

Interactions Among Beaver, Exotic Tree Species, and Aquatic Macroinvertebrates: Links Between Terrestrial and Aquatic Systems

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Abstract

We examine interactions among cottonwood forests and their associated animal communities through two separate studies and show the relationship between herbivore foraging, plant community composition and terrestrial-aquatic linkages. First, in managed rivers the presence of beavers may benefit exotic species invasions. In a recent study we found that beavers browsed native cottonwoods more than native species of willow or exotic species such as Russian olive and salt cedar. We show that beaver selected 51% more cottonwoods, and 80–85% fewer willow, Russian olive, and salt cedar than expected based on their abundance in the riparian community. After just two years of beaver browsing, exotics increased by 4–17%. Second, changes to the terrestrial plant community extend into aquatic habitats through litter fall and have a negative affect on stream invertebrates. With a leaf pack study we showed that native cottonwood and exotic salt cedar decompose at significantly different rates, and support significantly different aquatic arthropod communities. To conclude, we will discuss the implications for these patterns on riparian biodiversity and function.

Key Words

Beaver, ecosystem engineer, exotic, litter quality, Russian olive, tamarisk.

Introduction

Invasions by exotics are of global concern and can occur very rapidly (Gillis 1992; Kolar and Lodge 2001; Zavaleta et al. 2001). For example, in less than 150 years since its introduction (Everitt 1998; Gladwin and Roelle 1998), the exotic shrub salt cedar (*Tamarisk* spp.) now occupies more than 526 000 ha of riparian habitat throughout the western United States (Stevens 1985), in many cases displacing native riparian species. These figures are of concern because riparian forest communities are often centers of diversity, especially in the arid Western US (Naiman et al. 1993), where riparian areas comprise less than 3% of the landscape (Naiman et al. 1993).

Riparian forests in the United States, in general, are rapidly declining and are now considered an endangered habitat type (Noss et al. 1995). It is estimated that over 100 000 ha of riparian habitat are lost annually and that 70–84% has been destroyed, converted to other uses, or significantly degraded since European settlement (Noss et al. 1995). Riparian forests are threatened by agriculture, development, and river management that eliminate natural flood regimes critical to sexual regeneration of native species in these forests (i.e., *Populus* spp.) (Rood and Mahoney 1995; Mahoney and Rood 1998; Rood et al. 1998), as well as invasive species such as salt cedar, and Russian Olive (*Elaeagnus angustifolia*).

Although riparian habitat has dramatically declined, exotics have increased in abundance. At the landscape level, these changes are likely due to major transmogrification of riparian ecosystems as listed above. At the local level, however, dominant herbivores may be an important factor affecting the invasibility of exotics. For example, studies have shown selective herbivory by large ungulates and beaver can result in plant community shifts (Johnston and Naiman 1990; Pastor and Naiman 1992; Peinetti et al. 2001). If herbivores prefer native species, then selective herbivory could positively affect exotic species when natives and exotics co-occur.

Strong preference of particular plant species by important herbivores may be a mechanism for linking terrestrial plant communities with aquatic processes. The interface between terrestrial and aquatic communities is complex and incorporates many processes including: microclimate modification (e.g., light, temperature, and humidity), nutrient

input alteration to the adjacent soils and organic contribution to rivers from surrounding terrestrial vegetation (Gregory et al. 1991). Therefore, factors that affect riparian forest communities may also affect aquatic ecosystem processes and biodiversity. For example, studies have shown how the terrestrial plant community can affect aquatic processes at the landscape (Vannote et al. 1980; Corkum 1992), ecosystem (Gregory et al. 1991), stand (Helfield and Naiman 2001; Margolis et al. 2001), and species level (Schulze and Walker 1997; Bailey et al. 2001). However, studies examining the effects of exotic plant species on aquatic processes at any level are rare, but likely important due to the increased abundance of invasive exotics.

