Cottonwood Ecology Group, Northern Arizona University

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Research Notes for Land Managers

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Editor's Note

The following data sets, implications, and management recommendations are based upon ongoing field and common garden studies with Fremont (*Populus fremontii*) and narrowleaf (*Populus angustifolia*) cottonwood throughout Arizona, New Mexico, Utah, Nevada, Colorado, Montana and Idaho. They involve ongoing collaborations between the Blue Ridge Forest Service, AZ Game and Fish, Natural Resources Conservation Service, Bar T Bar Ranch, NAU grounds, Natural Channel Design, City of Flagstaff, Pinetop Game and Fish, Pinetop Forest Service, Bureau of Reclamation, Cibola National Wildlife Refuge, Ogden Nature Center, Utah Department of Natural Resources and the National Science Foundation to merge basic research and restoration. This issue includes brief reports on 10 major topics. ***We emphasize that many of these findings are preliminary, and many have not yet gone through the formal review process for publication, which can take years. These notes are meant to inform managers of our most current research findings and their management implications.*** Findings are presented in a short, readily accessible format. Each major topic is organized according to four subheadings listed as 1) Key Findings, 2) Major Lines of Evidence, 3) Major Conservation and Restoration Implications, and 4) Practical Recommendations. We welcome your feedback on these topics (Thomas.Whitham@nau.edu; Gery.Allan@nau.edu).

Climate change and the future of cottonwood riparian areas in the Southwest

Key Finding – Record droughts in the Southwest since 1996 have taken a toll on major vegetation types. Although mortality was highest for pinyon pine in common PJ woodlands, Fremont cottonwoods in rare riparian habitat suffered 20.7% mortality (Gitlin et al. 2006). These findings argue that it is important to understand the scope of the problem for riparian habitat throughout the Southwest and to take an aggressive stance on preventing future losses for a habitat type that is already considered threatened (Noss et al. 1995).

Three major lines of evidence – 1.1 - Climate change models predict that with continued warming and drought, the distribution of cottonwoods will be dramatically altered and will be eliminated from former areas of abundance (Gitlin & Whitham, unpub. data). The following figure shows the current distribution of cottonwoods (broadleaf Fremont and Eastern, narrowleaf and their naturally occurring hybrids) in a 4 state area of

Utah, Arizona, Colorado, and New Mexico. Using the Genetic Algorithm for Rule-set Prediction (GARP) model, panel (a) shows the potential niche distribution for narrowleaf (black) and broadleaf (light grey) cottonwoods, with medium grey showing the potential hybrid zone between species. The broadleaf cottonwoods currently have the largest niche of the cross types. Because cottonwoods only occur along creeks and rivers, panel (b) shows the potential niche map masked to show riparian areas only (species designations same as (a).

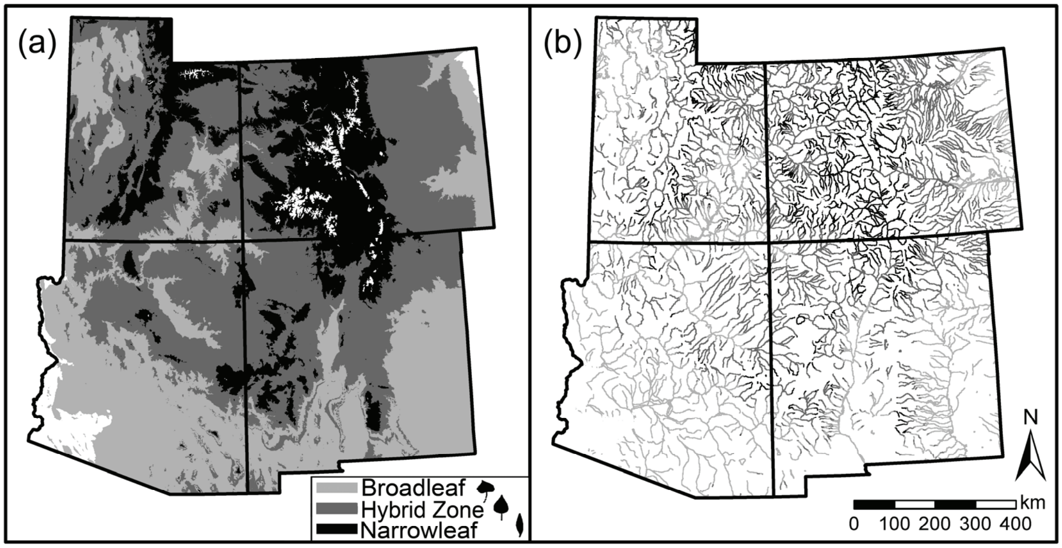


Figure 1. This panel shows the potential niche distribution of cottonwood modeled with GARP.

If you compare the current distribution of these cottonwoods (above Figure 1) with their projected distributions (right Figure 2) based upon increasing temperatures and declining moisture, note the dramatic shift in their distributions. **For example, the white area denotes regions of the Southwest that are largely devoid of cottonwoods; note how that area vastly increases with a climate change scenario that is generally accepted as being realistic (e.g., contrast above panel (a) with lower right hand panel below)** (Gitlin and Whitham unpub. data).

Future climate models predict greatly reduced *potential* distributions for cottonwood.

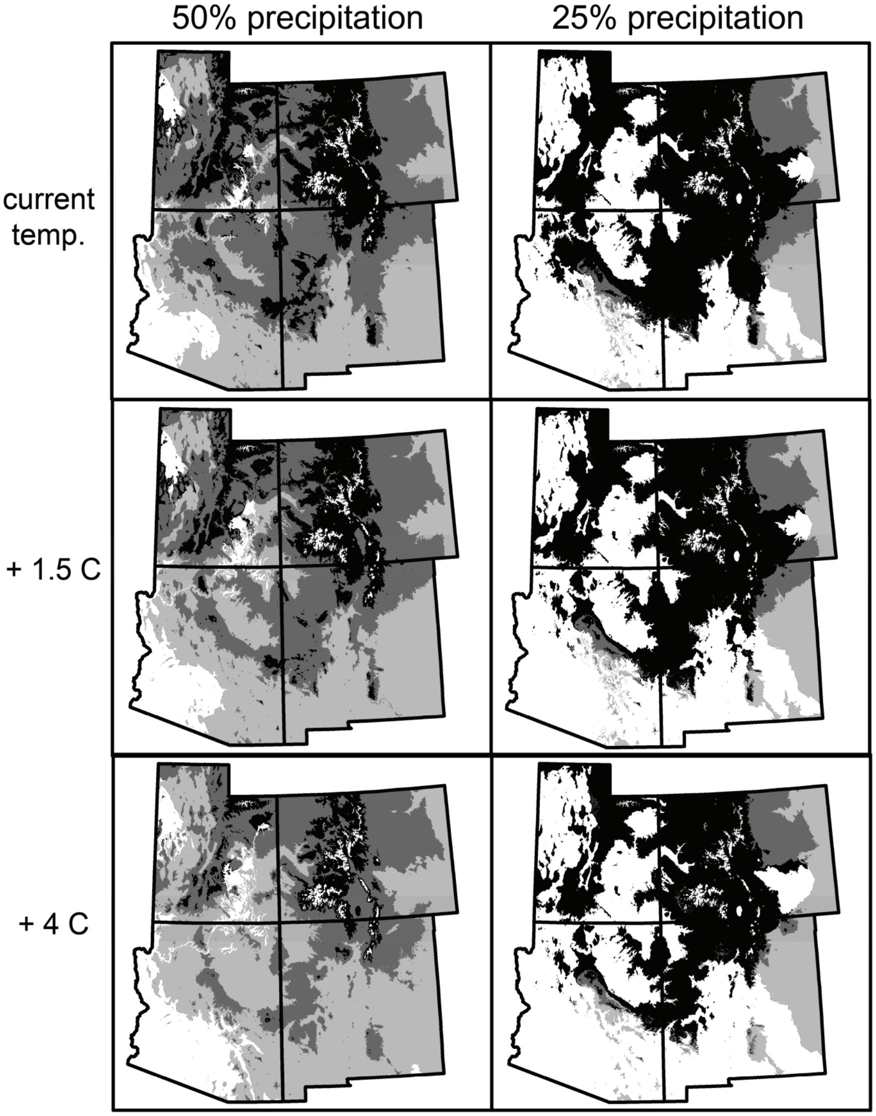


Figure 2. These panels indicate the potential distribution of cottonwood under several different combinations of increased temperature and decreased moisture.

1.2 - Broadleaf cottonwoods (Fremont and Eastern) and narrowleaf cottonwood are suffering much higher mortality than their naturally occurring hybrids (Gitlin & Whitham unpublished data). Across the Colorado Plateau, mortality levels of narrowleaf cottonwood, broadleaf and hybrid cottonwoods differed in 2003 and 2004 (Figure 3). Hybrids survived significantly better than either of their parental species. In 2003, 4% of F_1 type hybrids died, which was ~1/3 the mortality of narrowleaf and ~1/4 the mortality of broadleaf cottonwoods (panel a). The same patterns emerged in 2004; F_1 type hybrid mortality remained at 4%, while we recorded 23.3% of narrowleaf and 11.3% of broadleaf cottonwoods dead in that year (panel b).

