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THE EFFECTS OF LARGE HERBIVORES ON SMALL MAMMAL COMMUNITIES,
PLANTS AND ECOSYSTEM PROCESSES IN NORTHERN ARIZONA

By

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Dissertation

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for the degree of

Doctor of Philosophy
in Fish and Wildlife Biology

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The effects of large herbivores on small mammal communities, plants and ecosystem processes in northern Arizona

Chair: John Maron

Large herbivores are major drivers of community structure and function in many terrestrial systems. Through their direct effects on plants, large herbivores can influence the structure and complexity of habitats, the population abundance of animals that rely on those habitats, and the rates of ecosystem processes within those systems. These manifold impacts on systems are potentially magnifying, as removal of top predators and changes in land use have triggered large increases in large herbivore populations. Although increasing evidence suggests that large herbivores can critically shape the structure and function of the ecosystems they inhabit, few studies have detailed the direct and indirect effects of large herbivores on vegetation, animal populations, and ecosystem processes in the same system. Typically these varied impacts are studied in isolation and it is often unclear what the magnitude or sources of spatio-temporal variation in these effects might be. I used a large-scale replicated elk-exclusion experiment to determine the effects of elk on small mammal communities, plants, and ecosystem processes.

I found that five years of elk exclusion led to noticeable changes in small mammal communities; some small mammals increased in the exclosure while others declined on controls. These changes were likely due to increasing habitat quality inside the fences and declining habitat quality outside. Elk browsing also decreased the recruitment of two dominant deciduous species and the quantity of litter of both of these species deposited on the forest floor during the peak in litterfall. Elk similarly reduced the cover of nitrogen fixing forb species, and the decomposition rates of both aspen and maple litter were more rapid inside the fences after 2 years of decomposition. These results indicate that elk are influencing the quantity and quality of litter inputs into this system as well as the decomposition environment. Finally, I found that mixtures of deciduous and evergreen litter influenced decomposition dynamics, the net mineralization of nitrogen, and plant growth. These results suggest that shifts in litter quantity and quality from browsing ungulates could have important indirect effects on plant growth. Overall, this work indicates that elk can have effects on multiple components of the community and ecosystem in only a short five year time period.

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CHAPTER 1

INTRODUCTION AND OVERVIEW

BACKGROUND

The direct effects of large herbivores on plants have been studied extensively, and it is well known that large herbivores commonly influence plant growth, reproduction, and survival (Crawley 1983, Schowalter et al. 1986, Huntly 1991, Danell et al. 2006, Maron and Crone 2006, Gordon and Prins 2008). However, large herbivores can also exert indirect effects on other species (Rooney and Waller 2003, McCauley et al. 2006, Huntzinger et al. 2008). These indirect effects can occur when species modify habitats or resources in ways that influence other species (Wootton 1994, Abrams et al. 1996). For example, by reducing vegetation height and volume large herbivores can influence the structure and complexity of forested habitat, indirectly affecting species that rely on that habitat (Jones et al. 1994, Jones et al. 1997, Berger et al. 2001, Bailey and Whitham 2002a, Ogada et al. 2008). Large herbivores have been shown to have both positive and negative effects on the abundance of invertebrates including soil fauna, snails, and moths (Wardle et al. 2001, Wardle et al. 2004, Allombert et al. 2005, Huntzinger et al. 2008), as well as on vertebrates including lizards, birds, and small mammals (McShea and Rappole 1997, Keesing 1998, McShea and Rappole 2000, Ogada et al. 2008, Pringle 2008). These widespread effects across taxonomic groups point to large herbivores as being important determinants of community structure (Paine 2000).

In addition to influencing co-occurring species, large herbivores can also influence ecosystem processes (McNaughton 1976, Pastor and Naiman 1992, Pastor et al. 1993, McNaughton et al. 1997, Pastor and Cohen 1997). Large herbivores can increase, decrease, or have no effect on plant productivity, soil N cycling and net N mineralization (McNaughton 1979,

Pastor and Naiman 1992, McNaughton et al. 1997, Augustine and McNaughton 1998, Ritchie et al. 1998, Augustine et al. 2003, Pastor et al. 2006). The direction of these effects are determined by a variety of factors including herbivore identity, density, and foraging strategy (Bakker et al. 2004, Côté et al. 2004, Danell et al. 2006), as well as plant community composition, tolerance to herbivory, and ecosystem characteristics including soil fertility and climate (McNaughton et al. 1997, Augustine and McNaughton 1998, de Mazancourt and Loreau 2000, Bardgett and Wardle 2003).