In this manuscript we address two issues regarding the invasion of exotic tree species in riparian forests: 1) In a managed river, do beavers promote invasions of exotic tree species through preferential foraging on natives?; and 2) Can the community effects of foraging by beavers extend from terrestrial into aquatic habitats to differentially affect aquatic macroinvertebrates?

Herbivore Preferences on Riparian Forest Communities

In systems where native and exotic species co-occur, herbivore preference of native species can result in short-term increases in the abundance of exotic species. Along the Weber River, near Ogden Utah, cottonwoods are the dominant riparian tree species with willows, Russian olive, and salt cedar as smaller fractions of the riparian forest community. Over two years of monthly monitoring, we found that beavers significantly preferred native species to exotics ($n=314$ stumps, $df=3$, $X^2=373.8$, $p<0.0001$; Figure 1A). Specifically, beaver selected 51% more cottonwoods than expected. In contrast, 80–85% fewer willow, Russian olive and salt cedar were taken than expected.

These observationally derived patterns of beaver preferences were confirmed in a choice experiment ($df=3$, $X^2=11.43$, $p=0.01$; Figure 1B; Bailey et al. unpublished data). We placed 1.5 m cuttings of cottonwood, willow, salt cedar and Russian olive in a randomized block design at the rivers edge. After two nights of feeding, we found that beaver selected 133% more cottonwood branches than expected by chance. Similarly, the observed and expected values for willows were nearly identical, indicating that willows were taken in proportion to their abundance in the block. However, compared to their abundance, 66% fewer Russian olive and salt cedar branches were taken than expected; suggesting that they were avoided by beavers.

Such strong preferences for cottonwoods, which dominate riparian gallery forests along the Weber River, are likely to result in at least short-term changes in the local dominance of individual plant species. After two years of browsing, we found a significant switch in the proportion of each species in the stream margin community ($n=889$ trees, $df=3$, $X^2=9.53$, $p<0.023$; Figure 2A). Before beaver browsing, cottonwood trees co-dominated the stream margin community with willow (47% and 42%, respectively), Russian olive composed 7% and salt cedar just 4% of the individuals in the community. However, after two years, cottonwoods composed less than 26%, willow increased to 58%, Russian olive increased to 10% and salt cedar increased to 6% of the stream margin community. Beaver preference for cottonwoods benefited other native species (willow) and the two exotics.

When we examined the inner forest beyond the stream margin where willows were absent, we also found a significant switch in the proportion of each species ($n=99$ trees, $df=2$, $X^2=5.93$, $p=0.05$; Figure 2B). Before beaver browsing, the riparian community was 53% cottonwood, 20% Russian olive and 27% salt cedar. After two years of beaver browsing, cottonwoods significantly declined to 36%, Russian olive increased to 29% and salt cedar increased to 35% of the riparian forest community.

Overall, in just two years, cottonwoods declined by 17–21%, willow increased 17%, and cumulatively Russian olive and salt cedar increased by 4–17%, depending on the location assessed (i.e., stream margin or inner gallery forest). Our findings argue that short-term impacts of beavers on the dominant vegetation were rapid and caused a decrease in cottonwoods and an increase in exotics. Preference by herbivores for particular plant species can result in dynamic changes to the plant community and subsequent ecosystem structure and properties (Johnston and

