COMMUNITY HERITABILITY MEASURES THE EVOLUTIONARY CONSEQUENCES OF INDIRECT GENETIC EFFECTS ON COMMUNITY STRUCTURE

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Abstract.—The evolutionary analysis of community organization is considered a major frontier in biology. Nevertheless, current explanations for community structure exclude the effects of genes and selection at levels above the individual. Here, we demonstrate a genetic basis for community structure, arising from the fitness consequences of genetic interactions among species (i.e., interspecific indirect genetic effects or IIGEs). Using simulated and natural communities of arthropods inhabiting North American cottonwoods (*Populus*), we show that when species comprising ecological communities are summarized using a multivariate statistical method, nonmetric multidimensional scaling (NMDS), the resulting univariate scores can be analyzed using standard techniques for estimating the heritability of quantitative traits. Our estimates of the broad-sense heritability of arthropod communities on known genotypes of cottonwood trees in common gardens explained 56–63% of the total variation in community phenotype. To justify and help interpret our empirical approach, we modeled synthetic communities in which the number, intensity, and fitness consequences of the genetic interactions among species comprising the community were explicitly known. Results from the model suggest that our empirical estimates of broad-sense community heritability arise from heritable variation in a host tree trait and the fitness consequences of IGEs that extend from tree trait to arthropods. When arthropod traits are heritable, interspecific IGEs cause species interactions to change, and community evolution occurs. Our results have implications for establishing the genetic foundations of communities and ecosystems.

Key words.—Arthropods, community evolution, community genetics, cottonwood, extended community phenotype, indirect genetic effects, *Populus*.

Community ecology has yet to incorporate the evolutionary insights gained from studies of multilevel selection within species (Wade 1977; Craig 1982; Goodnight 1990a,b; Thompson et al. 2001; Whitham et al. 2003). In particular, the lack of a reliable field measure for group, species, or community heritability has prevented widespread acceptance of multilevel selection as an evolutionary force capable of influencing community structure (Hubbell 2001; Clark and Mclachlan 2003; Volkov et al. 2003; Hochwender and Fritz 2004). However, when individuals live within groups, components of fitness arising from conspecific interactions can be readily identified (Goodnight et al. 1992; Goodnight and Stevens 1997; Whitham et al. 2003). The fitness consequences of genetically based interactions among individuals in the same species, known as indirect genetic effects (IGEs), are now considered important in group and social evolution (Moore et al. 1997; Agrawal et al. 2001; Wade 2003).

An analogous mechanism involves genetic interactions among individuals in different species (Goodnight 1990a,b; Goodnight and Craig 1996; Swenson et al. 2000; Wade 2003). When these interactions have fitness consequences, the realized fitness of each species depends on the number and relative abundances of other species present within the community (E. V. Lonsdorf, S. M. Shuster, and T. G. Whitham, unpubl. ms.). Stated differently, when the fitnesses of all interacting species are affected at once, contextual, community-level selection occurs (Goodnight et al. 1992; Whitham et al. 2003). We define community-level selection as selection that requires interactions with at least one other species, that is, selection within a community context, where-

in individual relative fitness depends on the genetic and demographic composition of its community (Kerr and Godfrey-Smith 2002). We do not suggest that a community has fitness (e.g., Wilson 1997) or that differential extinction and proliferation of communities occurs.

Because the fitness consequences of genetic interactions among species alter the population frequencies of the alleles involved in these interactions, genetic differences among communities are likely to exist. Moreover, interactions among species and the fitness effects they impose are likely to undergo continuous change (Moore et al. 1997; Agrawal et al. 2001; Wade 2003). Therefore, when the traits involved in interspecific interactions are heritable, genetic interactions among individuals in different species are likely to evolve, and the number and relative abundances of species comprising the community are likely to change (Whitham et al. 2005). In the same way that IGEs may influence social evolution, we suggest that interspecific IGEs (IIGEs) could influence interspecific interactions and provide a basis for communities to evolve genetically and differentiate demographically.

Here, we describe methods for measuring broad-sense community heritability, H_C^2, an empirical estimate of the fraction of the total variation in community phenotype that is explained by IIGEs (Becker 1985; Falconer 1989; see also Goodnight 1990a,b). Our approach for measuring H_C^2 uses standard quantitative genetic methods. However, instead of estimating the phenotypic covariance of quantitative traits in related individuals, we estimate the phenotypic covariance of arthropod communities on related cottonwood trees. We also provide a mechanism by which cottonwood clones may

accumulate similar arthropod assemblages. We assert that measurable broad-sense community heritability arises when genetic variation in one species covaries with natural selection on one or more other species. Such genetic interactions among species cause natural selection to act within a community context. Thus, broad-sense community heritability, H_C^2, provides two types of information: (1) it measures the phenotypic covariance of communities on groups of related host organisms; and (2) it documents the existence of indirect genetic effects among species within communities (Craig 1982; Goodnight 1990a,b; Goodnight and Craig 1996; Moore et al. 1997; Swenson et al. 2000; Agrawal et al. 2001; Wade 2003).

We apply this approach to study phenotypic differences that appear within and among arthropod communities inhabiting genetically distinct groups of cottonwood tree clones. We present three sets of results. First, we review existing research that demonstrates the dependence of arthropod fitness on interactions between arthropod and host plant genes. Next, we report the methods and results of simulations in which arthropod fitness, abundance, and evolution—and thus arthropod community phenotype—depends explicitly on genetic interactions between simulated arthropods and their simulated host plants. Last, we apply our simulation results in a common-garden experiment, in which we measure the among-group component of the total phenotypic variance of 79 arthropod communities inhabiting groups of genetically identical trees, drawn from 20 genotypes within four cottonwood cross types. In this analysis, we document significant broad-sense community heritability under field conditions. These results, combined with our simulations, suggest that estimates of community heritability quantify the phenotypic consequences of selection caused by genetic interactions among species.

Our simulations and the consistent phenotypic responses that appeared within and among community generations in natural arthropod communities show that broad-sense community heritability can account for the resemblance among communities sharing common ancestry. Our use of established quantitative genetic methods to measure the existence of genetic variation within and among ecological communities, as well as the phenotypic covariance of genetically similar communities caused by IIGEs, demonstrates that genetic interactions among species can produce distinct community phenotypes and may lead to community evolution.

Arthropod Communities on Cottonwoods: A Review

Our research and that of our collaborators shows that the expression of genes in North American cottonwoods (*Populus* sp.), piñon pine (*Pinus edulus*), and Australian eucalypts (*Eucalyptus* sp.) results in extended phenotypes that influence community structure and ecosystem processes (Driebe and Whitham 2000; Dungey et al. 2000; Brown et al. 2001; Gehring and Whitham 2002; Chapman et al. 2003; Kuske et al. 2003; Whitham et al. 2003; Schweitzer et al. 2004, 2005a,b; Bailey et al. 2004, 2005, 2006; Wimp et al. 2005; Bangert et al. 2006; LeRoy et al. 2006). Genes underlying cottonwood extended community and ecosystem phenotypes control plant phytochemistry, particularly salicylate phenolic glycosides and condensed tannins (Lindroth et al. 1993; Harding et al. 2005; Rehill et al. 2005). These compounds affect diverse taxa at all trophic levels and at scales from common gardens to western North America (Floate et al. 1997; Martinsen et al. 1998; Bangert et al. 2005, 2006).

