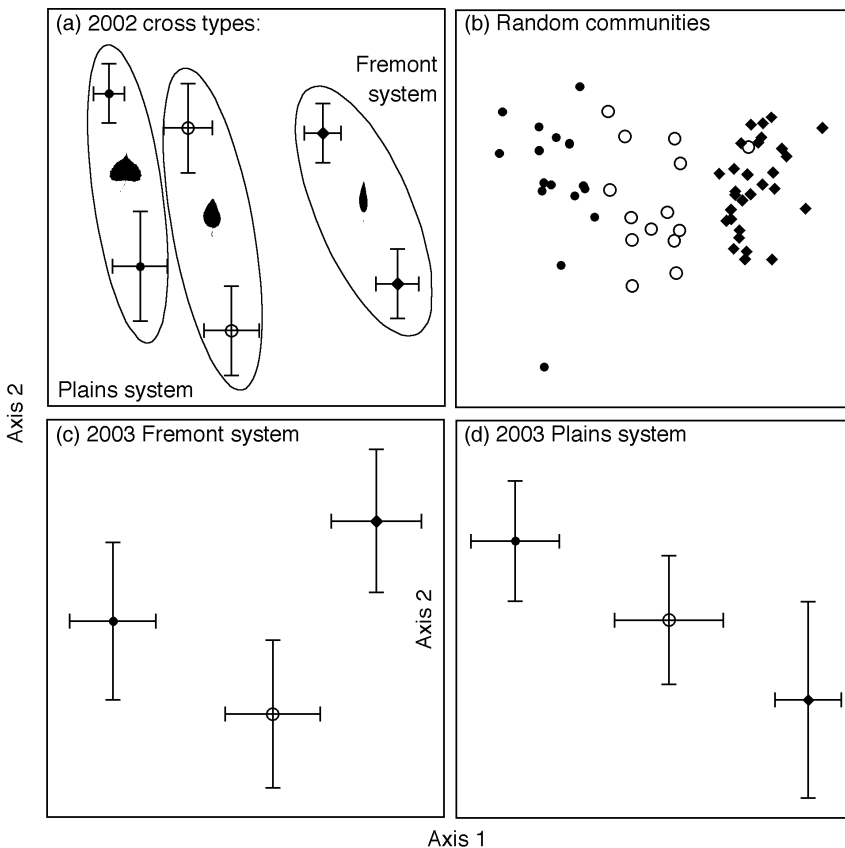
#### *Tree to regional scale patterns: arthropod community along a genetic continuum*

At the tree scale within each river, there was a significant negative relationship between host plant genetic distance and arthropod community similarity (Table 4). With an increase in genetic distance among individual trees the arthropod community was less similar in each river (Fig. 5a,b): arthropod community composition was changing with host plant genetic variation within each river across the

**Table 3** ANOVA table for geographical scale arthropod community compositions

Location	Source of variation	d.f.	SS	MS	F	P
Regional (2002)	Hybridizing System	1	6.73	6.73	32.55	0.0001
	Cross type	2	21.58	10.79	52.14	0.0001
	Cross type × System	2	2.56	1.28	6.18	0.0001
	Residual	309	63.94	0.21		
	Total	314	94.82			
Random communities (2002)	Cross type	2	6.60	3.30	20.42	0.0001
	Residual	59	9.54	0.16		
	Total	61	16.14			
Plains by narrowleaf (2003)	Cross type	2	3.97	1.98	6.86	0.0001
	River	2	2.64	1.32	4.57	0.0001
	Cross type × river	4	2.68	0.67	2.32	0.0002
	Residual	66	19.07	0.29		
	Total	74	28.27			
Fremont by narrowleaf (2003)	Cross type	2	4.34	2.17	7.45	0.0001
	River	3	6.91	2.33	7.90	0.0001
	Cross type × river	6	5.42	0.90	3.10	0.0001
	Residual	107	31.18	0.29		
	Total	118	47.93			

P-values are limited by the number of permutations for the test, e.g. 9999. The 2002 regional data set tests for differences between the two hybridizing ‘Systems’ and tree cross type. Random communities were constructed from the 2002 data to test the general effect of tree cross type while controlling for the different hybridizing system and environment. Since there was a strong hybridizing system effect on abundance for the 2002 data, these systems were analysed separately with the 2003 data and included ‘River’ as an environmental factor.