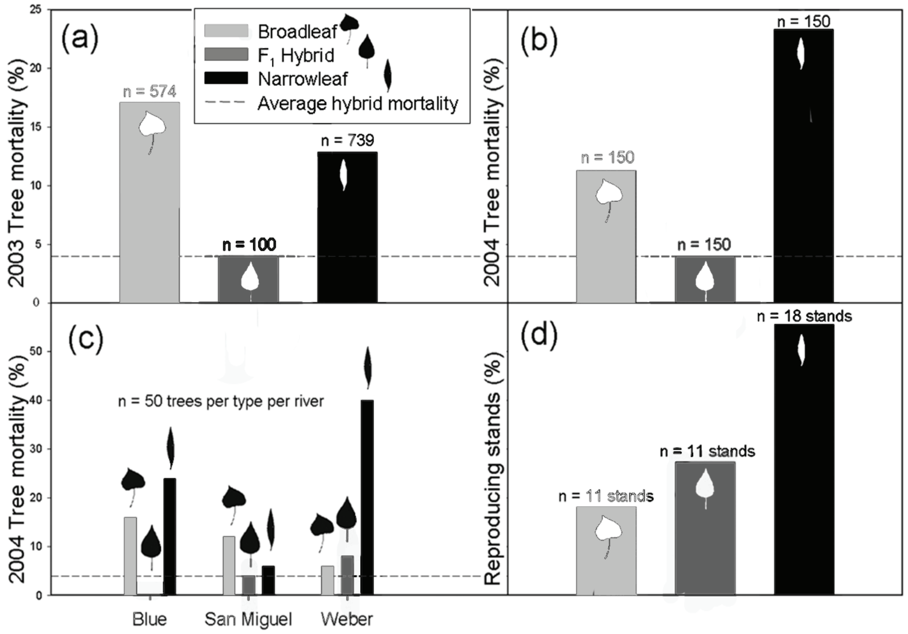


Figure 3. Natural hybrids show lower mortality than parental species (a-c), and broadleaf cottonwoods were found to have the lowest rates of reproduction (d).

Panel (c) shows that although the mortality patterns vary among individual rivers, the overall pattern is for natural hybrids to outperform their parental species. Panel (d) shows the patterns of reproduction in which broadleaf cottonwoods are lower than either natural hybrids or narrowleaf cottonwood. This is largely due to the fact that hybrids and narrowleaf cottonwood can reproduce via sprouting from the roots, whereas broadleaf cottonwoods such as Fremont can only reproduce via seedlings. So, in the absence of flooding events, which are largely eliminated by flood control, plants that clone have a reproductive advantage and are likely to better survive drought and reduced water flows due to agricultural and other human demands on water.

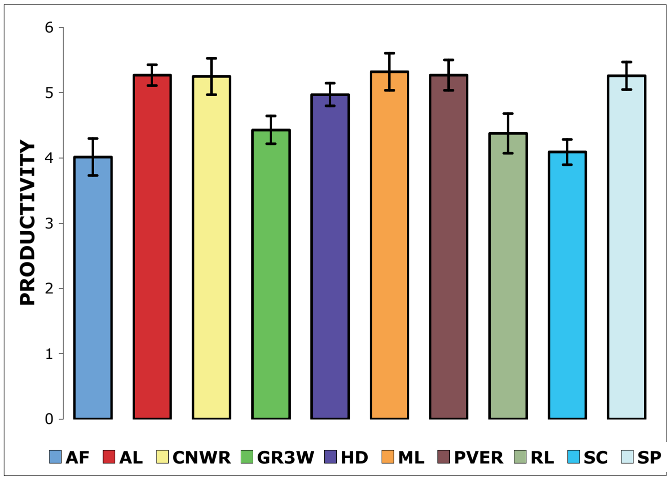


Figure 4. Fremont productivity significantly varies across populations.

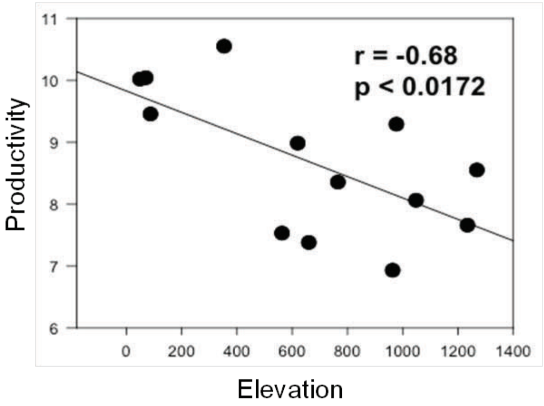


Figure 5. Plant productivity correlates with elevation of the source population.

1.3 - Local source populations may be best adapted to their current local environments. In 2007, we planted over 2000 Fremont cottonwoods that had been propagated from cuttings collected throughout the Basin and Range Hydrogeologic Province in Arizona (174,000 km^2). They were planted at Palo Verde Ecological Reserve, near Blythe, CA in collaboration with the Bureau of Reclamation and California Fish and Game. In addition to the restoration goals of the planting, we sought to find out if local source populations would perform better than source populations from more distant locations. Although it is commonly believed that local source populations will outperform those from farther away, we found that environmental distance is more important than geographic distance for initial survivorship 6 months after planting (Ferrier unpub. data).

As with initial survivorship, we also found that Fremont productivity (p=0.0001) is significantly different across populations (Figure 4 above), and significantly correlates to a generalized environmental cline, elevation (Figure 5 left) (Grady unpub. data). The population variation and clinal association we see in these plant traits may indicate that selection is driving evolutionary differences within this species. More importantly, environmental similarity of source populations to the restoration site will be an important predictor of survival and subsequent performance. We show this to be true for current climatic con-

-ditions, but as we move into a changing future, environmentally similar source populations in current time may shift out of the zone of adaptability for the future.

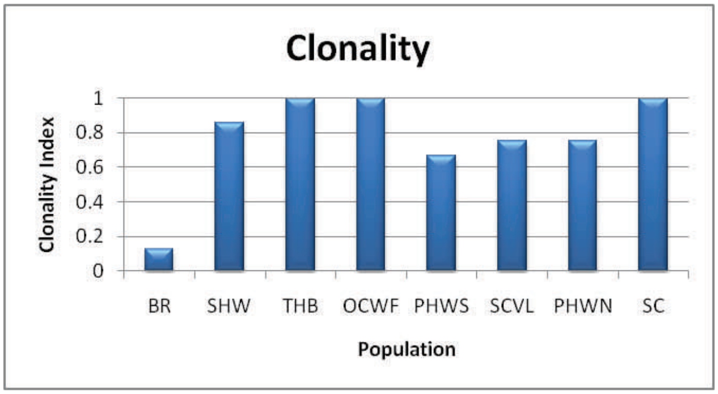
Major Conservation and Restoration Implications – The above findings suggest that predicted climate changes and other anthropogenic effects on the environment are negatively impacting riparian habitats of the Southwest. These effects are likely to represent major challenges to conservation and restoration. As climate change accelerates, we cautiously suggest that local source populations may no longer be best adapted to the local environment. Findings are beginning to emerge in ongoing studies in Canada, and Europe that provide supporting evidence of this concern. The restoration implications are so great that we can't afford to ignore them. Together, the above 3 independent data sets argue that it is very important to set up restoration experiments that explicitly test for climate change and for this hypothesis to be thoroughly investigated.

Practical Recommendations – Climate change is a 'wild card' that will likely require a change in restoration practices. We suspect that the scientific and restoration community is currently unprepared to deal with climate change. We suggest that managers devise alternative restoration strategies that incorporate climate change risk assessment. For example, our findings that naturally occurring hybrids are better than their parents in surviving drought argues that these hybrids should be considered for use in restoration. Furthermore, if the environment will change as much as models predict, then managers will need to seriously consider restoration with non-local genotypes in favor of genotypes from areas with evolutionary histories similar to what we think the 'local' environment has or will become. We recommend that restoration biologists establish plantings using different genotypes from known source populations that have been carefully tagged so that their performance can be quantified and future local restoration efforts can take advantage of this knowledge. Using climate change models, we can establish field trials using genotypes that would have been most appropriate 200 years ago, today, and 200 years into the predicted future. We emphasize that a field trial approach, to determine what 'native' populations are best able to survive in a changing environment, may be crucial to conservation and restoration efforts. The genetic differences among different tree genotypes are so pronounced that genetic effects must be considered in any restoration effort. Such experimental restoration plantings can rigorously test these findings and even short-term studies of climate change effects will help managers make appropriate restoration decisions. The time, land and monetary investment into restoration are so great that we cannot afford to plant genotypes that will ultimately fail with a changing climate. (Thomas.Whitham@nau.edu, Alicyn.Gitlin@nau.edu, Sharon.Ferrier@nau.edu, Kevin.Grady@nau.edu)

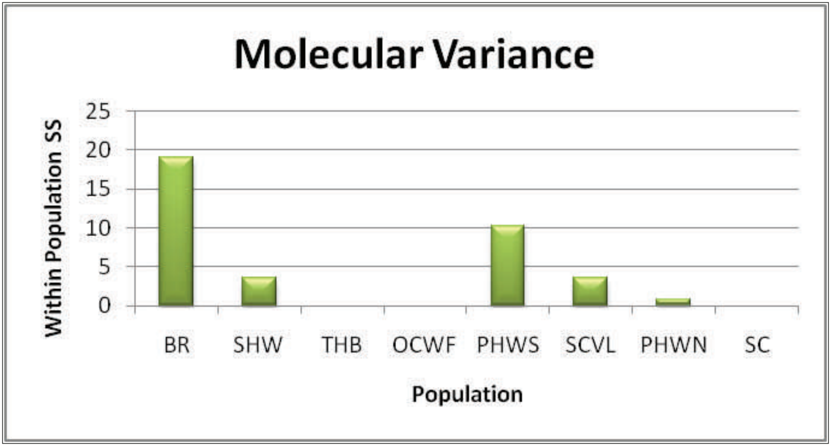
Range location, isolation, and climatic stress impact genetic diversity

Key Finding - Populations located at the edge of a species' range often persist at their physiological limits and in isolation from other sexually reproducing populations; the added stress of a warming and drying climate may be enough to tip the balance, resulting in low levels of genetic diversity. Species at the edge of their range tend to be distributed in small, isolated pockets. This structure results from two processes: 1) decline of a previously more widespread distribution, and 2) "founder events" or the long-distance dispersal of few individuals that persist in isolation, often through asexual reproduction (Hampe & Petit 2005). As riparian areas decline, dependent species' distributions also shrink. Regardless of which process is at work, the result of lost connectivity between populations is sexual isolation, inbreeding, and the potential for genetic drift, which could result in low genetic variation.

