A genetic similarity rule determines arthropod community structure

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Abstract

We define a genetic similarity rule that predicts how genetic variation in a dominant plant affects the structure of an arthropod community. This rule applies to hybridizing cottonwood species where plant genetic variation determines plant–animal interactions and structures a dependent community of leaf-modifying arthropods. Because the associated arthropod community is expected to respond to important plant traits, we also tested whether plant chemical composition is one potential intermediate link between plant genes and arthropod community composition. Two lines of evidence support our genetic similarity rule. First, in a common garden experiment we found that trees with similar genetic compositions had similar chemical compositions and similar arthropod compositions. Second, in a wild population, we found a similar relationship between genetic similarity in cottonwoods and the dependent arthropod community. Field data demonstrate that the relationship between genes and arthropods was also significant when the hybrids were analysed alone, i.e. the pattern is not dependent upon the inclusion of both parental species. Because plant–animal interactions and natural hybridization are common to diverse plant taxa, we suggest that a genetic similarity rule is potentially applicable, and may be extended, to other systems and ecological processes. For example, plants with similar genetic compositions may exhibit similar litter decomposition rates. A corollary to this genetic similarity rule predicts that in systems with low plant genetic variability, the environment will be a stronger factor structuring the dependent community. Our findings argue that the genetic composition of a dominant plant can structure higher order ecological processes, thus placing community and ecosystem ecology within a genetic and evolutionary framework. A genetic similarity rule also has important conservation implications because the loss of genetic diversity in one species, especially dominant or keystone species that define many communities, may cascade to negatively affect the rest of the dependent community.

Keywords: arthropod community composition, assembly rules, chemical composition, genetic composition, *Populus*, similarity rule

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Introduction

The assembly of communities has been a topic of considerable theoretical interest in community ecology (e.g. Gleason 1926; Clements 1936; MacArthur 1958; Cole 1983; Weiher & Keddy 1999a). One attempt to understand community assembly involves the formulation of assembly rules, which aim to identify the underlying ecological mechanisms that structure communities

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(e.g. Diamond 1975; Fox & Brown 1993; Weiher & Keddy 1999b). One example is Fox's rule that suggests that different guilds of small desert rodents will all be represented equally in a community before another species is added. Although the assembly rule approach has been subject to contentious debate (e.g. Strong *et al.* 1984; Wilson 1995; Kelt & Brown 1999; Simberloff *et al.* 1999; Stone *et al.* 2000; Brown *et al.* 2002), it is a useful heuristic for understanding community patterns (Belyea & Lancaster 1999; Booth & Larson 1999; Kelt & Brown 1999; Weiher & Keddy 1999a; Temperton *et al.* 2004).

Historically, two definitions have been used in the study of assembly rules. The first defines assembly as the fitting together of parts and thus, the assembly process includes assembly history and trajectory. These types of assemblages have then been manipulated and modelled (Robinson & Dickerson 1987; Drake 1990, 1991; Drake *et al.* 1993, 1999; Luh & Pimm 1993; Hraber & Milne 1997; Lockwood *et al.* 1997; Price & Morin 2004). The second definition refers to a collection of parts where a specific mechanism (e.g. competition) has been hypothesized to structure the assemblage (Fox & Brown 1993; Booth & Larson 1999; Fox 1999; Kelt & Brown 1999; Weiher & Keddy 1999b).

More recently, Knapp *et al.* (2004) have suggested that general ecological rules are useful and ecology would benefit from a rule-driven approach. For example, a simple ecological rule might state that grazing in mesic grasslands counters the effects of fire on plant community diversity. This rule is predictive and can be tested in other grasslands, and when the rule is broken, alternative hypotheses can be tested (Knapp *et al.* 2004). A remaining challenge is to develop formal ecological rules that will increase our ability to predict the assembly of ecological communities (Lawton 1999; Weiher & Keddy 1999a; Knapp *et al.* 2004). In this study, we take a genetic-based assembly rule approach. In this case, the collection of parts consists of a leaf-modifying arthropod guild, where host plant genetic and chemical compositions define a rule for determining how arthropod communities become structured in cottonwood hybrid zones. We refer to this rule as a genetic similarity rule.

Ecological assembly rules have had various degrees of success in predicting community structure, often revealing 'only tendencies' (Wilson 1999). Many assembly mechanics are internal to the community (e.g. competition and predation); thus the order of species addition and rate (e.g. history) are important and prediction of these assemblages has been difficult (Drake 1991; Drake *et al.* 1993; Kelt 1999). Consequently, the assembly process can appear chaotic and idiosyncratic. However, because genes are the products of long-term natural selection and evolution, a genetically based community assembly rule may improve predictability, compared to rules that rely upon ecological associations

that may fluctuate from year to year. A genetic-based approach is especially pertinent because it can facilitate the inclusion of evolutionary processes (e.g. natural selection) into community and ecosystem ecology (Schweitzer *et al.* 2004, 2005; Wimp *et al.* 2004, 2005). Although earlier studies have demonstrated a relationship between arthropod community structure and host plant genetic variation (e.g. Fritz & Price 1988; Maddox & Root 1990; Aguilar & Boecklen 1992; Dungey *et al.* 2000; Wimp *et al.* 2005), none have addressed chemical and community composition simultaneously in the context of a genetic similarity rule. Such a rule has the potential to increase our ability to predict community structure through the intermediate steps of gene products (i.e. plant chemistry), which provide a mechanistic basis for understanding community structure.