**Fig. 4** Regional scale arthropod community composition by host plant cross type. (a) 2002 ordination of the regional arthropod communities showing significant differences by general cross type (large ellipses) with a significant substructure by hybridizing system (error bars). Leaf symbols represent the general cross types with the Fremont communities in the upper portion and plains communities in the lower portion of the panel. (b) 2002 regional arthropod community with environment and hybridizing system randomized into the general cross type categories. (c) 2003 arthropod community on the Fremont × narrowleaf, and (d) plains × narrowleaf hybridizing systems. Panels a–d: ● = Fremont or plains cottonwoods; ○ = F<sub>1</sub> hybrids; and ◆ = backcross type cottonwoods. All ellipses and error bars represent 95% confidence intervals around the community centroids.



**Table 4** Mantel correlations between arthropod community composition and cottonwood AFLP composition

Location	All cross types				Hybrids only			
	<i>n</i>	<i>R</i> <sup>2</sup>	Mantel <i>t</i>	<i>P</i>	<i>n</i>	<i>R</i> <sup>2</sup>	Mantel <i>t</i>	<i>P</i>
Indian Creek, UT	30	0.1388	-8.18	< 0.0001	20	0.1240	-4.84	0.0010
San Miguel River, CO	12	0.1955	-3.52	0.0026	8	0.0957	-1.60	0.079
Blue River, AZ	29	0.2078	-8.87	< 0.0001	20	0.2927	-7.15	0.0001
Rio Nambe, NM	27	0.0755	-4.58	< 0.0001	18	0.0688	-2.91	0.008
Clear Creek, CO	13	0.0887	-2.16	0.02	8	0.1648	-1.72	0.06
St. Vrain Creek, CO	26	0.3310	-8.80	< 0.0001	16	0.0660	-2.68	0.016
Stands	10	0.3781	-2.99	0.0005	—	—	—	—
2002 Rivers	14	0.2853	9999	0.0001	<i>Fremont only</i>			
2003 Rivers	6	0.2871	9999	0.026	23	0.1852	-6.57	< 0.0001
*Region	137	0.0752	9999	< 0.0001				

*P*-values are determined from Mantel's *t*-approximation when sample size > 20 otherwise determined by 9999 randomizations. \*Corrected for spatial autocorrelation with a partial Mantel test.

region and cottonwood genetic composition significantly explained 8%–33% of the variation in community composition. This pattern is consistent with that observed by Bangert *et al.* (2006) in a common garden where environmental factors were minimized, and in the wild in the adjacent hybrid zone. The observed pattern of a significant relationship of genetic distance with arthropod community similarity was not entirely driven by the inclusion of both parental species and their hybrids. To address this, we conducted the analyses at finer scales. When the same analysis was performed only on the hybrid cross types, the relationships remained significant or nearly so (Table 4). Moreover, the relationship is significant within just the Fremont cross type (Table 4).

To address this hypothesis at larger scales, we quantified this relationship at the stand scale and found the same pattern: stands that had more similar genetic compositions had more similar arthropod communities and explained nearly 38% of the variation at this scale (Mantel  $r = -0.6149$ ;  $P < 0.001$ ; Fig. 5c).

At the river scale we conducted two analyses. First, in 2003, six rivers were analysed, where rivers with similar cottonwood AFLP genetic compositions had similar arthropod communities and explained nearly 29% of community variation at this scale (Mantel  $r = -0.5358$ ;  $P = 0.026$ ; Fig. 5d). Second, 14 hybrid zones showed significant variation in cottonwood cross type composition ( $\chi^2 = 122$ ;  $P < 0.001$ ; d.f. = 26). With cross type proportions as a surrogate for genetic composition, rivers with similar cross type proportions had similar communities when spatial autocorrelation was controlled with a partial Mantel test. This result explained nearly 29% of community variation at this scale (Mantel  $r = -0.5341$ ;  $P = 0.0003$ ; Fig. 6).