Genetic variation in cottonwoods is the most important factor affecting arthropod communities in the wild and in common gardens (Wimp et al. 2004, 2005; Bangert et al. 2005), and the fitness effects of individual tree genotypes on arthropod fitness are well documented (Whitham 1989, 1999; Wimp and Whitham 2001; McIntyre and Whitham 2003). Reciprocal transplant experiments of different aphid lineages on different tree lineages indicate that aphid fitness is likely to be influenced by an interaction between aphid genotype and tree genotype (Moran and Whitham 1988). Studies of variation in single sequence repeats (SSRs) in the galling aphid *Pemphigus betae* show high levels of genetic variation and that particular aphid SSRs covary with particular narrowleaf and hybrid cottonwood tree genotypes (Lushai et al. 2004; R. Foottit, G. Allen, and T. Whitham, unpubl. ms.). Interactions between different species of arthropods within cottonwood communities are less well documented but also appear to impose significant fitness effects (Dickson and Whitham 1996; Waltz and Whitham 1997; Martinsen et al. 2000; Wimp and Whitham 2001), suggesting that arthropod communities on cottonwood trees arise from within- and among-species interactions that influence the fitness of their associated arthropod populations.

MATERIALS AND METHODS

Univariate Summaries of Arthropod Community Phenotype

In our simulations and in our empirical study, we summarized the abundances of arthropod species comprising communities on different genotypes of cottonwood trees using nonmetric multidimensional scaling (NMDS; Faith et al. 1987; Minchin 1987; Clarke 1993). NMDS is based upon pairwise community dissimilarities generated by the Bray-Curtis dissimilarity coefficient (Faith et al. 1987; Minchin 1987; Clarke 1993). Thus, in our analyses, each clonal replicate within each tree genotype generated a single NMDS score, which summarized the composition of each community. The Bray-Curtis measure is appropriate for ecological data because: (1) its value is one when samples have no species in common; (2) its value is zero when samples are identical; (3) species that are jointly absent from samples do not affect the dissimilarity value among samples; (4) the addition of samples does not affect the dissimilarity values for other pairs of samples; (5) it registers differences in the total abundance among samples when the relative abundances are identical (Clarke and Warwick 2001); and (6) it successfully recovers simulated ecological gradients in ordination (Faith et al. 1987; Minchin 1987).

NMDS performs well when handling data with high beta diversity (Fasham 1977), but also efficiently handles data in which beta diversity is low (Minchin 1987). This point is critical in the cottonwood system, in which turnover rates approach 80% among trees of the same cross type (G. M. Wimp, unpubl. data). Previous work on the robustness of NMDS compared to other multivariate techniques, as well as

our own exploration, suggest that NMDS is less likely to create spurious sources of variation, which could be misattributed to plant genetic factors, than are other multivariate techniques, such as canonical discriminant analysis and principal component analysis (E. V. Lonsdorf, unpubl. data; see below). NMDS provides no specific information on the genetic basis for each score. The map of samples it produces is based on rank dissimilarities, not on species distributions (Minchin 1987). Because common and rare arthropod species are treated equally by NMDS, observed score values are not driven by a few common species, but instead represent community-wide patterns. Thus, NMDS seemed ideal for our purposes; it provided a robust ordination technique for community analysis because it captured the consequences of trait interactions among host cottonwoods and their dependent arthropods, and it summarized them as a single community phenotype.

Community Heritability

Our overarching goal was to explore the relationship between IIGEs, our presumed source of community-level selection, and their possible effects on variation in community phenotypes. If these phenotypic changes reflect changes in the genetic interactions among species within the community, then the outcome of community-level selection (i.e., selection within in a community context) can be called community evolution. We suggest that the underlying genetic basis for phenotypic variation among arthropod communities on cottonwood trees, what we consider quantifiable in estimates of broad-sense community heritability, H_C^2, should be proportional to the product of the broad-sense heritability of the tree trait used to identify genetically similar communities, θ_i, and the intensity of community-level selection, γ, relative to total selection in each ecological context, $(\gamma + E_n)$. Thus,

$$H_C^2 \propto H_\theta^2 \frac{\gamma}{\gamma + E_n}, \tag{1}$$

where H_θ^2 is broad-sense heritability of tree trait θ, and γ summarizes the intensity of the fitness consequences of genetic interactions between each arthropod species and its host plant. In equation (1), E_n represents all other potential sources of variation in the arthropod community, including IIGEs among community members, for example, intraguild and trophic interactions among the arthropod species (competition, predation, mutualism, disease). Because IIGEs from each of the above sources can contribute to total variation in community phenotype, they may each contribute to the measurable value of broad-sense community heritability (see below). Thus, estimates of H_C^2 can quantify more than just the heritability of the tree trait; they also include the phenotypic effects of individual-level as well as community-level selection, although we chose not to identify the relative contributions of selection in these contexts here (see Goodnight et al. 1992). Instead, we predicted that broad-sense community heritability would approach zero if any of the following were true: (1) variation in the plant trait was not heritable; (2) the strength of selection was zero, so that heritable variation within the tree had no fitness consequences for the dependent community; or (3) the ecological context from interactions

with species other than the host tree was much more important than the tree, that is, E_n was very large.

To illustrate this theory in detail, we performed a series of simulations in which phenotypically distinct arthropod communities were produced by genetic interactions among community members and their host plants. More specifically, we created communities in which we controlled and accounted for the number, intensity, and fitness consequences of the genetic interactions among the species comprising the community. We then applied the theory to an empirical study of an arthropod community on genetically variable host trees.

If the communities of arthropods were similar within replicates of individual tree genotypes, as well as distinct among different tree genotypes, then a one-way ANOVA of NMDS scores by tree genotype would identify the fraction of the total variation in community phenotype that was due to genetic differences among communities. We suggest that this simple analysis identifies the among-community fraction of the genetic variance affecting coevolving traits (sensu Goodnight and Craig 1996), that is, the fraction of total genetic variance that specifically influences the composition of arthropod communities on cottonwood trees.

A one-way ANOVA of NMDS scores used to identify differences in community phenotype is analogous to the standard method for identifying the broad-sense heritability of quantitative traits (H^2; Lynch and Walsh 1998; see also Becker 1985; Falconer 1989). For this reason, and because all cottonwood tree genotypes bearing arthropod communities that were included in our analyses were represented by multiple clones, we define community heritability in the broad sense, H_C^2, as the contribution of all genetic factors influencing community phenotypic variation: $H_C^2 = (\sigma_{\text{among genotype}}^2/\sigma_{\text{total}}^2)$ (Becker 1985; Falconer 1989; Lynch and Walsh 1998). Thus, in addition to providing a means for documenting the existence of indirect genetic effects among species within communities, estimates of H_C^2 provide a statistical estimate of the phenotypic covariance of communities on groups of related host organisms

Simulated Arthropods on Simulated Cottonwoods

To determine whether phenotypically distinct arthropod communities could be produced by genetic interactions among community members and their host plants, we modeled synthetic communities in which the number, intensity, and fitness consequences of the genetic interactions among species were explicitly known. We created synthetic trees in which a single trait influencing plant phytochemistry varied among tree genotypes and cross types. We next allowed simulated arthropods of different genotypes to sample trees in our simulated forest so that particular abundances of arthropod species became associated with each tree because of the interaction between tree and arthropod genotypes. We then used NMDS to collapse arthropod multispecies abundances for each tree into a single community phenotype for genetic analysis.