Here, we develop a genetic similarity rule based on the genetic structure of a naturally hybridizing plant complex, which exhibits significant genetic variation, gene flow, and heritable plant traits, many of which are important to the dependent community. We specifically focus on the relationship between hybridizing cottonwood tree species (*Populus*: Salicaceae), their hybrid derivatives, and the associated leaf-modifying arthropod community. Two species of cottonwoods, *Populus fremontii* (Fremont cottonwood) and *Populus angustifolia* (narrowleaf cottonwood) naturally hybridize and exhibit unidirectional introgression of Fremont genes into the narrowleaf genome (Keim *et al.* 1989; Whitham *et al.* 1999; Martinsen *et al.* 2001). Because these trees are dominants of a major riparian vegetation type, the genetic variation in these species is likely to have important community and ecosystem consequences (Whitham *et al.* 2003). Furthermore, as natural hybridization is found in diverse taxa worldwide and is thought to represent a major pathway in plant evolution (e.g. Stace 1987; Smith & Sytsma 1990; Rieseberg *et al.* 1996), studies of these dynamic systems may be especially revealing of the evolutionary processes for both the plant and their dependent communities. This genetic similarity rule does not invoke internal community dynamics or historical influences on community structure (e.g. competition or species addition-sequence as sources of contingency; *sensu* Lawton 1999), but rather relies on plant genetic composition to predict arthropod community composition.

The rule we propose states 'the genetic composition of a plant will influence the community structure of the dependent community.' We do not consider the assembly process, but rather final community composition because our work suggests that the contingencies of internal community dynamics, such as competition and predation, and environmental variation play a less important role relative to cottonwood genetics in structuring this arthropod community (Bangert 2004; Bangert *et al.* 2005).

The theoretical basis of this genetic similarity rule starts with the F_1 hybrid generation. Although F_1 individuals are

unique because they combine the genomes of two species, an F_1 individual can be genetically similar to either of the parental types depending upon the allelic contribution of each parent, and this may have ecological implications for the dependent community. For example, if an F_1 hybrid possesses a large proportion of ecologically important alleles (e.g. alleles for tannin production or chemical oviposition cues) from one parent, it should support an arthropod community that is similar to that parental type. Consequently, the community associated with F_1 individuals may resemble either parental type or be unique. We can then extend this aspect of the rule to include the parental species and hybrid cross types where: if a particular cross type is sampled, then we would expect a particular community phenotype. Along a genetic continuum among individual trees, another formulation of this rule would state: if individual plants are genetically similar, then they will support similar arthropod communities. We also expect that the arthropod community will respond to ecologically important products of genes (e.g. phytochemical composition; Martinsen *et al*. 1998; Driebe & Whitham 2000; Rehill *et al*. 2005) rather than directly to genetic composition. Thus, we hypothesize that plant chemistry is one potentially important mechanism that can mediate the relationship between genes and arthropod communities (Abrahamson *et al*. 2003; Fig. 1).

In this study, we take a multivariate approach in a common garden environment and consider the change in genetic composition among cottonwood cross types as a complement to studies that consider univariate measures of genes, chemistry, or community alpha diversity. This approach is informative because it incorporates all factors, and factor levels, simultaneously along with their interactions because these factors do not interact in a vacuum (Thompson 1994). Therefore, we may gain a more realistic perspective of the system under investigation and suggest areas for more detailed experimental studies (e.g. Doney *et al*. 2004; Knapp *et al*. 2004). We also compare the

community structure of an assemblage of arthropods, to the genetic composition of hybrid trees growing wild to assess the generality of the genetic similarity rule. We explicitly test four predictions: (i) genetic, chemical, and arthropod compositions are different among plant cross types (i.e. Fremont, F_1, backcross, and narrowleaf); (ii) plants with similar genetic compositions will have similar chemical and arthropod compositions; (iii) if chemistry is a significant mechanism (not implied to be the only mechanism) then we expect the strength of the relationship between genes and chemistry will be greater than that between chemistry and arthropods, which in turn will be greater than that between genes and arthropods (Fig. 1); and (iv) arthropod community structure changes as Fremont genes introgress into the narrowleaf genome. Testing these predictions is fundamental to the development of a genetically based community assembly rule and will allow us to progress to even finer levels of predicting community structure and composition based on the genetic variation of ecologically important traits.