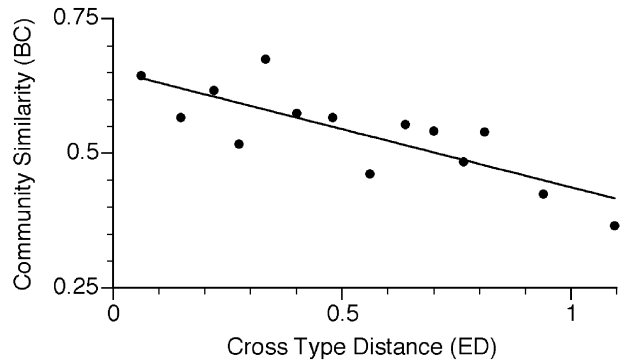
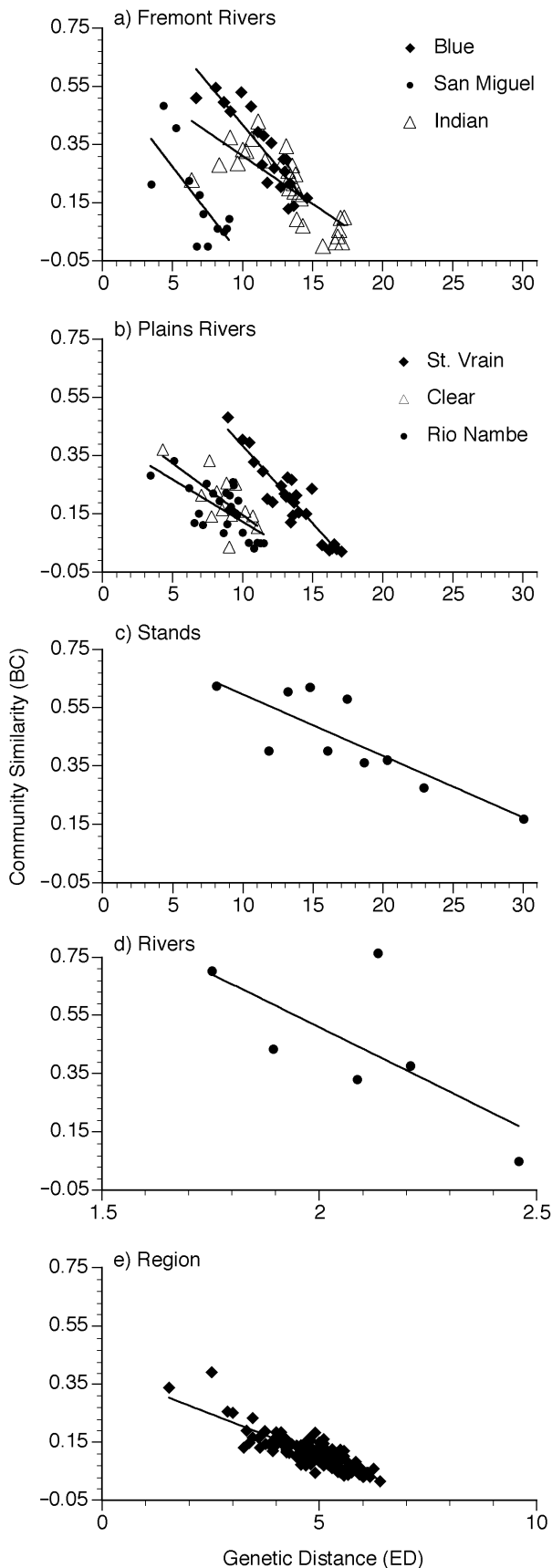
At the regional scale, we analysed 137 trees surveyed in 2003, across the extent of this study in a single analysis

to determine if this relationship was detectable at this scale. Across the regional extent, trees that had similar genetic compositions also had similar arthropod communities with 8% of community variation still explained at this scale. (Mantel  $r = -0.2742$ ,  $P = 0.0001$ ; Fig. 5e). These combined results suggest that local arthropod community patterns associated with host plant genetic composition was detectable across multiple geographical scales.

