

The role of plant resistance and tolerance to herbivory in mediating the effects of introduced herbivores

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Abstract While the generally negative consequences of introduced species are well known, little is appreciated on the role of the evolutionary history of plants with herbivores in mediating the indirect impacts of herbivory. We examined how variation in plant resistance and tolerance traits can mediate the effects of herbivory and can have differential indirect impacts on other species and processes. We used two examples of a native and an introduced herbivore, *Castor canadensis* (American beaver) and *Cervus elaphus* (Rocky Mountain elk) with *Populus* spp. to test a conceptual model regarding possible outcomes of species interactions with native and exotic mammalian herbivores. Using these two herbivore test cases, we make two predictions to create testable hypotheses across systems and taxa: First, adaptive traits of tolerance or resistance to herbivory will be fewer when exotic species feed on plant species with which they have no evolutionary history. Second, historical constraints of species interactions will allow for negative feedbacks to stabilize the effects of herbivory by a native species. Overall, these two case studies illustrate that plant resistance and tolerance traits can mediate the indirect consequences of herbivory on associated interacting species. Specifically, when there is no

evolutionary history between the plants and herbivores, which is often the case with species introductions, the effects of herbivory are more likely to reduce genetic variation and habitat mosaics, thus indirectly affecting associated species.

Keywords Beaver · Elk · Genes to ecosystems · Introduced herbivores · *Populus* · Resistance traits · Tolerance traits

Introduction

It is well established that the consequences of species introductions can be severe, including community disassembly (Sanders et al. 2003), wholesale losses of native species (Simberloff and Von Holle 1999), changes to soil biota and the processes they mediate (Vitousek and Walker 1989; Wolfe and Klironomos 2005; Reinhart and Calloway 2006), and overall ecosystem reorganization (Simberloff and Von Holle 1999; Parker et al. 2006). Introduced herbivores can be particularly problematic. Once introduced, 25% of exotic vertebrates (at least between Europe and North America) establish in the new landscape and can become pests (Jeschke and Strayer 2005), this is especially true when they are managed for human uses. Mammalian species such as red deer in New Zealand, feral pigs in Hawai'i, rabbits on Pacific Islands and beaver in Argentina and Chile are a few examples of vertebrate introductions that have

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large-scale effects on native plant communities and ecosystem processes (Vitousek 1986; Wardle et al. 2001; Eldridge and Simpson 2002; Anderson et al. 2006; Anderson and Rosemond 2007) that can even facilitate the invasion of other plant species (Parker et al. 2006). For example, introductions of rabbits on two continents have resulted in dramatic shifts in plant species richness and abundance due to rabbit herbivory, which has had large indirect effects on plant community composition, plant productivity, nutrient cycles and trophic interactions (Eldridge and Simpson 2002; Miller 2007; Bergstrom et al. 2009). While many of the mostly negative effects of introduced herbivores are clear, what is less apparent is the role of plant responses to introduced herbivores and how differential species traits, determined by evolutionary history, may facilitate or mitigate the consequences of the introduction at the population, community or even ecosystem level.

There are two primary mechanisms for plants to cope with herbivory, the evolution of resistance traits or tolerance traits. Plant resistance traits are typically characterized as having a negative effect on the fitness and/or performance of herbivores (Leimu and Koricheva 2006; Nunez-Farfan et al. 2007). Resistance traits are usually identified through choice experiments under the assumption that resistant plants should receive less herbivore damage than susceptible plants under natural conditions (Rausher 1992). Plant tolerance traits are those traits that enable the plant to persist on the landscape even with herbivore pressure, although they may be costly to the plant (Strauss and Agrawal 1999). Tolerance traits may include, but are not limited to, induced phytochemical responses (Tollrian and Harvell 1999; Strauss et al. 2002), changes to morphology (Ohgushi 2005), compensatory growth such as resprouting from the browsed portion of the plant or cloning to spread out the herbivore damage (Strauss and Agrawal 1999; Vesik and Westoby 2004). While often considered in mutually exclusive arenas, recent data have shown that a combination of resistance and tolerance traits may occur and be selected for simultaneously, which may enable a plant to persist in the environment of herbivores (Stowe 1998; Pilson 2000; Puustinen et al. 2004; Nunez-Farfan et al. 2007). Moreover, one might expect in systems where there is no past evolutionary relationship between a dominant plant and an introduced herbivore, that

evolved resistance and tolerance traits in the population are likely to be rare or absent, relative to those systems where plants and herbivores have a shared evolutionary background (Daehler et al. 1999; Parker et al. 2006; Bailey et al. 2007). For example, the presence or absence of a shared evolutionary history between plants and their herbivores can affect: (1) a plant's ability to persist on the landscape (Bailey et al. 2007), which can alter abiotic environmental conditions affecting associated species and ecosystem properties; (2) how much genetic variation there is within and among plant populations, which is fundamental to a species ability to respond to forces of natural selection and has extended consequences for associated species interactions, biodiversity and ecosystem function.

Figure 1 illustrates a conceptual model by which the effects of introduced herbivores can have variable consequences on associated communities and ecosystems compared to native herbivores. It demonstrates four possible outcomes, three of which are likely for native herbivores that have evolved with the plant community and one outcome which is likely with introduced herbivores with no evolutionary history. Categories one through three are likely to result in the greatest survival, higher genetic variation, the greatest possibility to respond to natural selection, and create habitat mosaics that may have positive indirect impacts on associated species and processes. In contrast, category four may result in the lowest survival, the least amount of genetic variation and result in habitat homogenization across the landscape that is likely to have negative impacts on associated species and processes. Here, we use two case studies of a native and an introduced herbivore, *Castor canadensis* (American beaver) and *Cervus elaphus* (Rocky Mountain elk), respectively, to examine these categories in well-studied *Populus* spp. ecosystems. We used this comparison to examine how variation in plant responses to herbivory may facilitate or mitigate the effects of introduced herbivory not only on the dominant plant, but also on associated arthropod and avian diversity, plant community dynamics as well as ecosystem functions, including trophic interactions and soil nutrient cycles. Using these two herbivore case studies, we make two predictions to generate future testable hypotheses: First, adaptive traits of tolerance or resistance to herbivory will be fewer when exotic species feed on

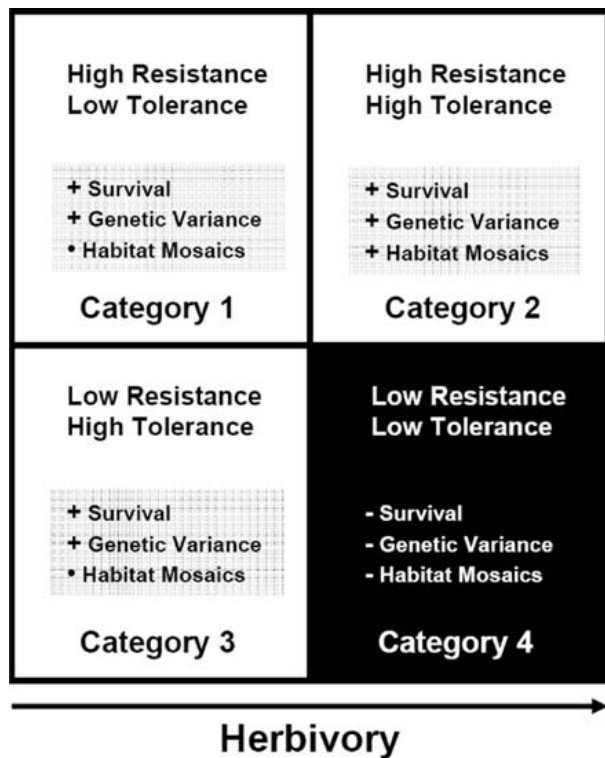


Fig. 1 Conceptual diagram illustrating how resistance and tolerance traits in plants may mediate the indirect effects of herbivory on associated species. We predict that when a population of plants expresses strong resistance or tolerance to a particular herbivore, plant survival will be high, population level genetic variation will be maintained, but habitat mosaics will be restricted to one class of plant (i.e. either unbrowsed resistant genotypes or browsed tolerant genotypes). When a population expresses strong resistance and tolerance, the outcome is similar, but habitat mosaics will also be greatest, likely maximizing diversity. In contrast, when there is low resistance and tolerance to a particular herbivore, such as when herbivores are introduced, survival will be low, genetic variance will be low, and habitat mosaics will be uncommon resulting in the greatest negative indirect effects on associated species. The symbol “•” represents a neutral outcome. The *black box* represents the predicted circumstances surrounding introduced herbivores

non-adapted plant species, which will result in greater mortality of the focal plant, low genetic variation in the remaining population of plants, and thus greater negative effects on associated species and ecosystem function due to a less diverse resource base (category 4 in Fig. 1). Second, evolutionary constraints of species interactions will allow for feedbacks to stabilize the effects of herbivory by a native species, creating a consistent habitat resource for associated interacting species (categories 1–3 in Fig. 1).