Materials and methods

Cottonwood system

Cottonwood trees are dominant species in many river systems in the western USA. Most rivers have two species, each in a different section of the genus *Populus* that naturally hybridize in a contact zone between the two parental species. Fremont cottonwood occupies the lower reaches of rivers, whereas narrowleaf cottonwood is found in the upper reaches (Eckenwalder 1984). Along the Weber River, Utah (and many other rivers across the western USA), narrowleaf cottonwood (*Populus angustifolia* James, sect. *Tacamahaca*) commonly hybridizes with Fremont cottonwood (*Populus fremontii* Watson, sect. *Aigeiros*) in an overlap zone, and exhibits unidirectional introgression whereby the F_1 generation only backcrosses with the narrowleaf parent. Subsequent backcrossing occurs only with narrowleaf cottonwoods resulting in a hybrid complex (Keim *et al*. 1989; Martinsen *et al*. 2001) comprising a continuum of genotypes from F_1 hybrids to narrowleaf cottonwoods. Because of the lack of backcrossing to the Fremont parent, there is a characteristic morphological gap between F_1 hybrids and Fremont cottonwood (Floate & Whitham 1993). Individual trees represent distinct genotypes and we use the term cross type to represent a genotypic class, e.g. F_1 hybrids collectively. Thus, there are four categories of cross types that can occur sympatrically: pure Fremont, F_1 hybrids, advanced backcross hybrids with narrowleaf, and pure narrowleaf cottonwood (Wimp *et al*. 2005). This hybrid complex provides a model system for the study of the genetic effect on community structure mediated by plant chemistry.
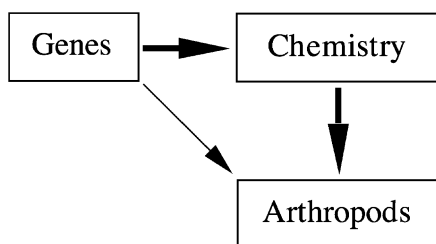

Fig. 1 A priori model of the relationship between genetic, chemical, and arthropod community structures suggests that arthropod community structure is determined by plant genetic composition via chemical composition of the plant. Bold arrows represent stronger relationships than thin arrows between factors and the arthropod community.

Cottonwood genetics and chemistry

All data were generated from tree genotypes planted randomly in an 11-year-old common garden in Ogden, Utah, USA. Trees were propagated from cuttings taken from wild-growing Fremont, F_1 hybrids, a range of backcross hybrids, and pure narrowleaf along the Weber River in Ogden, Utah. We studied the effects of plant genotype and introgression on phytochemical composition and arthropod community structure on 29 different genotypes (5 Fremont, 7 F_1 hybrid, 7 backcross hybrid, and 10 narrowleaf cottonwoods). Each tree was genotyped and their pure or hybrid status was confirmed with 35 species-specific, restriction fragment length polymophisms (RFLP; Martinsen *et al.* 2001). Although these are anonymous markers and do not represent genes that code for the secondary metabolites in this study, these markers do allow us to quantify the genetic distance among individuals. We calculated the genetic Euclidean distance between each genotype (e.g. Excoffier *et al.* 1992) in order to quantify the relationship between individual tree genetic, chemical, and arthropod compositions.

The aggregate composition of four ecologically important chemical species (nitrogen, salicortin, HCH-salicortin, and condensed tannins) was quantified on the common garden genotypes in 2001 and a subset of the trees in 2002. Nitrogen is often of critical importance to herbivores (Mattson 1980; White 1984). Condensed tannins and phenolic glycosides (salicortin and HCH-salicortin) are major secondary metabolites and have been shown to influence herbivore performance in the genus *Populus* (Palo 1984; Hemming & Lindroth 1995; Lindroth & Hwang 1996; Hwang & Lindroth 1997; Osier *et al.* 2000). Preliminary work indicated that salicortin and HCH-salicortin (hydroxy-cyclohexen-on-oyl-salicortin; Picard *et al.* 1994; R. Julkunnen-Tiitto, personal communication) were the major phenolic glycosides in this system (Rehill *et al.*, 2005). Chemical composition is genetically determined and was consistent between 2001 and 2002 (nitrogen: $R^2 = 0.4000$; condensed tannin: $R^2 = 0.9281$; salicortin: $R^2 = 0.9037$; HCH-salicortin: $R^2 = 0.9099$; composition: Mantel $r = 0.7964$, $t = 7.00$, $P < 0.0001$). The 2001 foliar concentrations (% dry weight), of each of these four chemicals on each tree, were used to calculate the chemical compositional Euclidean distance between individual trees for use in the Mantel procedure.

Leaves were sampled from trees on three occasions (21–24 May, 20–23 June, and 14–18 August 2001), and the means of the three sample periods of chemical percent dry weight, were used in our data analysis (Osier *et al.* 2000). These dates approximately encompass the time span of arthropod oviposition, larval development, and eclosion. Each sample consisted of 15–25 leaves and each leaf was removed by cutting at the lamina–petiole junction, including

the fifth or middle leaf from the current year's growth to standardize leaf age. All leaf samples were immediately frozen between blocks of dry ice and kept frozen until storage at –20 °C. Leaves were lyophilized and ground to pass a 40-mesh screen on a Wiley Mill. Nitrogen was measured using an elemental analyser (LECO); glycine *p*-toluenesulphonate served as the reference standard. After an exhaustive extraction of leaf tissue in 70% acetone with 1 mM ascorbate at 4 °C, condensed tannins were determined with the acid butanol assay (Porter *et al.* 1986) using tannins prepared from narrowleaf cottonwood as the standard (Hagerman & Butler 1980; Waterman & Mole 1994). Phenolic glycoside concentrations were quantified by high performance thin layer chromatography as described by Lindroth *et al.* (1993), and salicortin and HCH-salicortin were purified from cottonwood leaves by a modification of the methods of Lindroth *et al.* (1987) and used as standards.