Our simulation analysis had two goals that each dealt with statistical challenges inherent in our definition of community heritability. The first was to ensure that NMDS did not artificially manipulate components of variation within the extended phenotypes to produce false estimates of community

heritability. If the statistical conversion of multivariate data to a univariate score artificially altered phenotypic variation within or among tree genotypes, it would call into question our genetic interpretations of the actual arthropod community on *Populus*. Because we explicitly defined the relationship between tree phenotype and its associated arthropod community, we had a well-founded, a priori expectation that the relationship between tree phenotypic values and community NMDS scores reflected the selection imposed from plant to arthropod.

The second goal of our simulation was to apply fundamental, well-accepted theory from quantitative genetics and ecology to determine whether our measure of community heritability identified the phenotypic signature of the fitness consequences of genetic interactions among species. In our empirical work (see below), we predicted that if genetic interactions had no fitness consequences for arthropods settling on cottonwoods, there would be no differences in the composition of arthropod communities within or among cottonwood genotypes. Rejection of this hypothesis, in the form of an observed significant association of particular arthropod communities with individual plant genotypes, would provide evidence that community-level selection had occurred and that there was a strong genetic component to community structure. In our simulation, we modified the fitness consequences and the strength of genetic interactions among arthropods and their cottonwood hosts to determine the sensitivity of our measure of community heritability.

Simulation of Tree Phenotypes

To determine whether phenotypically distinct communities can be produced by genetic interactions among community members and their host plants, we modeled synthetic communities in which the number, intensity, and fitness consequences of the genetic interactions among species comprising the community were explicitly known. We assumed that a single trait, θ, (e.g., plant phytochemistry) varied among tree genotypes (i.e., the trait was heritable). We then used a general quantitative genetic model (Shaw et al. 1998) to separate genetic and environmental effects on the expression of phytochemical trait θ,

$$\theta_i = a_1 + a_2 + e_\theta, \quad (2)$$

where, a_1 was the additive effect of an allele on chromosome 1, a_2 was the additive effect of an allele on chromosome 2, e_θ was a uniformly distributed number that represented the residual deviation due to random environmental effects, $e_\theta \sim U(-e_\theta/2, e_\theta/2)$, and there was no dominance. Because e_θ was randomized across all individuals, there were no gene-by-environment (G × E) interactions (Shaw et al. 1998). Thus, the final phenotypic value, θ, equaled the sum of additive genetic effects, $(a_1 + a_2)$, plus the environmental deviation, e, following the standard definition of a phenotype (P), P = G + E.

Simulation of Arthropod Communities

On each of the 50 trees in our simulation (see below), we created a community of 25 dependent arthropod species according to the following assumptions. We assumed that the

ith tree trait, θ_i, represented potential habitat, and that the jth arthropod trait, z_j, like the host tree trait, was determined by a single locus with two alleles, such that,

$$z_j = b_1 + b_2 + e_z, \quad (3)$$

where, b_1 was the additive effect of an allele on chromosome 1, b_2 was the additive effect of an allele on chromosome 2, and e_z was a uniformly distributed number, $e_z \sim U(-(e_z/2), e_z/2)$, that represented the residual deviation due to random environmental effects. Like the tree trait, we assumed that there were two alleles for each jth arthropod species, C_j and D_j. Assuming that p_j represented the frequency of allele D_j in a population of arthropod species j, then the mean trait value, $\bar{z}_{ij}$, for a population of arthropod species, j, on cottonwood tree, i, was

$$\bar{z}_{ij} = 2p_j^2 D_j + 2p_j(1 - p_j)(C_j + D_j)$$
$$+ 2(1 - p_j)^2 C_j. \quad (4)$$

We modified the model of Ronce and Kirkpatrick (2001) to describe joint changes in population size, n_{ij}, and mean trait, $\bar{z}_{ij}$, as a function of tree trait, θ_i, for each arthropod species, j, on each tree, i.

$$\frac{d\bar{z}_{ij}}{dt} = \frac{\sigma^2_{G_{ij}}}{\sigma^2_{z_{ij}}} \gamma(\theta_i - \bar{z}_{ij}), \quad (5a)$$

$$\frac{dn_{ij}}{dt} = n_i\left[r\left(1 - \frac{n_{ij}}{K}\right) - \frac{\gamma}{2}\sigma^2_{z_{ij}} - \frac{\gamma}{2}(\theta_i - \bar{z}_{ij})^2\right], \quad \text{and} \quad (5b)$$

$$\frac{dp_{ij}}{dt} = \frac{d\bar{z}_{ij}}{dt}\frac{1}{2D_i - 2C_j}. \quad (5c)$$

In equation (5a), $\sigma^2_{G_{ij}}$ is the genetic variance of trait $\bar{z}_{ij}$, equal to $2p_i(1 - p_i)(2D_j - 2C_j)^2$, $\sigma^2_{z_{ij}}$ is the total phenotypic variance of trait z, equal to $\sigma^2_{G_{ij}} + \sigma^2_E$, γ is the strength of stabilizing selection by tree trait θ_i on insect trait $\bar{z}_{ij}$, and $(\theta_i - \bar{z}_{ij})$ represents the degree of maladaptation of the jth insect species on the ith host plant. Following Ronce and Kirkpatrick (2001), we assumed that the arthropod population followed logistic growth in which K represented its carrying capacity. The second and third terms inside the square brackets of equation (5b) represented two different demographic loads that would reduce arthropod population size. The first was due to stabilizing selection acting on variance around the mean arthropod trait, and the second was due to the evolutionary load difference between the arthropod mean trait, $\bar{z}$, and the habitat represented by tree trait, θ (Lande and Shannon 1996). The change in gene frequency over time (eq. 5c) was simply the change in trait value scaled by the quantitative trait differences of the two alleles.

We assumed that the gene frequency, p_{ij}^*, and trait value, $\bar{z}_{ij}^*$, of each arthropod species, j, on tree, i, at equilibrium would be:

$$p_{ij}^* = \begin{cases} 0 \\ \dfrac{\theta_i - 2C_i}{2D_i - 2C_i} \quad \text{and} \\ 1, \end{cases}$$