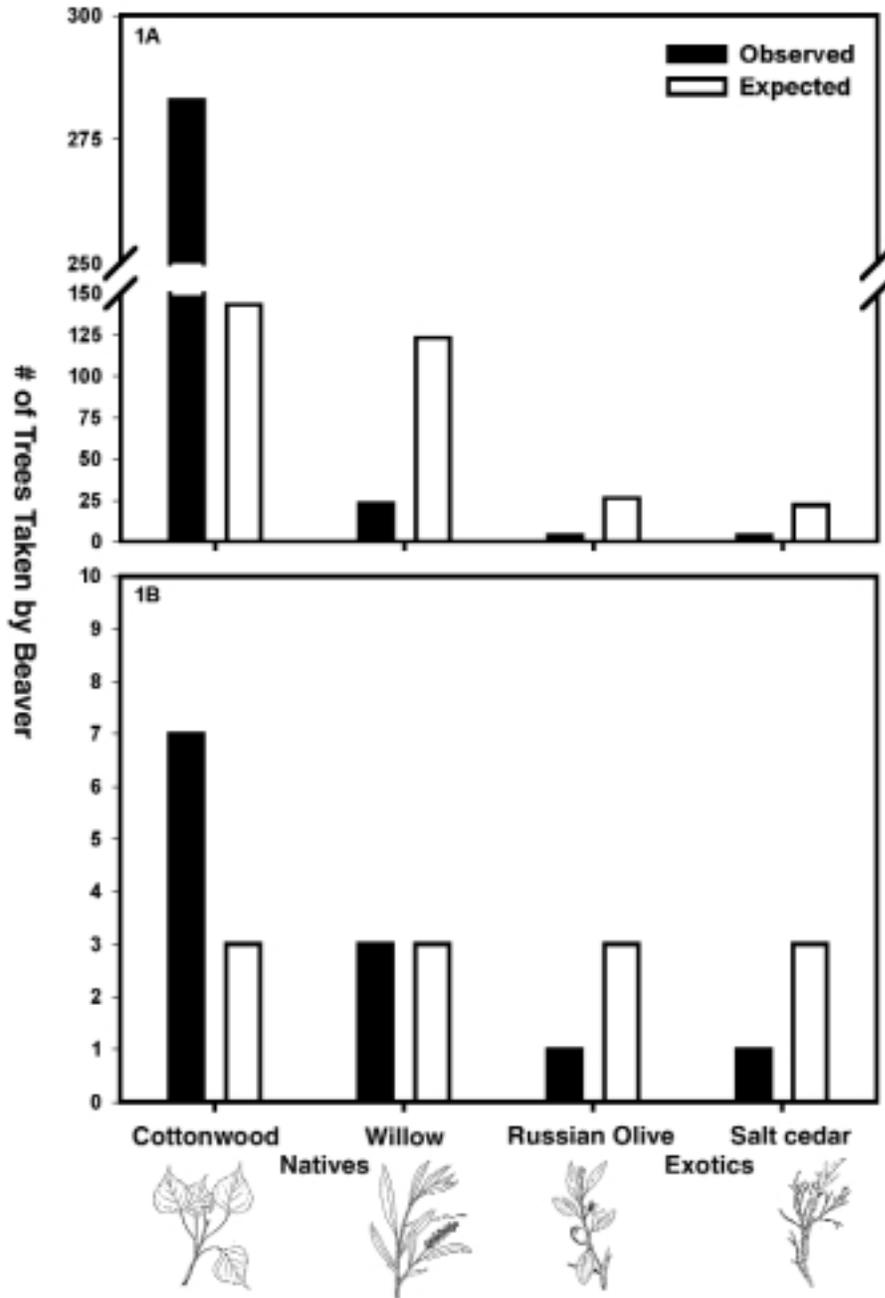


Figure 1. Beavers prefer natives and avoid exotics. There was a significant preference by beaver for cottonwoods over Russian olive or salt cedar. (A) After two years of browsing among 1302 trees, beaver selected 51% more cottonwoods than expected, willows were selected in proportion to their abundance, and 82-85% fewer Russian olive and salt cedar were selected than expected. (B) These patterns of preference were confirmed in a stream-side choice experiment where beaver selected >2X more cottonwoods than expected, selected willows in proportion to their abundance, and took 3X fewer Russian olive and salt cedar than expected.