## Discussion

### *Local genetic effects scale to the region*

Our findings show that arthropod communities respond to host plant cross type and the genetic gradient associated with these cross types. The strongest and most consistent pattern of arthropod composition followed this genetic gradient at the tree, stand, and river scales, and was still detectable at the regional scale. This suggests that arthropod communities are tracking fine scale plant genetic variation and that the morphological-based plant categories represent a more coarse, but important, resolution to this relationship. Categorical analysis (i.e. by cross type) of this community is important for two reasons. First, categorical analysis is conducive to studying the geographical mosaic of community structure and suggests testable evolutionary hypotheses. For example, the cross type by river interaction (Table 3) suggests that even though the community is discriminating among the host plant cross types in each river, individual species may be responding differently among hosts in different river systems. These different responses may be due to different hybridizing dynamics of the plants, and different arthropod adaptations across the region may result in the differential evolution of interspecific interactions, resulting in a geographical mosaic (*sensu* Thompson



**Fig. 6** 2002 mean arthropod community similarity vs mean cross type composition at the river scale. Cross type composition is a surrogate for genetic composition (see Fig. 2) and exhibits a similar pattern as the AFLP compositional analysis (see Fig. 4d).

2005). However, over the regional extent of this study, the arthropod community is responding to the general cross types with a substructure based on hybridizing system. Second, since there is a genetic basis to these cross types, our studies suggest that other communities on other host plants that express morphological variation may initially be analysed without molecular data (e.g. two different hybridizing oak complexes, Boecklen & Spellenberg 1990; Aguilar & Boecklen 1992; *Chrysothamnus nauseosus* Floate *et al.* 1996), to test the correlation between community composition and phenotype variation before pursuing expensive molecular work. Figure 6 suggests that the cross type analysis results in the same conclusion as the analysis using genetic data (Fig. 5d).

*Genetic components of community composition*

Based on previous studies, we expected that regional environmental variation would swamp out community patterns because of increased environmental contingency (*sensu* Lawton 1999) at large spatial scales. The patterns that we identified at the tree scale within rivers were strong enough to be detected at the regional scale across the extent of the Four-Corner States in the southwestern USA. (720 000 km<sup>2</sup>). This is in contrast to previous work that

**Fig. 5** 2003 mean arthropod community similarity vs mean genetic distance at multiple scales. Panels (a) and (b) represent analysis at the individual tree scale within six rivers. Panel (c) represents analysis at the stand scale where both genetic and community compositions are quantified across 8 trees within each of 10 stands. Panel (d) represents mean arthropod community similarity vs mean cottonwood genetic composition at the river scale. Data at the river scale were pooled within each river in a similar manner as at the stand scale. Panel (e) represents analysis on individual trees from across the Four Corner States region in the western USA. Note that the x-axis changes with spatial scale.

suggests that, if there is a genetic effect on composition (beta diversity), it will only be detectable at small scales, and the environmental effect will mask the genetic effect at large scales because of increasing environmental variation (Menge & Olson 1990; Stiling & Rossi 1995, 1996; Huston 1999; Johnson & Agrawal 2005). The variation in community composition that was explained by host plant genetic composition at the largest scale was declining but detectable. Also, as scale increased, genetic distance among units decreased because of different levels of aggregation with scale. Moreover, genetic composition may become more homogeneous with scale, whereas environmental factors become more heterogeneous and will eventually swamp out the genetic effect. Our data agree with these findings in that the genetic component explained much less of the variance in community composition at the largest scale and this suggests that, if the extent of this study was increased, the genetic effect would disappear. Current theories on local to regional diversity relationships (Huston 1999), however, do not include local genetic effects that produce regional patterns. If the genetic factor is strong it may compete with large regional environmental variation as scale increases, as in this study. Conversely, if the variability of genetic effects does not increase as fast as environmental variation, then the environment becomes a stronger factor in organizing dependent communities, and the genetic effects on the community decline (Bangert *et al.*, in review).

Current thinking is that among cross type changes in community composition (beta diversity) will add more to regional scale community composition (gamma diversity) at small scales, while within cross type species richness (alpha diversity) becomes increasingly more important at large scales because species richness accumulates and becomes gamma diversity at the largest scale (Loreau 2000; Gering & Crist 2002). When host plant genetic variation is large, we predict that beta diversity should be important at multiple scales, while alpha diversity will still be important at larger scales as predicted (Loreau 2000; Gering & Crist 2002; Bangert *et al.* 2005). In this study we did not partition gamma diversity into alpha and beta diversity (e.g. Crist *et al.* 2003); however, in other studies in this and other systems, alpha diversity is often not statistically significant at the local scale but beta diversity can be strong at both local and regional scales, thus increasing gamma diversity (Wimp *et al.* 2004, 2005; Bangert *et al.* 2005; Bangert & Slobodchikoff 2006).