$$\bar{z}_{ij}^* = \begin{cases} 2C_i, & \text{if } \theta_i < 2C_i \\ \theta_j, & \text{if } 2C_i < \theta_i < 2D_i \\ 2D_i, & \text{if } \theta_i > 2D_i. \end{cases} \quad (6)$$
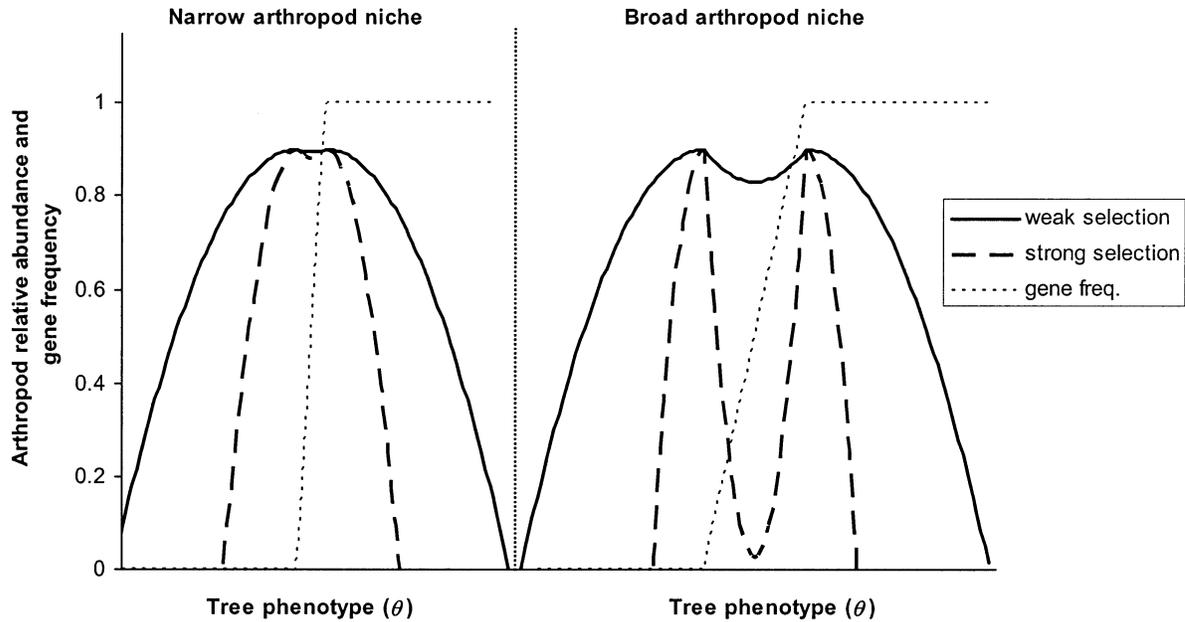
FIG. 1. The two sources of demographic load, variance in arthropod trait, z, and evolutionary load, can create relatively complex associations between tree phenotype, θ, and the predicted arthropod abundance for each species, n^* (scaled from zero to one in this figure), as a function of the range in niche space. High genetic variation underlying niche breadth and strong selection (dashed line) increase demographic load due to variance in arthropod trait, relative to low genetic variation and weak selection (solid line); the dotted line illustrates the predicted arthropod gene frequency that creates a phenotype, z, that matches tree phenotype, θ, within the potential niche space.

Because we limited the range in niche space of each arthropod species to between $2C$ and $2D$, arthropod alleles would become fixed when θ_i was above or below 2C or 2D, respectively.

The predicted abundance of each arthropod species, j, on tree, i, n_{ij}^*, was

$$n_{ij}^* = K\left[1 - \frac{\gamma}{2}\sigma_{z_{ij}}^2 - \frac{\gamma}{2}(\theta_i - \bar{z}_{ij}^*)^2\right] + E_{n_{ij}}, \qquad (7)$$

where $E_{n_{ij}}$ was a uniformly distributed random number, $E_{n_{ij}} \sim U(-E_{n_{ij}}/2, E_{n_{ij}}/2)$, that represented the residual difference in population size of arthropod species, j, on tree, i, caused by ecological interactions other than the tree, (e.g., predators, competition, disease). The relative effect of E_n on predicted abundance was proportional to the carrying capacity. For example, if carrying capacity, K, was 100 (as it is in our simulations) and $E_n = 30$, then the abundance range predicted by tree phenotype would range between zero and 100 ± 15. The relative effect of E_n on n^* was thus proportional to $E_n/2K$.

We emphasize that as a consequence of our assumptions, the two sources of demographic load, variance in arthropod trait, z, and evolutionary load, can create relatively complex associations between tree phenotype, θ, and the predicted arthropod abundance for each species, n^*, as a function of the range in niche space (Fig. 1). With a narrow niche range relative to the plant phenotype, the arthropod gene frequency should either be fixed at zero or one, resulting in very low trait variance ($\sigma_{z_{ij}}^2 \sim 0$) and high evolutionary load ($\theta_i \neq \bar{z}_{ij}$). In contrast, with a broad niche range relative to plant phenotype, arthropod gene frequency is more likely to fall between zero and one, resulting in higher trait variance ($\sigma_{z_{ij}}^2 > 0$) and very little evolutionary load ($\theta_i = \bar{z}_{ij}$).

Note that equation (7) takes on the definition of a traditional phenotype, $P = G + E$, where phenotype P represents arthropod population, n_{ij}, G represents the terms in parentheses, which include genetically determined plant and arthropod traits; and E represents the environmental causes of variation in arthropod population size. Equation (7) illustrates our assumption that the abundance of each arthropod species, and therefore the arthropod community on each tree, is determined by the strength of the interaction between tree and arthropod phenotypes, $(\gamma/2)(\theta_i - \bar{z}_{ij}^*)^2$, relative to variation in ecological context, $E_{n_{ij}}$.

Simulations

As explained above, we used the results of our simulations to satisfy two statistical goals underlying our methods for analyzing community heritability. Our first goal was to correctly quantify the relationships between tree phenotype, selection due to IIGEs, and arthropod community phenotype. To achieve this, we compared tree phenotypes with NMDS scores as a function of selection strength and ecological context. We predicted that the strength of the relationship would increase as community-level selection increased and ecological variation decreased. Recall that two demographic load terms described earlier (eqs. 5b and 7) caused population size to decline when arthropod trait variance was greater than zero and/or when the arthropod's mean trait value did not match host plant phenotype. We required NMDS to capture the complexity of associations between each arthropod abundance and plant phenotype as a function of arthropod niche

range and selection. Furthermore, we required the NMDS scores to be continuous and normally distributed, assumptions made when genetic analyses are applied to traditional phenotypes (Lynch and Walsh 1998).

Our second goal was to determine whether our measures of community heritability identified the phenotypic signature of the fitness consequences of genetic interactions among species. To achieve this, we varied the terms in equation (1) to determine whether our measure of community heritability was sensitive to changes in broad sense heritability of tree trait, H_θ^2, the intensity of community-level selection, γ, and total selection in each ecological context, $(\gamma + E_n)$. We predicted that community heritability would increase as plant heritability increased, selection increased, or ecological variation decreased. Meeting both of our statistical goals would indicate that significant estimates of community heritability in our empirical study revealed the existence of genetic interactions between plant trait variation and arthropod fitnesses that altered the ecological and evolutionary contexts of these natural communities.

For our simulation experiments, we used four alleles to create 10 genotypes (four homozygotes and six possible heterozygotes) and replicated each genotype five times, for a total of 50 individual trees. We could have created many more trees, but we limited the number to resemble the empirical work described below. We performed our simulation (community analysis and statistical analysis described below) under two levels of heritability for plant trait, θ, eight levels of the strength of selection, γ, and five levels of variation in ecological context, $E_{n_{ij}}$. We replicated each of the 80 factor-level combinations 100 times and reported the average community heritability. We used Matlab (ver. 6.5.1; Mathworks, Inc., Natick, MA) for all simulations (see Appendix I, available online only at http://dx.doi.org/10.1554/05-121.1.s1).

Sampling Arthropod Communities on Common Garden Cottonwoods

To investigate the tendency for genetically distinct host trees to support phenotypically distinct communities in the field, we surveyed the leaf modifying arthropod community on *Populus* (14 species from five orders and seven families). Because these gall-forming and leaf-rolling arthropods live in close association with their cottonwood hosts, we expected them to exhibit high fidelity to tree genotype. Also, because heritable traits underlie arthropod decisions about oviposition and gall formation, and because these decisions are made in response to heritable phenological and chemical cues present in trees (Abrahamson et al. 1993), we considered genetic correlations likely to arise among these associated traits in arthropods and in cottonwood trees.