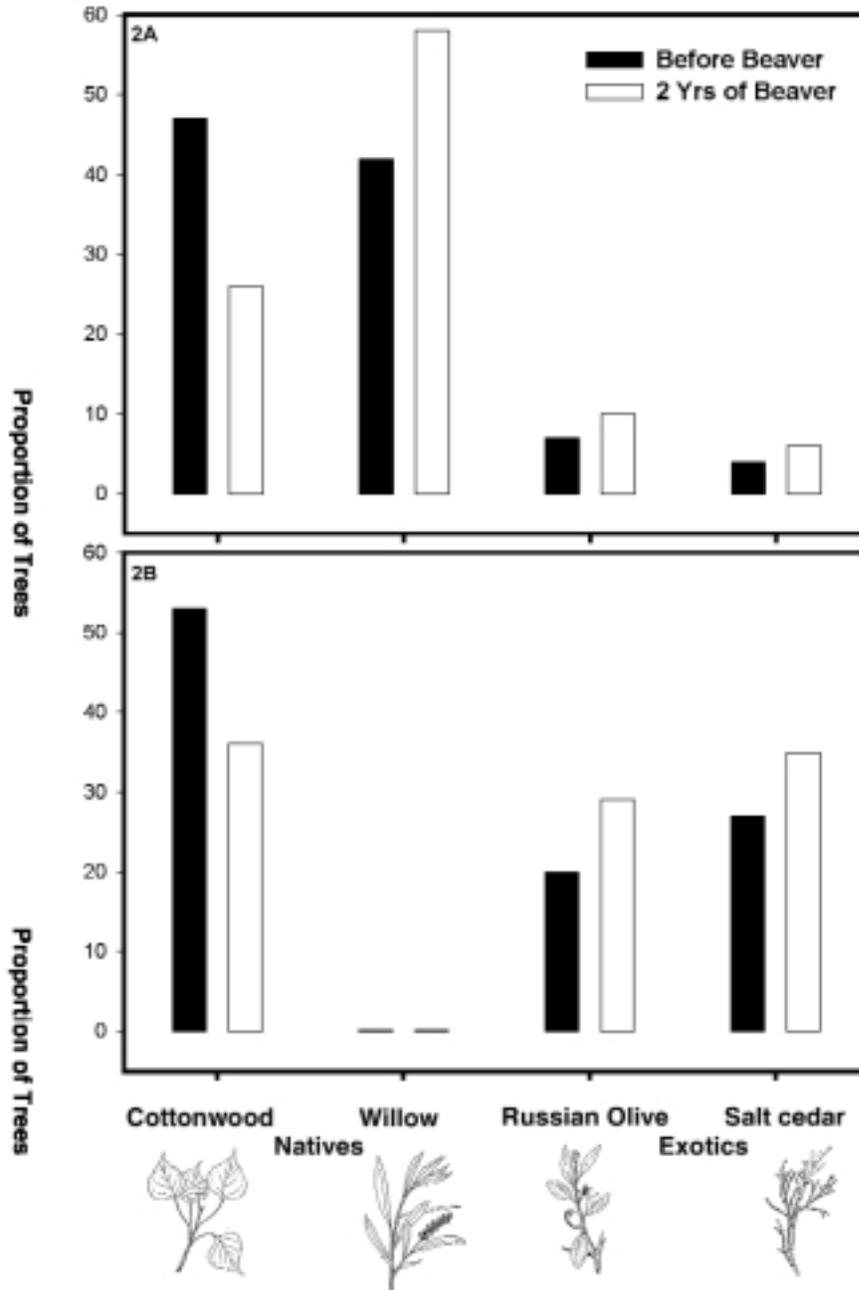


Figure 2. Exotics increase by 4-17%: The proportion of cottonwood, willow, Russian olive, and salt cedar in the riparian gallery forest switched after two years of beaver browsing. With repeat surveys of 1302 trees, natives dominated the riparian forest community. (A) At the stream margin cottonwoods and willows composed 89% of the community with Russian olive and salt cedar making up 11% of the community when willows were present. After two years of selective felling by beavers, natives still composed 84% of the community and exotics species increased to 16%. (B) In the inner forest where willows were absent (n=99 trees), cottonwoods comprised 53% of the trees, with Russian olive 20% and salt cedar 27%. However, after two years of selective felling by beavers, cottonwoods decline to 36% and Russian olive and salt cedar increased to 64%. Across both stream margin and inner forest, cottonwoods declined by 17-21%, willow increased 17%, and cumulatively Russian olive and salt cedar increased by 4-17% in just two years.