Two major lines of evidence - 1.1 - Isolated stands were found to be 6.9 times more clonal than larger, intact populations. The above result comes from a recent study comparing a large (10,000+ trees), intact population (BR) of narrowleaf cottonwood with 7 small (50-200 trees), iso-



Clonality Index = 1 – [(G-1)/(N-1)], where G = # of unique multi-locus genotypes, and N = # of ramets sampled.



lated populations across Arizona's Rim Country at the southern edge of the species' range (Bothwell & Whitham unpub. data). Plants often exhibit asexual reproduction when environmental stress makes sexual reproduction too physically demanding. Clonal growth is also common to "founder" populations, providing a means of persistence in the absence of mates available for sexual reproduction.

1.2 - Molecular variance is 2.6 times higher and percent polymorphic loci 1.6 times higher in the larger, intact population (Blue River - BR). Note that for three populations, all "individuals" consist of a single clone; there is zero genetic diversity (above figure). Clonal growth may be an adaptation that acts as a buffer, allowing plants to survive through times of stress and isolation. Yet if conditions allowing for sexual reproduction do not follow, it will be important to understand the repercussions of associated low genetic diversity.

Major Conservation and Restoration Implications – Diversity begets diversity. Arthropod species richness has been shown to accumulate with genetic diversity of foundation trees such as narrowleaf cottonwood (Wimp et al. 2004, Bangert et al. 2008), and several studies have shown that different genotypes of this tree support different arthropods, soil microbes, trophic interactions, and ecosystem processes (Shuster et al. 2006, Bailey et al. 2006, Schweitzer et al. 2008). Conservation and restoration efforts that manage for genetic diversity of foundation species will get the most bang for their buck by attracting a more diverse associated community. The stability that comes with a more complex community helps safeguard against disease and loss of functional niches and ecosystem services, thereby protecting the time and money invested into restoration projects.

Practical Recommendations – Especially in the southwest, at the rear edge of many species' ranges, a stand of several hundred trees may in fact consist of only a handful of individual clones, each of which are genetically identical. Collecting stock from opposite ends of stands or from many different stands is an inexpensive way to ensure the highest level of genetic diversity for restoration plantings. Connectivity is also an important consideration in planning the location of restoration projects. Given that cottonwood pollen can travel up to 35km, restoration projects planted within range of outside sources of sexual recruitment will have a greater likelihood of naturalization and continued success.

(Helen.Bothwell@nau.edu)

Stress experienced by foundation species such as narrowleaf cottonwood is likely to have a cascading effect on total ecosystem biodiversity.

Genetic diversity in Fremont cottonwood and its implications for a diverse dependent community ranging from microbes to vertebrates


H. Bothwell

Key Finding - Genetic variation among individual Fremont cottonwood trees has a major effect in defining community structure, ecosystem processes, and biodiversity. In other words, tree genotype (i.e., the genetic makeup of an individual tree) is very important in conservation and restoration. Recent studies have clearly shown that different tree genotypes support different insect communities and ecosystem processes (e.g., Schweitzer et al. 2005, Shuster et al. 2006, Bailey et al. 2006) and that greater genetic diversity in stands promotes greater biodiversity (Wimp et al. 2004).

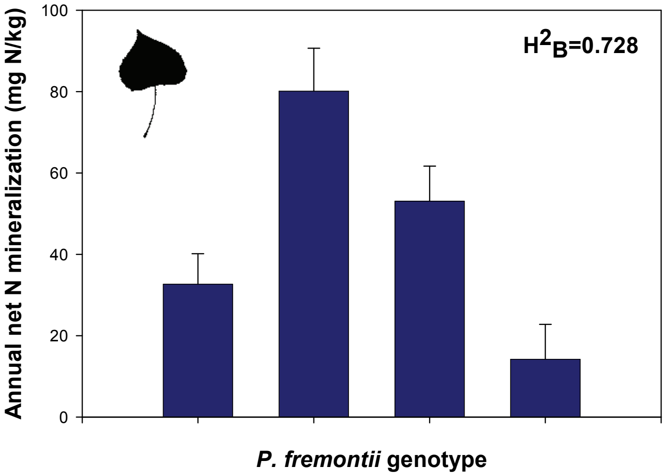
Three major lines of evidence – 1.1 – When different cottonwood genotypes are cloned and grown together in common garden field trials, their survival and performance varies dramatically. Thus, it is important to include a genetics perspective in their conservation and restoration. For example, when cottonwoods are randomly selected from the wild, cloned and planted in a common garden, some genotypes show 100% mortality, while others show 0% mortality and exhibit 2 meters growth per year. These differences are genetically based, suggesting that genetic variation is critical for conservation and restoration, and may represent the key to success or failure in a restoration effort, especially if climate change is also involved.

1.2 - In common garden studies, we've found that 73% of the variation in annual net nitrogen mineralization is due to plant genetic effects, whereas only 27% is due to environmental effects (Schweitzer et al., unpublished data). For example, in the following figure, net nitrogen mineralization in the soil beneath replicated individual tree genotypes varies dramatically from one tree genotype to another. Some trees have innately high nitrogen mineralization rates while others are far lower. Because this is an important ecosystem process that affects a major soil nutrient, the genetic control of this process is important to understand and utilize in conservation and restoration efforts.

1.3 - Similarly, 65% of the variation in the arthropod community living on Fremont cottonwood is due to plant genetic effects, whereas only 35% is due to environmental effects (Shuster et al. 2006). In combination, the determination of tree survival, the community of organisms that live on these trees and the ecosystem processes of energy and nutrient flow is largely under genetic control.

Genetic variation is a powerful tool for conservation and restoration, and may represent the key to success or failure in a restoration effort, especially if climate change is involved.

Genetic factors explain nearly 73% of the variation in annual rates of N mineralization (varying eight-fold in annual rates)



Major Conservation and Restoration Implications - It is important to conserve genetic diversity in Fremont cottonwood to meet the challenges of riparian habitat loss and a changing environment brought about by climate change. Genetic diversity is central to the preservation of biodiversity in riparian communities because different tree genotypes support different communities and ecosystem processes. Even though Fremont cottonwood is widespread throughout the Southwest, loss of genetic diversity in this foundation species is likely to result in the loss of biodiversity. While it is widely recognized that the conservation of genetic diversity is important for the preservation of rare and endangered species, it may be even more important to conserve genetic diversity in abundant foundation species such as cottonwoods because of the large dependent community they support (Whitham et al. 2003, Whitham et al. 2006). Studies by Wimp et al. (2004) show that nearly 60% of the variation in the diversity of an insect community composed of over 207 species is dependent upon the genetic diversity of the individual stands of trees they occupied. This has now been repeated and shown to work at local to regional levels (Bangert et al. 2005, 2006a,b, 2007). The following four articles provide case studies highlighting the role of tree genetic diversity to associated community biodiversity and the health of key ecosystem functions.

Practical Recommendations – Genetically survey cottonwood populations, with the goal of matching the genetic variation in wild sites with that of restoration sites. This sounds expensive and difficult, but with our current facilities (the state of the art Environmental Genetics and Genomics facility at Northern Arizona University), we have surveyed Fremont cottonwoods throughout their range in the southwestern U.S. Furthermore, with the recent sequencing of the cottonwood genome (the first tree to be sequenced just as the human genome has been sequenced) (Tuscan et al. 2006), we are now in a position to understand the conservation genetics of Fremont cottonwood as has never been accomplished with any other tree species.

(Thomas.Whitham@nau.edu)

Diversity is more than meets the eye

Key Finding - Genotypic variation in host trees is an important driver of arthropod evolutionary processes, such as race formation and speciation. In a recent study, Evans et al. (2008) found that mites (*Aceria parapopuli*) are genetically differentiated according to host tree genetics. Different cryptic species of mites are locally adapted to individual cottonwood genotypes.

Two Major Lines of Evidence - 1.1 - Population genetic analyses of both mites and their cottonwood hosts indicate a strong correlation between cryptic species of mite and underlying tree genetics. Mites respond most significantly to host genotype at the cross type level, and they are more strongly differentiated among F1 hosts when compared with the parental species, *P. angustifolia.* To a lesser degree, cryptic species of mites also show distinct clustering at the level of individual tree genotype (figure below).

1.2 - Reciprocal transfer experiments demonstrate that mites significantly prefer natal compared to non-natal host trees ($P > 0.05$). Greenhouse trials were conducted to remove environmental variation and pinpoint genetic effects. Results support the above genetic findings. Even when species do not appear morphologically distinct, studies such as this highlight the importance of underlying genetic variation to the differential fitness and survival of dependent organisms.


H. Bothwell

Major Conservation and Restoration Implications - Genetic variation of foundation species has important consequences for the evolution of dependent organisms. *Aceria parapopuli* is morphologically considered a single species across all *Populus* hosts (Kiefer 1940). Although morphologically indistinct, this study reveals much differentiation at the genotypic level. Cryptic speciation may be a beginning stage in the evolution of new species. This raises an important point. Biodiversity is likely much greater than currently estimated as based on morphological classification. The example of strong host genetic effects driving genetic divergence (i.e., evolution) in mites is a model that likely holds true for a wide variety of dependent organisms.