Arthropod community

Common garden trees. We collected abundance data in 2002 for 16 leaf-modifying arthropods on the common garden genotypes. This community interacts directly with leaf tissue and is likely to be most sensitive to the underlying genetic and chemical structure of the plant (Price *et al.* 1987; Dreger-Jauffret & Shorthouse 1992; Mani 1992; Abrahamson *et al.* 2003). This group is composed of leaf-gallers, -tiers, -rollers, -folders, and -miners. These arthropods leave distinctive species-specific structures that allow quantification whether the organism is present or not (Price *et al.* 1987; Floate & Whitham 1993). Most of the animals in this study have been identified to species in previous community surveys (Floate & Whitham 1995; Wimp & Whitham 2001; Wimp *et al.* 2005) and are maintained in a reference collection in the Colorado Plateau Museum of Arthropod Biodiversity at Northern Arizona University. Because some members of this community are known to affect the richness and abundance of diverse taxa including birds, arthropods and fungi (e.g. Dickson & Whitham 1996; Martinsen *et al.* 2000; Bailey & Whitham 2003), they can be considered important or keystone species that affect a much larger community. We surveyed approximately 45 shoots per tree (average 320 leaves) from approximately 6–8 m high in the canopy during the last week of August 2002 after leaf structures had matured, but before leaf abscission occurred (e.g. Floate & Whitham 1993). When replicates of a genotype were surveyed, the mean community associated with that genotype was used.

Observational field trees. To increase the generality of this genetic similarity rule and to constrain our results to hybrid individuals, we re-analysed a subset of trees from Wimp *et al.* (2004). The genetic composition of F_1 and backcross hybrids was quantified using amplified

fragment length polymorphism (AFLP; Vos *et al.* 1995) data that yielded 48 polymorphic loci across three different primer combinations from 25 trees growing wild along the Weber River hybrid zone (14 F_1 hybrids and 11 backcross hybrids). Additionally, we collected abundance data for the entire arthropod community composed of 101 species including herbivores, predators, and leaf modifiers on the same 25 hybrid genotypes with visual surveys conducted several times over the course of the season (Wimp *et al.* 2004; see Wimp *et al.* 2005 for methods).

Data analysis

Composition. Since we were interested in the relationship between genetic, chemical, and community compositions, we adopted the approach of correlating the compositional matrices throughout the study and we treated the chemical and genetic compositional matrices as 'communities' of chemicals and genetic markers (Legendre & Legendre 1998; Dungey *et al.* 2000). First, we analysed genetic, chemical, and community composition by cross type. Multivariate Euclidean distance matrices were constructed for each of the predictor variables, genes and chemistry. Euclidean distance measures the genetic or chemical compositional distance between two individual trees in multidimensional space by the standard formulae:

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

where, y_{1j} represents individual 1 and marker (or chemical) j, and y_{2j} represents individual 2 and marker (or chemical *j*) summed over all pairwise comparisons (Excoffier *et al.* 1992; Legendre & Legendre 1998; Peakall *et al.* 2003) resulting in trees that are more closely related to have low *ED*. A similarity matrix was constructed for the response variable (arthropod community) between each pair of trees utilizing the Bray–Curtis coefficient because Euclidean distance is not an appropriate metric for community data (Legendre & Legendre 1998):

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

where, *W* is the sum of the minimum abundances between sample *A* and *B*, divided by the total abundance of arthropods on the two trees (Faith *et al.* 1987; Legendre & Legendre 1998; Dungey *et al.* 2000). Thus, the Bray–Curtis coefficient scales between 0 and 1 and measures the proportion similarity between two samples where 1 = perfect similarity. The compositional matrices were quantified with a nonparametric ordination procedure that utilizes the ranks of the similarities (nonmetric multidimensional scaling, NMDS; Kruskal 1964; Faith *et al.* 1987; Minchin 1987; Legendre & Legendre 1998) and places the multi-variate data into two dimensions. Analysis of similarity

(ANOSIM) was used to quantify differences among cross types and is analogous to an *F*-test where distances or similarities within groups are compared to between group differences. ANOSIM *r* values measure the strength of these differences and scale between –1 and 1. Subsequent *P* values were determined through a randomization procedure (Clarke 1993; Manly 1997; Legendre & Legendre 1998; Anderson 2001; Clarke & Warwick 2001). These procedures have been successfully used for the analyses of chemical and community composition in both plant and animal studies (e.g. Dungey *et al.* 2000; Foster & Tilman 2000; Wimp *et al.* 2005). Finally, we regressed the arthropod community matrix against each of the four chemical species and the proportion of Fremont markers in the common garden trees with a nonparametric linear regression (Anderson 2001) to test the hypotheses that community composition changes both with concentrations of chemicals and the introgression of Fremont genes into the narrowleaf genome. We used the ordination scores to graphically present the relationships among factors (see Clarke & Warwick 2001 and Abrahamson *et al.* 2003 for a similar use of this procedure).

Mantel correlations. In order to evaluate the compositional relationship between genes, chemistry, and arthropods, we conducted Mantel and partial Mantel tests on the similarity and distance matrices among the three factors (Legendre 1993; Legendre & Legendre 1998). The arthropod and chemical data were natural log transformed prior to the calculation of the matrices to improve linearity. In these Mantel tests the Mantel's *t* approximation and associated *P* value were used to evaluate the strength of these relationships (Fortin & Gurevitch 1993; Casgrain & Legendre 2001). To further evaluate the model that tree chemical composition is a potential mechanistic link between genetic and arthropod compositions, partial Mantel tests were used (analogous to partial correlations; Legendre & Fortin 1989; Fortin & Gurevitch 1993; Legendre 1993; Manly 1997; Legendre & Legendre 1998; Casgrain & Legendre 2001; Vellend 2004). For the observational field data, we performed a Mantel test between the arthropod community and the AFLP genetic matrices utilizing only the hybrid trees, which eliminated the pure parental species from the analysis. This more restrictive analysis allowed us to determine if the genetic and arthropod variation within the hybrids alone was sufficient to exhibit significant relationships.

