
Benefits of Conservation of Plant Genetic Diversity to Arthropod Diversity

RANDY K. BANGERT,*†† RICHARD J. TUREK,† GREGORY D. MARTINSEN,‡ GINA M. WIMP,§ JOSEPH K. BAILEY,* AND THOMAS G. WHITHAM*

*Department of Biological Sciences and the Merriam-Powell Center for Environmental Research, Northern Arizona University, P.O. Box 5640, Flagstaff, AZ 86011-5640, U.S.A.

†Department of Mathematics and Statistics, Northern Arizona University, Flagstaff, AZ 86011-5717, U.S.A.

‡EcoPlan Associates, 701 W. Southern Avenue, Mesa, AZ 85210, U.S.A.

§Department of Entomology, University of Maryland, College Park, MD 20742, U.S.A.

Abstract: *We argue that the genetic diversity of a dominant plant is important to the associated dependent community because dependent species such as herbivores are restricted to a subset of genotypes in the host-plant population. For plants that function as habitat, we predicted that greater genetic diversity in the plant population would be associated with greater diversity in the dependent arthropod community. Using naturally hybridizing cottonwoods (*Populus* spp.) in western North America as a model system, we tested the general hypothesis that arthropod alpha (within cross-type richness) and beta (among cross-type composition) diversities are correlated with cottonwood cross types from local to regional scales. In common garden experiments and field surveys, leaf-modifying arthropod richness was significantly greater on either the F_1 (1.54 times) or backcross (1.46 times) hybrid cross types than on the pure broadleaf cross type (*P. deltoides* Marshall or *P. fremontii* Watson). Composition was significantly different among three cross types of cottonwoods at all scales. Within a river system, cottonwood hybrid zones had 1.49 times greater richness than the broadleaf zone, and community composition was significantly different between each parental zone and the hybrid zone, demonstrating a hierarchical concentration of diversity. Overall, the habitats with the highest cottonwood cross-type diversity also had the highest arthropod diversity. These data show that the genetics of habitat is an important conservation concept and should be a component of conservation theory.*

Key Words: arthropod composition, arthropod richness, cottonwoods, host-plant cross-type diversity, natural hybrids, *Populus* spp.

Beneficios de la Conservación de Diversidad Genética de Plantas para la Diversidad de Artrópodos

Resumen: *Argumentamos que la diversidad genética de una planta dominante es importante para la comunidad dependiente asociada porque las especies dependientes, como herbívoros, están restringidas a un subconjunto de genotipos en la población de plantas hospederas. Para plantas que funcionan como hábitat, predijimos que la mayor diversidad genética en la población de plantas estaría asociada con mayor diversidad en la comunidad de artrópodos dependiente. Utilizando álamos (*Populus* spp.) naturalmente hibridizantes en Norteamérica occidental como sistema modelo, probamos la hipótesis general de que las diversidades alfa (riqueza intra tipo de cruza) y beta (riqueza inter tipo de cruza) de artrópodos están correlacionadas con los tipos de cruza de álamos desde escalas locales a regionales. En experimentos de jardín comunes y muestreos de campo, la riqueza de artrópodos modificadores de hojas fue significativamente mayor en la F_1 (1.54 veces) o en híbridos de retrocruza (1.46 veces) que en el tipo de cruza pura de hoja ancha (*P. deltoides* Marshall or *P. fremontii* Watson). La composición fue significativamente diferente en los tres tipos de cruza de álamos en todas las escalas. En un sistema ripario, las zonas de álamos híbridos tenían 1.49 veces más que la riqueza de la zona de hoja ancha, y la composición de la comunidad fue significativamente diferente entre cada*

††email rkb@dana.ucc.nau.edu

Paper submitted October 3, 2003; revised manuscript accepted June 10, 2004.

zona parental y la zona híbrida, lo que demuestra una concentración jerárquica de la diversidad. En general, los hábitats con la mayor diversidad de tipos de cruza de álamos también tuvieron la mayor diversidad de artrópodos. Estos datos muestran que la genética del hábitat es un concepto importante en conservación y debe ser un componente de la teoría de conservación.

Palabras Clave: álamos, composición de artrópodos, diversidad de plantas hospederas, híbridos naturales, *Populus* spp., riqueza de artrópodos

Introduction

As the discipline of conservation biology has moved beyond a science focused on crisis and triage, new approaches have become available. At the forefront, single-species conservation approaches have been used to protect multiple species based on their special attributes as umbrella, keystone, or indicator species (Simberloff 1998), but it has been suggested that, to increase conservation efficiency, the U.S. Endangered Species Act (ESA) should be amended to focus on habitats (Carroll et al. 1996).

Alternative concepts are concerned with more general hypotheses about the conservation of diversity. These hypotheses include habitat conservation, biodiversity hotspots (Dobson et al. 1997; Reid 1998), zones of transition (Smith et al. 2001), biogeographic crossroads (Spector 2002), and the conservation of processes (Ashley et al. 2003) rather than single species. Finally, molecular techniques coupled with population genetics have greatly enhanced conservation science (e.g., Keim et al. 1989; Bouzat et al. 1998; Ashley 1999; Bellinger et al. 2003). In conservation genetics, molecular techniques are used to determine where to concentrate conservation efforts to maximize heterozygosity for the species of concern (e.g., Meffe 1996; Prior et al. 1997). Conservation genetics, however, is typically a focal-species approach that disregards the importance of genotype to community interactions and the maintenance of biodiversity. Here, we used a combined approach in which we considered the genetic diversity of a hybridizing complex of a dominant plant and its dependent assemblage of other organisms (e.g., Dungey et al. 2000; Whitham et al. 2003).

In systems of plant-animal interactions where host plants are habitat, different plant cross types enhance beta diversity in arthropod communities (Floate et al. 1996). In the wild and in common gardens of known pedigree, arthropod richness is greatest on naturally hybridizing *Eucalyptus* spp. in Australia (Whitham et al. 1994; Dungey et al. 2000). A galling aphid (*Pemphigus betae*) is more abundant on genetically susceptible backcross cottonwood hybrids, and the presence of this aphid increases community richness, including arthropods, fungi, and birds (Whitham et al. 1999). Similarly, in the Rocky Mountains of the western United States and Canada, natural cottonwood hybrid zones are the strongest factor in-

fluencing the geographical distribution of *P. betae* (Floate et al. 1997). Overall, from within a tree to the geographic scale, plant hybridization affects the abundance of diverse organisms from microbes to vertebrates (Whitham et al. 1999).

Cottonwoods provide a model system in which to study the relationship between host plant genetic diversity and arthropod community diversity across many scales because different species of cottonwoods naturally hybridize in a contact (i.e., hybrid) zone along most rivers in the western United States (Eckenwalder 1984a; Fig. 1). Many argue that hybrid zones are areas with high rates of both plant and animal evolution that result in high diversity (Carroll et al. 1996; Whitham et al. 1999; Prance 2000). For example, hybrid zones are analogous to biogeographic crossroads (Spector 2002) because, where multiple cross types converge, arthropod diversity is greatest. In a cottonwood hybrid zone on the Weber River in northern Utah, cottonwood genetic diversity was evaluated based on 40 restriction fragment length polymorphic (RFLP) loci and was two to six times greater on the first hybrid generation (F₁) and backcross hybrid cross types compared with either of the pure parental species. Moreover, there is often greater arthropod and avian richness associated with these hybrids (Whitham et al. 1999), and arthropod community composition is different among cottonwood cross types (Floate & Whitham 1995), resulting in high beta diversity. For example, across multiple cottonwood stands, cottonwood gene diversity explains 60% of arthropod community diversity (Wimp et al. 2004). Where plants hybridize, patterns of arthropod diversity may reflect the underlying patterns of genetic diversity in their host plant.