Practical Recommendations - Conservation of genetic diversity in common foundation species (at the species, hybrid, population, and individual levels) is a powerful way to insure the

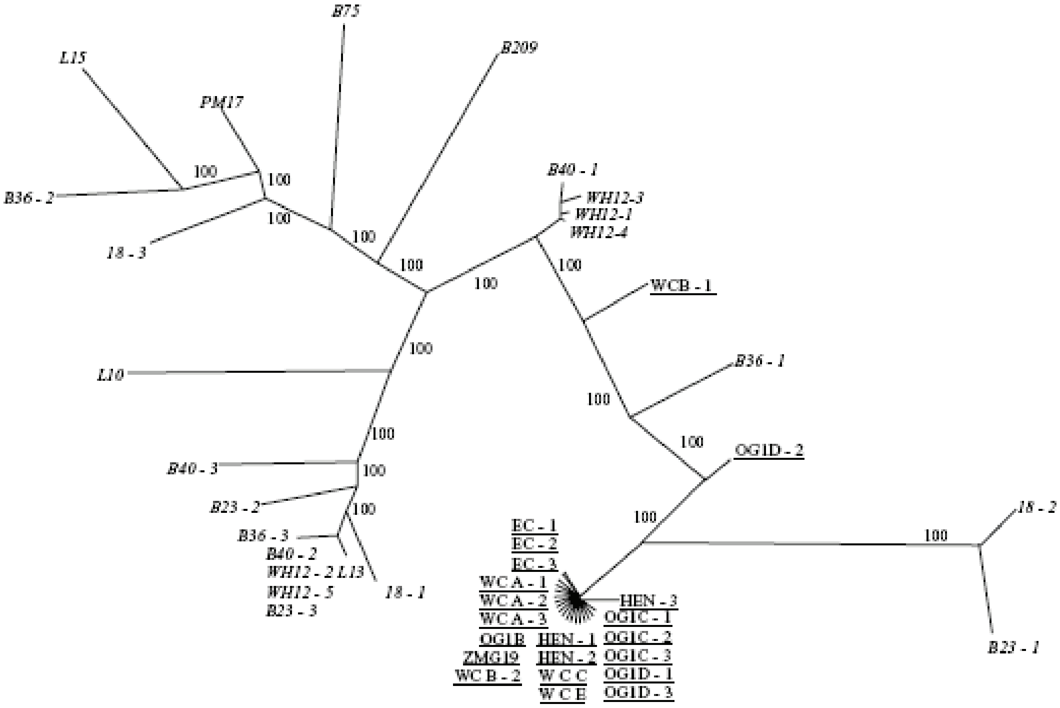


Figure 1. This Neighbor-Joining tree based on Cavalli-Sforzachord distances of mite populations reveals significant differentiation among cottonwood crosstypes. Mites on *P. angustifolia* (underlined) shows moderate differentiation, while F1 hybrid crosstypes (italics) show high levels of differentiation. Each branch represents a host tree genotype and number of mite galls investigated per host. Note the large bootstrap values at the nodes signifying strong support for differentiated branches among F1s (Fig. reproduced from Evans et al. 2008).

maintenance of fertile grounds for evolutionary processes to take place and the continued survival of a diverse dependent community of organisms. The importance of intraspecific variation in performance and survival by environment has been recognized since Clausen et al.'s 1940 pioneer study of *Potentilla glandulosa* grown along an elevation gradient. Evans et al.'s work argues for the extension of this concept such that intraspecific variation in dependent organism genetics produces varied fitness responses based on the "environment" of host genotype. Variation is the building block of evolution. Divergence and speciation often take place on time scales beyond the scope of scientific investigations and management planning; yet by managing for genetic diversity within common host trees, we can provide an environment in which these processes are allowed to thrive in the associated community. When funding and time allow, it is ideal to use a wide variety of different genotypes in restoration. A species designation does not always mean that one-size-fits-all. Awareness of and management plans that take into consideration variation and local adaptation *within* species will ensure "environments" that allow for maximized performance, survival, and evolutionary potential of *all* groups within species.

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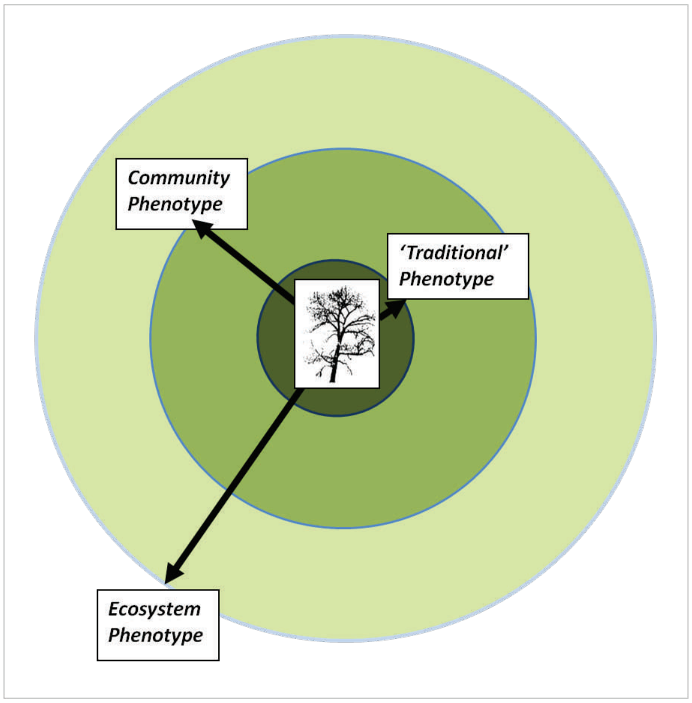
Interspecific indirect genetic effects (IIGEs): the influence of tree genetics reaches far into the surrounding community and ecosystem



Whitham *et al.* 2003, Shuster *et al.* 2006, Whitham *et al.* 2006

Key Finding - Foundation species are those which maintain structure and the stability of key ecosystem processes that the associated community of organisms depends on (Ellison *et al.* 2005**). The emerging field of community genetics strives to understand how the genetic make-up of foundation species organizes these processes such that similar tree genotypes will also share similar *extended phenotypes* (i.e., similar associated communities, ecosystem processes, and structure) (right figure).** One way that trees interact with the surrounding ecosystem is through *interspecific indirect genetic effects* (IIGEs). Wojtowicz *et al.*'s work with litter-dwelling arthropods provides a good example of this (unpub.).

> **"When one tugs at a single thing in nature, he finds it attached to the rest of the world."**
>
> **- John Muir**

Major Lines of Evidence - 1.1 - In Wojtowicz *et al.*'s study, tree genetics appears to be organizing the abundance of key functional groups through their interaction with chemical and structural traits of cottonwood trees. Abundance of millipedes (decomposer) and mites (a mix of fungal feeders and predators) is influenced by the genetic gradient created by the Fremont-narrowleaf cottonwood hybrid system. We suspect these animals are responding to the variation in genetically-linked chemistry of decomposing litter from these trees (figure on following page). Note, this model suggests that millipede abundance is not directly responding to tree genetics, but seems to be regulated through the influence of bound condensed tannins and lignin content of the litter.

1.2 - The number of litter webs of a common family of spider (Agelenidae) tracks the same genetic gradient that millipedes and mites do. Interestingly, the influence of tree genetics on litter web abundance is strongest close to the trees ($R^2 = 0.40$, $p = 0.0001$), but rapidly decreases with increased distance from the trees' base. We are currently investigating whether differences in litter depth among the cottonwood tree cross types are responsible for this pattern.

Major Conservation and Restoration Implications - The arthropods (insects, spiders, millipedes, centi-

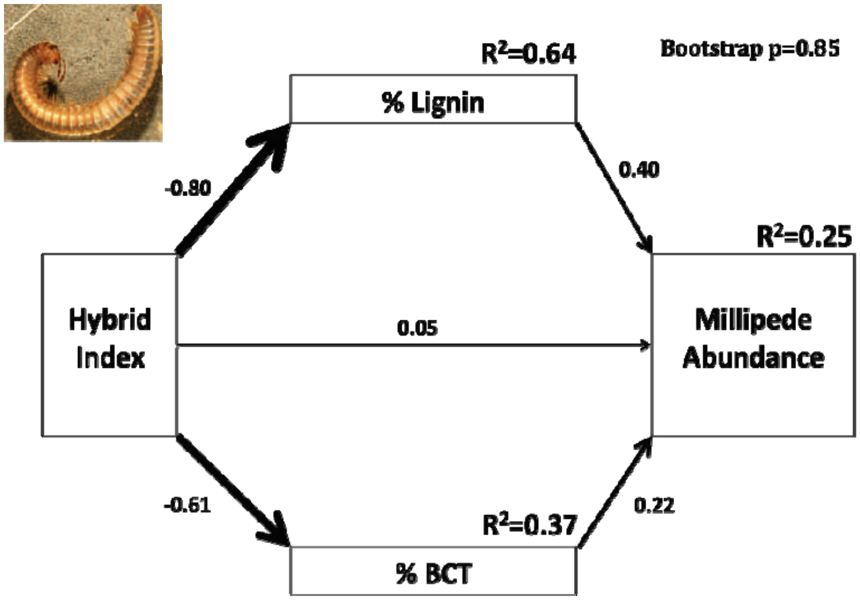


Fig. 1. The model illustrates the relationship between a cottonwood tree's genetic position in the Fremont-narrowleaf hybrid system (hybrid index), litter chemistry, and millipede abundance. Trees with a hybrid index near 1 are Fremont, near 0 are narrowleaf, and near 0.5 are F_1 hybrids. A tree's hybrid index can be thought of as its genetic identity along the breeding continuum between the two parental species. Numbers above the arrows (path coefficients) represent the strength of the relationship between variables (in rectangles). For example, the path coefficient between hybrid index and % lignin suggests a strong relationship of increasing lignin content of the litter with a decreasing hybrid index score (i.e. narrowleaf trees have higher lignin content than Fremont trees). R^2 above variables represent the amount of variation in that variable explained by the model. The high bootstrap score suggest that the model fits the data very well.

pedes, mites, etc) associated with litter and soil are intimately tied to decomposition and nutrient cycling processes. They can influence decomposition by directly eating decomposing litter, by preying on the decomposers, or preying on the predators of decomposers. Because these animals are important regulators of a fundamental ecosystem function (nutrient cycling), they are important in all managed and unmanaged terrestrial systems. Therefore, scientists and managers need to understand what variables influence litter arthropod abundance, community structuring, and function.