Although increasing evidence suggests that large herbivores can critically shape the structure and function of the ecosystems they inhabit (McNaughton 1985, McInnes et al. 1992, Palmer et al. 2008), few studies have detailed the direct and indirect effects of large herbivores on vegetation, animal populations, and ecosystem processes in the same system. Typically these varied impacts are studied in isolation and it is often unclear what the magnitude or sources of spatio-temporal variation in these effects might be. In addition, the same outcome of herbivory (e.g. reduction in understory plant biomass) could influence both co-occurring species as well as ecosystem properties. For example, elk (*Cervus elaphus*) browsing led to a large reduction in the abundance of aspen trees (*Populus tremuloides*), which are hosts to galling sawflies that are eaten by insectivorous birds (Bailey and Whitham 2002a, b, Bailey et al. 2007). Thus, the indirect effects of elk may cascade to influence ecosystem properties (due to changes in the phytochemistry of litter being deposited on the forest floor (e.g. Schweitzer et al. 2004), while at the same time influencing insect abundance and the bird behavior (Bailey and Whitham 2002a). Understanding these complex interactions requires an approach that considers multiple components of communities and ecosystems.

In addition, the effects of large herbivores may be magnified today because ungulates (especially white-tailed deer, *Odocoileus virginianus*) exist at much higher densities in many places than they did historically (McShea et al. 1997). These high densities are leading to dramatic changes in plant communities in many systems (Alverson et al. 1988, Garrott et al. 1993, McShea et al. 1997, Waller and Alverson 1997, Warren 1997, Côté et al. 2004, Heckel et al. 2010), including reductions in plant species richness and diversity and declines in plants that are important for human use (Balgooyen and Waller 1995, Horsley et al. 2003, Potvin et al. 2003, Rooney et al. 2003, McGraw and Furedi 2005). Furthermore, these changes may lead to different alternative stable states (Stromayer and Warren 1997, Augustine et al. 1998) in communities, which may or may not be desirable for managers (Westoby et al. 1989, Laycock 1991). It is therefore critical that we understand how high densities of ungulates are influencing ecosystems so that managers have the tools they need to make important decisions regarding the future of our forests.

Finally, a majority of the studies documenting large herbivore effects on communities use fenced exclosures and they compare plant and animal communities inside versus outside the fences after some time period (Tiedemann and Berndt 1972, Moulton 1978, Bock et al. 1984, Putman et al. 1989, Keesing 1998, Ritchie et al. 1998, Wardle et al. 2001, Steen et al. 2005, Lkeintjes Neff et al. 2007). These studies typically show increased or decreased abundances of particular species as a result of a release from browsing pressure, and it is often unclear what temporal sequence of events led to these changes, or how quickly those changes occurred. This likely depends on how strongly herbivores suppress plants, and a growing number of studies are showing a rapid response of some plants (e.g. deciduous species) to a release from browsing

pressure (Bailey and Whitham 2002, Beschta 2005, Hebblewhite et al. 2005, Kaye et al. 2005, Bailey et al. 2007, Kauffman et al. 2010).

For my dissertation, I studied the effects of Rocky Mountain elk (*Cervus elaphus*) on small mammal communities, plants, and ecosystem properties in northern Arizona. There are now approximately 30,000-35,000 elk (post-hunt adults as of 2009) in the mountains of northern Arizona (Arizona Game and Fish Department 2010), and elk density is much higher now than it was historically (Allen 1996, Truett 1996). Rocky Mountain elk are the main ungulate at this site, though there are occasional sightings of both mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*).

Furthermore, heavy herbivory of aspen (*Populus tremuloides*) and maple (*Acer grandidentatum*) by elk has likely led to the decline of these species at this site over the last 25 years (Martin 2007). To study the impacts of elk herbivory we initiated a large-scale elk exclusion experiment during the fall of 2004. We created three large (3 m high) exclosures (~10 ha in size) encompassing entire snow-melt drainages along the Mogollon Rim area of northern Arizona in Coconino National Forest. In addition, each of these exclosure drainages was paired with an unfenced drainage nearby. Using a variety of methods we documented changes in plant and small mammal community composition between May of 2004 (before the fences were erected), and July of 2009.