Although there is no consensus on the importance of hybridization in conservation, some believe that hybrids are bad because they dilute genetic purity or species integrity (O'Brien & Mayr 1991) and are less fit (Price & Waser 1979). Consequently, hybrids are not officially recognized under the ESA. Plant species commonly hybridize (Arnold 1997), however, and hybrids are found in the fossil record (e.g., hybrid cottonwoods date to 12 million years BP; Eckenwalder 1984b, 1996). Furthermore, plant hybrids are often as fit as the parental species (Arnold & Hodges 1995; Rieseberg 1995; Schweitzer et al. 2002), and natural hybridization as a speciation process may be responsible for as much as 80% of the diversity of

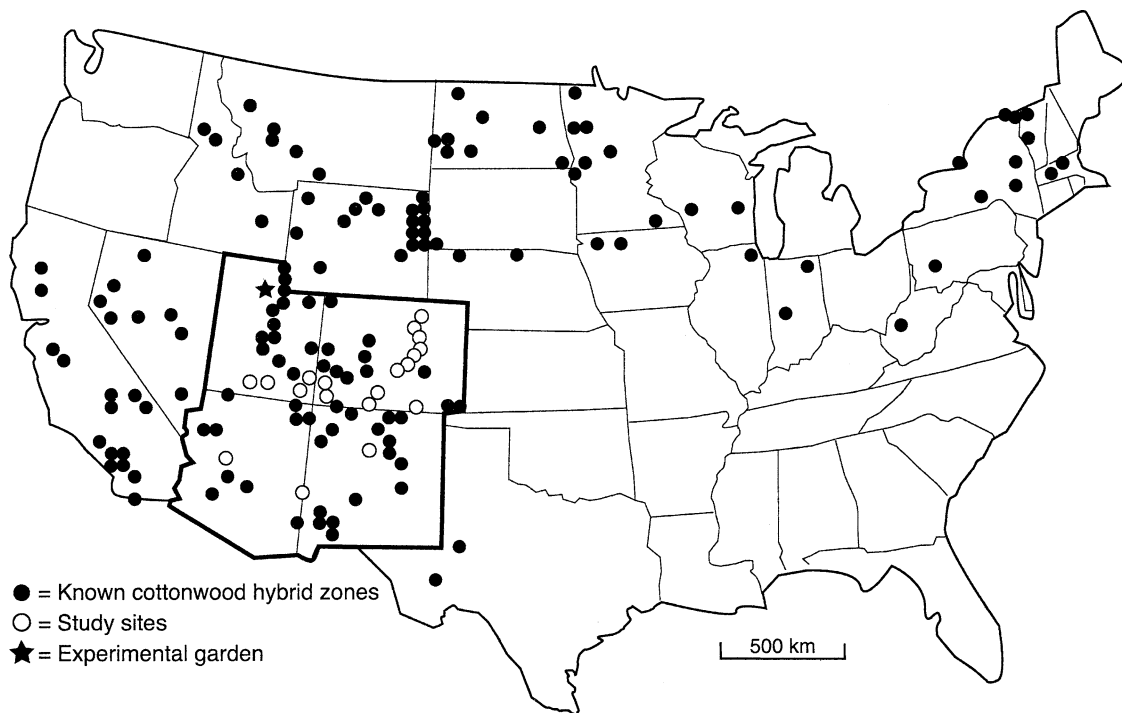


Figure 1. Distribution of cottonwood hybrid zones, the experimental common garden, and our study sites in the United States (after Eckenwalder 1984a).

terrestrial plants (Stace 1987). As a result, hybrids are now considered for conservation on a case-by-case basis, and two hybrids have been listed under the ESA (Whitham & Maschinski 1996). Thus, hybrids—particularly when formed under natural conditions—need consideration in conservation theory.

We concerned ourselves with richness and compositional patterns of an arthropod assemblage associated with two cottonwood species and their hybrids in the southwest region of North America. Studies of arthropods on hybrids often consider only species-specific population patterns and community density in determining patterns of resistance and do not consider community richness and composition (Aguilar & Boecklen 1992; Fritz et al. 1994; Fritz et al. 1998). Different species exhibit variable responses to parental and hybrid hosts (Fritz et al. 1994; Graham et al. 2001), leading to the expectation that community-level patterns may be too messy to disentangle (Fritz et al. 1999; Lawton 1999). Here, we examined community richness and composition and addressed the following four hypotheses: (1) natural cottonwood hybrids in common environments have the highest species richness and are compositionally dissimilar from the parental cross types; (2) arthropod composition is not different within a cross type between different environments, which addresses environment by cross-type interactions; (3) natural cottonwood hybrid zones are centers of arthropod diversity because of higher cross-type diversity; and (4) the patterns of diversity are stable across

multiple scales including a common garden, sites within a river, and at a regional scale across oceanic drainage basins that involve different hybridizing species.

Methods

Cottonwood Hybridization

Cottonwoods are found in most river systems in western North America, and there are commonly two species, one at high and one at low elevations, that hybridize in a contact zone between the two parental species (Eckenwalder 1984a; Fig. 1). *Populus angustifolia* James (narrowleaf cottonwood, section *Tacamabaca*) hybridizes with *P. fremontii* Watson (Fremont cottonwood, section *Aigeiros*) on the Pacific slope of North America west of the Continental Divide, and hybridizes with *P. deltoides* Marshall (plains cottonwood, section *Aigeiros*) on the Atlantic slope east of the Continental Divide, both resulting in an F_1 . Hereafter, the Pacific and Atlantic drainage basins are referred to as slopes.

Patterns of hybridization between narrowleaf cottonwood and the two species in the section *Aigeiros* (collectively referred to as the broadleaf cross type) are similar (Floate et al. 1997), and these two *Aigeiros* species are closely related based on phenetic and genetic analyses (Eckenwalder 1996; W. Young, personal communication). Furthermore, these hybridizing systems exhibit

unidirectional introgression, where the F_1 generation crosses only with the narrowleaf parent, resulting in a backcross generation. Subsequent backcrossing occurs only with the narrowleaf parent, resulting in a complex backcross swarm that becomes more like the narrowleaf with each backcross event (Keim et al. 1989; Martinsen et al. 2001). The hybrid zones are distinguished by high genetic diversity (Whitham et al. 1999) that can be characterized categorically as cross-type diversity. The zones range in size from a few kilometers up to 1000 river km. This results in a model system for studying the relationship between cottonwood cross-type diversity and an associated arthropod assemblage at multiple spatial scales.

We classified trees into four cross-type categories across multiple rivers, based on the strong correlation between tree morphology, tree genotype, and environment (Floate & Whitham 1995; Floate et al. 1997). The broadleaf cross type (section *Aigeiros*) grows in the lower reach and hybrid zone along a river, and the F_1 hybrids grow only in the hybrid zone. Backcross hybrids grow mostly in the hybrid zone and become increasingly rare farther upriver from the hybrid zone (Martinsen et al. 2001). The narrowleaf cross type is rare in the hybrid zone and common in the upper reach of a river. Complex backcross and pure narrowleaf trees are indistinguishable in the field without genetic data, but the backcross/narrowleaf cross type is composed mostly of backcross hybrids in the hybrid zone and almost exclusively of pure narrowleaf in the narrowleaf zone (Keim et al. 1989; Martinsen et al. 2001). In previous studies on trees of known genetic composition, the insect community does not distinguish between the backcross and narrowleaf cross types (Floate & Whitham 1995; G.M.W., unpublished data), and their chemical compositions are not different (Schweitzer et al. 2004; B. Rehill, unpublished data). Hence, we classified these trees as backcross hybrids in the hybrid zone and as narrowleaf cross types in the upper reach of a river. Hybrid zones were delineated from either parental zone based on the presence of either F_1 or broadleaf cottonwoods.