The genetic makeup of individual cottonwood trees can have important impacts on the community and ecosystem and can determine both the number and kinds of species present. It is an important factor in organizing who and how much is there, as well as the efficiency of key ecosystem functions. The genetics of trees can indirectly influence arthropods that regulate nutrient cycling. Our understanding of this effect can aid in the selection of genotypes that may be preferable in restoration projects or highlight the importance of conserving different individual genotypes within a species.

Practical Recommendations - Research investigating the role of plant genetics on litter arthropods is still in its infancy. Therefore, it is recommended that land managers opt for strategies that increase the genetic diversity of individuals in restoration and conservation projects. By preserving plant genetic diversity, managers will increase the diversity of litter chemistry and litter layer architectural traits (e.g. depth, litter morphology, layering in the litter, etc) that influence those arthropods most important in regulating nutrient cycling.

> **Because litter arthropods are important regulators of a fundamental ecosystem service (nutrient cycling), they are important in all managed and unmanaged terrestrial systems.**

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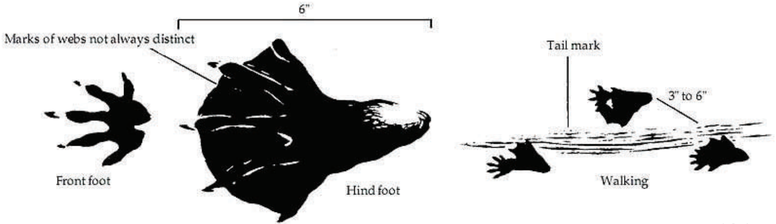
The Cottonwood Ecology website is a great resource where you can learn more about research happening in your own backyard. We are dedicated to bringing research into the hands of those best suited to put it into practice. On the website, you will find links to full-length publications that expand upon the topics discussed here as well as homepages of contributors to this publication. We encourage communication, feedback, questions, and collaboration. Keep your eyes open for links to upcoming events such as restoration workdays and the screening of the PBS special: Genes to Ecosystems.

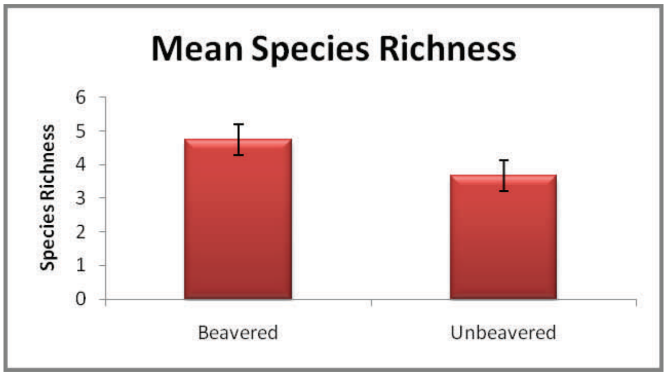
Beavers drive biological diversity

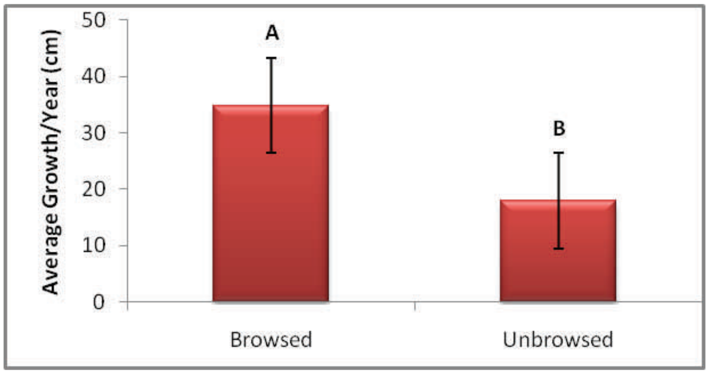


USDA

Key Findings - Mammalian herbivores, such as the beaver, alter riparian stand composition and generate genetic structure within stands through differential herbivory. A classic example of a foundation species and ecosystem engineer, beavers may be increasing biodiversity at the landscape scale by creating a more heterogeneous habitat of browsed and unbrowsed trees, which in turn supports different associated communities. By cutting trees for feeding and construction material for dams and lodges, beaver affect fish populations (Hagglund and Sjoberg 1998), stream flow (Hammerson 1994), nutrient cycling and availability (Naiman et al. 1994), individual species of arthropods (Martinsen et al. 1998, Bailey and Whitham 2006), vegetation diversity (Mitchell 1999), tree architecture (McGinley and Whitham 1985) as well as many other species and ecosystem functions.

Two major lines of evidence - 1.1 - Resprouts of Fremont cottonwood which have been felled by beaver support significantly greater arthropod species richness than the juvenile growth of 'unbeavered' paired control trees (left figure below: N= 98, Wilcoxon Signed-Rank test p=0.01). Measurements indicate that shoot elongation in browsed trees is nearly twice that found in unbrowsed trees (right figure below: p<0.0001). Analysis of key nutritional and defensive chemical compounds also confirmed that the resprout growth of browsed trees has higher nitrogen (p= 0.003), salicortin and HCH-salicortin, (p=0.001 and p=0.03, respectively) as well as lower lignin (p= 0.0001) content than juvenile growth of control trees.





1.2 - Condensed tannins are cottonwood defensive compounds that are under genetic control (Whitham et al. 2006, Woolbright et al. 2008; Figure following page). Beavers selectively fell trees with lower condensed tannins, such as *P. fremontii*, thereby altering riparian stand composition and genetic structure (Fig. 1C; Bailey et al. 2004). Both Fremont and narrowleaf cottonwood resprout from the stump (McGinley & Whitham 1985), but *P. fremontii* suffers greater mortality because unlike *P. augustifolia* and hybrids, it typically does not produce clonal runners (Schweitzer et al. 2002). Selective beaver herbivory can result in significant impacts due to the combined effects of beaver avoidance of high tannin genotypes and differential resprouting of various cross types. This likely constitutes a natural selection event where beavers have repatriated following their near extirpation from the West (Sandoz 1964).


Bilby Research Center/Ryan Belnap

In a recent study, selective felling by reintroduced beaver altered stand-level tannin concentration of surviving trees, such that cottonwood genotypes high in condensed tannins increased 3-6X after just 5 years (Fig. 1D; Whitham et al. 2006), significantly changing the composition of cottonwood stands. Fig. 1 illustrates the links between a mapped trait of a foundation tree and an ecosystem engineer whose selective foraging feeds back to the differential survival of various tree cross types and genotypes within these cross types. Even within stands of pure species of cottonwood, beavers discriminate among genotypes and act as agents of natural selection. Figure 2 shows