Case study systems

Two well-studied common herbivores (one native and one exotic) that interact with *Populus* spp. in the Intermountain West of the US were utilized to examine the prediction that evolved resistance strategies in plants are broken down when herbivores are introduced which in turn also impacts indirect effects at the population, community and ecosystem level. The comparison of these two case studies should be illustrative of the impacts of native and exotic herbivores and thus represent good models with which to test our predictions for various reasons. First, both herbivores (beaver and elk) are dominant browsers that can have landscape level impacts (Hobbs 1996; Wright et al. 2002). Second, both plant species (*Populus angustifolia* and *P. tremuloides*) are dominant forest trees with established effects on associated biodiversity and ecosystem function (Madritch et al. 2006, 2007; Bailey and Whitham 2007; Schweitzer et al. 2008). Furthermore, both trees are classified as the same genus, *Populus*, and while occupying different clades and different sections within the genus (*Populus* and *Tacamahaca*, respectively; Eckenwalder 1996; Hamzeh and Dayanandan 2004), they share many conserved traits related to the tolerance and resistance to herbivory, including the ability to resprout after damage and similar suites of secondary compounds (condensed tannins and phenolic glycosides; Palo 1984; Rehill et al. 2006; Schweitzer et al. 2008). Additionally both *Populus* species share many common invertebrate herbivores, including *Phyllocolpa* spp., which make leaf edge galls. In both systems, the galling structure has been shown to positively affect associated arthropod diversity (Bailey and Whitham 2003). In combination, this parity in study systems make them ideally suited to illustrate the potential role of plant response to herbivory in facilitating or mitigating the effects of introduced herbivores.

Exotic herbivores on *Populus tremuloides*

Populus tremuloides Michx. (trembling aspen) has the largest distribution of any North American deciduous tree species, is recognized for supporting many unique associated plant, insect and bird species and has important impacts on ecosystem processes. *P. tremuloides* is a resilient tree species that can

survive fires in the Intermountain Western US by resprouting from roots, which contributes to the long-term persistence of *P. tremuloides* across landscapes (Mitton and Grant 1996). However, throughout the Western US, *P. tremuloides* forests are in decline (Romme et al. 1995; Baker et al. 1997; Kay 1997; Bailey and Whitham 2002) and browsing by large introduced ungulates is considered to be one of the important causes of the change in populations of aspen (Romme et al. 1995; Kay 1997; Baker et al. 1997; Bailey and Whitham 2002; Hessler 2002a, b). Because of substantial environmental and economic value of *P. tremuloides*, this decline is of considerable concern (Romme et al. 1995; Baker et al. 1997; Bailey and Whitham 2002).

Populus tremuloides ecosystems in northern Arizona provide a good case study in which to study the effects of an introduced herbivore (Rocky Mountain elk; *Cervus elaphus*). In northern Arizona, Rocky Mountain elk were introduced in 1918 (Hoffmeister 1986; Rolf 2001) and population levels of elk on the Colorado Plateau in Arizona have been as high as 35,000 individuals (www.azgfd.gov). In an effort to remedy the negative effects of elk herbivory, 2 m high elk exclosures (mesh fencing) have been established throughout the Coconino National Forest by the US Forest Service (Rolf 2001) following fire to allow *P. tremuloides* forests, as well as understory plant communities, to establish and regenerate (Rambo and Faeth 1999; Kay and Bartos 2000; Rolf 2001; Bailey and Whitham 2002, 2003). A native species of elk (*Cervus elaphus merriamii*) occurred in Arizona but its distribution was limited to the White Mountains of eastern Arizona and was extirpated by 1914 (Hoffmeister 1986). Thus, populations of *P. tremuloides* in northern Arizona had no evolutionary history with a large browsing herbivore such as elk.

Native Herbivores on *Populus angustifolia*

Populus angustifolia James (narrowleaf cottonwood) riparian forests in the United States are rapidly declining and are now considered threatened (Noss et al. 1995; Gitlin et al. 2006). It is estimated that over 100,000 ha of riparian habitat are lost annually (Finch and Ruggiero 1993) and that 70–84% of riparian habitat has been destroyed, converted to other uses, or significantly degraded since European settlement (Noss et al. 1995). These figures are of

particular concern because riparian communities are often centers of diversity, especially in arid regions of the US (Finch and Ruggiero 1993; Naiman et al. 1993). Riparian habitats support many threatened and endangered species, and they provide critical habitat for Neotropical migrant birds (Knopf 1985). In these riparian habitats, beaver and *P. angustifolia* interact to affect the regeneration and maintenance of this community.

Through their feeding and dam-building activities, beaver (*Castor canadensis*) act as a keystone species to have disproportionate impacts on the community (Naiman et al. 1986, 1994; Johnston and Naiman 1990; Jones et al. 1994). Once a major herbivore of riparian habitats, beaver were heavily trapped and extirpated from most of North America by the turn of the nineteenth century (Jenkins and Busher 1979), but in the last several decades they have returned to much of their former range and their numbers have increased dramatically. Their reduced populations during most of the twentieth century however, may not have had a significant impact on the evolution of *Populus*-beaver interactions as this time period represents less than one generation of a long-lived species such as *P. angustifolia*. Beaver browsing impacts vegetation and can change competitive interactions among dominant species (McNaughton 1976; Johnston and Naiman 1990), and the disturbances they create greatly alter landscapes (e.g. beaver dams; Naiman et al. 1986, 1994). Thus, the overall broad distribution of beaver have resulted in a long history of interaction with *P. angustifolia* in the western US and along the Weber River in northern Utah.

Plant resistance and tolerance to herbivory

Much research has shown that mammalian herbivores respond to variation in phytochemistry in plants (Bryant 1981; Basey et al. 1990; Verheyden-Tixier and Duncan 2000; Pusenius et al. 2002; O'Reilly-Wapstra et al. 2002, 2004; Bailey et al. 2004). However, relatively few studies demonstrate that herbivores can act as agents of natural selection on plant traits in general and defensive phytochemistry in particular (Mauricio and Rausher 1997; but see Stinchcombe and Rausher 2001, 2002; Bailey et al. 2004, 2007). While the specific phytochemical traits

that confer resistance to the two *Populus* species differ between the herbivores (Fig. 2a, b), for both *P. angustifolia* and *P. tremuloides* there does appear

to be some resistance to herbivory in the population. Specifically, in a choice experiment where 5 replicates of 12 genotypes of *P. angustifolia* were