To separate genetic and environmental hypotheses that might account for among-community patterns, cuttings from *P. fremontii* (Fremont cottonwood), *P. angustifolia* (narrow-leaf cottonwood), F$_1$ hybrid (*P. fremontii* × *P. angustifolia*), and backcross hybrid (BC; F$_1$ × *P. angustifolia*) cottonwood trees growing naturally along the Weber River, Utah, were established in a common garden. Pure and hybrid status as well as specific tree genotypes were determined using 35 species-specific restriction fragment-length polymorphism

(RFLP) markers (Keim et al. 1989; Martinsen et al. 2001). Multiple cuttings used per tree allowed clonal replication within genotypes. Trees within stands were blocked to reduce potential within-garden site effects. All trees in this study were approximately 10 years old, were about 10 m tall, and had reached reproductive maturity.

Focusing on the lower canopy of each of these trees and counting the numbers of each arthropod species identifiable during a 2-min survey, we censused 79 trees with three to six replicate clones per genotype for the leaf-modifying communities. The 14 members of the leaf-modifying arthropod community on *Populus* included four species of aphids (Homoptera: Aphididae: *P. betae*, *P. populicaulis*, *P. populitransversus*, *Thecabuis populicondupifolius*), seven species of lepidopterans (Lepidoptera: Gelechiidae: *Anacampsis niveopulvella*, gelechiid 2; Gracillaridae: gracillarids 1, 2; Tortricidae: tortricids 1–3), one sawfly (Hymenoptera: Tenthredinidae: *Phyllocolpa* sp.), one beetle (Coleoptera: Psoidae: psoid sp. 1), and one mite (Acari: Eriophyidae: *Aceria parapopuli*).

Genetic Analysis of Community Phenotypes

Because our experimental design incorporated genetic variation within and between host cottonwood species and their naturally occurring hybrids (i.e., four cross types; *P. fremontii*, *P. angustifolia*, F$_1$ hybrid, and BC hybrid), we analyzed our empirical study using three methods of increasing genetic resolution: (1) a line cross/joint scaling analysis of the effect of cross type; (2) nested ANOVA with genotype nested within cross type; and (3) a one-way ANOVA of genotype for each of the four cross types. This sequence allowed us to determine whether within- or between-species comparisons accounted for more of the total variation in community phenotype in our study and to determine the extent to which our inferences from this system may apply to other systems. All three analyses assumed that each NMDS score acted as a trait whose genetic basis can be evaluated (Hochwender and Fritz 2004). We emphasize that one of the goals of our simulation was to evaluate this assumption as well.

Our line cross/joint scaling analysis combined a line cross method (Cavalli 1952; Hayman 1958) and a joint scaling test (Mather and Jinks 1982) to yield a regression technique that determined whether additive or dominant genetic effects influenced the expression of community phenotype in hybridizing species (Lynch and Walsh 1998). Significant plant additive or dominant genetic effects on a community would indicate that differences between species were important determinants of arthropod community.

Our nested ANOVA, of genotypes nested within cross type, using the standard methods for estimating broad-sense heritability of quantitative traits, (Becker 1985; Falconer 1989), allowed us to estimate the relative effects of genotype and cross type. To summarize total variation in community phenotype, and to determine the total contribution of genetic factors underlying arthropod community differences, we calculated the broad-sense heritability of community phenotype, H_C^2, from nested ANOVAs of NMDS scores as the proportion of variation that is due to genotype relative to total variation. However, because segregational variance from genetic differences between the cottonwood species comprising our pa-

rental host plant cross types (Fremont, narrowleaf) were exposed within the BC hybrids (Lynch and Walsh 1998), differences between genotypes could arise from either within a single species or genetic differences between species in this cross type. Therefore, our nested ANOVA, while providing a way to identify the relative contributions of genotype and cross type to estimates of community heritability, does not provide unequivocal evidence of genetic variation within a species.

Thus, to treat each cross type separately and determine whether variation within a species has important community-level consequences, we also conducted a one-way ANOVA of community phenotype within each of the four tree cross types. This approach is analogous to the standard method for identifying dam effects in a half-sib breeding design (Falconer and McKay 1996). Significant heritability estimates within the parental tree species would suggest that the genetic variation within species, rather than or in addition to between species, was important for predicting the structure of the dependent community. We analyzed common-garden communities in the same manner as the simulation data, although due to unequal sample sizes, the lower 90% confidence intervals for our within-lineage analyses were estimated as in Becker (1985; see Appendix II, available online only at http://dx.doi.org/10.1554/05-121.1.s2).

RESULTS

Simulations

Our simulations indicated that NMDS is indeed an appropriate tool for identifying the interaction of plant phenotype and selection on a dependent arthropod community. That is, NMDS did not create spurious variance in community phenotype and instead acted as a trait whose genetic basis can be evaluated using standard quantitative genetic methods. As the strength of selection increased, the slope of the relationship between tree phenotype and the arthropod community NMDS score increased (Fig. 2). As the ecological variation increased, the relationship between tree phenotype and NMDS score became weaker. Furthermore, NMDS captured the effects of two sources of demographic load illustrated by the slightly nonlinear relationship between NMDS and tree phenotype. When niche range was constrained to zero so that only the evolutionary load term was included, the relationship between NMDS and plant phenotype was linear (E. Lonsdorf, S. Shuster, and T. Whitham; unpubl. data).

One-way ANOVA of NMDS scores across cottonwood genotypes in our simulated communities showed significant among-genotype variation in arthropod community structure, indicating that the fitness consequences of genetic interactions between arthropods and their host plants had produced recognizable community phenotypes. Furthermore, our estimate of community heritability was sensitive to changes in plant trait heritability, the strength of selection by the plant trait on each arthropod, and the amount of ecological variation (Fig. 3). As selection increased, community heritability increased and the rate of increase declined with increasing ecological variation. Consistent with equation (1), our overall estimate of broad sense community heritability, H_C^2, was scaled by plant heritability, such that H_C^2 was higher when

plant heritability was also higher (Fig. 3a) and lower when plant heritability was lower (Fig. 3b).

Plant Genetic Basis of Arthropod Community Variation in a Common Garden

The results of our three analyses of the galling community on cottonwoods consistently indicated that genetic variation within an individual host plant species explained more variation in community phenotype than genetic variation between host plant species. First, the line cross analysis and joint scaling test showed weak, nonsignificant additive and dominant effects between the two cottonwood species. The simplest additive model could not be rejected ($\chi^2 = 1.68$, df $= 2$, $P = 0.43$) and the additive effect was not significant (0.10 ± 0.13; $t = 0.76$, $P = 0.29$).

Second, a nested-ANOVA of NMDS scores with genotypes nested within cross types showed that tree genotype accounted for approximately three times more of the total variation in arthropod community phenotype (57%) than tree cross type (19%). Both genotype and cross type, however, accounted for significant variation in arthropod community structure (Table 1). Because line cross analysis indicated weak or no additive effects and because arthropod community differences between cross types were small compared to differences within, it is unlikely that segregational variance in the BC cross type contributed much to differences between genotypes.