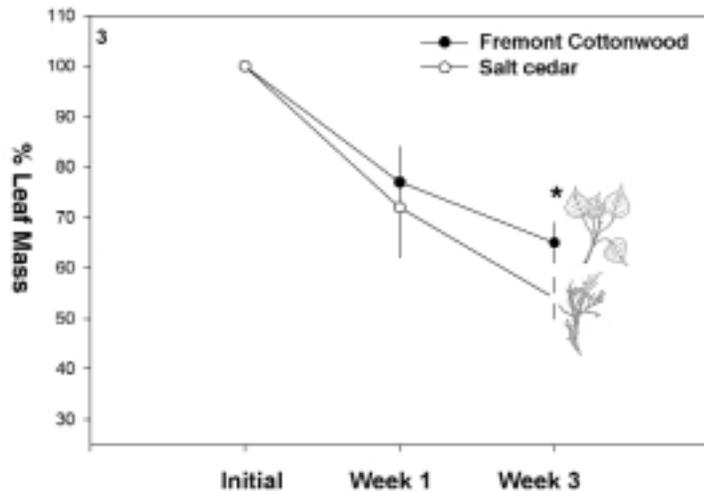


Figure 3. Fremont cottonwood decomposes slower than salt cedar. Using 3 mm mesh bags, salt cedar leaves lose biomass faster than Fremont cottonwood leaves after three weeks in the water (adapted from Bailey et al. 2001).

Naiman 1990; Pastor and Naiman 1992; Ritchie et al. 1998; Sirotnak and Huntley 2000; Peinetti et al. 2001) particularly if the herbivore is abundant, a keystone species, or an ecosystem engineer. For example, Johnston and Naiman (1990) showed that beaver preferred to harvest aspen trees over other riparian forest trees. This preference resulted in changes to the abundance and composition of the riparian plant community. After beaver browsing, riparian plant communities originally dominated by aspen were replaced with alder and spruce. Other effects of beaver browsing include changes in the distribution of important arthropod herbivores and communities (Martinsen et al. 1998), and alterations of ecosystem properties such as nutrient cycling patterns in streams (Naiman et al. 1986; Naiman et al. 1988).

Effects of Native and Exotic Litter on Stream Macroinvertebrates

Relatively few studies have examined how native and exotic leaf litter differentially affect aquatic macroinvertebrate communities (Boulton et al. 1997; Schulze and Walker 1997). Because beaver browsing can alter the abundance of native and exotic tree species, they may also alter litter quality and quantity that falls into the stream and affect aquatic macroinvertebrates.

Along Wet Beaver Creek, AZ, we examined the effects of native Fremont cottonwood (*Populus fremontii* L.) and exotic salt cedar (*Tamarix* spp.) litter on the aquatic macroinvertebrate community (Bailey et al. 2001). Using 3 mm mesh leaf packs we quantified the decomposition rates of cottonwood and salt cedar litter and aquatic macroinvertebrate richness, abundance, and composition after one and three weeks in the stream. The leaves of salt cedar and cottonwood differ both morphologically and chemically. Fremont cottonwood leaves have low tannin concentrations and are generally regarded as a good food resource for arthropods (Driebe and Whitham 2000). Salt cedar leaves have relatively high concentrations of tannins and are generally regarded as a poor food resource for arthropods (El-Beheiry and El-Kady 1998). In addition to leaf litter as a food resource, cottonwood leaves are broader than salt cedar and may provide better habitat and protection from predators for aquatic macroinvertebrates (Dobson 1994).