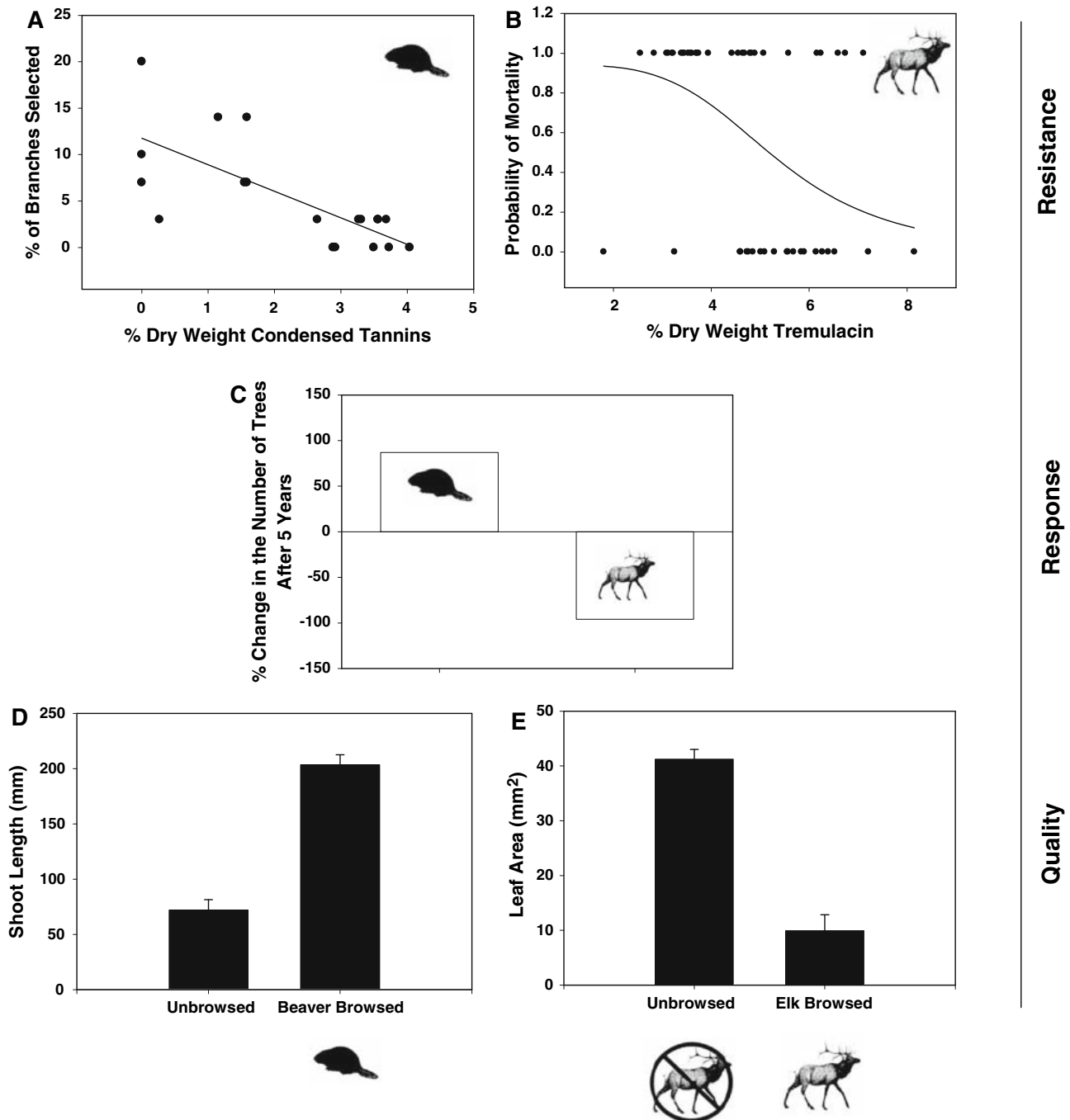


Fig. 2 Plant resistance and tolerance traits are important to patterns of mammalian herbivory, plant persistence on the landscape, and subsequent plant quality after herbivory. In the case of native beaver-*Populus angustifolia*, where plants express strong resistance (a) and tolerance (c), the consequences of herbivory are largely positive (i.e. nearly a 100%

increase in the number of individuals and improved plant quality (d). In contrast, when the expression of resistance and tolerance traits are weak (b), as in the case of the introduced elk-*P. tremuloides*, the consequences of herbivory are largely negative (c) (i.e. rapid mortality and poor plant quality; e)

randomly placed in a stream adjacent to active beaver herbivory, beaver preferred trees low in bark condensed tannins (Fig. 2a: $F_{(1,11)} = 5.53$, $r^2 = 0.36$, $P = 0.041$). In a similar experimental choice experiment in which 60 unbrowsed *P. tremuloides* were excluded from elk herbivory for 5 years and then exposed to elk, we found that the phenolic glycoside, tremulacin, was positively related to *P. tremuloides* survival (Fig. 2b: 2002: $X^2 = 21.23$, $P < 0.0001$). Furthermore, repeat surveys of the population showed that the effect became stronger through time after fence removal (2005: $X^2 = 30.36$, $P < 0.0001$; Bailey et al. 2007). While these data indicate the presence of phytochemical resistance traits within *P. angustifolia* and *P. tremuloides* populations, understanding the frequency of these traits in the population is fundamental to understanding the impacts of herbivory.

In landscape level surveys of phytochemistry in *P. angustifolia* and *P. tremuloides* populations, the frequency of resistance traits in the population is remarkably different. For example, in a survey of 50 genotypes of *P. angustifolia* from 6 sites along the Weber River, 90% of the trees had a concentration of condensed tannins in bark that was greater than 4% (dry mass [DM]). These data are consistent with a long-term ecological and evolutionary history of interaction resulting in most of the individuals within the population of *P. angustifolia* demonstrating resistance to beaver herbivory. In contrast, 90% of the population of *P. tremuloides* in northern Arizona have a susceptible foliar phytochemical phenotype. In a survey of 100 individuals from 10 sites north of the San Francisco Peaks in northern Arizona, 25% of the population had a concentration of tremulacin great enough to give them a 50% chance of survival after herbivory by elk, and only 10% of the population had an 80% chance of survival. These results are consistent with data reported in Bailey et al. (2007) and suggest that the interaction of elk and *P. tremuloides* in these forests is a relatively recent dynamic as genetic variation in *P. tremuloides* forests of northern Arizona have not changed in response to this selective pressure imposed by elk. This is likely due to the fact that *P. tremuloides* are a long-lived tree (~150 years) and elk have been introduced in less than one generation time (i.e., 91 years ago). A response in *P. tremuloides* to this selective pressure is made more difficult as sexual reproduction in the last 100 years is considered rare due to fire management

techniques (Romme et al. 1997). Because of the inability of aspen to respond to selection by elk, genetic variation in these populations is likely to be low.

There is a rich literature on plant responses to herbivory that include induced morphological, physiological and phytochemical changes to plant tissues (see reviews by Strauss and Agrawal 1999; Ohgushi 2005). One fundamental plant tolerance response to herbivory that may be critical to plant persistence is coppicing or resprouting. Coppice is plant tissue that sprouts from the existing and previously browsed plant stem. In *P. angustifolia* riparian forests, such as along the Weber River where we conducted our studies, beaver felling of trees can also stimulate regeneration through root sprouting (McGinley and Whitham 1985; Martinsen et al. 1998). We estimate that from a single felled tree approximately 20–40 cm in diameter, as many as 30 or more young *P. angustifolia* can sucker from the roots and even more can coppice from the stump. Figure 2c shows the 5 year change (%) in the number of individual trees across nine sites on the Weber River, UT. Overall, there was nearly a 100% increase in the number of *P. angustifolia* trees 5 years after beaver herbivory. As sexual regeneration is rare in *P. angustifolia* riparian forests, particularly when the rivers are managed (Mahoney and Rood 1998), resprouting may represent a major factor in the formation of *P. angustifolia* clones in which a single clone may be composed of over 160 mature ramets and occupy approximately 25 m of riverbank (clone 18, Weber River, personal observation). Furthermore, when 115 young trees were experimentally felled to simulate beaver cutting, 91% resprouted from both coppicing and root suckers. These asexually derived *P. angustifolia* express juvenile architectural traits rather than the mature traits of the larger trees from which they were derived (e.g., shoot lengths are nearly four times as long as those of adjacent unbrowsed *P. angustifolia*, Fig. 2d; Bailey and Whitham 2006b), and they exhibit very different phytochemical phenotypes than mature trees (Martinsen et al. 1998; Rehill et al. 2006).