RESEARCH OBJECTIVES

Small mammals may be particularly sensitive to changes in habitat structure due to the activities of ungulates (Keesing 1998, 2000). In order to understand how elk influence small mammals in northern Arizona I had the following research questions:

- Do ungulates influence habitat structure and complexity?

- Do large herbivores indirectly influence small mammal population abundance through effects on their habitat?
- Do large herbivores influence small mammal species richness and diversity?

Long term U.S. Forest Service ungulate exclosures in Coconino National Forest (erected 1985-2000) revealed dramatic differences in the understory vegetation composition and structure inside versus outside the fences in 2005. For example, in a small fenced area near the field site, there was a dense stand of young aspen ramets (clonal recruits) as well as high abundance of several locally rare understory species including lupine (*Lupinus* spp.), paintbrush (*Castilleja* spp.), and columbine (*Aquilegia* spp.), and these species were entirely absent outside (E. Parsons, *personal observation*). Because a thicker understory and the presence of plants with seeds in the exclosures (e.g. *Lupinus* produces seeds that are eaten by rodents) could provide both food for small mammals and a refuge from predators we hypothesized that elk browsing decreases small mammal abundance and richness. We predicted that the exclusion of elk would lead to increases in understory vegetation as well as increases in small mammal abundance and richness inside the fences.

We initiated a large-scale small mammal live-trapping program in May of 2004 and we used capture-mark-recapture methods to determine whether elk influenced small mammal relative abundance and diversity. We also measured habitat variables that might be important to small mammals (e.g. woody debris, percentage of grass and forbs, etc.) during the same time period and we determined habitat preferences of two of the most common species to see if they selected vegetation characteristics that were influenced by elk.

The long-term U.S. Forest Service exclosures also had higher abundance of deciduous canopy trees including aspen, willow (*Salix* spp.), and maple (E. Parsons, *personal observation*).

Deciduous species (such as these) tend to have higher quality litter (e.g. high levels of nitrogen, low levels of secondary defense compounds) as compared to litter from evergreen trees (Aerts 1995, Chapman et al. 2006). Because decomposition rates of high quality litter are faster than that of low quality litter, increases in deciduous species inside exclosures has the potential to increase high quality litter deposits and influence N cycling and N availability (Pastor et al. 1988, Pastor and Naiman 1992). We hypothesized that elk were preventing the regeneration of deciduous species at our sites and slowing down rates of N cycling. We predicted that elk exclusion would lead to regeneration of deciduous species, this would lead to a greater quantity of high quality litter reaching the forest floor, and this would affect soil N dynamics. For my research on the effects of large herbivores on plants and ecosystem processes I wanted to answer the following questions:

- Do large herbivores influence the quantity of leaf litter inputs? How do these effects vary spatially, across topographic gradients where tree composition changes?
- Do large herbivores influence the quality of leaf litter inputs?
- Do large herbivores influence decomposition rates?
- Do large herbivores influence soil nitrogen availability through changes in the quantity and quality of leaf litter inputs?

In order to determine whether elk influence N cycling we 1) quantified tree abundance and growth, 2) quantified litter quality characteristics and decomposition rates of the most common trees, 3) determined treatment effects on the decomposition rates of litter, and 4) measured rates of net N mineralization in response to different types of litter. We focused on abundance, growth, and litter quantity of aspen, maple, and white fir because these three species are the most dominant canopy trees at our field site, and litter from these three species makes up

~85% of the litter deposited during the peak in litterfall (October-November in northern Arizona).

In addition to their direct effects on plants (e.g. ungulate browsing reducing aspen height), large herbivores can also indirectly affect plants. For example, in a beech-maple forest in Pennsylvania, unpalatable understory forbs (i.e. forbs not eaten by deer) were significantly smaller in plots with deer access as compared with fenced exclosures (Heckel et al. 2010). These “non-consumptive effects” are hypothesized to be a result of large herbivore induced declines in soil quality as well as decreased leaf litter depth which may negatively affect plant growth (Heckel et al. 2010). I asked the following research question about herbivore-induced indirect effects on plants:

- Do the effects of large herbivores on leaf litter inputs influence plant germination, establishment, and growth?