Arthropod Assemblage

We examined plant cross type as the factor responsible for structuring a leaf-modifying arthropod assemblage. Our primary interest was in the richness and composition across scales ranging from individual trees to four states (Utah, Colorado, Arizona, and New Mexico) in the western United States (Fig. 1). Arthropods are important in studies of diversity because they account for a large proportion of animal diversity (Kremen et al. 1993), they are relatively easy to survey (Oliver & Beattie 1993), and they are important contributors to ecological processes (Fisher 1998). Also, many members of this leaf-modifying assemblage have the potential to be keystone engineers (Jones et al. 1994; Whitham et al. 1999; Bailey

& Whitham 2003); therefore, this assemblage should have important effects that extend to the arthropod community at large (Price et al. 1987). Leaf-modifying arthropods interact directly with leaf tissue and are sensitive to the underlying genetic structure of the host plant (Price et al. 1987; Dreger-Jauffret & Shorthouse 1992; Mani 1992; Price 2003). This group is composed of leaf-gallers, -tiers, -rollers, -folders, and -miners. These animals leave distinctive species-specific structures that allow us to quantify their assemblage in the field whether or not a species is present (Opler 1974; Price et al. 1987; Floate & Whitham 1993; Price et al. 1998). For the purposes of this study, we classified these organisms as morphospecies based on their characteristic structures. Finally, 23 of the 25 morphospecies were found at the extremes of the geographical extent of this study, indicating a single species pool.

Data Collection and Analysis

We surveyed trees during July and August 2002 after leaf structures were initiated but before autumn leaf abscission occurred (Floate & Whitham 1993). We constructed a species-by-tree data matrix from surveys on an average of 45 shoots per tree (average 320 leaves) from 6–8 m high in the canopy. Twenty trees per zone were sampled haphazardly within a pure broadleaf zone, a hybrid zone, and a pure narrowleaf zone. Cross types in the hybrid zone were intermixed along the length of the zone. Rivers and zones were located opportunistically, depending on land-use patterns and access. We sampled 44 zones on 21 rivers and trees from a common garden (during the period from 2000 to 2002 in Ogden, Utah) from $105^{\circ}52'W$ to $113^{\circ}W$ and $33^{\circ}13'N$ to $41^{\circ}10'N$ (Fig. 1). This resulted in a total sample of 959 trees and more than 16,000 individual, modified leaf structures representing 25 morphospecies.

To address the question of the genetic component of diversity (cottonwoods as habitat) in common environments (i.e., hybrid zones), we used a two-factor split-plot analysis of variance (ANOVA) with cross type and slope (i.e., Pacific and Atlantic drainages) as the factors and river as a blocking variable. We then compared mean richness among cross types. We calculated mean richness per tree within each cross type in a hybrid zone and used these means as the measure of richness for that hybrid zone because each hybrid zone had different proportions of cross types.

We compared community composition by cross type with a powerful and robust nonparametric ordination procedure, nonmetric multidimensional scaling (NMDS) and an analysis of similarity (ANOSIM; Faith et al. 1987; Minchin 1987, 1999; Clarke 1993) that has been used successfully in analyses of community composition in both animal and plant studies (e.g., Oliver & Beattie 1996; Dungey et al. 2000). The ANOSIM procedure tests for differences between groups in a manner analogous

to an F test by comparing within-group similarity to between-group similarities (ANOSIM r ; Legendre & Legendre 1998), with p values determined by a randomization procedure (Clarke 1993; Manly 1997)

We used a subset of the data to address the hypothesis that community composition was driven primarily by the cottonwood genetic component. If cottonwood genetics is important, arthropod composition within either parental cross type will not be different between a pure zone and an adjacent hybrid zone. For example, arthropod composition on Fremont cottonwoods in the Fremont zone will not be different from the arthropod composition on Fremont cottonwoods in the hybrid zone. Arthropod composition on Fremont cottonwoods, however, will always be different than the composition on narrowleaf cottonwoods. Five rivers with a broadleaf zone and a hybrid zone, each with at least five broadleaf trees, were selected. We also used the same criterion to select seven rivers with both a pure narrowleaf zone and a hybrid zone.

To experimentally support our observational data and to further control for environmental effects, we tested differences in composition between four cross types in an 11-year-old common garden containing trees of known genetic composition determined by previous RFLP analysis (Martinsen et al. 2001). Genotypes were planted in the garden of common soil type (Fischer et al. 2004) in a randomized-interspersed design, and trees were selected randomly for this study. Because these trees were of known genetic composition, we could distinguish between the backcross and narrowleaf cross types. In 2000 and 2001, we conducted timed visual surveys for arthropod structures on 200 shoots per tree on 10 trees per cross type. For the 2002 common garden data, we sampled trees in the same manner as the field study. Community and genetic composition were compared with NMDS and ANOSIM.

To address the hypothesis that diversity was greatest in hybrid zones, we again used a two-factor split-plot ANOVA with river as a blocking variable nested within slope, and compared total richness per zone. The three zones were delineated as pure broadleaf, hybrid, and pure narrowleaf. Because richness is correlated with abundance (the density effect—Denslow 1995; Chazdon et al. 1999), we rarefied richness on abundance to the zone with the lowest abundance within each river (Gotelli & Colwell 2001). We then compared composition between zones with NMDS and ANOSIM analyses by combining all trees (20) within each zone by river into a single community.

Finally, to address the hypothesis that patterns of diversity are stable across scales, we compared patterns of total regional richness among cross types within hybrid zones. We constructed sample-based accumulation curves (Colwell 1997) and modeled the differences of the first 20 trees along each curve to meet the assumptions of linear regression. For example, we calculated the dif-

ference in richness between each accumulating observation and constructed curves of these differences. For each curve, the corresponding differences were regressed on the square of the reciprocal of the observation number. We ran diagnostic tests on the regression curves to check assumptions such as normality, equal variances, absence of autocorrelation, and model adequacy. We then compared the ensuing equations with F tests to determine whether there were significant differences in species accumulation curves among cross types. We modeled the first 20 trees because differences in richness are manifest early in the accumulation process.

We examined community composition by cross type at the single hybrid zone scale and the regional slope scale with NMDS and ANOSIM. At the smallest scale, cross-type composition was analyzed from two separate hybrid zones, one from each slope with similar proportions of the cross types. At the slope scale, cross-type composition was analyzed for all hybrid zone trees. Because the slope scale of composition involved 305 trees, the communities from 5 individual trees were combined into a single community for a more efficient presentation of the data. These communities were both qualitatively and quantitatively similar to the analysis on single-tree communities.

Finally, we conducted a general analysis for indicator species for the four cross types across all zones and rivers (Dufrene & Legendre 1997). Indicator value analysis evaluates the affinity of a species for a cross type and the distribution of that species across all sample units independent of other species. Thus, the indicator value represents the percent occurrence of that species within a cross type with p values calculated via a randomization procedure.

Results

Cross-Type Effects on Arthropod Diversity

Backcross trees had significantly more species per tree than the broadleaf cross type and the F_1 cross type was intermediate ($F_{2,17} = 15.37$, $p < 0.001$; Fig. 2). Although there were river and slope (i.e., Pacific versus Atlantic drainages) effects, there was no slope-by-cross-type interaction, suggesting that the cross-type effect is stable along the environmental gradient from the Colorado Plateau to the Colorado Front Range, where both of these hybridizing systems show similar patterns of richness.