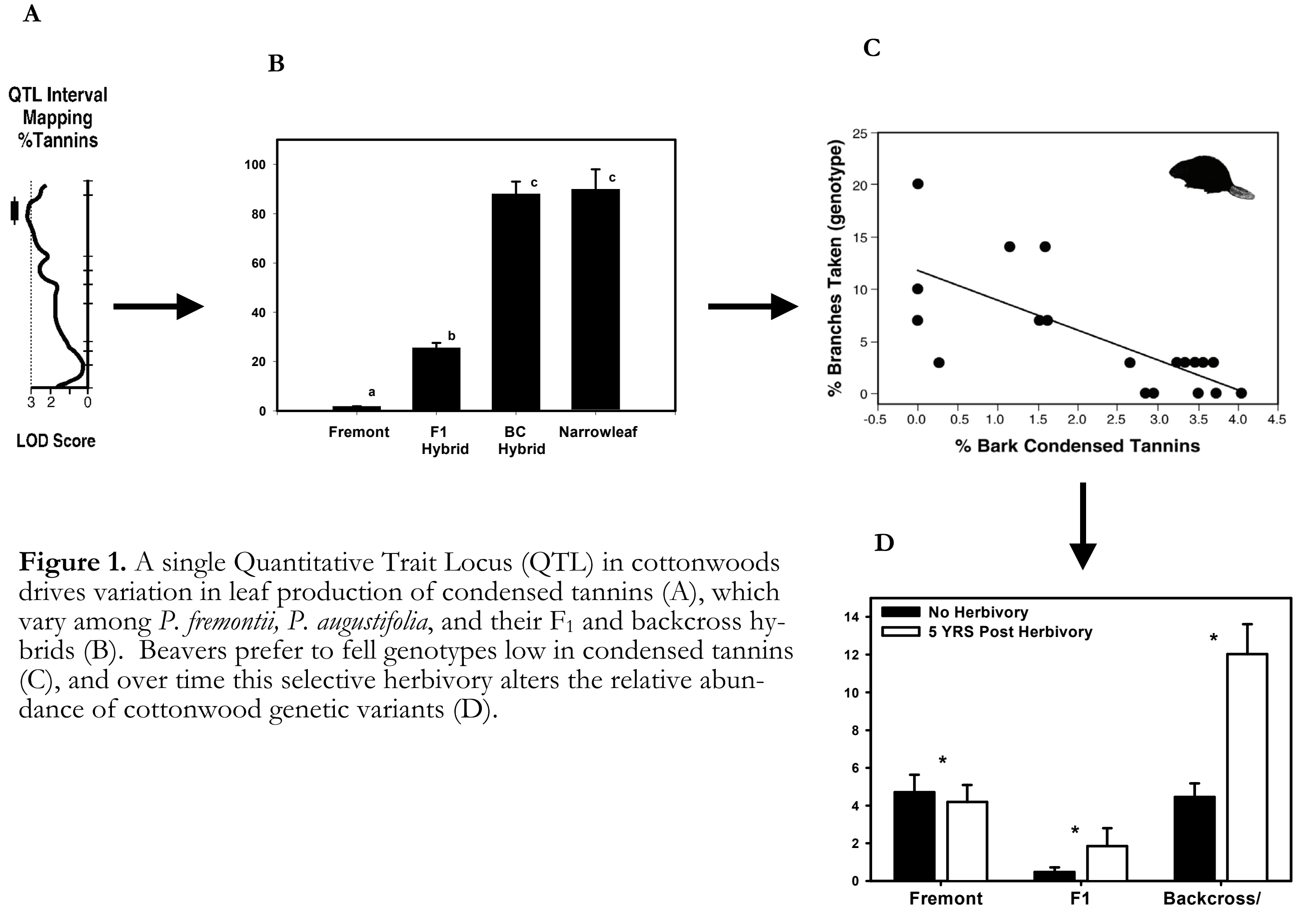


Figure 1. A single Quantitative Trait Locus (QTL) in cottonwoods drives variation in leaf production of condensed tannins (A), which vary among *P. fremontii, P. augustifolia*, and their F_1 and backcross hybrids (B). Beavers prefer to fell genotypes low in condensed tannins (C), and over time this selective herbivory alters the relative abundance of cottonwood genetic variants (D).

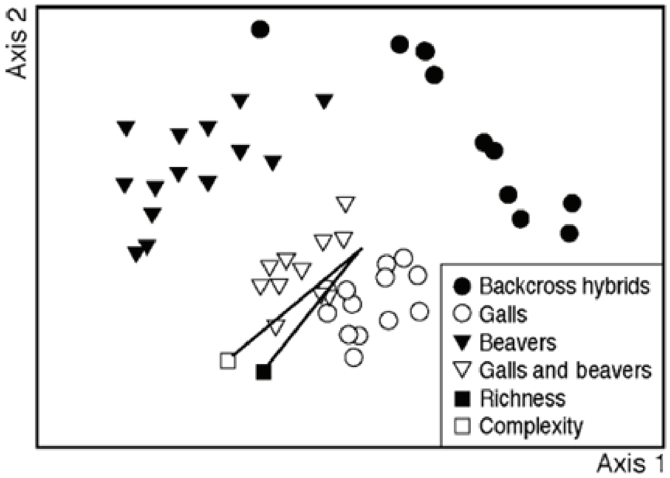


Figure 2. Arthropod communities on resprout growth of beaver-felled trees (▼) differed from those of control backcross hybrid trees (●), as shown by non-metric multidimensional scaling. Resprout growth of beaver-felled trees also attracted gall-forming sawflies (*Phyllocolpa* spp.), which solicited another set of arthropods (○). Open triangles show the combined effects of beavers and sawflies on the arthropod community. All groups were significantly different from one another and from the control group (ANOSIM). Vector analysis (DECODA) revealed that these treatments significantly increased both arthropod richness and complexity (□ and ■, respectively) relative to the control group (Bailey & Whitham 2007).

how a higher trophic level may be altered due to selective beaver herbivory; arthropod community composition varies across cottonwood genotypes, and thereby tracks beaver-induced changes in stand composition (Walker et al., unpub. data).

Major Conservation and Restoration Implications - Beaver were historically present in most North American streams but were extirpated over large areas by the beginning of the 20th century due to the fur trade. After almost complete extirpation in the late 1800's, beaver are now recolonizing some of their former range (Jenkins & Busher 1979). Because of the important role they play in structuring riparian environments and regulating ecosystem processes, beaver are integral to healthy riparian systems. Studies examining interactions between foundation or keystone species have shown that one or two influential species can affect ecological communities and biodiversity at a large scale (Helfield & Naiman 2006, Bailey & Whitham 2007). This project supports those findings, showing that in riparian areas where beaver are actively browsing *P. fremontii*, arthropod species richness is increased and shoot elongation on browsed trees is nearly twice that of control trees. Defensive chemistry and nutritional content of unbrowsed trees is significantly different from that of browsed trees. Both of these traits are under genetic control and likely drive the observed differences in arthropod community composition and structure.

Southwestern riparian systems are hotspots of biodiversity that are rapidly disappearing and considered threatened (Noss et al. 1995). In most instances, cottonwood genetics, phytochemistry, and beaver herbivory likely interact to increase overall biodiversity. Because arthropods are the basis of a food chain for many insectivorous birds and mammals, beaver-cottonwood-arthropod interactions provide a window into the functional foundation of an entire ecosystem. The genetically-based indirect interactions presented here are merely the first links in complex networks resulting from the interactions between two dominating foundation species.

Beavers are an important part of the ecosystem, and culling should be discouraged under normal circumstances.

Practical Recommendations - When considering rivers or riparian zones for protection, preference should be given to those that contain the greatest diversity of species and habitat. Since beaver have been shown to positively influence biodiversity and habitat heterogeneity, preserving riparian areas with resident beaver populations should facilitate the maintenance of complex interactions and diverse communities.

Beavers are an important part of the ecosystem, and culling should be discouraged under normal circumstances. However, in situations where cottonwood stands have been reduced to a few individuals, beavers may have a negative effect.

We also suggest that it may be feasible to identify beaver-unpalatable cottonwood genotypes for restoration planting, such as those that are high in condensed tannin defensive chemistry.

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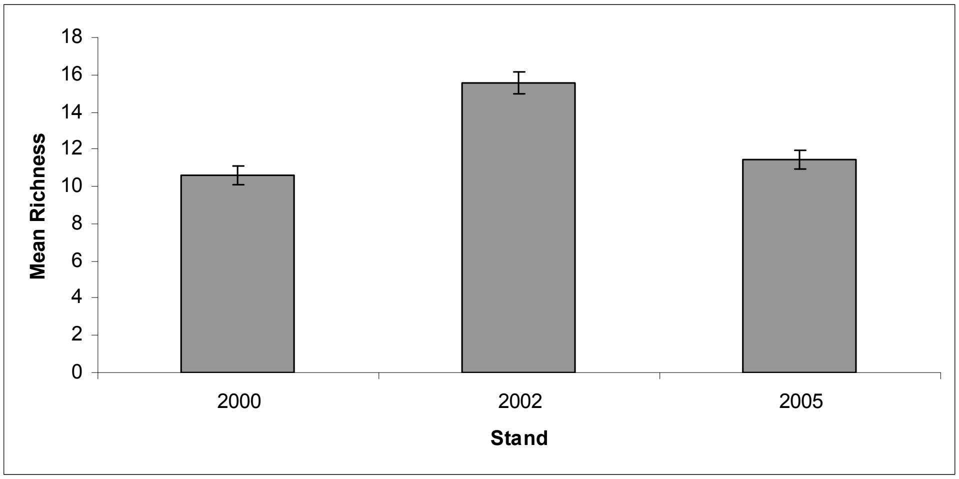
Bilby Research Center/Ryan Belnap

Stand age, competition, and planting densities affect biodiversity and habitat quality of restored communities.

Key finding - As trees in a restoration stand age, they begin to compete with one another, resulting in branch dieback, simplified branch architecture, and reduced growth that negatively affect biodiversity.

Two major lines of evidence - 1.1 - The left figure shows arthropod species richness in stands of different ages in which the oldest stand (only 7 years old and planted in 2000) has the lowest species richness (Hagenauer et al. unpub. data). This decline is associated with canopy closure, the dieback of lower branches, and reduced tree architectural complexity. Mean arthropod species richness was found to be significantly different among these three stands of Fremont cottonwood trees. They represent a chronosequence, with the three adjacent stands planted in 2000, 2002, and 2005. All groups are significantly different (F = 33.08, df = 2, p < 0.0001). Bars represent ± 1SE. We predict that with fur-



1.2 - The communities associated with different aged stands are very different from each other (Hagenauer et al. unpub. data). Figure 2 shows an ordination in which each dot represents the arthropod community of an individual tree. Dots close together have similar communities while dots far apart are very different. Note that the communities on trees in different aged stands are clustered together and that the communities are significantly different for the trees in each stand even though they are all nearby one another in the Cibola National Wildlife Refuge. We believe that the difference is due to plant stress in which stressed trees in older stands that compete with one another support very different insects than those in younger stands that do not have closed canopies. Studies with pines show that plant stress has a major negative effect on reducing biodiversity (Stone et al. in press).