Results

Genetic, chemical and arthropod compositions are different among plant cross types

Our studies support our first prediction that genetic, chemical, and arthropod compositions are different among

Table 1 Analysis of similarity (ANOSIM) r values and associated P values reveal that genetic, chemical and arthropod community compositions by cross type exhibit similar patterns in the common garden

	Fremont		F$_1$		Backcross	
	r	P	r	P	r	P
Genes: Euclidean distance						
F$_1$	0.945	0.001	—	—	—	—
Backcross	1.000	< 0.001	0.816	0.001	—	—
Narrowleaf	1.000	0.001	0.998	< 0.001	0.411	< 0.001
Overall ANOSIM	0.811	< 0.001				
Chemistry: Euclidean distance						
F$_1$	0.878	0.001	—	—		
Backcross	0.679	0.003	0.658	0.001	—	—
Narrowleaf	0.589	< 0.001	0.374	0.005	−0.016	0.46
Overall ANOSIM	0.412	< 0.001				
Arthropods: Bray–Curtis similarity						
F$_1$	0.559	0.003	—	—	—	—
Backcross	0.730	0.001	0.466	0.001	—	—
Narrowleaf	0.871	< 0.001	0.607	< 0.001	−0.023	0.54
Overall ANOSIM	0.491	< 0.001				

All groups are different except for the backcross and narrowleaf cross types, which form a single group for chemical and arthropod compositions. The difference between backcross and narrowleaf genetic composition is due to large variance in the backcross group. Larger values of r indicate small mean within-group ranks relative to mean between-group ranks, analogous to an F-test.
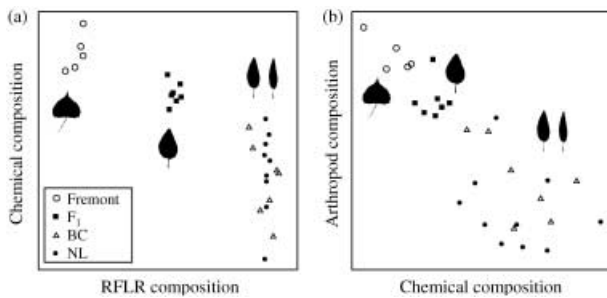

Fig. 2 Ordination scores from the NMDS procedure represent cottonwood genetic, chemical, and arthropod compositions on the common garden trees. All three factors exhibit similar patterns by cross type. Compositions of the F$_1$ cross types are intermediate between the Fremont and narrowleaf cross types and the backcross and narrowleaf cross types are most similar. These patterns are expected in any unidirectional hybridizing complex. Each point represents the composition of a single individual tree, where points close in ordination space are more compositionally similar than points that are distant, thus axes are unit-less. Panel (a) shows that chemical composition is correlated with genetic composition, and panel (b) shows that arthropod composition is correlated with chemical composition.

plant cross types (Table 1; Fig. 2a). In the common garden trees, the backcrosses exhibited the greatest dispersion as expected (dispersion: $P = 0.01$, Anderson 2001), which is likely due to recombination of the two parental genomes in this cross type (after Rieseberg & Ellstrand 1993). Although parental genomes recombine, with each unidirectional

backcross event the Fremont genome is progressively diminished and becomes more similar to the narrowleaf genome (*sensu* Rieseberg & Ellstrand 1993; Martinsen *et al.* 2001). There were also significant genetic differences between F$_1$ and backcrosses in the field trees (ANOSIM; $r = 0.5233$, $P < 0.0001$).

The patterns of chemical composition were similar to the above findings of genetic composition. The backcross and narrowleaf cross types did not differ significantly in their overall chemical composition and they form a single group. The chemical composition of the F$_1$ group is intermediate between the other two groups and there were significant differences in chemical composition among these three groups (Table 1; Fig. 2a, b). Additionally, univariate analysis suggests that F$_1$ arthropod community structure was significantly correlated with HCH-salicortin ($R^2 = 0.1827$; $F_{1,27} = 6.03$; $P = 0.0003$). Similarly, backcross/narrowleaf arthropod community structure was significantly correlated with condensed tannins ($R^2 = 0.2479$; $F_{1,27} = 8.90$; $P = 0.0001$).

Arthropod community composition was significantly different at the cross-type level. Arthropod community composition on the common garden trees was different among Fremont, F$_1$ hybrids, and backcross/narrowleaf cross types, exhibiting patterns similar to the genetic and chemical compositional patterns (Table 1; Fig. 2b).

If genes control tree chemistry and arthropod community structure, then compositional patterns for all three factors (genetic, chemical, and arthropod composition) should be similar at the cross type level. In other words,

Table 2 Mantel and partial Mantel *r* values for the relationships between the genetic, chemical, and arthropod compositions (after Legendre 1993)

	Genes	Chemistry	Arthropods
Genes	—	0.631***	−0.411***
Chemistry	0.539***	—	−0.505***
Arthropods	−0.137 NS	−0.348***	—

Mantel *r* values are reported in the upper right triangle. Partial Mantel *r* values are in the lower left triangle of the table where correlations between variables are reported when the third factor is held constant. *P* values associated with the Mantel tests are based on Mantel's asymptotic *t*. *P* values for the partial Mantel tests are based on 9999 randomizations (***$P < 0.001$; NS, nonsignificant). Arthropod and chemistry data were LN transformed, prior to the calculation of their distance matrices, to improve linearity. RFLP genetic data were not transformed.