Neither the broadleaf nor the backcross/narrowleaf cross types exhibited differences in composition between their pure and the hybrid zones (ANOSIM: broadleaf $r = -0.02$, $p = 0.57$; backcross/narrowleaf $r = 0.05$, $p = 0.13$; Fig. 3). These data support our hypothesis that the cross-type effect on community composition was stronger than the environmental effect (i.e., a cross type growing in a pure zone does not exhibit differences from the same

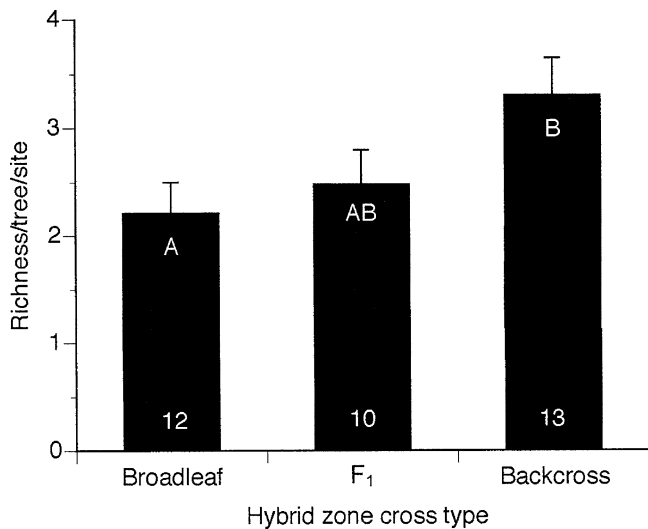


Figure 2. Mean arthropod richness by cottonwood cross type per tree per hybrid zone ± 1 SE. Different letters represent significant differences between treatment classes determined by Tukey's least significant difference. Numbers within bars represent the number of replicate hybrid zone sites.

cross type growing in an adjacent hybrid zone). Furthermore, there was significant separation of communities between the two cross-type extremes ($r = 0.92$, $p < 0.001$; Fig. 3), which further supports the hypothesis that cross type had a stronger influence than environmental factors on this group of arthropods.

COMMON GARDEN EXPERIMENT

Observational field data from multiple river systems demonstrated that cross-type effects on this assemblage of arthropods were important. To experimentally determine whether the genetic effects would be as consistent as our field data suggested, we quantified patterns of species composition in an 11-year-old common garden, where environmental effects were largely eliminated. Two major patterns emerged. First, patterns of species composition were similar across all 3 years in the common garden, where the community composition on backcross and narrowleaf trees was not different (all $p > 0.67$). The Fremont and F_1 hybrid cross types supported different communities (2000–2001, $p < 0.05$; 2002, $p < 0.001$), and the composition on the backcross/narrowleaf cross type was different from that on the Fremont and F_1 cross types (all $p < 0.001$; Fig. 4a–c). This result agreed with our compositional patterns in the field and supported the categorization of the backcross and narrowleaf cross types as a single group.

Second, genetic composition for the 2002 trees exhibited a similar pattern where all cross types had different genetic compositions (all pairwise $p \leq 0.001$; Fig. 4d),

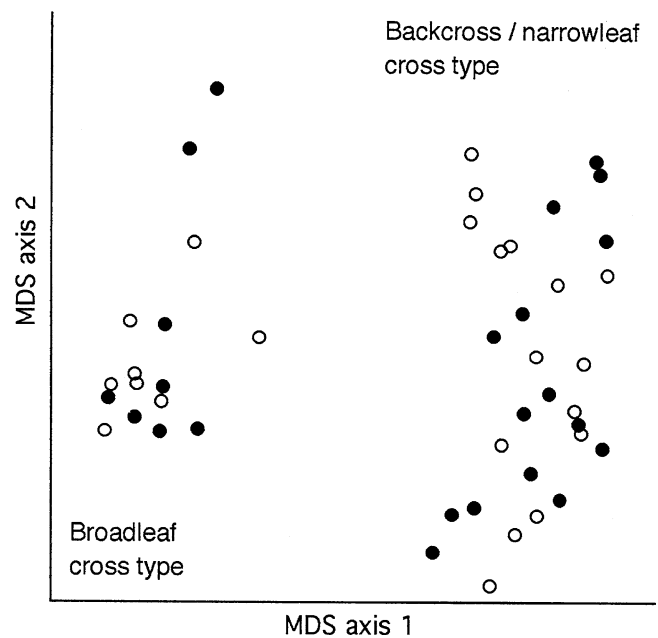


Figure 3. Nonmetric multidimensional scaling (NMDS) ordination of arthropod community composition on cottonwood cross types between the pure (●) and hybrid (○) zones. Community composition is different between cottonwood cross types but not different within a cross type between zones. The NMDS procedure produces plots in which each point represents a single community. Points that are close together are more similar, with respect to Sorenson's similarity index, than points that are distant; thus, MDS axes are without units.

and trees with similar genetic compositions had similar community compositions (Mantel $t = 5.60$, $p < 0.001$, Fig. 4c–d). These results support the observational data indicating that composition was strongly correlated with cross type in this leaf-modifying assemblage. The genetic diversity of the host plant, then, should be an important conservation consideration.

Cottonwood Habitat

Cottonwood hybrid zones supported the greatest total richness and were significantly more rich in arthropod species than the pure broadleaf zones, but the cottonwood hybrid zones did not differ from the narrowleaf zones across multiple rivers ($F_{2,16} = 5.88$, $p = 0.012$; Fig. 5a). There were no significant slope, river, or slope-by-river interaction terms.

Community composition was also significantly different among all three zones (overall ANOSIM $r = 0.40$, $p < 0.001$; Fig. 5b). Although the environments associated with the different zones probably affected total richness and composition, these results further suggest that cottonwood genetic diversity mediates environmental

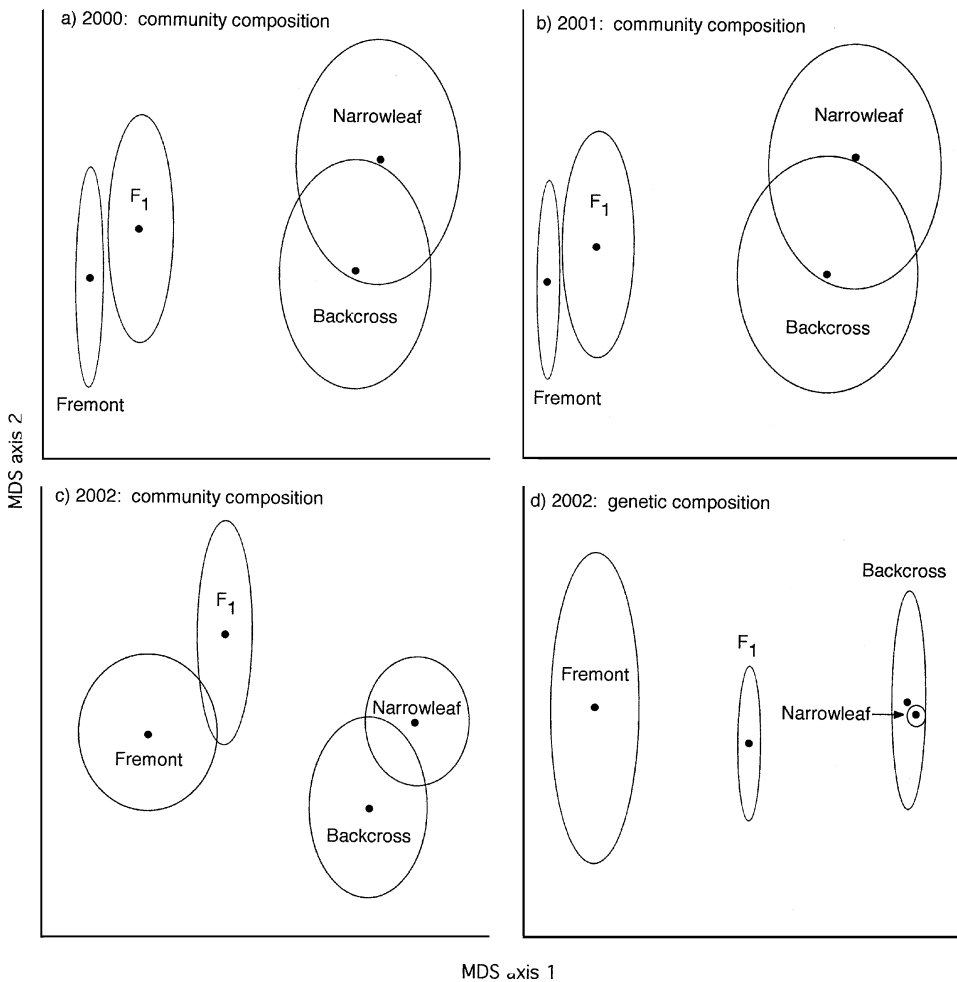


Figure 4. (a-c) Arthropod morphospecies composition on trees of known genetic composition. (d) Genetic composition on trees in the common garden. Both the arthropod and genetic compositions show the same pattern across 3 years in an experimental common garden. Solid symbols are ordination centroids with 95% confidence ellipses.