While the size (dbh) of *P. angustifolia* and *P. tremuloides* were nearly comparable between these study systems (trees generally less than 20 cm in diameter), *P. tremuloides* did not coppice as vigorously as *P. angustifolia*. We also found no

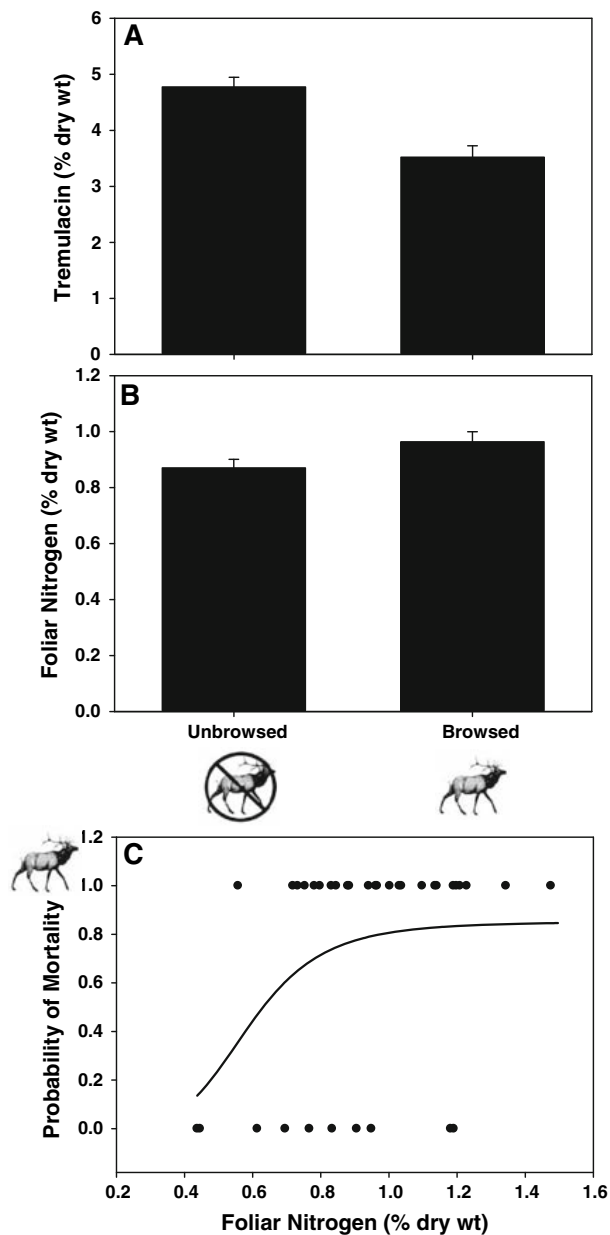


Fig. 3 In the case of introduced elk-*Populus tremuloides*, when *P. tremuloides* express tolerance traits such as coppicing from the browsed trunk, the foliage is less well defended (a) and more nutritious (b). Subsequently, elk are more likely to re-browse the resprout foliage resulting in increased mortality through time (c)

evidence of root suckering in *P. tremuloides* after browsing by elk. Similar to *P. angustifolia*, resprouting *P. tremuloides* also exhibited very different phytochemical and architectural phenotypes relative to adjacent unbrowsed *P. tremuloides* (Bailey and Whitham 2003). Importantly, the phytochemical differences in *P. tremuloides* make them even more

susceptible to repeated herbivory by elk. When leaf foliage of 40 browsed *P. tremuloides* was compared to foliage of 60 adjacent unbrowsed *P. tremuloides* that were experimentally protected by a fence, the concentration of tremulacin was 26% lower in browsed plants (Fig. 3a). In contrast, nitrogen concentration was 9% higher in browsed versus unbrowsed plants (Fig. 2b). While high tremulacin concentration conveys initial resistance in *P. tremuloides* to elk herbivory, when we examined the phytochemical traits that were correlated with *P. tremuloides* mortality in the 40 browsed *P. tremuloides*, we found that nitrogen concentration was positively correlated with *P. tremuloides* mortality (Fig. 3c). Both the resprout and phytochemical response in *P. tremuloides* to elk herbivory have little effect to enable *P. tremuloides* to persist on the landscape, therefore our research indicates that elk herbivory can reduce *P. tremuloides* numbers by 96% in just 5 years after a fire (Fig. 2c). Of those *P. tremuloides* that persist, they were generally of poor nutritional quality and had leaves that were 75% smaller than those of unbrowsed *P. tremuloides* (Fig. 2e). These herbivore-induced changes in both species of *Populus* ultimately had significant indirect effects on a diverse community of organisms.

Indirect effects of herbivory on biodiversity

Variation in the response of associated species to plant traits may be critical to how the effects of introduced herbivores cascade across higher levels of organization. One herbivore commonly found on many species of *Populus* is a galling sawfly *Phyllocolpa* spp. (Tenthredinidae). *Phyllocolpa* is commonly found both on *P. tremuloides* in montane forests of northern Arizona (*Phyllocolpa bozemanni*) and in *P. angustifolia* riparian forests (*Phyllocolpa* spp.) and is considered a keystone species as it creates a fold on the margin of a leaf that other invertebrate species utilize. On *P. angustifolia*, beaver herbivory positively affected the abundance of the *Phyllocolpa* spp. sawfly through changes to host plant architecture (Fig. 4), including increased shoot length. *Phyllocolpa* spp. gall abundance was 7–14 times greater on beaver resprout foliage than on adjacent non-resprout foliage. On *P. tremuloides* trees, elk herbivory negatively affected the

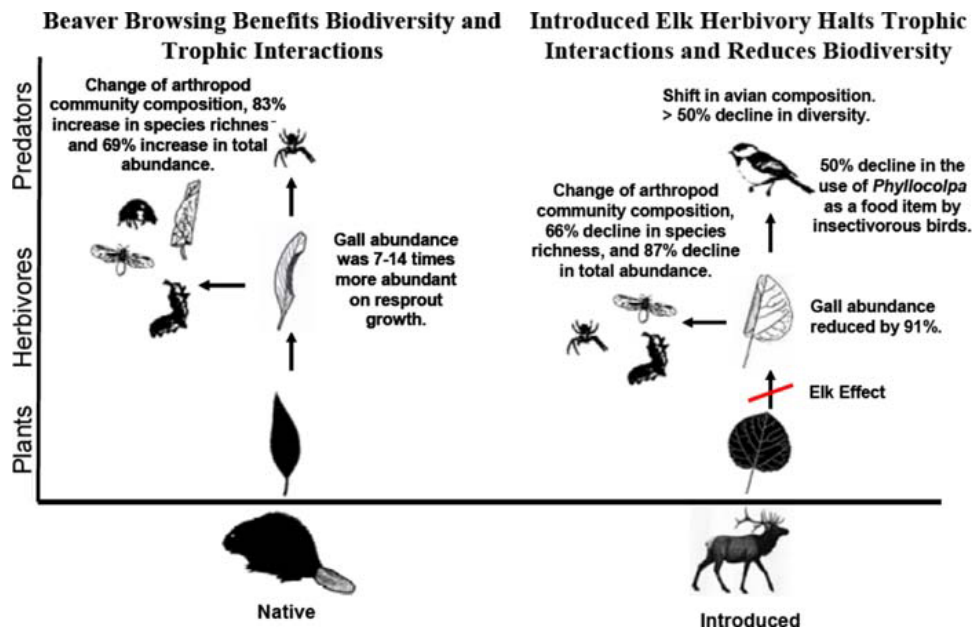


Fig. 4 The indirect consequences of herbivory on associated arthropod communities and trophic interactions vary depending upon the plant response to herbivory. Overall, native beaver herbivory increases habitat complexity and improves plant quality positively affecting a keystone galling herbivore and a diverse community of associated arthropods. In contrast, reduction in habitat complexity due to high herbivory and mortality of *Populus tremuloides* by the introduced herbivore

(Rocky Mountain elk) and reduced plant quality negatively affected a similar galling herbivore species (*Phyllocolpa bozemanii*). Moreover, elk indirectly and negatively, affect insectivorous birds which feed on the gall, reduce arthropod diversity that occupy the gall, and shift avian community composition at the stand level resulting in a 50% decline in overall diversity

abundance of *Phyllocolpa bozemanii* through changes to host plant architecture (Bailey and Whitham 2006a). As a result, *P. bozemanii* gall abundance is 91% lower on elk resprout foliage than on adjacent non-resprout foliage. Therefore, as *Phyllocolpa* spp. occurs on both species of *Populus*, but responds differently to herbivory, this comparison provides the opportunity to examine the consequences of differential effects of native and exotic species on biodiversity and ecosystem function.