Third, a one-way ANOVA of NMDS scores of genotypes within each cross type indicated that genetic variance within individual host plant species can be used to account for variation among dependent arthropod communities (Fig. 4b). We calculated significant heritability estimates for both parental types (Fremont $H_C^2 \pm 95\%$ CI $= 0.65 \pm 0.47$; narrowleaf $H_C^2 = 0.60 \pm 0.47$), and also within the BC cross type ($H_C^2 = 0.80 \pm 0.20$). However, we observed no significant heritability within the F_1 cross type ($H_C^2 = 0.013 \pm 0.19$). Overall, our three statistical methods indicated that genetic variation within host plant species accounted for more of the total variation in arthropod community than genetic variation between host plant species.

DISCUSSION

Together, our simulation and empirical results indicated that indirect genetic effects on the fitness of community members can produce distinct arthropod communities with statistically distinguishable phenotypes. We found that NMDS, the statistical approach we used to transform each multivariate community phenotype into a univariate score suitable for quantitative genetic analysis, accurately represents variation in community phenotype within and among host plant genotypes (Fig. 2). Our results also suggest that IIGEs are expressed when a plant trait is heritable, when that trait imposes selection upon arthropods, and when the fitness effects of the trait on arthropods are not swamped by other sources of selection. We assert that the consequences of IIGEs on community phenotype can be measured in estimates of broad-sense community heritability, H_C^2. Moreover, when we increased selection intensity due to IIGEs, the value of H_C^2 increased, that is, communities became more distinct (Fig.
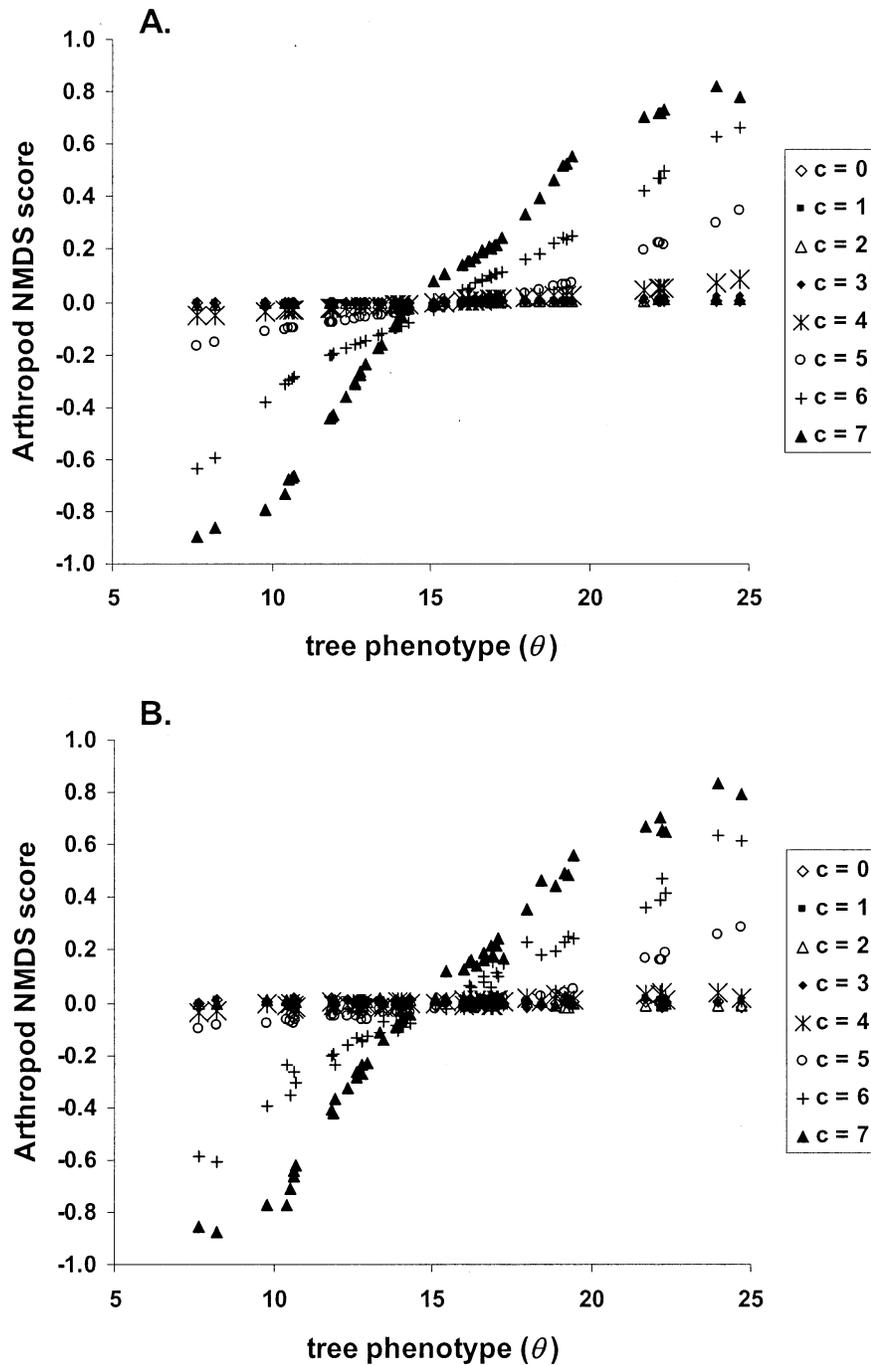
FIG. 2. Nonmetric multidimensional scaling (NMDS) acts as a trait whose genetic basis can be evaluated using standard quantitative genetic methods. Each set of points represents the relationship between tree phenotype (θ) and arthropod community structure (NMDS score) created by selection intensity, γ, (= $[0.0000792 \times 2.51]^c$), from the tree and other environmental sources, E_N, (cf. eqs. 1 and 7). The relative effect of E_n on each species is proportional to $E_n/2K$. As the strength of selection increased (c in γ above), the slope of the relationship between tree phenotype and the arthropod community NMDS score increased; as the ecological variation increased (A: E_N = 0 vs. B: E_N = 60), the relationship between tree phenotype and NMDS score became weaker. NMDS also captured the effects of two sources of demographic load illustrated by the slightly nonlinear relationship between NMDS a tree phenotype. When niche range was constrained to be zero so that only the evolutionary load term was included, the relationship between NMDS and plant phenotype was linear (not shown).
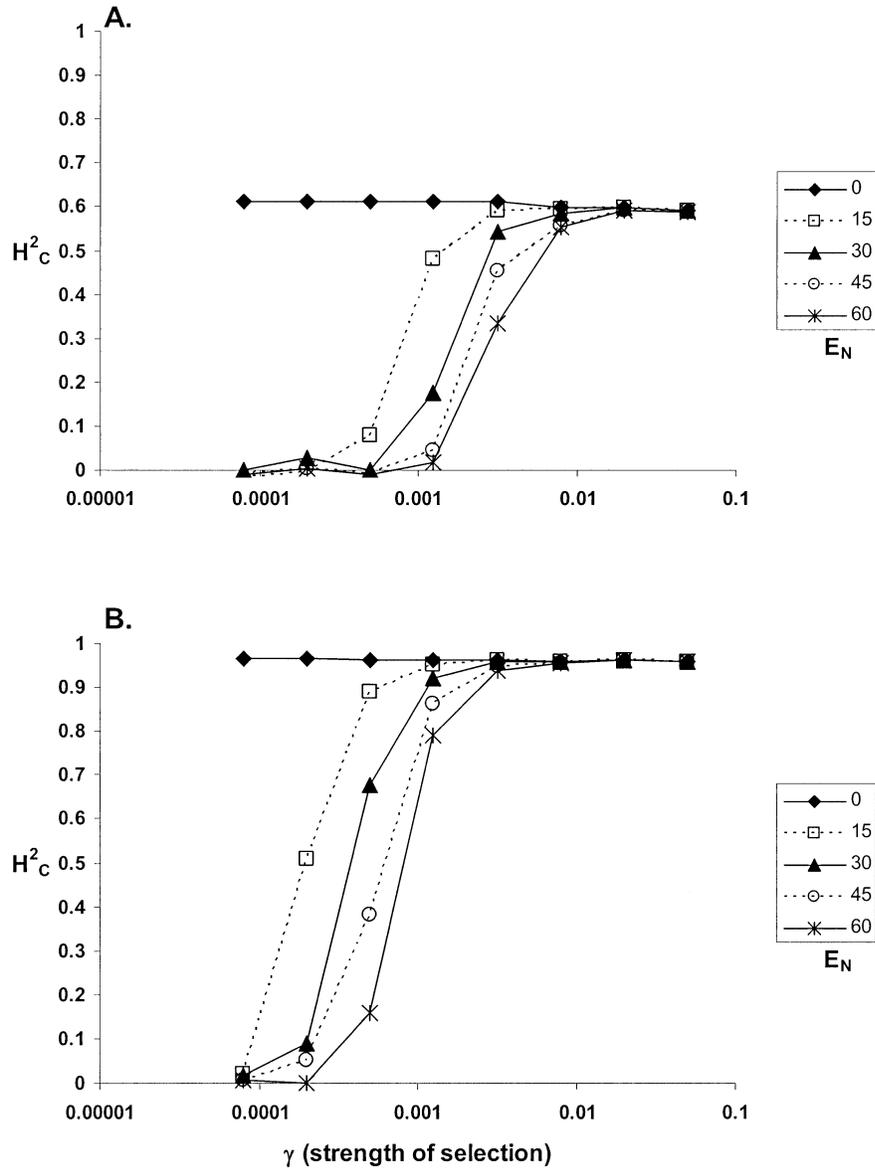
FIG. 3. The relationship between community heritability, plant trait heritability, the strength of selection of plant trait on each arthropod and the amount of ecological variation; as selection (γ) increased, community heritability increased, and the rate of increase declined with increasing ecological variation (E_N); our overall estimate of broad sense community heritability, H^2_C was scaled by plant heritability, such that H^2_C was lower when plant heritability was lower (A) and higher when plant heritability was higher (B).