variation. For example, the community of the hybrid zone site on the Verde River was located in broadleaf ordination space because it contained no backcross trees. Conversely, the hybrid site on Birch Creek was located in narrowleaf ordination space because it was composed of 95% backcross trees (Fig. 5b).

Species Diversity at Multiple Scales

SPECIES RICHNESS

Patterns of leaf-modifier richness in hybrid zones exhibited similar patterns at the regional scale on both the Pacific and Atlantic slopes. This leaf-modifying assemblage is strongly correlated with cottonwood cross types at the individual tree and river scales. The F₁ and backcross cross types supported more total leaf modifiers regionally than the broadleaf cross type (F₁ versus broadleaf: $F_{3,51} = 4.07$, $p < 0.0114$; backcross versus broadleaf: $F_{3,51} = 6.51$, $p = 0.0008$), but the F₁ and backcross cross types were not significantly different (F₁ versus backcross: $F_{3,51} = 0.85$, $p = 0.4709$; Fig. 6). The regional F₁ curve was still increasing, indicating that F₁s eventually accumulated most of the species from both parents along with unique

species, whereas the other two curves reached an apparent asymptote (Fig. 6). In fact, the backcross cross type required another 90 trees to add one more species. This illustrates how patterns of species richness can accumulate differently at different scales. One or both of the hybrid cross types, however, exhibited significantly greater richness than the broadleaf cross type across multiple scales—from single trees to the region—supporting the hypothesis that hybrid trees are host to more species than parental hosts at multiple scales.

ASSEMBLAGE COMPOSITION

The pattern of species composition in the common garden was also found in individual hybrid zones and across slopes. Arthropod composition in hybrid zones was significantly different among all three cross types at the river scale and the slope scale (ANOSIM: all pair wise $p < 0.0001$; Fig. 7), suggesting that cross type had an influence on both community richness and structure. It might be expected that environmental variability and community assembly history (i.e., contingency sensu Fritz et al. 1999; Lawton 1999) obscure community-wide patterns especially at large spatial scales. The bottom-up genetic

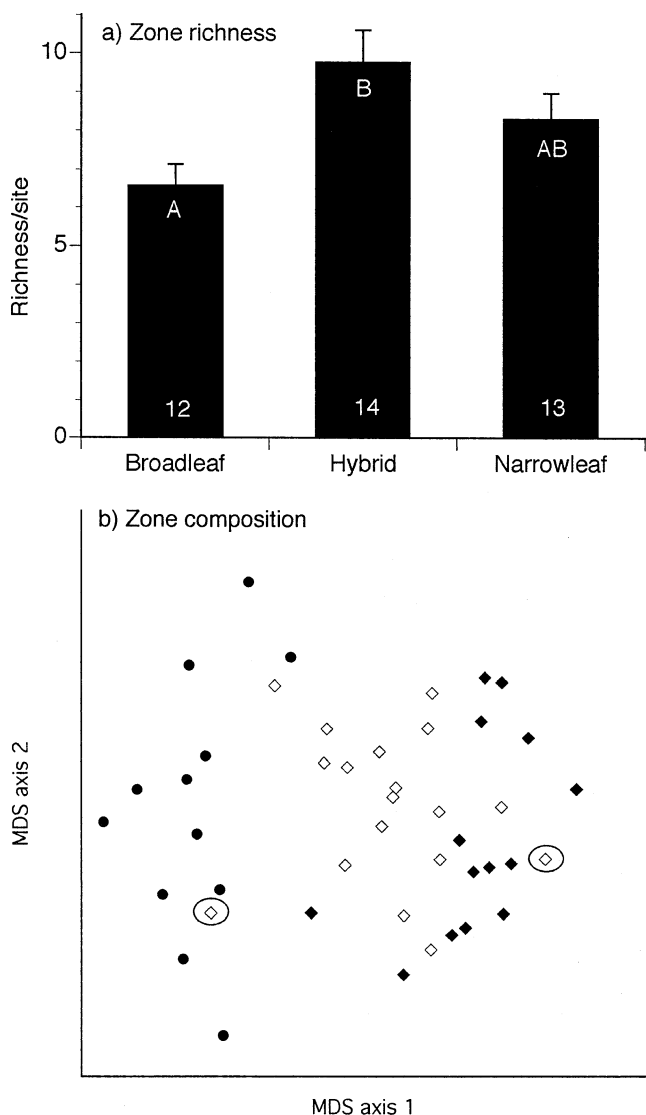


Figure 5. (a) Arthropod total richness in the three cottonwood zones across replicate rivers. Error bars represent ± 1 SE, different letters represent significant differences between treatment classes, and the numbers within bars represent the number of replicates. The (b) nonmetric multidimensional scaling ordination of arthropod community composition is different in the broadleaf (\bullet), hybrid (\diamond), and narrowleaf (\blacklozenge) zones across replicate rivers. The hybrid zone sites that are circled in panel (b) were similar in cottonwood cross-type composition to the pure zones.

basis to richness and species composition, though, resulted in an emergent property in the form of repeatable patterns at all scales in two different hybridizing systems. At the largest scale, 56% of the morphospecies were significant indicators (all $p < 0.05$) of cross type, where each cross type had 3 to 4 indicator species, resulting in differences in assemblage composition.

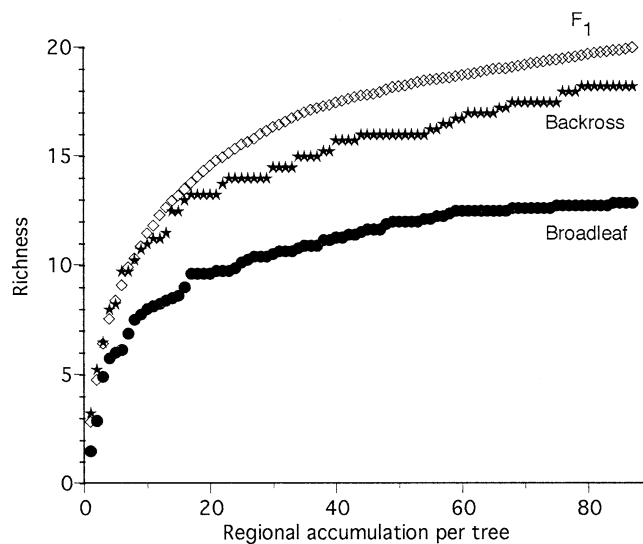


Figure 6. Total arthropod species accumulation for all cottonwood hybrid zones across the extent of this study rarified to the number of trees in the F₁ cross type as the limiting factor.