Fig. 3 On average, arthropod communities become less similar as plant genetic distance increases (i.e. small genetic distance indicates more closely related trees). Genetic distances of the common garden trees (solid circles) were based on RFLP markers. The genetic distances of the naturally growing trees in the wild (open triangles) were based on AFLP marker data and only include the F_1 and backcross hybrids, thus removing the leverage of the two pure parental species from the analysis.

genetic variation among cross types should be associated with a similar pattern of phytochemical variation and a similar pattern of arthropod community variation among cross types. For all three factors, the backcross/narrowleaf were not significantly different in composition (Table 1). Moreover, the Fremont and backcross/narrowleaf arthropod communities do not overlap, and both significantly differ from the F_1 cross type community. Importantly, the community associated with the F_1 cross type is intermediate between the two parentals, i.e. the F_1 community does not lie outside of the parentals. This pattern argues that the community response may be either additive or dominant to Fremont cottonwood (*sensu* Hochwender & Fritz 2004; R. K. Bangert, unpublished). Community composition was also significantly different between the F_1 and backcross hybrids for the entire arthropod community on the observational trees growing in the wild (ANOSIM; $r = 0.3867$, $P < 0.001$).

These three factors exhibit similar patterns based on cross type, where the F_1's are intermediate between the two parental species and the backcrosses and narrowleaf form a single group. In general, the genetic composition shows the strongest differences among cross types, followed by chemical composition, with the arthropod community exhibiting the smallest differences among cross types (Table 1). This pattern is expected if host-plant chemistry is one potential intermediate link between plant genetic composition and arthropod community composition. In summary, we show that at the cross-type level, genetic, chemical, and arthropod compositions all exhibit similar patterns of differentiation.

Similar genetic, chemical, and arthropod compositions

Our second prediction that plants with similar genetic compositions will have similar chemical and arthropod
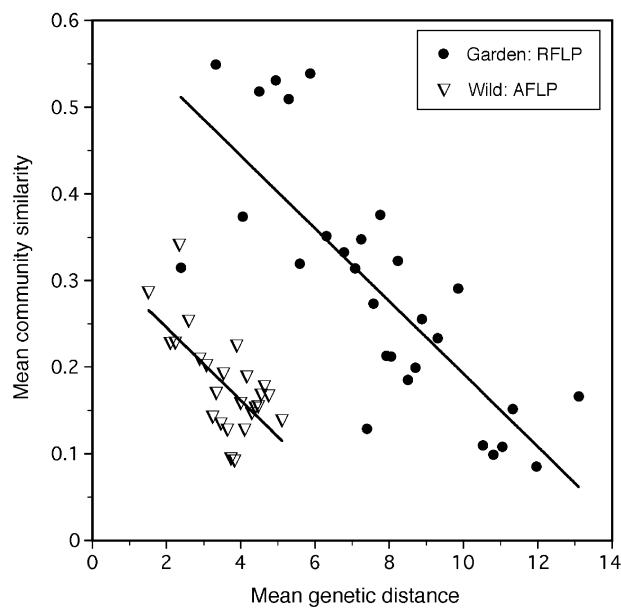
compositions was supported in both the common garden and studies on trees growing naturally in the wild. In the common garden, there were strong relationships between genetic, chemical, and arthropod compositions (Fig. 2). However, the strongest relationship was between genetic and chemical compositions and the weakest, but still significant relationship, was between genetic and arthropod compositions, with the chemical and arthropod relationship intermediate (Mantel *r* values in upper right triangle of Table 2). This pattern is consistent with the model (Maruyama 1997) that arthropods respond to plant genetic composition via plant chemical composition (Fig. 1), although further experimental work needs to confirm causation.

Similarly, in our studies in the wild, using only hybrid trees (i.e. no pure Fremont or pure narrowleaf trees included in the analyses), we obtained the same basic pattern with a much larger arthropod community (i.e. 101 species including herbivores, predators, parasitoids, and leaf modifiers). Using AFLP molecular markers, open triangles in Fig. 3 show that trees with similar genetic compositions also had similar arthropod compositions (Mantel $r = -0.3166$; Mantel $t = -4.21$; $P < 0.0001$; Fig. 3). Thus, with two independent data sets and two different genetic marker systems (i.e. RFLP and AFLP), the same patterns emerged (Fig. 3). Although the slopes of the relationship are similar, the

intercepts are different because the pure parentals were not used in the analysis of the field trees.

These studies also allow us to reject the hypothesis that the pattern of arthropod community similarity is driven by the inclusion of different plant species. Because the above studies utilized only hybrid trees, the highly significant relationship between genetic distance of trees and arthropod community similarity confirms that this relationship is not dependent upon the inclusion of different tree species in the analysis. Future studies need to study these relationships at even finer levels of plant genetic variation.