One possible way that large herbivores may indirectly affect plants is by reducing the diversity of litter types that mix on the forest floor. For example, declines in both aspen and maple due to elk browsing could decrease the quantity of these litter types (and the extent of mixing) deposited on the forest floor during the peak in leaf litterfall. Litter mixtures often have unpredictable decomposition dynamics (Gartner and Cardon 2004), including changing quantities of plant available N (Finzi and Canham 1998). Thus it is possible that herbivore-induced changes in plant-litter mixtures could indirectly influence plant growth by changing the rate of nutrient cycling or the quantity of available nutrients for plants. In order to investigate whether this was a possible mechanism we examined whether litter mixtures influenced decomposition dynamics as well as plant growth and net N mineralization using both a field and greenhouse experiment. To do this we decomposed bags composed of individual litter or a

mixture of maple, aspen, and white fir (*Abies concolor*), and measured mass loss and N content. We also grew four understory plants (whose seeds were collected at the field site) in soil amended with maple, aspen, or white fir litter alone, or in mixture, and we measured effects on plant emergence, growth, and net N mineralization.

GENERAL RESULTS

Small mammals

I found that large herbivores affected the relative abundances of some of the species of small mammal between 2004 -2009. Specifically, the relative abundance of voles, mice, and woodrats was influenced by the elk exclosures, but not the relative abundance of red squirrels, chipmunks, or rock squirrels (Fig. 2.2.1). Voles increased inside the exclosures, however, woodrats and mice relative abundance remained roughly the same inside the fences while declining outside the fences. These changes are likely explained by increasing habitat quality inside the fences for some species and declining habitat quality outside the fences for others. Voles inhabit the more mesic areas of the snow-melt drainages and are often caught in areas of high grass cover, and it is likely that both grass cover and height have increased inside the exclosures since 2004. Also, elk browsing has eliminated much of the understory outside of the fences and aspen and maple have declined over the last 25 years (Martin 2007, Martin et al. *unpublished results*). Thus, it is possible that elk-induced declines in understory biomass are continuing to decrease habitat quality for mice as well as woodrats. I also found that red squirrel middens increased inside exclosures (Fig. 2.2.2), and small mammal species richness increased as well (Fig. 2.2.3).

Litter mixtures

In a field decomposition experiment, I found that a mixture of aspen, maple, and white fir litter increased the decomposition rate of aspen litter, but did not change the decomposition rate of either maple or white fir (Fig. 3.3.1A). Also, the mixtures changed litter N dynamics by increasing the N content of aspen while lowering the N content of white fir (Fig. 3.3.1B). This result is surprising because many authors have hypothesized that high quality litter (high in N, fast to decompose) can speed up the decomposition rate of low quality litter (low in N, slow to decompose) either through leaching of nutrients or fungal translocation (Gessner et al. 2010). However this work shows that the reverse may occur: we found that the low quality litter (white fir) lost N while the high quality litter (aspen) gained N and decomposed more rapidly. I also found in a greenhouse experiment that four understory plants had higher biomass at the end of the experiment in the mixture (litter from same three species), as compared to individual litter treatments (Fig. 3.3.2), and this is likely explained by the mixtures increasing the mineralization of N (Fig. 3.3.4).

Litter quantity and quality

I found that elk browsed a large percentage of the deciduous trees at our site, but only a small percentage of the evergreens (Fig. 4.4.1). Furthermore, this resulted in a much higher quantity of both maple and aspen leaves being deposited inside exclosures as compared to non-fenced control drainages (Fig. 4.4.2). In addition, litter from the deciduous species (aspen and maple) decomposed much more rapidly than litter from the evergreen species (Fig. 4.4.2B), but there was no difference in the rate of net N mineralization below litter bags of the three species. However, I found that elk influenced the decomposition environment; maple and aspen litter decomposed more rapidly inside the exclosures and compared to outside. This could have been

due to elk-induced differences in abiotic factors affecting decomposition such as temperature and moisture, or to differences in soil fertility or decomposer communities. And while elk did not affect forb species richness or diversity, the cover of N-fixing forbs (Fig. 4.4.6) and trees was significantly higher inside the fences in 2009 indicating that elk may affect N inputs by reducing the cover of high quality (high N) plant species. Overall, these results indicate that elk can have significant effects on plant species composition and decomposition processes in a short, 5 year time period.