Discussion

Our experimental and observational studies from a common garden and from individual rivers on both the Pacific and Atlantic slopes of the Rocky Mountains supported the concept that the genetic diversity of a dominant species is important to its dependent community (e.g., Dungey et al. 2000). These data showed four major patterns: (1) the highest arthropod richness (i.e., alpha diversity) was associated with the genetically most diverse cross types; (2) hybrid zones had the greatest host-plant genetic diversity and arthropod richness; (3) there was high arthropod beta diversity among host-plant cross types; and (4) these patterns were found at both local and regional scales. All four have several major implications for conservation.

Genes as Community Organizers

Tree cross type was a stronger component in structuring this leaf-modifying assemblage than the environment at multiple scales ranging from individual trees to hundreds of trees across hundreds of kilometers. Several lines of evidence support the genetic argument. At both the smallest and largest scales, at least one of the hybrid cross types was host to more arthropod species than the pure broadleaf parent in common environments in both observational and experimental studies. Community composition was different among tree cross types and on trees of known genetic composition in a common garden environment. This pattern was also observed in the field even though there was much greater environmental variability at the regional scale across 21 rivers. This arthropod assemblage was distinguishable between the two parental

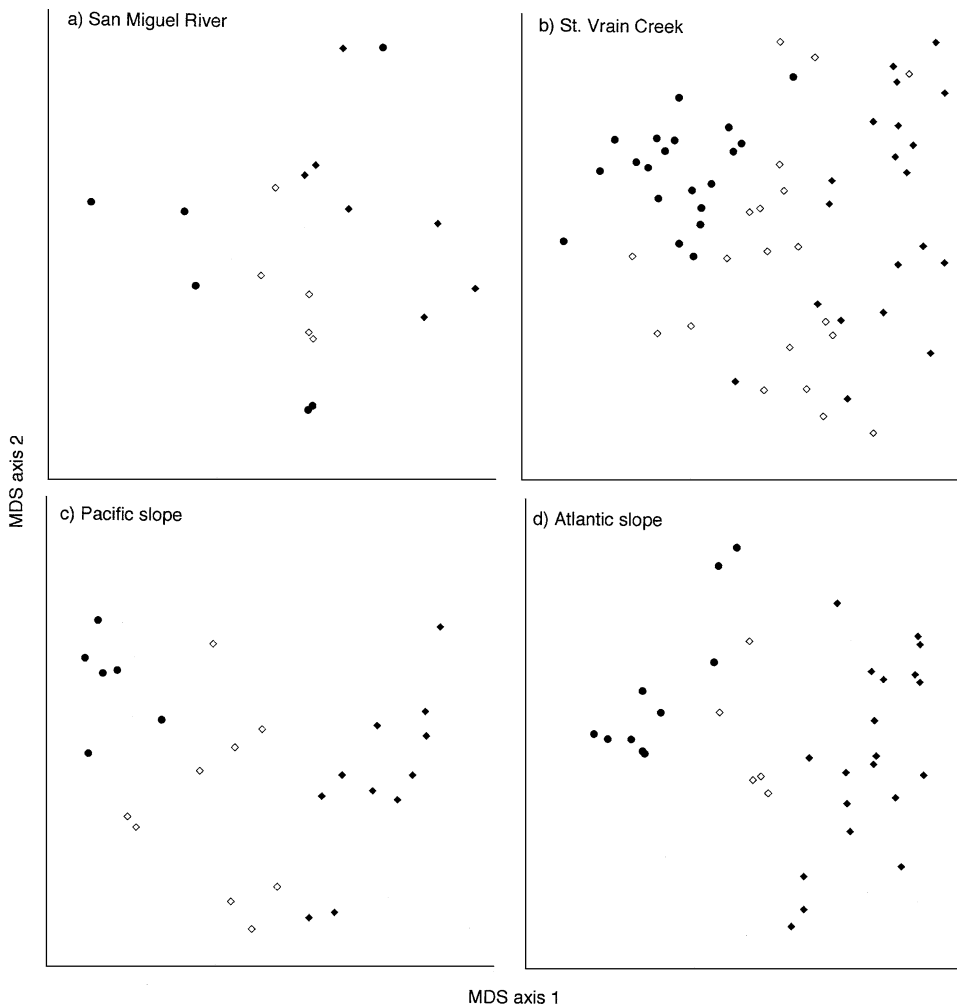


Figure 7. Nonmetric multidimensional scaling ordinations of arthropod community composition on broadleaf (●), hybrid (◇), and backcross/narrowleaf (◆) cross types at the river scale in the (a) Pacific and (b) Atlantic regions and at the (c) Pacific and (d) Atlantic regional scales.

cross types but was not distinct within a parental cross type between different environments (i.e., pure and hybrid zones). This indicates that the environment-by-gene interaction affecting this assemblage is relatively weak and that cross type is the stronger factor.

Hybrid zones had greater richness than the pure broadleaf zones, in part because of greater cottonwood cross-type diversity (i.e., genetic diversity; Whitham et al. 1999). Initially, this indicated that this assemblage was responding to different host species. However, there is gene flow between the two parental species, resulting in a hybrid swarm, and this arthropod assemblage had greater richness on hybrid trees.

Greater species richness is not always evident on hybrids (Boecklen & Spellenberg 1990), but community composition is often different between hybrids and parental classes (Boecklen & Spellenberg 1990; Fritz et al. 1994), resulting in high beta diversity. In the cottonwood system, arthropod compositional differences were not solely the result of different host species but instead resulted from different hybrid cross types within this host-plant species complex. This is important because several of these leaf modifiers increase the diversity of the

free-living arthropod and avian communities (Whitham et al. 1999), so even small differences in leaf-modifier richness could result in large differences in overall diversity. Also, differences in community composition result in an increase in overall diversity. Consequently, our data show (1) that we need to rethink the reputed negative role of hybrids in ecology and conservation (Carroll et al. 1996; Whitham & Maschinski 1996; Whitham et al. 1999), and (2) that all cross types are necessary to maintain maximum host-plant diversity.

Because there is significant gene flow among tree cross types (e.g., 21% of Fremont molecular markers can introgress into the narrowleaf genome; Martinsen et al. 2001), there is the potential for increased genetic diversity and, consequently, the heritability of factors responsible for community structure (Whitham et al. 2003). For example, a genetic basis for ecosystem function has been demonstrated in cottonwoods (Fischer et al. 2004; Schweitzer et al. 2004), and aquatic decomposition is different across cottonwood cross types (Driebe & Whitham 2000). Finally, host-plant gene diversity explains 60% of arthropod community diversity (G.M.W., unpublished data). When the host plant is the habitat, there is the

potential that the genetic diversity of the habitat might structure community composition (e.g., Fritz & Price 1988; Floate et al. 1996). Where there is high genetic variability among plants, herbivore diversity should be greatest (Whitham et al. 1999). Therefore, natural hybrid zones may represent diversity hotspots and should be important focal points for the conservation of biodiversity and ecological and evolutionary processes (Whitham et al. 1999; Prance 2000; Ashley et al. 2003).

Conservation of Hybrid Zones

In general, riparian cottonwood corridors in the Rocky Mountain region comprise only 2 to 5% of the landscape, are heavily affected by human activities (e.g., Dobkin et al. 1998), and are used by as many as 22 and 28% more vertebrate species than surrounding ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests or piñon (*Pinus edulis* Engelm.)/juniper (*Juniperus* spp.) woodlands, respectively (Finch & Ruggiero 1993). The riparian cottonwood corridors we studied were embedded within the ponderosa or piñon/juniper habitat types. Within this species-rich riparian habitat, arthropod diversity was concentrated in hybrid zones and further concentrated on both of the hybrid cross types relative to the broadleaf cottonwood parent, resulting in a hierarchical concentration of diversity. Thus, cottonwood corridors are local hotspots of diversity, similar to geographic crossroads, because two plant species come into contact. Hybrid zones are zones of genetic transition because there is a transition between species resulting in high levels of plant genetic diversity that enhances arthropod alpha and beta diversity (Whitham et al. 1999). Because riparian corridors are dendritic in nature, they effectively infiltrate the landscape but are also susceptible to fragmentation; thus, there is the potential for large effects on multiple species through both infiltration and fragmentation. Moreover, by conserving entire riparian corridors, cottonwood zones can remain dynamic and adjust to climate change as zones of transition (Smith et al. 2001; Araújo 2002). These results support the concept that habitat conservation is more efficient than single-species conservation, resulting in the conservation of both evolutionary (Ashley et al. 2003) and ecological processes.