Chemistry as a potential intermediate link

The garden data are strongly consistent and further support our third prediction (*sensu* Legendre 1993; Maruyama 1997) of a genetic similarity rule with phytochemistry as one potential mechanism mediating the relationship between plant genes and the arthropod community (Fig. 1; lower left triangle of Table 2). Chemical composition is still strongly correlated with genetic composition when arthropod composition is controlled, and arthropod composition is strongly correlated with chemical composition when genetic composition is controlled. However, when chemical composition is held constant, there was no longer a significant relationship between arthropod and genetic composition. This pattern is consistent with the causative model, that at the community level arthropods are responding to plant genetics via plant chemistry (values in lower left triangle, Table 2; after Legendre 1993; Maruyama 1997). Again, further experimental work is needed to demonstrate causation.

Fremont introgression

Our fourth prediction, that introgression affects the structure of the dependent community was also supported. Leaf-modifying arthropod community structure on the garden trees changed along the genetic continuum as Fremont genes introgress into the narrowleaf genome ($R^2 = 0.3224$; $F_{1,27} = 12.85$, $P < 0.00$; Fig. 4). This result further supports our genetic similarity rule and argues that introgression between these two species strongly influences the composition and structure of dependent arthropod communities.

Discussion

A plant genetic similarity rule predicts chemical and arthropod community structure

Our general hypothesis is that plant genetic composition influences arthropod community structure (Maddox & Root 1990; Whitham *et al.* 1999; Dungey *et al.* 2000;
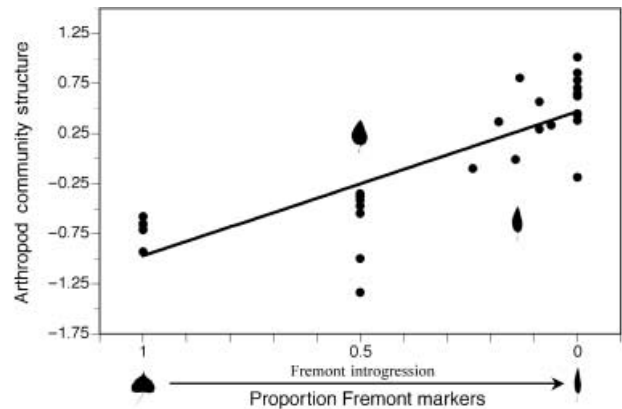
Fig. 4 Arthropod community structure changes with the introgression of Fremont RFLP markers into the narrowleaf genome. The ordinate axis represents arthropod community structure based on the ordination scores from the NMDS procedure (after Clarke & Warwick 2001).

Hochwender & Fritz 2004; Wimp *et al.* 2004, 2005), thus placing community ecology into a genetic and evolutionary-based framework (Whitham *et al.* 2003). For example, selective pressures on particular plant genotypes have the potential to exert selective pressures on the dependent community.

Our data support a genetic similarity rule in several ways. Similar genotypes have similar chemistries and arthropod communities. Genetic variation within the hybrid complex is sufficient to explain the relationship between genes and arthropod compositions and these patterns were not exclusively driven by the pure parental species. The leaf-modifying guild and the full arthropod community (e.g. Wimp *et al.* 2005) support this similarity rule. And, these patterns are found in both common garden and wild settings.

Our findings are different from those derived from other assembly rule studies in that we adopt a broad approach that encompasses genetic, chemical, and arthropod compositions and their combined interactions. We also consider phytochemistry as one likely mechanism that structures the dependent community. This is important because if ecological rules can be defined, then community composition and other ecological processes may be more predictable (Bangert 2004; Knapp *et al.* 2004). For example, when specific markers are identified that are correlated with gene products and dependent herbivores, then community structure can be more accurately predicted when the genetic composition, or cross type, of an individual plant is known (e.g. Wimp *et al.* 2005).

We also consider and reject two alternative hypotheses. First, our results were exclusively driven by the differences in community composition between two pure cottonwood species. We reject this hypothesis because when we

examined community composition on the hybrid cross types alone (i.e. parental species were excluded), we found that the relationship between arthropod community structure and genetic composition was still highly significant. Furthermore, in a previous study (Bangert 2004), the 'hybrid only' pattern held in six other river systems across the region, which argues that this is a general pattern. Second, our patterns were the result of the contributions of a single keystone species, and do not represent a community-wide response. We reject this hypothesis because 38–52% of the leaf-modifying arthropods were significant contributors to the observed patterns among cross types, suggesting a community-wide response to cottonwood genetic variation. Most importantly, studies that have observationally and experimentally examined individual leaf modifiers in isolation have demonstrated major plant genotype effects on their distribution and abundance (e.g. galling aphids, Dickson & Whitham 1996; leaf-rolling moths, Martinsen *et al*. 2000; galling mites, McIntyre & Whitham 2003). The fact that many of these leaf modifiers occupy different tree genotypes and/or cross types (e.g. galling mites on F_1 hybrids, galling aphids on complex backcrosses) reduces their interactions and probability that any single leaf modifier will drive the distribution of all others.

An evolutionary framework for community ecology

Community ecology has been described as unmanageable because communities are subject to high levels of contingency resulting from the large number of interacting factors (Lawton 1999). Studies at lower (population) and higher (macroecology) levels are more tractable because there is either less contingency or emergent patterns become expressed, respectively (Lawton 1999). In our study system, discrete community patterns were expressed at three levels: among individuals, within a common garden, and within a river drainage. We believe that community studies in systems driven by bottom-up plant genetics (see Hunter & Price 1992 for a discussion of bottom-up factors) reveal stable community patterns rather than 'weak, fuzzy generalizations' (Lawton 1999). Our results, and those of others, support the idea that plant genetics can influence community structure in a wide range of organisms from microbes to vertebrates (Whitham *et al*. 2003), and across scales from metres to 720 000 km2 (Bangert 2004).