DISSERTATION FORMAT

The following chapters were formatted for individual publication in specific peer-reviewed scientific journals. Though they have not yet been submitted, the first two are currently in revision for submission in 2011. I worked on these manuscripts extensively with my advisor John Maron, as well as with Tom Martin and Cory Cleveland and they are all listed as co-authors. Because these chapters were a collaborative effort I use the collective “we” throughout all three manuscripts.

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CHAPTER 2
ELK HERBIVORY ALTERS SMALL MAMMAL ASSEMBLAGES IN HIGH
ELEVATION DRAINAGES

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Abstract

Heavy herbivory by ungulates can substantially alter habitat, but the indirect consequences of habitat modification for animal assemblages that rely on that habitat are not well studied. We explored short-term responses of small mammal communities to recent exclusion of Rocky Mountain elk (*Cervus elaphus*) in high elevation riparian drainages in northern Arizona. We used 10 ha elk exclosures paired with unfenced control drainages to examine how browsing influenced habitat use, relative abundance, richness, and diversity of a small mammal assemblage. We found that the small mammal assemblage changed significantly after six years of elk exclusion. Relative abundance of voles (*Microtus mexicanus*) increased in exclosure drainages, likely due to an increase in habitat quality. However, the relative abundances of woodrats (*Neotoma neomexicana*) and two species of mice (*Peromyscus maniculatus* and *P. boylii*) decreased in the controls, while remaining stable in exclosures. This decline was likely due to the fact that mice selected habitats high in shrub cover, and shrub cover declined in control drainages during our study. Thus, elk removal may have maintained or improved habitat for mice inside the exclosures while habitat quality and mouse abundance both declined outside the fences. Finally, small mammal species richness increased in the exclosures relative to the controls while species diversity showed no significant trends. Together, our results show that abundant large herbivores can structure assemblages of small mammals in just a few years. Moreover, exclusion of abundant large herbivores can yield rapid responses by vegetation that may enhance habitat quality for small mammal populations.

Introduction

Individual species can indirectly affect sympatric heterospecifics by altering their habitat (Jones et al. 1997, Pringle 2008). These species are known variously as ecosystem engineers, keystone species, and strong interactors (Paine 1966, 1969, MacArthur 1972, Jones et al. 1994), but they share a common ability to modify resources available to co-occurring species (Jones et al. 1997, Fox-Dobbs et al. 2010). Habitat modifiers can increase the richness and abundance of sympatric species when they create new habitats (Crooks 2002), or when they increase habitat heterogeneity by creating a mosaic of engineered and non-engineered patches on the landscape (Jones et al. 1997). Habitat modifiers can also decrease the richness and abundance of co-occurring species by lowering overall habitat quality (Keesing 1998, McCauley et al. 2006, Keesing et al. 2006, McCauley et al. 2008, Keesing et al. 2008). These negative effects are particularly poorly understood, because they are less dramatic than the wholesale destruction or creation of habitat that some engineering species impose. Experiments that test the impacts of these habitat modifiers on other members of the community are critically needed (Wright and Jones 2004, Pringle et al. 2007).

Ungulates are not typically thought of as ecosystem engineers but they can have strong impacts on general features of habitat. Due to their high energy requirements and their increasing abundance (Côté et al. 2004, McGraw and Furedi 2005), species such as deer and elk can strongly modify vegetation structure (McNaughton et al. 1988, Rooney and Waller 2003, Danell et al. 2006, Martin 2007). Reductions in vegetative cover due to ungulate browsing have the potential to impact the abundance and diversity of species that rely on the three-dimensional structure of vegetation as habitat (Grant et al. 1982, Smit et al. 2001). For example, large herbivores can reduce bird abundance and diversity by changing the cover of shrubs and saplings

(McShea and Rappole 2000, Berger et al. 2001, Martin 2007, Ogada et al. 2008). Alternatively, large herbivores such as elephants (*Loxodonta africana*) can increase the abundance of arboreal lizards by damaging trees and creating refuges for the lizards (Pringle 2008). Whether large herbivores increase or decrease abundance and diversity will likely depend on several factors including herbivore density, productivity, and the specific life history requirements of the co-occurring species (Crooks 2002, Côté et al. 2004, Rooney et al. 2004, Pringle et al. 2007).