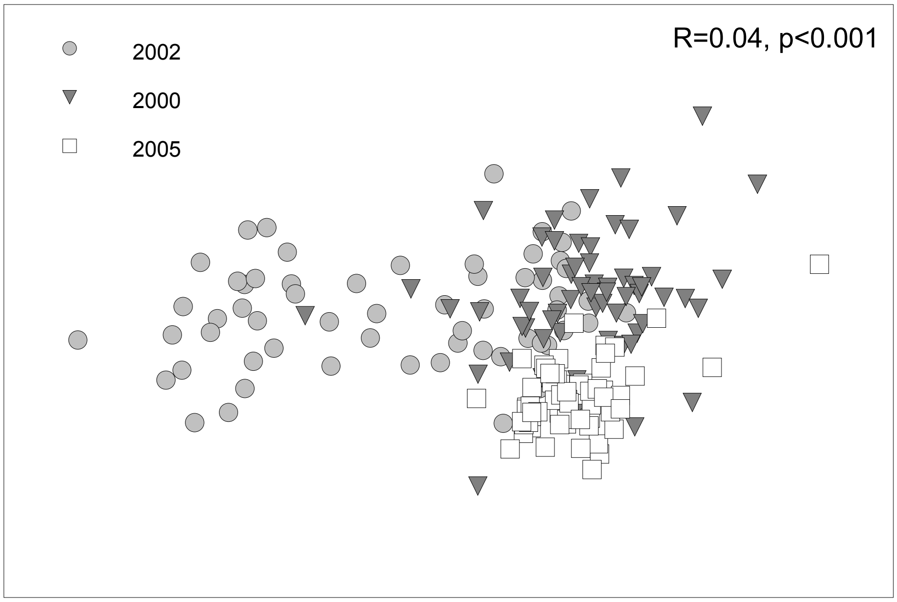


Figure 2. The above NMDS (nonmetric multi-dimensional scaling) shows differences in arthropod communities pooled across four months from a chronosequence of *P. fremontii* trees planed in 2000, 2002, and 2005. All three groups are significantly different (ANOSIM R = 0.04, p < 0.001). Thus, different aged stands are supporting very different communities even though they are growing in close proximity.

Major Conservation and Restoration Implications - Once canopy closure occurs, competition increases and biodiversity declines. This is a common pattern recorded for canopy closure and increased stress resulting from competition. Furthermore, these studies show that variation in stand age will support the greatest overall diversity. In wild rivers that periodically flood, a mosaic of stand ages is typical and stand density varies greatly. Although more research of wild stands is needed, we suspect that the density of trees in wild stands is lower than current management and restoration practices call for.

Practical Recommendations – Plant trees at lower densities to reduce competition and to increase branch architectural complexity. This should result in lower planting and maintenance costs. Because large, even-aged stands in the wild are not common, we recommend simulating these block sizes in restoration to provide a mosaic of block sizes, stand densities and stand ages that will maximize habitat heterogeneity and biodiversity.

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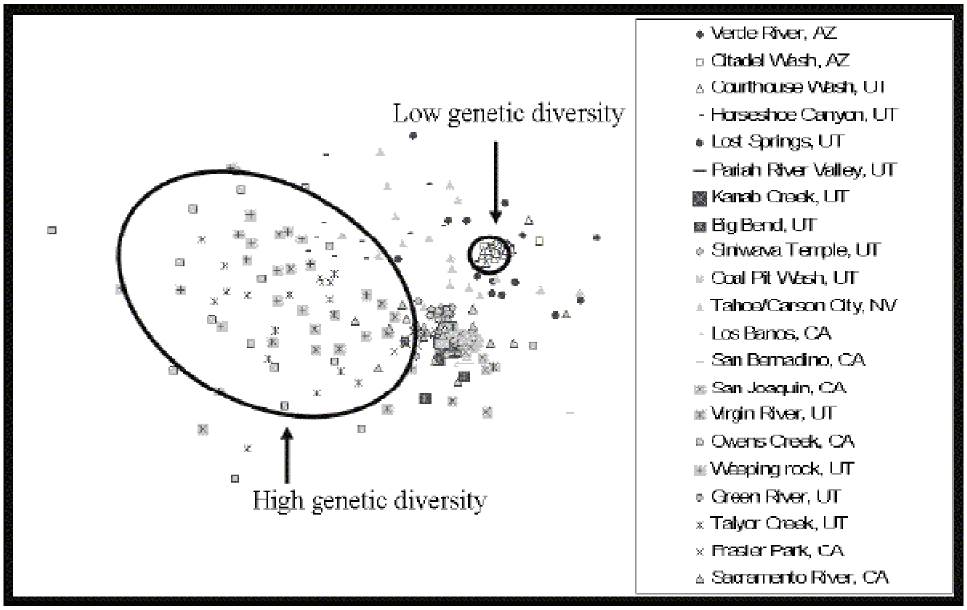
Restoration sites should aim to mirror the genetic structure of wild populations

Key Finding – The genetic structure of restored cottonwood plantings in many National Wildlife Refuges does not match wild populations. In other words, as currently designed, these restoration efforts are using only a fraction of the genetic diversity and structure found in the wild. We emphasize that this observation is not meant to be critical of these important restoration efforts; it simply represents the state of the art and demonstrates that the inclusion of genetics into restoration has yet to be achieved. Because of the major efforts currently underway in riparian restoration, we believe that the work within this field can serve as a model for other restoration practices, which have not yet developed to this level of understanding.

Major lines of evidence - 1.1 - A recent study by Honchak et al. (unpub. data) provides evidence showing that the genetic structure of Fremont cottonwood in restored



areas differs greatly from that found in natural stands. The right figure shows an NMDS ordination of AFLP genetic data from 21 populations of *P. fremontii* (362 individuals). It shows that the variation in genetic diversity in 'natural' stands of Fremont cottonwood fluctuates across its range. Natural stands are defined as stands that show no obvious signs of having been planted and are generally in more remote areas with little or no human habitation. The circles show extremes of genetic variation in which one study site exhibits great genetic variation (i.e., large circle), whereas another site shows low genetic diversity (i.e., small circle).

Similar studies of 11 restoration sites in Arizona show that the genetic structure in these 'restored' populations is on average far less than that found in the wild, and most are very similar to one another. In other words, one restored site is genetically similar to another, whereas nearly all wild populations over the same area are genetically differentiated. The fact that natural stands are so genetically differentiated suggests that incorporating a wider range of genotypes would benefit restoration.

Major Conservation and Restoration Implications – Best restoration efforts to date lack knowledge of the genetic structure of natural populations, which in turn will affect the species they support. Because different tree genotypes support different communities of organisms and ecosystem processes, genetically differentiated populations of Fremont cottonwood across the Southwest will also support different communities and ecosystem processes. Thus, genetic structure is important to quantify, maintain, and simulate in restoration efforts.

Practical Recommendations – Use a genetic approach, which is currently available and not cost prohibitive to define the tree genotypes that are best to use in restoration. We recommend a two pronged approach. First, using the genetic structure of nearby tree populations as a guide, restoration should promote the use of genotypes that simulate the genetic structure of these nearby populations. Where no local stands have survived, we recommend planting a mix of genotypes from the region to determine what genotypes will survive best at this specific site. Subsequent use of these genotypes will maximize survival and simulate the genetic structure of more diverse wild stands. Second, because climate change is a 'wild card', restoration ecologists should hedge their bets by planting genotypes recommended by current climate change models that allow us to predict the source of genotypes most likely to do best under future conditions predicted to prevail at the local restoration site. We emphasize that this is very doable with today's technology and is not cost prohibitive (see first section on climate change models)

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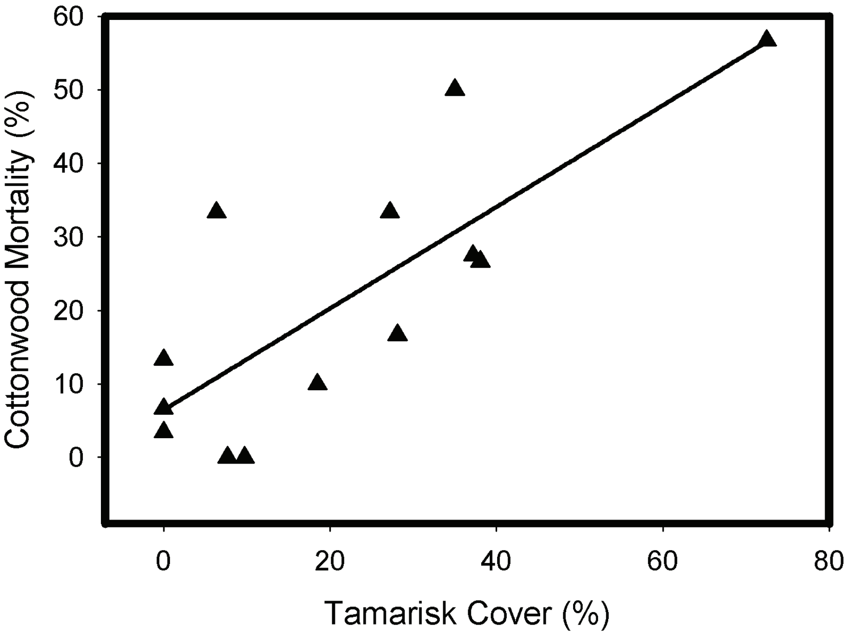
Invasion ecology: Interactions with exotic Tamarisk

Key Finding – Increased tamarisk cover predicts increased broadleaf cottonwood mortality on the Colorado Plateau. We expect climate change to interact with this exotic to exacerbate the problems of riparian restoration. Although we recognize that there are mixed views on the value of tamarisk, three major facts emerge. First, it is an exotic. Second, while the distribution of tamarisk has increased dramatically, the distribution of cottonwoods and willows have dramatically declined over the same time period. Third, they do not support the same communities of organisms. We suspect that the interaction of an exotic species and climate change creates an even more unfavorable environment for Fremont cottonwood and willows.