Overall, salt cedar decomposed faster than cottonwood. There was a significant species effect ($F=6.27$, $p=0.023$), as well as a time effect ($F=24.81$, $p<0.001$), but no species by time interaction ($F=0.85$, $p=0.371$). Cottonwoods and salt cedar had similar litter decomposition rates after one week in the water; cottonwood leaf litter lost 23% of its mass, and salt cedar lost 28% of its leaf mass (mean leaf mass lost \pm 1SE = 0.23 ± 0.02 and 0.28 ± 0.04 , respectively; Figure 3). However, after three weeks, salt cedar lost a total of 12% more leaf mass than cottonwood leaves (mean leaf mass lost \pm 1SE = 0.35 ± 0.02 and 0.46 ± 0.03 , respectively).

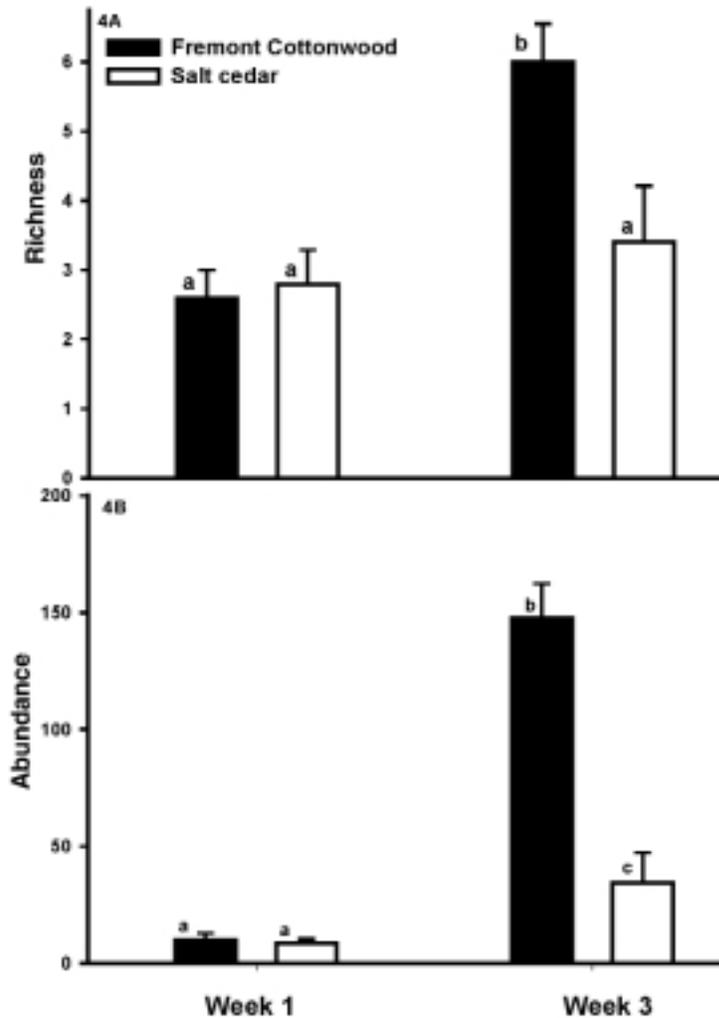


Figure 4. Macroinvertebrate richness and abundance greater on cottonwood. After initial litter-bag colonization, aquatic macroinvertebrate richness is twice as great on Fremont cottonwood leaves as it is on salt cedar leaves at three weeks. After three weeks, aquatic macroinvertebrate abundance is four times greater on Fremont cottonwood leaves as it is on salt cedar leaves (adapted from Bailey et al. 2001).