Here we quantified the short-term responses of an entire rodent community to experimental cessation from heavy elk herbivory. Small mammal populations are often influenced by microhabitat characteristics such as protective cover and vegetation complexity (Birney et al. 1976, Dueser and Porter 1986) and thus may be particularly susceptible to herbivore-driven changes in these vegetation components (Grant et al. 1982, Smit et al. 2001). Although a handful of studies have documented such effects, the vast majority of research has examined impacts of domestic grazers on small mammal abundance (Schmidt et al. 2005, Steen et al. 2005, Torre et al. 2007). Impacts of domestic grazers on habitat might be quite different from wild grazers given differences in their freedom to roam and breadth of diet, such that the effects of wild grazers on small mammals remain unclear.

We examined the influence of Rocky Mountain elk (*Cervus elaphus*) on small mammal communities in a high elevation riparian forest in north-central Arizona. We compared three drainages that had been recently fenced (starting in 2004) to exclude elk with three paired unfenced drainages. Our goal was to determine the speed with which different components of the small mammal assemblage responded to the cessation of herbivory from fencing. We estimated the relative abundance of seven species of small mammal in plots open or recently

closed to elk, as well as determined how recent elk exclusion influenced the composition and diversity of the small mammal community.

Methods

Study sites

Our study sites were a series of parallel high elevation (2350 m) drainages along the Mogollon Rim in Coconino National Forest in north-central Arizona. The canopy vegetation in these drainages is characterized by aspen (*Populus tremuloides*), canyon maple (*Acer grandidentatum*), New Mexico locust (*Robinia neomexicana*), Gambel Oak (*Quercus gambellii*), white-fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), white pine (*Pinus monticola*) and ponderosa pine (*Pinus ponderosa*). The woody understory vegetation includes Utah serviceberry (*Amelanchier utahensis*), elderberry (*Sambucus glauca*) and other shrubs in the family Rosaceae. Dominant herbs include bracken fern (*Pteridium aquilinum*), western sneezeweed (*Dugaldia hoopesii*), pine thermopsis (*Thermopsis pinetorum*), and Canada violet (*Viola elaphus*). Further description of the study site can be found in Martin (1998, 2007).

The large mammalian herbivores that use these drainages are Rocky Mountain elk (*Cervus elaphus nelsoni*), mule deer (*Odocoileus hemionus*), and Coues white-tailed deer (*Odocoileus virginianus couesi*). Rocky Mountain elk were by far the most abundant large herbivore in our system (in 2007 and 2008, they produced 97 % of the ungulate scat piles on our study drainages, *unpublished data*). Rocky Mountain elk were introduced to northern Arizona from Yellowstone National Park in 1913 (Arizona Game and Fish Department 2010), roughly thirty years after the native elk subspecies (*Cervus elaphus merriami*) became extinct (Truett 1996). There are now approximately 30,000 – 35,000 post-hunt adult Rocky Mountain elk in Arizona (Arizona Game and Fish Department 2010), and current elk abundance in the forests of

the southwest is much higher than historic abundance (Allen 1996, Truett 1996). We commonly see elk on our sites, as well as evidence of heavy herbivory in the drainages (Martin 2007).

The small mammals that use these high-elevation drainages include: rock squirrel (*Spermophilus variegatus*), American red squirrel (*Tamiasciurus hudsonicus*), Mexican woodrat (*Neotoma mexicana*), northern pocket gopher (*Thomomys talpoides*), gray-collared chipmunk (*Tamias cinereicollis*), Mexican vole (*Microtus mexicanus*), brush mouse (*Peromyscus boylii*), deer mouse (*Peromyscus maniculatus*), and Merriam's shrew (*Sorex merriami*). Deer mice and brush mice are similar in size and appearance and were only successfully distinguished after early summer 2006.

To determine how heavy elk herbivory affects small mammal communities, we identified three pairs of drainages (6 drainages total) in large canyons near the rim of the Mogollon Plateau. Each drainage pair within a canyon was separated by ~ 200 m, and canyons containing pairs of drainages were separated by ~ 2 km. We randomly assigned one drainage from each pair to receive an ungulate exclusion treatment (*see Table 1 for detailed locations*). This consisted of a 2.5 m tall fence that was attached to metal fence posts 0.3 m above ground level to allow predator access. Fences had two strands of high tension wire above them to bring the fence to a height of 3 m. Each fence enclosed a 10 ha section of drainage, which comprised the majority of each drainage. Fences were constructed during fall and winter 2004, and paired control drainages were left unfenced. The fences excluded elk but not mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), and mountain lions (*Puma concolor*).