TABLE 1. Results of a nested ANOVA of arthropod community phenotypes (summarized by nonmetric multidimensional scaling scores) with tree genotype nested within cross type to identify differences in the composition of arthropod communities within cottonwood cross types.

Source	df	Sum of squares	Mean square	F ratio	Prob $> F$
Cross type	3	0.604	0.202	10.184	$<.0001$
Genotype(cross)	16	2.192	0.137	6.926	$<.0001$
Error	59	1.167	0.020		
Total	78	3.964			

3). Thus, any observation of significant H^2_C means that there is a genetic basis for interactions between species, a requirement for community evolution (Goodnight 1990a,b; Goodnight and Craig 1996). Furthermore, our ability to detect significant H^2_C for existing communities indicated that community-level selection and phenotypic divergence among communities had already occurred.

Our simulation results are substantiated by our analysis of natural arthropod communities on cottonwoods in a common garden. Our estimates of community heritability indicated that approximately 56–63% of the phenotypic variation among communities was explained by genetic variation among clones (Fig. 4). We also found IIGEs appearing within a single cottonwood species, rather than between species, indicating that our results apply to a wide range of systems
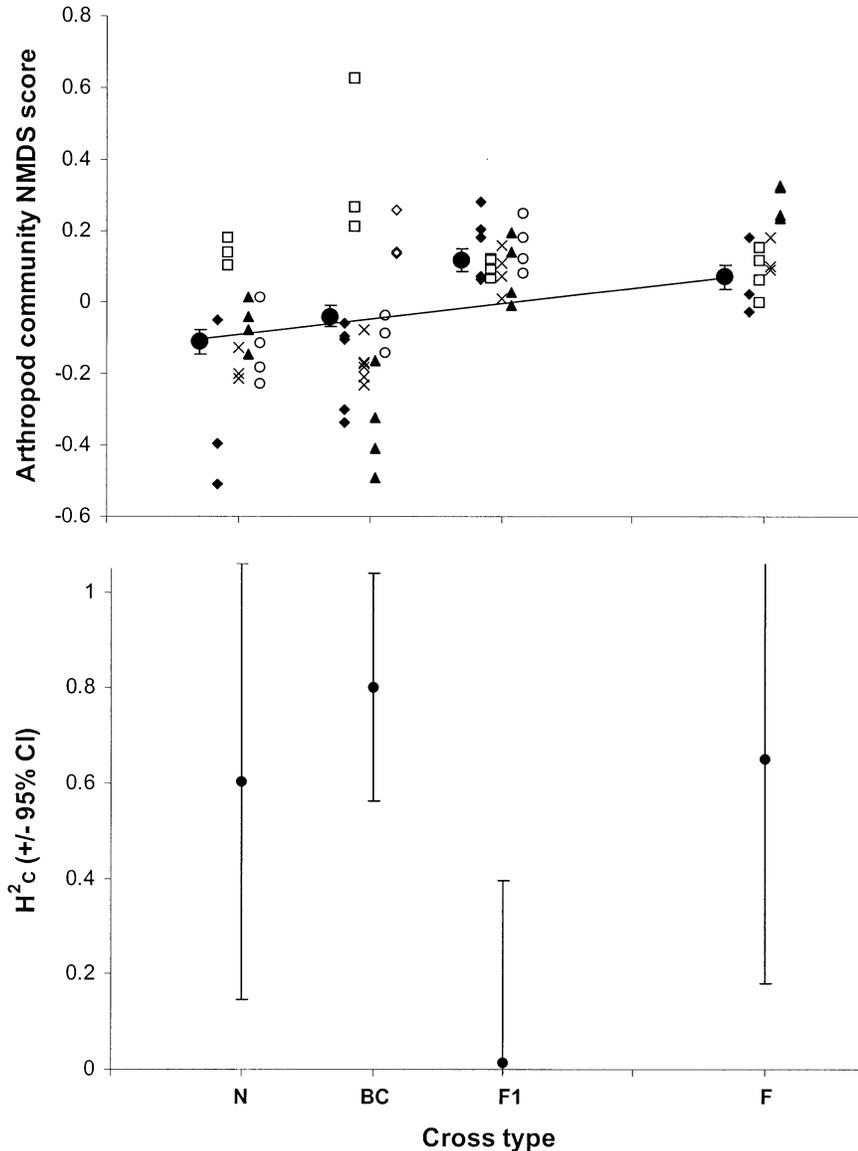
FIG. 4. (A) Genetic variation within, rather than between, individual host plant species structures the dependent arthropod community. The line cross analysis and joint scaling test showed weak, nonsignificant additive and dominant effects between the two host plant species. The simplest additive model could not be rejected ($\chi^2 = 1.6843$, df = 2, $P = 0.43$) and the additive effect was not significant (additive effect $\pm$ SE = 0.10 $\pm$ 0.13, $t = 0.76$, $P = 0.29$). Large, filled circles represent adjusted means of cross type arthropod community plus/minus one standard from a nested ANOVA; each of the small symbols represent individuals of each genotype within each of the four cross types; similar symbols in different cross types do not represent similar genotypes. (B) One-way ANOVA of nonmetric multidimensional scaling scores of genotypes within each crosstype indicated that genetic variance within host plant species can be used to account for variation among dependent arthropod communities. Heritability estimates for both parental types (Fremont [F] $H^2_C = 0.65$ $\pm$ 0.47; narrowleaf [N] $H^2_C = 0.60 \pm 0.47$), and also within the backcross hybrid (BC) cross type ($H^2_C = 0.80 \pm 0.20$) were significant. We observed no significant heritability within F_1 cross type ($H^2_C = 0.013 \pm 0.19$).