Overall, decomposing cottonwood leaves supported a more diverse arthropod community. There was a species \times time interaction showing strong differences in macroinvertebrate richness ($F=5.77$, $p=0.029$; Figure 4A) and abundance ($F=31.97$, $p<<0.001$; Figure 4B), on a per-leaf-pack basis, between treatment groups through time. After one week, aquatic macroinvertebrate taxonomic richness did not differ between the two leaf types. However, from week one to week three, the macroinvertebrate richness of cottonwood litter increased ~ 2.5 times, while no significant increase was detected on salt cedar over the same period. The fact that richness did not continue to increase on salt cedar leaves was surprising because new macroinvertebrate taxa should continue to colonize the leaf material. Most importantly, after three weeks, macroinvertebrate richness on cottonwood litter was twice as high as that on salt cedar (mean richness $\pm 1SE = 6.0 \pm 0.55$ vs. 3.4 ± 0.81 species per leaf pack).

For both leaf types, macroinvertebrate colonization increased predictably through time. After one week, there was no difference in macroinvertebrate abundance between cottonwood and salt cedar litter (mean abundance $\pm 1SE$

= 9.8 ± 3.06 and 8.6 ± 1.69). Macroinvertebrate abundance in leaf packs with cottonwood leaves was ~15 times greater at three weeks than at one week. Macroinvertebrate abundance on salt cedar was only four times greater at three weeks than at one week. However, macroinvertebrate abundance after three weeks was ~4 times greater on cottonwood leaves than on salt cedar leaves (mean abundance \pm 1SE = 147.4 ± 14.92 and 34.6 ± 12.83 , respectively).

The long-term implications and the mechanisms behind these patterns are still unclear. However, successful exotic invasions by plants and animals of other aquatic ecosystems have shown similar negative effects for native species diversity. Boulton et al. (1997) found that riparian forests dominated by an exotic species had significantly lower invertebrate fauna in the hyporheic zone than riparian forests dominated by native vegetation. In Australia, Schulze and Walker (1997) also reported that native eucalyptus and exotic willow leaves decomposed at different rates and structured macroinvertebrate communities differently.

Implications

From these data we have made two main points. First, preference by beavers for native plant species can favor exotic riparian species. The activities of beavers, which are keystone species in terrestrial and aquatic systems, provide a clear link between terrestrial and aquatic processes. In managed systems, where sexual regeneration of native riparian species is rare, selective foraging by beaver could dramatically alter the riparian forest community. Our study is over a short period of time for long-lived species and does not explore the long-term asexual response of these species to beaver herbivory. It does suggest, however, that factors that alter the quantity, quality or diversity of terrestrial litter input may be important determinants of stream processes at multiple scales, and may extend to higher trophic levels.

Second, changes in the terrestrial riparian forest plant community can affect aquatic macroinvertebrates. Because plant invasions are occurring rapidly and are potentially replacing native vegetation, the linkages between terrestrial and aquatic habitats (such as those we have demonstrated here) are likely to have important effects on biodiversity. Our study suggests that changes in terrestrial plant communities due to herbivory, by arthropods or mammals, can result in changes to the dependent aquatic macroinvertebrate community. These data indicate that native and exotic plant species are not equivalent and that specific plant species can be important to aquatic macroinvertebrate community composition and biodiversity.

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Literature Cited

- Bailey, J.K.; Schweitzer, J.A.; Whitham, T.G. 2001. Salt cedar negatively affects biodiversity of aquatic macroinvertebrates. *Wetlands* 21:442–447.
- Boulton, A.J.; Scarsbrook, M.R.; Quinn, J.M.; Burrell, G.P. 1997. Land use effects on the hyporheic ecology of five small streams near Hamilton, New Zealand. *New Zealand Journal of Marine Freshwater Research* 31:609–622.
- Corkum, L.D. 1992. Spatial patterns of macroinvertebrates along rivers within and among biomes. *Hydrobiologia* 239: 101–114.
- Dobson, M. 1994. Microhabitat as a determinant of diversity: stream invertebrates colonizing leaf packs. *Freshwater Biology* 32:565–572.
- Driebe, E.; Whitham, T.G. 2000. Cottonwood hybridization affects tannin and nitrogen content of leaf litter and alters decomposition. *Oecologia* 123:99–107.
- El-Beheiry, M.A.H.; El-Kady, H.F. 1998. Nutritive value of two *Tamarix* species in Egypt. *Journal of Arid Environments* 38:529–539.
- Everitt, B.L. 1998. Chronology of the spread of *Tamarisk* in the central Rio Grande. *Wetlands* 18:658–668.