Although cottonwoods are not endangered species, riparian habitat, especially in the western United States, is designated as threatened as a result of human activity (Noss et al. 1995). Approximately 100,000 ha of cottonwood habitat is lost every year (Finch & Ruggiero 1993), resulting in a significant loss of habitat that could have a potential effect on hundreds of species across multiple trophic levels and major taxonomic groups. Because multiple taxa respond to these hybridizing swarms, the conservation of cottonwood diversity should result in the conservation of associated species diversity. Thus, hybrid zones are a model system that incorporates mul-

multiple conservation issues: habitat conservation, the genetics of habitat, natural hybrids, diversity hotspots, geographic crossroads, and zones of transition (Dobson et al. 1997; Reid 1998; Smith et al. 2001; Spector 2002). Dominant plants define many habitats (e.g., ponderosa forest or green ash woodlands; Finch & Ruggiero 1993). In addition, many dominant plants hybridize (e.g., oaks [*Quercus* spp.], Boecklen & Spellenberg 1990; piñon, Christensen et al. 1995; rabbitbrush [*Chrysothamnus* spp.], Floate et al. 1996; eucalypts [*Eucalyptus* spp.], Dungey et al. 2000; and sagebrush [*Artemisia*], Graham et al. 2001), and plant and animal interactions comprise a large proportion of biotic relationships. Thus, the consideration of habitat genetic diversity can be a general and efficient approach to conserving both process and diverse assemblages of both plants and animals.

Acknowledgments

We thank the following people and organizations for access to cottonwood trees: Ogden Nature Center; S. Romero and the people of the Nambe Pueblo; V. Cuthair, the Ute Mountain Tribal Park Enterprise, the Ute Mountain Environmental Programs, and the Ute Mountain Tribal Council; C. Valdez and the Southern Ute Tribe; the Colorado Nature Conservancy; City of Boulder Open Space and Mountain Parks; Denver Mountain Parks; and Jefferson County Open Space. The comments of K. Haskins, P. W. Price, P. Service, S. M. Shuster, J. A. Schweitzer, J. A. Smallwood, J. G. B. Oostermeijer, G. K. Meffe, E. Main, and two anonymous reviewers significantly improved this paper. Funding was provided by National Science Foundation grant DEB-0078280 and the Merriam-Powell Center for Environmental Research.

Literature Cited

- Aguilar, J. M., and W. J. Boecklen. 1992. Patterns of herbivory in the *Quercus grisea* x *Quercus gambelii* species complex. *Oikos* **64**:498-504.
- Araújo, M. B. 2002. Biodiversity hotspots and zones of ecological transition. *Conservation Biology* **16**:1662-1663.
- Arnold, M. L. 1997. *Natural hybridization and evolution*. Oxford University Press, Oxford, United Kingdom.
- Arnold, M. L., and S. A. Hodges. 1995. Are natural hybrids fit or unfit relative to their parents? *Trends in Ecology & Evolution* **10**:67-71.
- Ashley, M. V. 1999. Molecular conservation genetics. *American Scientist* **87**:28-35.
- Ashley, M. V., M. F. Willson, O. R. W. Pergams, D. J. O'Dowd, S. M. Gende, and J. S. Brown. 2003. Evolutionary enlightened management. *Biological Conservation* **111**:115-123.
- Bailey, J. K., and T. G. Whitham. 2003. Interactions among elk, aspen, galling sawflies, and insectivorous birds. *Oikos* **101**:127-134.
- Bellinger, M. R., J. A. Johnson, J. Toepfer, and P. Dunn. 2003. Loss of genetic variation in greater prairie chickens following a population bottleneck in Wisconsin, U.S.A. *Conservation Biology* **17**:717-724.
- Boecklen, W. J., and R. Spellenberg. 1990. Structure in herbivore communities in two oak (*Quercus* spp.) hybrid zones. *Oecologia* **85**:92-100.