and were not simply an epiphenomenon created by the hybridization process (Table 2). Using line cross analysis, we found no significant additive genetic effects between tree species. Furthermore, a nested ANOVA suggested that only 19% of variation in communities was due to differences between tree cross types, as compared to 57% of variation due to differences among genotypes within cross types. Our results suggest that variation in the outcome of genetic interactions between tree and arthropod species is primarily

caused by genetic variation among individuals within tree and arthropod species.

Because we observed significant estimates of H^2_C, we conclude that indirect genetic effects exist between cottonwoods and their dependent galling communities. These selection events occurred consistently within the clonal replicates of the 20 tree genotypes in our garden, leading to consistent arthropod communities, evidently produced by similar intensities of community-level selection. It is well known that

TABLE 2. Results of three genetic analyses indicate that differences in community phenotype among individual trees were caused by genetic interactions between arthropods and cottonwood genotypes within two distinct parental cottonwood species, not due to genetic variation generated by hybridization.

Indirect genetic effect	Line cross analysis	Nested ANOVA	One-way ANOVAs
Between hybridizing host species Reason	Weak effects no additive or dominant	Weak effects 19% of variance between cross type	na
Within host species Reason	na	Strong effects 57% of variance within cross type	Strong effects narrowleaf $H_c^2 = 0.60\ (0.46)$ Fremont $H_c^2 = 0.65\ (0.47)$

different communities of arthropods become associated with genetically distinct plants (see review above). We suggest that observations of phenotypically similar communities on genetically similar plants provide evidence for the existence of community-level selection and for genetically based variation in the underlying phenotype that creates selection. Estimates of H_C^2 measure the phenotypic covariance of communities inhabiting genetically identical host plants and provide a quantitative summary of how strongly genetic interactions between plants and their symbionts (IIGEs) may influence the overall community composition. We discuss elsewhere (Whitham et al. 2003) how the total intensity of community-level selection may be partitioned into its constituent effects using contextual analysis (Goodnight et al. 1992).

Our results provide important definitions for the study of community genetics. Despite apparent similarities between evolution as it occurs within individual species and evolution at the community level, the terms *community heritability, community-level selection*, and *community evolution*, as we use them here, are not strictly analogous to the more familiar terms *heritability, selection*, and *evolution*, as they are used in studies of quantitative traits in diploid populations. Falconer and McKay (1996, p. 123) defined heritability in the broad sense, H^2, as ''the extent to which individuals' phenotypes are determined by the[ir] genotypes,'' or more explicitly, the ratio of the genetic variance, V_G, to total phenotypic variance, V_P, where V_G is measured as the among-group component of the total phenotypic variance, when groups consist of clonal individuals.

We define community heritability in the broad sense, H_C^2, as the among-group component of the total phenotypic variance of arthropod communities, when communities inhabit groups of clonal host plants. As such, our definition identifies the contribution of all genetic factors influencing observed community phenotype; that is, H_C^2 [$\sigma_{\text{among genotype}}^2/\sigma_{\text{total}}^2$]. Thus, H_C^2 is computationally analogous to the standard quantitative genetic definition of broad-sense heritability for diploid organisms (Becker 1985; Lynch and Walsh 1998). However, our definition differs from that of Goodnight (1990a,b; Goodnight and Craig 1996), who focused on community-level traits that were transmissible from one community generation to the next. This definition is similar to the quantitative genetic definition of narrow-sense heritability, and thus is distinct from ours.

While significant broad-sense heritability, H^2, indicates that selection could change the average value of a quantitative

trait, it is a poor predictor of how much change can occur because dominance and epistasis contribute to the total genetic variance that H^2 measures. Similarly, while significant broad-sense community heritability, H_C^2, indicates that community-level selection could change the average community phenotype, it too is a poor predictor of how much change can occur because genetic variation within species as well as the phenotypic consequences of genetic interactions among species are part of the total phenotypic variance. Significant estimates of H_C^2 demonstrate the existence of a genetic basis for community organization (Tables 1, 2), that is, they show that genetically similar host species accumulate similar assemblages of symbionts in a predictable and repeatable way. Regardless of whether this pattern arises from active habitat selection by arthropods or from viability selection on arthropods, the composition of the community is recognizable in a repeatable way because some individuals are present on host plants and others are not.

Falconer and McKay (1996, p. 185; also Lande and Arnold 1983; Phillips and Arnold 1989) defined the selection differential, S, on quantitative traits as ''the mean phenotypic value of individuals selected as parents, expressed as a deviation from . . . the mean phenotypic value of all the individuals in the parental generation before selection was made.'' We define community-level selection as selection that requires interactions with at least one other species, wherein individual relative fitness depends on the genetic and demographic composition of its community. Such selection occurs within a community context and does not imply that communities differentially proliferate or become extinct.

Falconer and McKay (1996, p. 185) defined evolution, or the response to selection, R, as, ''the difference of mean phenotypic value between the offspring of the selected parents and the whole of the parental generation before selection.'' Here is where our definition of community evolution departs most from standard quantitative genetic terminology. Similar to our definition of community-level selection, we define community evolution as a change in genetic interactions between two or more species (Goodnight 1990a,b; Goodnight and Craig 1996), that is, evolution in a community context. We suggest that IIGEs are likely to cause such changes and may, in the process, change the overall composition of the community, that is, change in the number and relative abundances of species that comprise it.

Our findings support the concept of extended community phenotypes in which genes have effects at levels higher than the population (Whitham et al. 2003; Johnson and Agrawal

2005). The signatures of these phenotypes are revealed by distinct community phenotypes, which are heritable. Clearly, significant estimates of H_C^2 demonstrate the existence of a genetic basis for community organization (Tables 1, 2). That is, they show that genetically similar plant species and genotypes within a species accumulate similar arthropod species in a predictable and repeatable way. Moreover, like estimates of H^2, which measure genetic variation within a single species underlying a quantitative trait, H_C^2 measures genetic variation within a species underlying the structure of its dependent community, which we have described as a quantitative trait using NMDS.

In summary, significant estimates of broad-sense community heritability, H_C^2, provide three types of useful information: (1) they demonstrate that a genetic basis of community structure exists; (2) they provide evidence that community-level selection has occurred as a result of genetic interactions among multiple species (IIGEs); and (3) when longitudinal estimates of H_C^2 are possible, they provide a quantitative estimate of the realized response of the community phenotype to selection due to indirect genetic effects among species. This result has major implications for establishing the genetic foundations of communities and ecosystems.

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