The *Phyllocolpa* spp. can be considered a keystone species as it creates a structure (i.e. a leaf fold) that provides habitat for many other species such as aphids and spiders that utilize the space within the fold for shelter and food (Cappuccino 1993; Dickson and Whitham 1996; Martinsen et al. 2000; Bailey and Whitham 2003; Nakamura and Ohgushi 2003). In *P. tremuloides* forests, the presence of this sawfly can increase average arthropod richness by 66% and abundance by 87% (Fig. 4; Bailey and Whitham 2003). Using non-metric multi-dimensional scaling (NMDS) ordination of individual species, standardized to species maxima, Bailey and Whitham

(2003) found that arthropod community composition differed significantly when galls were present on *P. tremuloides* ramets than when galls were absent. These data suggest that localized shelters created by modifying plant leaves have community-wide effects. Of the 33 arthropod species documented in this study, more were found on galled leaves than on non-galled leaves. For example, at least 90% of the abundance of 5 herbivorous arthropod species and 6 predaceous species were found within the galls (Bailey and Whitham 2003).

Phyllocolpa bozemanii is also an important food item for insectivorous birds associated with *P. tremuloides* forests (Bailey and Whitham 2003). However, elk herbivory strongly negatively affects the abundance *P. bozemanii* through changes to *P. tremuloides* (i.e. architecture, chemistry; Fig. 2e) and thus could indirectly and negatively affect insectivorous birds. In fact, when the number of galls was experimentally held constant on browsed and unbrowsed *P. tremuloides*, there was no difference in bird predation of galls (Bailey and Whitham 2003). This demonstrated that elk browsing reduced

insectivorous bird foraging on *P. tremuloides* ramets by 50%. At the stand level, elk browsing interacted to affect avian communities. In the spring of 2000, 22 migratory bird species were surveyed inside and outside five similar-aged *P. tremuloides* stands that were protected from elk herbivory by an enclosure. NMDS ordinations (coupled with analysis of similarity) showed that the avian community was significantly different inside and outside of the enclosure (Bailey and Whitham 2006a) and that elk herbivory resulted in a 50% decline in avian diversity at these sites.

In contrast to the negative effects of elk herbivory on arthropod diversity and trophic interactions with avian predators, the effects of beaver herbivory on *Phyllocolpa* spp. increased arthropod diversity and maintained trophic interactions. For example, arthropod community composition was significantly different on *P. angustifolia* trees with *Phyllocolpa* spp. relative to those without the galling insect, species richness was 83% greater and there were 69% more individuals. Overall, the difference in the effects of beaver versus elk herbivory on arthropod community composition was driven by the response of the plants. Variation in the response of plants then had extended effects on associated arthropods because of the preference of sawflies for vigorously growing plant tissues (Price 1991).

Indirect effects of herbivory on associated plant communities

The effects of introduced herbivores on associated biodiversity are not limited to species which also utilize the focal plant as we have described above, but may also extend indirectly to other plant communities. For example, using repeat surveys of six riparian forest sites that had been heavily influenced by beaver herbivory, we found a negative relationship between the proportion of trees at the site that had been cut by beaver out of the total number of trees at the site initially and the number of new exotic tree seedlings which colonized the site. In sites where beaver had removed a greater proportion of the mature trees, there were fewer new exotics (Fig. 5a; $r^2 = 0.18$, $F_{(1,30)} = 6.12$, $P = 0.017$). We hypothesized that this was due to the resprout response of *P. angustifolia* to beaver herbivory and the potential

change in the number of individuals at the site after 5 years. Consistent with this prediction we found that the number of new *P. angustifolia* after 5 years was negatively correlated with new colonization by exotic seedlings (Fig. 5b; $r^2 = 0.33$, $F_{(1,30)} = 14.45$, $P = 0.0007$; Bailey, unpublished data). These included *Ulmus pumila* (Siberian elm), *Eleagnus angustifolia* (Russian Olive), *Tamarix chinensis* (salt cedar), which are particularly invasive and known for displacing native species (Brock 1994; Katz and Shafroth 2003). In contrast to the hypothesis that native herbivores remove native plants from the system enabling exotic species to colonize, these results are consistent with an adaptive response of the plant to the herbivore, beaver, which may slow the spread of exotics by occupying habitat with ramet production.

The lack of plant resistance traits to the introduced elk in northern Arizona impacts not only the dominant species in the forest but also to adjacent understory species, with consequences for native people in the area. In northern Arizona, the Native American culture is rich, with many federally recognized Native American tribes, and the field collection and use of ethnobotanical plants are common by the Diné and Hopi people (Moerman 1996; Nabhan et al. 2004). Many species within the local ecosystem are used in one way or another as food items, pharmaceuticals, craft materials, and ceremonial items that are important for the traditions of a culture as well as the daily well being of individuals within that culture (the field of ethnobotany). We explored the impacts of introduced elk on ethnobotanical plant species richness and abundance as well as the richness and abundance of plants specifically used for craft, food, ceremonies and medicine across six paired enclosure and control sites (described above). Elk herbivory negatively impacted total plant species richness, abundance as well as the richness and abundance of all classes of ethnobotanicals (i.e., ceremonial, medicinal, craft and food species; Fig. 5c, d). For example, there was a 55% decline in the number of ethnobotanical species and 62% decline in the total abundance of ethnobotanical plants when elk were present. In particular, there was a 74% decline in the abundance of plants used for medicinal purposes and an 87% decline in the species richness of medicinal plants (Bailey et al., unpublished). These results indicate that elk may reduce the availability of

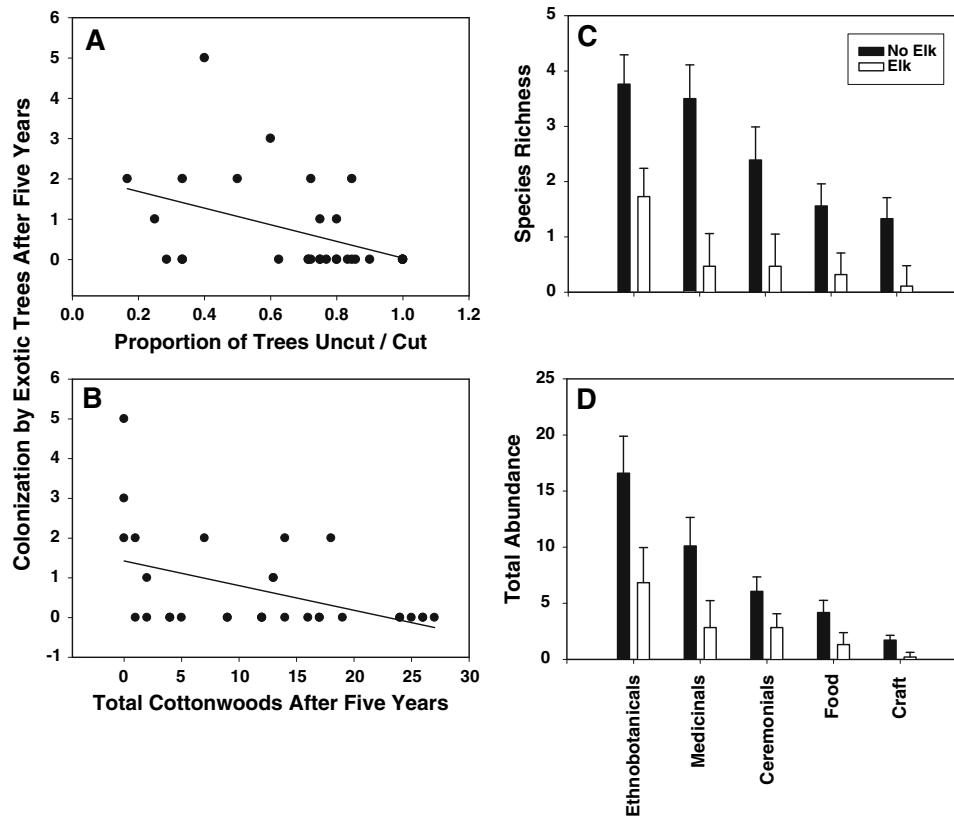


Fig. 5 The indirect consequences of herbivory on associated plant communities vary depending upon the plant response to herbivory. In the beaver-*Populus angustifolia* case study, the resprout response of *P. angustifolia* was negatively correlated with future colonization of invasive exotics, such as *Ulmus pumila* (Siberian elm), *Eleagnus angustifolia* (Russian olive),