- Gillis, A.M. 1992. Keeping aliens out of paradise: Government agencies and environmental groups are looking for ways to keep nonnative animal and plant pests out of Hawaii. *Bioscience* 42:482–485.
- Gregory, S.V.; Swanson, F.J.; McKee, W.A.; Cummins, K.W. 1991. An ecosystem perspective of riparian zones: focus on links between land and water. *Bioscience* 41:540–551.
- Gladwin, D.N.; Roelle, J.E. 1998. Survival of plains cottonwood (*Populus deltoides* subsp. *Monilifera*) and salt cedar (*Tamarix ramosissima*) seedlings in response to flooding. *Wetlands* 18:669–674.
- Helfield, J.M.; Naiman, R.J. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* 82:2403–2409.
- Johnston, C.A.; Naiman, R.J. 1990. Browse selection by beaver: effects on riparian forest composition. *Canadian Journal of Forest Research* 20:1036–1043.
- Kolar, C.S.; Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16:199–204.
- Mahoney, J.M.; Rood, S.B. 1998. Streamflow requirements for cottonwood seedling recruitment — an integrative model. *Wetlands* 8:634–645.
- Margolis, B.E.; Raesly, R.L.; Shumway, D.L. 2001. The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. *Wetlands* 21:554–563.
- Martinsen, G.D.; Driebe, E.M.; Whitham, T.G. 1998. Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. *Ecology* 79:192–200.
- Naiman, R.J.; Melillo, J.M.; Hobbie, J.E. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67:1254–1269.
- Naiman, R.J.; Johnston, C.A.; Kelley, J.C. 1988. Alteration of North American streams by beaver. *Bioscience* 38:753–762.
- Naiman, R.J.; Decamps, H.; Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3:209–212.
- Noss, R.F.; LaRoe III, E.T.; Scott, J.M. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. US Department of the Interior, National Biological Service, Washington, DC, USA Biological Report 28.
- Pastor, J.; Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139:690–705.
- Peinetti, H.R.; Menezes, R.S.C.; Coughenour, M.B. 2001. Changes induced by elk browsing in the aboveground biomass production and distribution of willow (*Salix monticola* Bebb): their relationships with plant water, carbon, and nitrogen dynamics. *Oecologia* 127:334–342.
- Ritchie, M.E.; Tilman, D.; Knops, J.M.H. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165–177.
- Rood S.B.; Mahoney, J.M. 1995. River damming and riparian cottonwoods along the Marias River, Montana. *Rivers* 5:195–207.
- Rood, S.B.; Kalischuk, A.R.; Mahoney, J.M. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman river, Alberta, Canada. *Wetlands* 8:557–570.
- Schulze, D.J.; Walker, K.F. 1997. Riparian eucalypts and willows and their significance for aquatic invertebrates in the River Murray, South Australia. *Regulated Rivers* 13:557–577.
- Sirotnak, J.M.; Huntley, N.J. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology* 81:78–87.
- Stevens, L. 1985. Invertebrate herbivore community dynamics on *Tamarix chinensis* loueiro and *Salix exigua* Nuttall in the Grand Canyon, Arizona. Masters Thesis Northern Arizona University, Flagstaff, AZ.

Vannote, R.L.; Minshall, W.M.; Cummins, K.W.; Sedell, J.R.; Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130–137.

Zavaleta, E.S.; Hobbs, R.J.; Mooney, H.A. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution*. 16:454–459.