In this study, we considered the general genetic composition of a dominant tree that defines a major riparian community type. However, by refining future analyses to include only those genetic markers that represent important ecological traits (e.g. condensed tannins; Whitham *et al*. 2003; Schweitzer *et al*. 2004, 2005), predictive power can be expected to improve. In this system at local and regional scales, there are several species that are significant

indicators of different cottonwood cross types (Bangert *et al*. 2005; Wimp *et al*. 2005). For example, two independent studies (Bangert *et al*. 2005; Wimp *et al*. 2005) found that 33–56% of the species were significant indicators of the four cross types and that some species are able to detect the difference between complex backcross and narrowleaf trees that otherwise require molecular analysis to differentiate. Failure to account for factors such as plant genetics may reduce the predictive power of models of community assembly.

Because we have demonstrated a genetic basis to community structure in this cottonwood system, we can state a simple genetic similarity rule that may apply to other plant–animal systems: in plant or animal species (or hybrid complexes) with large genetic variability, the associated communities of dependent organisms will differ with respect to plant genotypes or cross-type classes (e.g. Maddox & Root 1990; Aguilar & Boecklen 1992; Floate & Whitham 1995; Floate *et al*. 1996; Dungey *et al*. 2000; Hochwender & Fritz 2004; Wimp *et al*. 2005). Conversely, in systems with low plant genetic variability we predict that the environment will be a stronger factor in community structure (Bangert 2004). One corollary to this genetic similarity rule is that by knowing the insect community, we should be able to predict plant cross type (Floate & Whitham 1995). This should be possible with the development of additional plant genetic data that quantifies the expression of ecologically important alleles for particular traits that different insect species or herbivore suites respond to (*sensu* Maddox & Root 1990). Thus, we have a genetic similarity rule that goes beyond simple pattern documentation (Keddy & Weiher 1999; Kelt & Brown 1999) to a prediction of indicator species, and suites of dependent species (Bangert *et al*. 2005; Wimp *et al*. 2005).

Because genetically dissimilar cottonwoods support dissimilar arthropod communities, we should also expect that greater genetic variation at the stand level would also be associated with greater diversity in the arthropod community and higher trophic levels. In support of this hypothesis, Wimp *et al*. (2004) found that in the wild, genetic variation at the stand level in cottonwoods accounted for 59% of the variation in the diversity of an arthropod community composed on 207 species. We believe these findings are consistent with our genetic similarity rule and argue that the conservation of genetic diversity in a dominant tree such as cottonwoods could be important for conserving the diversity of the dependent community (Bangert *et al*. 2005).

While many community studies do seem to result in fuzzy generalizations, weak tendencies, or appear chaotic (e.g. Drake 1991; Lawton 1999; Wilson 1999), our genetic-based similarity rule can improve predictions of community-level studies involving plant–animal interactions. This rule is analogous to what other authors have identified as

domains or basins of attraction (Holling 1973; Thompson *et al.* 2001), alternative stable states in ecology (Hraber & Milne 1997; Beisner *et al.* 2003; Elmqvist *et al.* 2003), or deterministic chaos and self-organization (Drake *et al.* 1999), whereby order emerges at the community level. Our study is supported by the Hraber & Milne (1997) model where community assembly has genotype-based assembly rules that act as basins of community attraction.

Our studies argue that this *Populus* system has domains of community attraction that change as genes recombine through hybridization and introgression. Plant cross type defines these basins of attraction, e.g. the Fremont, F_1, or backcross/narrowleaf classes, because within any one class there is genetic variability resulting in variability in community composition. However, each cross type is well defined, and community composition predictably reflects these genotypic changes. Alternatively, these basins of attraction can be viewed as an adaptive landscape with different community peaks (*sensu* Weiher & Keddy 1999b; Thompson *et al.* 2001) represented by genotypic category.

Because plant genetic variation acts as a bottom-up force, strong emergent properties such as the structuring of arthropod communities occur. In this sense, the vagaries of contingency (e.g. environmental factors) become less important, and the ability of genes to organize biological systems becomes a prominent factor. Our genetic similarity rule arises from these emergent properties and suggests that (i) plant genotypes predictably affect herbivore community composition via plant chemistry (e.g. Bangert 2004); (ii) arthropods can be used as traits that rival the plant's own morphological traits used in taxonomic classification (Floate & Whitham 1995); (iii) greater genetic diversity among trees in a stand will be associated with greater diversity in the dependent community (Wimp *et al.* 2004); and (iv) in systems with low genetic variability, the environment will be a stronger factor in community assembly than plant genetic composition (Bangert 2004). Moreover, this rule can be extended to investigate whether plant genetics influence other ecological processes such as species interactions (Thompson 1994), or ecosystem processes like decomposition and nitrogen mineralization rates (Schweitzer *et al.* 2004, 2005; LeRoy *et al.* 2005). In conclusion, we argue that a genetic similarity rule provides both increased predictive power for understanding community structure and provides an evolutionary framework for investigating community assembly and associated ecosystem processes.

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