Tamarix chinensis (salt cedar) across 6 sites (a, b). While likely, unrelated to the response of *P. tremuloides* to elk herbivory, the introduced elk negatively affected a culturally important plant community. Elk herbivory reduced ethnobotanical plant richness and abundance as well as the richness and abundance of medicinal, ceremonial, craft and food species (c, d)

medical resources to Native American cultures as well as limit the potential number of ailments that may be treated. The pattern was similar for plants used as food, craft and ceremony. Food plant abundance was 69% lower in the presence of elk and food plant richness was 80% less. Craft plants, potentially used in the making of Kachinas or baskets, were 88% lower in abundance in the presence of elk with 93% fewer species. And finally, ceremonial plants were 60% less abundant with 84% fewer species in the presence of elk. While we don't know the specific mechanisms of linkage between aspen and understory plant communities, research indicates that the presence of aspen leads to particular associated plant species (Rambo and Faeth 1999). When aspen are removed from sites, these communities are lost. In combination, these results indicate that an overlooked effect of species introductions are

the negative indirect impacts of introductions and management strategy on associated plant communities and the cultural groups that utilize them.

Indirect effects of herbivory on ecosystem processes

Ungulate herbivory can have profound effects on ecosystem processes in forests by directly altering soil physical and chemical properties through trampling and inputs of urine and dung and indirectly by changing plant species composition, productivity as well as litter and root inputs (Pastor and Cohen 1997; Ritchie et al. 1998; Bardgett and Wardle 2003; Harrison and Bardgett 2008). These effects may be especially important when the herbivore is an introduced species (Wardle et al. 2001; Eldridge and

Simpson 2002). Utilizing the elk exclosures described above in *P. tremuloides* ecosystem in northern Arizona, Stritar et al. (2009) found that reductions in plant biomass due to herbivory (and possibly trampling by elk) resulted in significant differences in soil carbon (C) and nitrogen (N) dynamics in soils, across a time since fire chronosequence. When averaged over sites, pools of organic C, total N and microbial biomass N were 22, 23 and 37% higher (respectively) in the absence of herbivory (i.e. inside of the exclosures). In contrast they report that the activity of potential C-degrading extracellular enzyme activity and soil NO_3^- , as measured with in-field resin bags, were 43 and 63% lower, respectively, inside of the exclosures (without elk). These data suggest that herbivory by the introduced elk have significant effects on C and N accumulation when elk are absent (i.e. increased plant biomass inputs from litter). However, plants utilize and microbial communities immobilize much of these nutrients, reducing the amount of mineralized N that could be lost. Herbivory by elk alters C and N accumulation and potentially increases the chances for losses of mineralized N due to leaching of NO_3^- from the system, with the absence of uptake by either microbes or plants. While the issue of herbivore density is important, anecdotal evidence indicates that in *P. tremuloides* systems where elk are native, herbivory has been shown to have no effect on total pools of C and N or on N availability as measured with in-field resin bags, relative to aspen stands inside elk exclosures (after 35 years; Binkley et al. 2003; Singer and Schoenecker 2003; Schoenecker et al. 2004), although N export does occur due to elk movements (Schoenecker et al. 2004).

No comparable data from the beaver-*P. angustifolia* system exist. Nonetheless, the literature suggests that shifts in species composition with herbivory may have significant impacts on plant community composition and soil nutrient dynamics (Pastor and Naiman 1992; Naiman et al. 1993, 1994; Johnston 2001; Rosell et al. 2005). Anecdotally, the effects of beaver in their native range are dependent on site-specific conditions such as habitat, relief and soil type (Johnston et al. 1995; Rosell et al. 2005). However the activities of beaver are thought to have an overall stabilizing effect on riparian ecosystems by maintaining early stages of succession and improving water quality which positively impact many other associated

species (Naiman et al. 1993; Rosell et al. 2005). Increases in the plant population of *P. angustifolia* genotypes with higher condensed tannins (due to selective felling of trees with lower bark condensed tannins; Bailey et al. 2004) may result in nutrient conservation in riparian soils as previous work in this and other systems indicates that condensed tannins slow rates of litter decay and rates of net N mineralization to ultimately conserve N in systems when the forest is composed of trees with high concentrations of condensed tannins (Hättenschwiler and Vitousek 2000; Kraus et al. 2003; Schweitzer et al. 2004, 2008). For example, at the stand level, condensed tannin inputs from leaf litter explain up to 63% of annual rates of net N mineralization in the field along the Weber River in northern Utah (Schweitzer et al. 2004). While these results may have similar effects in ecosystems where the elk is native (but see above) or when beaver are introduced, relatively little data are available to compare differential ecosystem consequences of herbivory by natives versus exotics on soil nutrient processes. Therefore, the indirect consequences of herbivory by native and exotic species on ecosystem processes are largely unknown and deserving of future research attention.

Conclusions and future directions

Overall, with these two plant-herbivore case studies, we illustrate that plant resistance and tolerance traits can mediate the indirect consequences of herbivory on associated interacting species. Specifically, when there is no evolutionary history between the plants and herbivores, the indirect effects of herbivory are more likely to be negative (Category 4 in Fig. 1). For example, the introduced elk-*P. tremuloides* interaction revealed a low frequency of resistance in the population and weak expression of tolerance traits. This led to the rapid mortality of *P. tremuloides* and the generally poor quality in the individuals that remained on the landscape. These effects had negative consequences on an important galling insect, the arthropod community that occupied the galls, as well as their avian predators. Introduced elk also negatively impacted ecosystem processes such as trophic interactions and soil nutrient processes. In contrast, when there is an evolutionary history between plant and herbivore, there is an increased chance that

tolerance traits may have evolved which enable plants to persist on the landscape. Such tolerance traits can maintain genetic variation in the population, and create habitat mosaics that positively affect biodiversity (Category 2 in Fig. 1). For example, the native beaver-*P. angustifolia* interactions revealed a high frequency of resistance in the population. In addition, *P. angustifolia* also responded positively to beaver herbivory through coppicing and resprouting from the roots. The resprout foliage was vigorous and tended to positively affect arthropod diversity and negatively affect the colonization and encroachment of new exotic trees. While these two cases represent examples for category 2 and category 4 of the conceptual model (Fig. 1), it is thought that plants which have high resistance and tolerance to herbivory are likely rare. Therefore, these categories may represent the tails of the ecological distribution of plant-herbivore systems. However, when herbivores are introduced, outcomes associated with category 4 are likely. For example, beaver in Chile, deer in Argentina, rabbits in Australia, possums in New Zealand, deer in Canada all represent category 4 introductions with strong negative effects on associated biodiversity and ecosystem function largely due to the lack of resistance and tolerance traits in the population (see other papers in this issue—Martin et al. 2009; Oduor 2009; O'Reilley-Wapstra and Cowan 2009; Relva 2009; Wallem 2009).

The two case studies described here illustrate the importance of understanding the evolution of resistance and tolerance traits and how they mediate indirect effects to other levels of organization as well as provide a framework for future hypothesis testing. Based upon the conceptual model (Fig. 1), we expect the largest negative ecological effects of herbivory will occur when there is little genetic variation for resistance/tolerance traits and the largest positive interactions to occur when there is significant genetic variation for resistance/tolerance traits as characterized by categories 4 and 2, respectively. Studies that experimentally examine the role of evolutionary interactions between plants and their herbivores to separate the effects of resistance and tolerance to maintaining genetic variation, habitat mosaics in plant populations and indirect impacts on associated species are fundamental to this prediction. Expansion of these studies to other comparative systems will allow us to broaden the inferences about indirect

effects of species introductions and gain insight into the mechanisms of the unintended consequences of species interactions.