Our findings are consistent with the idea that host plant genetic composition extends beyond the host phenotype to affect other organisms that interact with cottonwood cross types. In this case we found that arthropod community structure is strongly correlated with host plant genetic composition at local and regional levels, in agreement with a genetic similarity rule (Bangert *et al.* 2006). This is

analogous to narrow sense heritability where individual trees host communities that are similar to communities on closely related trees. However, because host plant genetic variation acts as a bottom-up force, (Hunter & Price 1992) these strong emergent properties result. Dawkins (1982) promoted the idea that genes can have an extended effect beyond the individual and, more recently, Whitham *et al.* (2003) applied this concept to ecological communities. Our data support the idea that arthropod communities are keying into the genetic composition of cottonwood cross types, possibly through the chemical composition of the host (Bangert *et al.* 2006). In this sense, arthropod communities become an extension of the cottonwood genome. Given that arthropods are sensitive to host plant traits that are genetically controlled (e.g. chemistry: Dungey *et al.* 2000; Osier & Lindroth 2001; resistance: Moran & Whitham 1990; Mopper *et al.* 1991; leaf shape: Floate & Whitham 1995; this paper), it is perhaps not surprising that they would closely track genetic composition via these traits (e.g. Bangert *et al.* 2006). Other studies of cottonwood genetic diversity also support this idea, finding that 13 different species of herbivores and predators tracked genetic differences across cottonwood cross types (Wimp *et al.* 2005) and were reliable indicator species of the cross types (Bangert *et al.* 2005; Wimp *et al.* 2005).

## Conclusions

Our study addresses two points that are key issues in community ecology. First, by incorporating a community genetics approach (Whitham *et al.* 2003), we find that the genetic variation generated by interspecific hybridization is an important factor responsible for organizing arthropod communities. Shuster *et al.* (2006) used quantitative genetic methods to propose a model that these patterns are not simply the aggregate result of single species population dynamics. They suggest that community-level patterns are the result of interactions among community members including interactions with the host plant, resulting in changes in community-level gene frequencies (*sensu* Wilson 1997). Thus, the community level patterns identified here are potentially more than the sum of individual responses and not driven by a single abundant species (e.g. Bangert *et al.* 2006). This results in strong patterns that hold over a wide range of spatial scales. Second, the arthropod communities we studied show high levels of beta diversity (i.e. compositional change along a genetic gradient), where previous studies generally find community diversity correlated with environmental gradients (e.g. Veech *et al.* 2002; Johnson & Agrawal 2005).

Natural hybridization and genetic variability are important and common in plants (e.g. Stace 1987; Smith & Sytsma 1990); therefore, the effects of plant genetic variation on many ecological processes may be as important as plant

species diversity. The work in the cottonwood system involving mammalian and insect herbivory also show that the effects of cottonwood genes extend beyond the cottonwood individual and population to influence external ecological processes (e.g. Martinsen *et al.* 2000; Wimp & Whitham 2001; Whitham *et al.* 2003; Wimp *et al.* 2004, 2005). The results of other studies suggest that this is not merely phenomenological, but may be common in other diverse systems when viewed in this context (e.g. Boecklen & Spellenberg 1990; Aguilar & Boecklen 1992; Floate *et al.* 1996; Hochwender & Fritz 2004). If a genetic similarity rule is a general concept then studies of community ecology may benefit from the incorporation of genetics into community concepts, eventually taking a perspective of evolution by natural selection to higher levels of biological organization (e.g. Wilson 1992, 1997; Johnson & Boerlijst 2002).

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This work was the result of a large collaboration that collectively is interested in the genetic effects of a dominant plant on phytochemistry and dependent animal community members. R. K. Bangert, G. M. Wimp, and T. G. Whitham are concerned with arthropods and community analyses. G. J. Allan, N. Meneses, G. D. Martinsen, and P. Keim investigate genetic structure in cottonwood hybrid zones. R. J. Turek studies the theoretical applications of nonparametric approaches to ecological studies.

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