Major line of evidence – Across the Colorado Plateau, surveys by Gitlin and Whitham (unpub. data) show that as cover of tamarisk increases in individual stands, so does the mortality of cottonwoods ($R^2 = 0.62$, $n = 13$, $P = 0.001$). The right figure shows that as tamarisk increases in abundance, there is a direct negative relationship with cottonwood mortality such that 62% of the variation in cottonwood mortality is predicted by the abundance of tamarisk.



Major Conservation and Restoration Implications – For successful cottonwood and willow establishment, it is important to remove tamarisk.

Practical Recommendations – In addition to tamarisk removal in restoration efforts, we recommend the identification of tamarisk resistant cottonwood genotypes. As there is undoubtedly great genetic variation in the ability of Fremont cottonwood to survive competition with tamarisk, it would be beneficial to identify these genotypes for potential use in areas where continued threat of tamarisk invasion is highest. An initial start along these lines would be to propagate the Fremont cottonwood survivors in stands that have been invaded by tamarisk and compare them in field trials with Fremont cottonwoods that have not experienced tamarisk. Again, this is not cost prohibitive as such trials could be conducted along with current restoration efforts.

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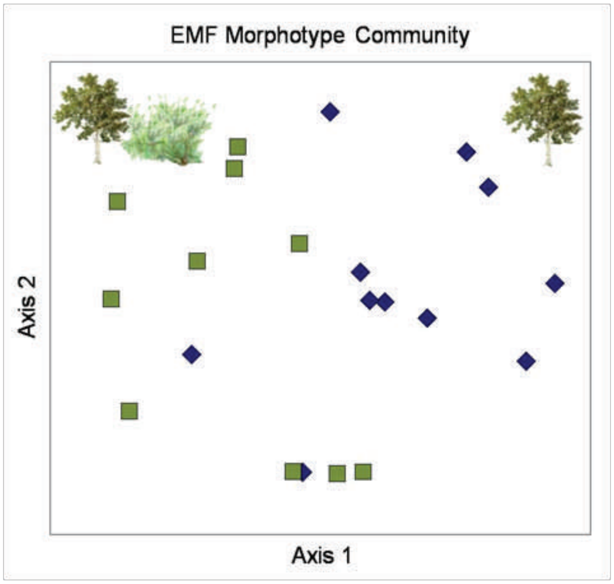
Tamarisk alter the structure of ectomycorrhizal fungal communities of cottonwoods

Because each EMF species may function differently and provide a unique service to the host tree, it is most beneficial for the EMF community to be large and diverse.

Key Finding – Exotic tamarisk (*Tamarix* spp.) alter the structure of ectomycorrhizal fungal (EMF) communities of neighboring cottonwoods. Invasive species are one of three major causes of biodiversity loss, along with habitat loss and climate change (Magoulick & DiStefano 2007). Tamarisk, or salt cedar, is one of the most aggressive exotics in the Southwest, and these findings argue that tamarisk may not only be able to directly outcompete native riparian species but is also capable of disrupting vital belowground mutualisms with mycorrhizal fungi, upon which native species are highly dependent for establishment and growth.

Two major lines of evidence – 1.1 – The presence of tamarisk decreases EMF colonization and species richness and alters the EMF community structure of nearby cottonwoods (Meinhardt & Gehring, unpub. data). Because each EMF species may function differently and provide a unique service to the host tree (e.g., sequestration of a particular nutrient, protection from adverse soil conditions), it is most beneficial for the EMF community to be large and diverse. The right figure shows an NMDS ordination with two distinct EMF communities, one from cottonwoods with tamarisk neighbors (■)and one from cottonwoods with tamarisk absent from their rooting zones (◊). Each point represents the EMF community of a cottonwood tree. Points closer together are more similar, while points



further away from each other indicate more dissimilar communities.

1.2 – Tamarisk have a fertilization effect on surrounding soil. Analyses of soil collected in the field from under cottonwoods with and without tamarisk neighbors showed that tamarisk significantly increases nitrate (NH_3). This fertilization via leaf exudates and litter deposition may be one mechanism by which tamarisk disrupts mycorrhizal mutualisms. Increased nutrient availability can be beneficial for other plants, but when nutrients are abundant, there is little or no need for a plant to form associations with mycorrhizal fungi (Johnson et al. 2003). Without mycorrhizae, the effects of environmental or soil stresses are not mediated for a plant; these stresses will become increasingly important in the face of climate change.

Major Conservation and Restoration Implications – The above findings suggest that tamarisk is disrupting vital mutualisms between mycorrhizal fungi and native cottonwoods. Because tamarisk does not associate with mycorrhizal fungi, its domination of an area is hypothesized to degrade the composition and function of mycorrhizal communities (Wolf et al. 2008). The lack of mycorrhizal fungi in the soil is likely to reduce the natural establishment of cottonwoods and the success of restoration efforts. Therefore, it may be necessary to inoculate restoration sites with mycorrhizal fungi prior to planting.

Practical Recommendations – Successful restoration of cottonwood may require assessments of the soil chemistry and mycorrhizal communities of a proposed site. The impacts of tamarisk on soil chemistry and belowground communities are not well understood. In order to be proactive, land managers should consider evaluating the soil chemistry and mycorrhizal communities of sites previously invaded by tamarisk. Such assessments can allow for poor soil conditions to be improved (e.g., flooding to reduce soil salinity, inoculation to increase mycorrhizal fungi) before enormous time and monetary investments are made in a restoration project.

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Brian Layton Cardall Memorial Scholarship Fund

Brian Layton Cardall was born on December 7, 1976. He grew up in Salt Lake City Utah. He traveled widely, lived life fully, cared about his family and trained intensely for his career in science. Brian earned a bachelor's degree from Utah State University where he studied the chemical defenses of newts against predatory garter snakes with one of the great professors of herpetology, Dr. Edmund Brodie Jr. Brian went on to complete a Masters' degree at Utah State University in Dr. Karen Mock's laboratory, where, using skills he was developing in molecular genetics, he showed that suckers in Lake Bonneville, Utah, were actually two distinct species.

In 2007, Brian became a graduate student in my laboratory. He applied for and received a Science Foundation Arizona fellowship in the first year they were offered, and became interested in "community genetics," the study of how genetic variation within one species may influence the distribution, abundance and reproduction of other species. In association with Dr. Tom Whitham's Cottonwood Ecology group, Brian's work took several directions. His cottonwood work focused on locations in Arizona and Utah in which invasive salt cedar or Tamarisk had changed riverbanks that had once been populated by cottonwood trees. Brian's research suggested that particular genetic variants of cottonwoods are resistant to invasion by salt cedar, a discovery that could revolutionize river restoration efforts in areas where salt cedar is abundant. Brian also became interested in *Diorabda* beetles, another invasive species that eats Tamarisk. And consistent with community genetics theory, Brian showed that beetles preferred to eat certain salt cedar plants and avoid others. Brian began to work independently with Dr. Tom Dudley at the University of California, Santa Barbara to understand the genetic basis of such preferences.

Brian liked to collaborate. He studied aspen dendrochronology with Jeff Kane and Tony Chang. He investigated the effects of beavers on riparian vegetation with Rachel Durben and Faith Walker. He explored the history of Tamarisk invasions with Alicyn Gitlin and David Smith. He developed molecular genetic markers that he, Kenyon Mobley and I plan to use to explore sexual selection in marine isopods in Mexico. Brian loved his work. It never seemed to represent work to him. He seemed charmed by the beauty and complexity of nature, and Brian wore the largest of his infectiously large smiles when in the field with his daughter Ava, she riding on his shoulders or strapped to his chest, facing outward so she could see the world through her father's inquisitive and perceptive eyes.

Brian Cardall was one of the most outstanding people I have ever known. He was a consistently friendly, hard working, intelligent, witty and even-tempered guy. He was a kind and gentle human being. He was a devoted father and a caring husband. And in my view, Brian had all of the intellectual, creative and scientific tools he needed to become one of the most outstanding scientists of his generation. I have been, and will continue to be inspired by Brian Cardall; my student, my colleague, and my friend.

– Stephen M. Shuster

The **Brian Layton Cardall Memorial Scholarship Fund** has been established to honor the memory of our beloved friend and colleague who died on June 9, 2009 at the age of 32. This fund will be used to provide scholarship support to outstanding PhD candidates at Northern Arizona University whose dissertation research focuses on conservation biology, for which Brian held a passionate interest. Donation can be made through the following websites **BrianCardall.com**, **https://alumni.nau.edu/giving.aspx?fnds=01610**, or mailed directly to:

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Helen Bothwell
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The Cottonwood Ecology Group is an interdisciplinary research team composed of scientists from Northern Arizona University, Evergreen State College, West Virginia University, The University of Tennessee-Knoxville and The University of Wisconsin-Madison. Emphasizing the need to understand how genetic variation in primary producers structures communities, affects species distribution, and alters ecosystem-level processes, current research focuses on the interactive effect of genetics and hybrid fitness in cottonwoods, arthropod diversity and community structure, plant defensive chemistry, and evolution. As dominant trees, cottonwoods are central to the structure and ecosystem functioning of foundation riparian forests of North America Rivers. Common gardens located at The Nature Center in Ogden, Utah, the Arboretum at Flagstaff, the Cibola National Wildlife Refuge on the lower Colorado River in Arizona, Lethbridge in Alberta, Canada, as well as riparian field sites ranging from Arizona to British Columbia provide the opportunity for our group of investigators, collaborators, graduate students, and undergraduate students to investigate the significant ecological interactions of a genus with great ecological, conservation, economic, and restoration value.

NORTHERN ARIZONA UNIVERSITY

Cottonwood Ecology Group