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References

- Anderson CB, Rosemond AD (2007) Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia* 154:141–153
- Anderson CB, Griffith CR, Rosemond AD et al (2006) The effects of invasive North American beavers on riparian plant communities in Cape Horn, Chile Do exotic beavers engineer differently in sub-Antarctic ecosystems? *Biol Conserv* 128:467–474
- Bailey JK, Whitham TG (2002) Interactions among fire, aspen and elk affect insect biodiversity: reversal of a community response. *Ecology* 83:1701–1712
- Bailey JK, Whitham TG (2003) Interactions among fire, elk, aspen, galling sawflies and insectivorous birds. *Oikos* 101:127–134
- Bailey JK, Whitham TG (2006a) Indirect trait-mediated interactions between cottonwoods and beavers positively affect sawfly abundance. *Ecol Entomol* 31:294–297
- Bailey JK, Whitham TG (2006b) Biodiversity is related to indirect interactions among species of large effect. In: Ohgushi T, Craig T, Price PW (eds) *Indirect interaction webs: nontrophic linkages through induced plant traits*. Cambridge University Press, UK
- Bailey JK, Whitham TG (2007) Biodiversity is related to indirect interactions among species of large effect. In: Ohgushi T, Craig T, Price PW (eds) *Indirect interaction webs: nontrophic linkages through induced plant traits*. Cambridge University Press, UK, pp 306–328
- Bailey JK, Schweitzer JA, Rehill BJ et al (2004) Beavers as molecular geneticists: a genetic basis to the foraging of an ecosystem engineer. *Ecology* 85:603–608
- Bailey JK, Irschick DJ, Schweitzer JA et al (2007) Selective herbivory by elk results in rapid shifts in the chemical composition of aspen forests. *Biol Invasions* 9:715–722
- Baker WL, Munroe JA, Hessel AE (1997) The effects of elk on aspen in the winter range in Rocky Mountain National Park. *Ecography* 20:155–165
- Bardgett RD, Wardle DA (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258–2268
- Basey JM, Jenkins SH, Miller GC (1990) Food selection by beaver in relation to inducible defenses of *Populus tremuloides*. *Oikos* 59:57–62

- Bergstrom DM, Lucieer A, Keifer K et al (2009) Indirect effects of invasive species removal devastate a World Heritage Island. *J Appl Ecol* 47:73–81
- Binkley D, Singer F, Kaye M et al (2003) Influence of elk grazing on soil properties in Rocky Mountain National Park. *For Ecol Manage* 185:239–247
- Brock JH (1994) *Tamarix* spp. (salt cedar), an invasive exotic woody plant in arid and semi-arid riparian habitats of western U.S.A. In: de Waal LC, Child LE, Wade PM, Brock JH (eds) Ecology and management of invasive riverside plants. Wiley, New York, pp 27–44
- Bryant JP (1981) Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. *Science* 313:889–890
- Cappuccino N (1993) Mutual use of leaf-shelters by lepidopteran larvae on paper birch. *Ecol Entomol* 19:399–401
- Daehler CC, Anttila CK, Ayres DA et al (1999) Evolution of a new ecotype of *Spartina alterniflora* (Poaceae) in San Francisco Bay. *Am J Bot* 86:543–546
- Dickson LL, Whitham TG (1996) Genetically-based plant resistance traits affect arthropods, fungi, and birds. *Oecologia* 106:400–406
- Eckenwalder JE (1996) Systematics and evolution in *Populus*. In: Stettler RF, Bradshaw JDH, Heilman PE, Hinckley TM (eds) Biology of *Populus* and its implications for management and conservation. NRC Research Press, Ottawa, pp 7–30
- Eldridge DL, Simpson R (2002) Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. *Basic Appl Ecol* 3:19–29
- Finch DM, Ruggiero LF (1993) Wildlife habitats and biological diversity in the Rocky Mountains and northern Great Plains. *Nat Areas J* 13:191–203
- Gitlin AR, Stultz CM, Bowker MA et al (2006) Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conserv Biol* 20:1477–1486
- Hamzeh M, Dayanandan S (2004) Phylogeny of *Populus* (Salicaceae) based on nucleotide sequences of chloroplast trnT-trnF region and rDNA. *Am J Bot* 91:1398–1408
- Harrison KA, Bardgett RD (2008) Impacts of grazing and browsing by large herbivores on soils and soil biological properties. In: Gordon IJ, Prins HHT (eds) The ecology of browsing and grazing. Ecological studies 195. Springer, Berlin, Heidelberg, pp 201–216
- Hättenschwiler S, Vitousek PM (2000) The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends Ecol Evol* 15:238–243
- Hessl A (2002a) Aspen, elk, and fire: the effects of human institutions on ecosystem processes. *Bioscience* 52:1011–1022
- Hessl A (2002b) Interactive effects of human activities, herbivory and fire on quaking aspen (*Populus tremuloides*) age structures in western Wyoming. *J Biogeogr* 29:889–902
- Hobbs NT (1996) Modification of ecosystems by ungulates. *J Wildl Manage* 60:695–713
- Hoffmeister DF (1986) Mammals of Arizona. University of AZ Press, Tucson
- Jenkins SH, Busher PE (1979) *Castor canadensis*. *Mammal Species* 120:1–8
- Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. *Proc Nat Acad Sci* 102:7198–7202
- Johnston CA (2001) Wetland soil and landscape alteration by beaver. In: Richardson JL, Vepraskas MJ (eds) Wetland soils. CRC Press, Boca Raton, pp 391–409
- Johnston CA, Naiman RJ (1990) Browse selection by beaver: effects on forest composition. *Can J For Res* 20:1036–1043
- Johnston CA, Pinay G, Arens C et al (1995) Influence of soil properties on the biogeochemistry of a beaver meadow hydrosequence. *Soil Sci Soc Am J* 59:1789–1799
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373
- Katz GL, Shafroth PB (2003) Biology, ecology, and management of *Eleagnthus angustifolia* (Russian olive) in western North America. *Wetlands* 23:763–777
- Kay CE (1997) Is aspen doomed? *J For* 4–11
- Kay CE, Bartos DL (2000) Ungulate herbivory on Utah aspen: assessment of long-term exclosures. *J Range Manag* 53:145–153
- Knopf FL (1985) Significance of riparian vegetation to breeding birds across an altitudinal cline. In: Riparian ecosystems and their management: reconciling conflicting uses. (Johnson RR, Ziebell CD, Patten DR, Ffolliot PF, Hamre RH (tech. coords.). USDA For Serv Gen Tech Rep RM-120, pp 105–111
- Kraus TEC, Dahlgren RA, Zasoski RJ (2003) Tannins in nutrient dynamics of forest ecosystems—a review. *Plant Soil* 256:41–66
- Leimu R, Koricheva J (2006) A meta-analysis of genetic correlations between plant resistances to multiple enemies. *Am Nat* 168:E15–E37
- Madritch MD, Donaldson JR, Lindroth RL (2006) Genetic identity of *Populus tremuloides* litter influences decomposition and nutrient release in a mixed forest stand. *Ecosystems* 9:528–537
- Madritch MD, Jordan LM, Lindroth RL (2007) Interactive effects of condensed tannin and cellulose additions on soil respiration. *Can J For Res* 37:2063–2067
- Mahoney JM, Rood SB (1998) Streamflow requirements for cottonwood seedling recruitment—an integrative model. *Wetlands* 18:634–645
- Martin JL, Stockton SA, Allombert S, Gaston AJ (2009) Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: lessons from a deer introduction. *Biol Invasions* (this issue)
- Martinsen GD, Driebe EM, Whitham TG (1998) Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. *Ecology* 79:192–200
- Martinsen GD, Floate KD, Waltz AM et al (2000) Positive interactions between leaf-gallers and other arthropods enhance biodiversity on hybrid cottonwoods. *Oecologia* 123:82–89
- Mauricio R, Rausher MD (1997) Experimental manipulation of putative selection agents provides evidence for the role of natural enemies in the evolution of plant defense. *Evolution* 51:1435–1444
- McGinley MA, Whitham TG (1985) Central place foraging by beavers (*Castor canadensis*): a test of foraging predictions