- Bouzat, J. L., H. H. Cheng, H. A. Lewin, R. L. Westemeier, J. D. Brawn, and K. N. Paige. 1998. Genetic evaluation of a demographic bottleneck in the greater prairie chicken. *Conservation Biology* **12**:836–843.
- Carroll, R., C. Augspurger, A. Dobson, J. Franklin, G. Orians, W. Reid, R. Tracy, D. Wilcove, and J. Wilson. 1996. Strengthening the use of science in achieving the goals of the Endangered Species Act: an assessment by the Ecological Society of America. *Ecological Applications* **6**:1–11.
- Chazdon, R. L., R. K. Colwell, and J. S. Denslow. 1999. Tropical tree richness and resource-based niches. *Science* **285**:1459a.
- Christensen, K. M., T. G. Whitham, and P. Keim. 1995. Herbivory and tree mortality across a piñon pine hybrid zone. *Oecologia* **101**:29–36.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**:117–143.
- Colwell, R. K. 1997. EstimateS: statistical estimation of species richness and shared species from samples. University of Connecticut, Storrs. Available from <http://viceroy.ceb.uconn.edu/estimates> (accessed May 2004).
- Denslow, J. 1995. Disturbance and diversity in tropical rain forests: the density effect. *Ecological Applications* **5**:962–968.
- Dobkin, D. S., A. C. Rich, and W. H. Pyle. 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. *Conservation Biology* **12**:209–221.
- Dobson, A. P., J. P. Rodriguez, W. M. Roberts, and D. S. Wilcove. 1997. Geographic distribution of endangered species in the United States. *Science* **275**:550–553.
- Dreger-Jauffret, F., and J. D. Shorthouse. 1992. Diversity of gall-inducing insects and their galls. Pages 8–33 in J. D. Shorthouse and O. Rohfritsch, editors. *Biology of insect-induced galls*. Oxford University Press, New York.
- Driebe, E. M., and T. G. Whitham. 2000. Cottonwood hybridization affects tannin and nitrogen content of leaf litter and alters decomposition. *Oecologia* **123**:99–107.
- Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species definition: the need of an asymmetrical and flexible approach. *Ecological Monographs* **67**: 345–366.
- Dungey, H. S., B. M. Potts, T. G. Whitham, and H.-F. Li. 2000. Plant genetics affects arthropod community richness and composition: evidence from a synthetic eucalypt hybrid population. *Evolution* **54**:1938–1946.
- Eckenwalder, J. E. 1984a. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections *Aigeiros* and *Tacahamaca*. II. Taxonomy. *Canadian Journal of Botany* **62**:325–335.
- Eckenwalder, J. E. 1984b. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections *Aigeiros* and *Tacahamaca*. III. Paleobotany and evolution. *Canadian Journal of Botany* **62**:336–342.
- Eckenwalder, J. E. 1996. Systematics and evolution of *Populus*. Pages 7–32 in R. F. Stettler, H. D. Bradshaw Jr., P. E. Heilman, and T. M. Hinckley, editors. *The biology of Populus*. National Research Council Press, Ottawa, Canada.
- Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**:57–68.
- Finch, D. M., and L. F. Ruggiero. 1993. Wildlife habitats and biological diversity in the Rocky Mountains and northern Great Plains. *Natural Areas Journal* **13**:191–203.
- Fischer, D. G., S. C. Hart, and T. G. Whitham. 2004. Genetic variation in water-use parameters in cottonwoods: ecosystem implications. *Oecologia*: in press.
- Fisher, B. L. 1998. Insect behavior and ecology in conservation: preserving functional species interactions. *Annals of the Entomological Society of America* **91**:155–158.
- Floate, K. D., and T. G. Whitham. 1993. The “hybrid bridge” hypothesis: host shifting via plant hybrid swarms. *The American Naturalist* **141**:651–662.
- Floate, K. D., and T. G. Whitham. 1995. Insects as traits in plant systematics: their use in discriminating between hybrid cottonwoods. *Canadian Journal of Botany* **73**:1–13.
- Floate, K. D., G. W. Fernandes, and J. A. Nilsson. 1996. Distinguishing intrapopulation categories of plants by their insect faunas: galls on rabbitbrush. *Oecologia* **105**:221–229.
- Floate, K. D., G. D. Martinsen, and T. G. Whitham. 1997. Cottonwood hybrid zones as centres of abundance for gall aphids in western North America: importance of relative habitat size. *Journal of Animal Ecology* **66**:179–188.
- Fritz, R. S., and P. W. Price. 1988. Genetic variation among plants and insect community structure: willows and sawflies. *Ecology* **69**:845–856.
- Fritz, R. S., C. M. Nichols-Orians, and S. J. Brunsfeld. 1994. Interspecific hybridization of plants and resistance to herbivores: hypotheses, genetics, and variable responses in a diverse herbivore community. *Oecologia* **97**:106–117.
- Fritz, R. S., B. M. Roche, and S. J. Brunsfeld. 1998. Genetic variation in resistance of hybrid willows to herbivores. *Oikos* **83**:117–128.
- Fritz, R. S., C. Moulia, and G. Newcombe. 1999. Resistance of hybrid plants and animals to herbivores, pathogens, and parasites. *Annual Reviews of Ecology & Systematics* **30**:565–591.
- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**:379–391.
- Graham, J. H., E. D. McArthur, and D. C. Freeman. 2001. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae) XII. Galls on sagebrush in a reciprocal transplant garden. *Oecologia* **126**:239–246.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* **69**:373–386.
- Keim, P., K. N. Paige, T. G. Whitham, and K. G. Lark. 1989. Genetic analysis of an interspecific hybrid swarm of *Populus*: occurrence of unidirectional introgression. *Genetics* **123**:557–565.
- Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7**:796–808.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* **84**:177–192.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. 2nd edition. Elsevier, Amsterdam.
- Mani, M. S. 1992. Introduction to cecidology. Pages 3–7 in J. D. Shorthouse and O. Rohfritsch, editors. *Biology of insect-induced galls*. Oxford University Press, New York.
- Manly, B. F. J. 1997. *Randomization and Monte Carlo methods in biology*. 2nd edition. Chapman and Hall, New York.
- Martinsen, G. D., T. G. Whitham, R. J. Turek, and P. Keim. 2001. Hybrid populations selectively filter gene introgression between species. *Evolution* **55**:1325–1335.
- Meffe, G. K. 1996. Conserving genetic diversity in natural systems. Pages 41–76 in R. C. Szaro and D. W. Johnston, editors. *Biodiversity in managed landscapes*. Oxford University Press, Oxford, United Kingdom.
- Minchin, P. R. 1987. Simulation of multidimensional community patterns: towards a comprehensive model. *Vegetatio* **71**:145–156.
- Minchin, P. R. 1999. DECODA: database for ecological community data. Version 3.00 b06. Australian National University, Canberra.
- Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. *Endangered ecosystems of the United States: a preliminary assessment of loss and degradation*. Biological report 28. U.S. National Biological Service, Washington, D.C.
- O’Brien, S. J., and E. Mayr. 1991. Bureaucratic mischief: recognizing endangered species and subspecies. *Science* **251**:1187–1188.
- Oliver, I., and A. J. Beattie. 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* **7**:562–568.
- Oliver, I., and A. J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology* **10**:99–109.
- Opler, P. A. 1974. Oaks as evolutionary islands for leaf-mining insects. *American Scientist* **62**:67–73.

- Prance, G. 2000. The failure of biogeographers to convey the conservation message. *Journal of Biogeography* **27**:51-53.
- Price, M. V., and N. M. Wasser. 1979. Pollen dispersal and optimal outcrossing in *Delphinium nelsoni*. *Nature* **227**:294-297.
- Price, P. W., G. W. Fernandes, and G. L. Waring. 1987. Adaptive nature of insect galls. *Environmental Entomology* **16**:15-24.
- Price, P. W., G. W. Fernandes, A. C. F. Lara, J. Brawn, H. Barrios, M. G. Wright, S. P. Ribeiro, and N. Rothcliff. 1998. Global patterns in local number of insect galling species. *Journal of Biogeography* **25**:581-591.
- Price, P. W. 2003. Macroevolutionary theory on macroecological patterns. Cambridge University Press, Cambridge, United Kingdom.
- Prior, K. A., H. L. Gibbs, and P. J. Weatherhead. 1997. Population genetic structure in the black rat snake: implications for management. *Conservation Biology* **11**:1147-1158.
- Reid, W. V. 1998. Biodiversity hotspots. *Trends in Ecology & Evolution* **13**:275-280.
- Rieseberg, L. H. 1995. The role of hybridization in evolution: old wine in new skins. *American Journal of Botany* **82**:944-953.
- Schweitzer, J. A., G. D. Martinsen, and T. G. Whitham. 2002. Cottonwood hybrids gain fitness traits of both parents: a mechanism for their long-term persistence? *American Journal of Botany* **89**:981-990.
- Schweitzer, J. A., J. K. Bailey, B. J. Rehill, G. D. Martinsen, S. C. Hart, R. L. Lindroth, P. Keim, and T. G. Whitham. 2004. Genetically based trait in a dominant tree affects ecosystem processes. *Ecology Letters* **7**:127-134.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single species management passé in the landscape era? *Biological Conservation* **83**:247-257.
- Smith, T. B., S. Kark, C. J. Schneider, R. K. Wayne, and C. Moritz. 2001. Biodiversity hotspots and beyond: the need for preserving environmental transitions. *Trends in Ecology & Evolution* **16**:431.
- Spector, S. 2002. Biogeographic crossroads as priority areas for biodiversity conservation. *Conservation Biology* **16**:1480-1487.
- Stace, C. A. 1987. Hybridization and the plant species. Pages 115-127 in K. M. Urbanska, editor. *Differential patterns in higher plants*. Academic Press, New York.
- Whitham, T. G., and J. Maschinski. 1996. Current hybrid policy and the importance of hybrid plants in conservation. Pages 103-112 in J. Maschinski, D. H. Hammond, and L. Holter, technical editors. *Southwestern rare and endangered plants: proceedings of the second conference*. General technical report RM-283. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado.
- Whitham, T. G., P. A. Morrow, and B. M. Potts. 1994. Plant hybrid zones as centers of biodiversity: the herbivore community of two endemic Tasmanian eucalypts. *Oecologia* **97**:481-490.
- Whitham, T. G., G. D. Martinsen, K. D. Floate, H. S. Dungey, B. M. Potts, and P. Keim. 1999. Plant hybrid zones affect biodiversity: tools for a genetic based understanding of community structure. *Ecology* **80**:416-428.
- Whitham, T. G., et al. 2003. Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* **84**:559-573.
- Wimp, G. M., W. P. Young, S. A. Woolbright, G. D. Martinsen, P. Keim, and T. G. Whitham. 2004. Conserving plant genetic diversity for dependent for animal communities. *Ecology Letters* **7**:776-780.