- and the impact of selective feeding on *Populus fremontii*. *Oecologia* 66:558–562
- McNaughton SJ (1976) Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science* 191:92–94
- Miller C (2007) Rabbits lay waste to Macquarie Island. *Front Ecol Environ* 5:5
- Mitton JB, Grant MC (1996) Genetic variation and the natural history of quaking aspen. *Bioscience* 46:25–31
- Moerman DE (1996) An analysis of the food plants and drug plants of native North America. *J Ethnopharmacol* 52:1–22
- Nabhan GP, Coder M, Smith SJ et al (2004) Woodlands in crisis: a legacy of lost biodiversity and the Colorado Plateau. University of Arizona Press, Tuscon
- Naiman RJ, Melillo JM, Hobbie JE (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67:1254–1269
- Naiman RJ, Decamps H, Pollock M (1993) The role of riparian corridors in maintaining regional biodiversity. *Ecol Appl* 3:209–212
- Naiman RJ, Pinay G, Johnston CA et al (1994) Beaver influences on the longterm biogeochemical characteristics of Boreal drainage networks. *Ecology* 75:905–921
- Nakamura M, Ohgushi T (2003) Positive and negative effects of leaf shelters on herbivorous insects: linking multiple herbivore species on a willow. *Oecologia* 136:445–449
- Noss RF, LaRoe ET III, Scott JM (1995) Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. U.S. Department of the Interior, National Biological Service, Washington, DC, Biological Report 28
- Nunez-Farfan J, Fornoni J, Valverde PL (2007) The evolution of resistance and tolerance to herbivores. *Ann Rev Ecol Evol Syst* 38:541–566
- O'Reilly-Wapstra, JA, Cowan, P (2009) Native plant/herbivore interactions as determinants of the ecological and evolutionary effects of invasive mammalian herbivores: the case of the common brushtail possum. *Biol Invasions* (this issue)
- O'Reilly-Wapstra JM, McArthur C, Potts BM (2002) Genetic variation in resistance of *Eucalyptus globulus* to marsupial browsers. *Oecologia* 130:289–296
- O'Reilly-Wapstra JM, McArthur C, Potts BM (2004) Linking plant genotype, plant defensive chemistry and mammal browsing. *Funct Ecol* 18:677–684
- Oduor AMO, Gómez JM, Strauss SY (2009) Invasional meltdown or biotic resistance?: differential effects of exotic vertebrate and invertebrate herbivores on plant invasion. *Biol Invasions* (this issue)
- Ohgushi T (2005) Indirect interaction webs: herbivore-induced effects through trait change in plants. *Ann Rev Ecol Evol Syst* 36:81–105
- Palo RT (1984) Distribution of birch (*Betula* spp.), willow (*Salix* spp.), and poplar (*Populus* spp.) secondary metabolites and their potential role as chemical defense against herbivores. *J Chem Ecol* 10:499–520
- Parker JD, Burkepile DE, Hay ME (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science* 311:1459–1461
- Pastor J, Cohen Y (1997) Herbivores, the functional diversity of plant species and the cycling of nutrients in ecosystems. *Theor Popul Biol* 51:165–179
- Pastor J, Naiman RJ (1992) Selective foraging and ecosystem processes in boreal forests. *Am Nat* 139:690–705
- Pilson D (2000) The evolution of plant response to herbivory: simultaneously considering resistance and tolerance in *Brassica rapa*. *Evol Ecol* 14:457–489
- Price PW (1991) The plant vigor hypothesis and herbivore attack. *Oikos* 62:244–251
- Pusenius J, Prittinen K, Heimonen J et al (2002) Choice of voles among genotypes of birch seedlings: its relationship with seedling quality and preference of insects. *Oecologia* 130:426–432
- Puustinen S, Koskela T, Mutikainen P (2004) Direct and ecological costs of resistance and tolerance in the stinging nettle. *Oecologia* 139:76–82
- Rambo JL, Faeth SH (1999) Effect of vertebrate grazing on plant and insect community structure. *Conserv Biol* 13:1047–1054
- Rausher MD (1992) The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. *Evolution* 46:616–626
- Rehill BJ, Whitham TG, Martinsen GD et al (2006) Developmental trajectories in cottonwood phytochemistry. *J Chem Ecol* 32:2269–2285
- Reinhart KO, Calloway RM (2006) Soil biota and invasive plants. *New Phytol* 170:445–457
- Relva MA, Nuñez MA, Simberloff D (2009) Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown. *Biol Invasions* (this issue)
- Ritchie MA, Tilman D, Knops JMH (1998) Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165–177
- Rolf J (2001) Aspen fencing in N. Arizona: a 15 y perspective. *Proc Rocky Mtn Res Station. USDA Forest Service. RMRS-P-18:193–196*
- Romme WH, Turner MG, Wallace LL et al (1995) Aspen, elk, and fire in northern Yellowstone National Park. *Ecology* 76:2097–2106
- Romme WH, Turner MG, Gardner RH et al (1997) A rare episode of sexual reproduction in Aspen (*Populus tremuloides* Michx) following the 1988 Yellowstone fires. *Nat Areas J* 17:17–25
- Rosell F, Boszér O, Collen P et al (2005) Ecological impacts of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mamm Rev* 35:248–276
- Sanders NJ, Gotelli NJ, Heller NE et al (2003) Community disassembly by an invasive ant species. *Proc Nat Acad Sci* 100:2474–2477
- Schoenecker KA, Singer FJ, Zeingenfuss LC et al (2004) Effects of elk herbivory on vegetation and nitrogen processes. *J Wildl Manage* 68:837–849
- Schweitzer JA, Bailey JK, Rehill BJ et al (2004) Genetically based trait in dominant tree affects ecosystem processes. *Ecol Lett* 7:127–134
- Schweitzer JA, Madritch MM, Bailey JK et al (2008) From genes to ecosystems: the genetic basis of condensed tannins and their role in nutrient regulation in a *Populus* model system. *Ecosystems* 11:105–120
- Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biol Invasions* 1:21–32

- Singer FJ, Schoenecker KA (2003) Do ungulates accelerate or decelerate nitrogen cycling? *For Ecol Manage* 181:189–204
- Stinchcombe JR, Rausher MD (2001) Diffuse selection on resistance to deer herbivory in the ivyleaf morning glory, *Ipomea hederacea*. *Am Nat* 158:376–388
- Stinchcombe JR, Rausher MD (2002) The evolution of tolerance to deer herbivory: modifications caused by the abundance of insect herbivores. *Proc R Soc Lond* 269:1241–1246
- Stowe K (1998) Experimental evolution of resistance in *Brassica rapa*: correlated response of tolerance in lines selected for glucosinolate content. *Evolution* 52:703–712
- Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. *Trends Ecol Evol* 14:179–185
- Strauss SY, Rudgers JA, Lau JA et al (2002) Direct and ecological costs of resistance to herbivory. *Trends Ecol Evol* 17:278–285
- Stritar ML, Schweitzer JA, Hart SC et al (2009) Introduced mammalian herbivore alters soil processes after fire. *Oikos* (in review)
- Tollrian R, Harvell CD (1999) The ecology and evolution of inducible defenses. Princeton University Press, Princeton
- Verheyden-Tixier H, Duncan P (2000) Selection for small amount of hydrolysable tannins by a concentrate-selecting mammalian herbivore. *J Chem Ecol* 26:351–358
- Vesk PA, Westoby M (2004) Sprouting ability across diverse disturbances and vegetation types worldwide. *J Ecol* 92:310–320
- Vitousek PM (1986) Biological invasions and ecosystem processes: can species make a difference? In: Mooney HA, Drake J (eds) *Biological invasions in North America and Hawaii*. Springer, New York, pp 163–176
- Vitousek PM, Walker LR (1989) Biological invasion of *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. *Ecol Monogr* 59:247–265
- Wallem P, Anderson CB, Martínez Pastur G, Lencinas MV (2009) Using assembly rules to measure the resilience of riparian plant communities to beaver invasion in subantarctic forests. *Biol Invasions* (this issue)
- Wardle DA, Barker GM, Yeates GW et al (2001) Introduced browsing mammals in natural New Zealand forests: aboveground and belowground consequences. *Ecol Monogr* 71:587–614
- Wolfe BE, Klironomos JN (2005) Breaking new ground: soil communities and exotic plant invasion. *Bioscience* 55:477–487
- Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101