Trapping protocol

We used capture-mark-recapture methods (Armstrup et al. 2005) to determine how elk exclusion influenced small mammal relative abundance and community composition. We captured small mammals during the summers of 2004-2009 using both Sherman (8 x 9 x 23 cm) and Tomahawk (13 x 13 x 41 cm) live-traps. In each summer, we had three primary trapping sessions (in May, June, and July) with each session lasting four days and three nights. Sherman traps were placed on a permanently marked 10 x 25 trapping grid (250 traps total with 10 m spacing) located at the center of each exclosure and control drainage. Trapping grids encompassed the more mesic drainage bottoms to halfway up the xeric ridges and thus included a range of vegetation and habitat features. In addition to Sherman traps, twenty-five Tomahawk traps were placed on the trapping grid so we could catch the larger rodents. These were placed on alternating grid lines at every 3rd and 7th trap station.

During each trapping period, traps were baited with a combination of rolled oats and bird seed scented with peanut-butter (Shermans) or unshelled peanuts (Tomahawks), and were covered with closed-cell foam for protection from heat and cold. Traps were checked once in early morning and once before night fall of each day. We simultaneously trapped animals on each drainage of a pair and traps were moved to the next drainage pair after each 3-day, 4-night trapping session was completed. All trapped animals were given a uniquely numbered metal Monel ear tag (*National Band and Tag Company, Newport, Kentucky*) for individual identification. Because shrews and northern pocket gophers were rarely captured, they were not included in the analysis.

Relative abundance, diversity and species richness

We calculated the relative abundance of all species (in all drainages and for all primary trapping sessions) as the number of unique individuals captured divided by sampling effort, *Equation 1* (Slade and Blair 2000). We estimated relative abundance using an index rather than a population estimator such as those provided in Program MARK (White and Burnham 1999) because we were primarily interested in the relative difference in abundance between treatments as opposed to an absolute estimate of abundance. Furthermore, abundance estimators based on statistical models (Otis et al. 1978, Nichols and Pollock 1983), may provide high bias and inconsistent results when population density and samples are low (McKelvey and Pearson 2001). Most of our species exist at relatively low population density, and our estimates of abundance were inappropriate when we used these methods. Thus, we decided that relative abundance would provide the most appropriate way to track differences between exclosures and non-fenced controls for all species in this analysis.

$$\textit{Equation 1: Relative abundance} = \frac{\textit{unique individuals}}{\textit{sampling effort}}$$

We calculated sampling effort as shown by *Equation 2* (Beauvais and Buskirk 1999). Because traps were checked twice a day for three mornings and four evenings (from 2006 to 2009), all animals had the potential of being caught a maximum of seven times (i.e. intervals = 7) during a trapping session. During 2004 and 2005, however, traps were only checked once a day (and thus animals could only be caught a maximum of four times during each trapping session) so we used four trap intervals in our calculations for sampling effort for these two years. We subtracted sprung traps (closed traps without animals in them) from traps*intervals because these traps were not available to catch animals. However, we multiplied sprung traps by 0.5 before subtraction because the best estimate of when traps close (and thus became unavailable) is half

way between intervals (Beauvais and Buskirk 1999). This method corrects for trap saturation and variation in trap-springing by site or time and provides a more accurate measure of sampling effort than simply multiplying traps by trapping intervals (Nelson and Clark 1973, Beauvais and Buskirk 1999). Sampling effort was important to quantify at our field site because physical disturbances, including direct sun, wind, rain, and hail, as well as animals (mostly black bears), caused our traps to close.

$$\textit{Equation 2: Sampling effort} = (\textit{traps} * \textit{intervals}) - (\textit{sprung traps} * 0.5)$$

We first determined yearly estimates of relative abundance for all drainages by separately averaging the relative abundance for each species for May, June, and July. We then calculated paired-drainage differences by subtracting the non-fenced control drainage estimate for a species from the paired enclosure estimate. By examining changes in paired differences over time (as opposed to simply comparing enclosure and control averages), we were able to control for variation in relative abundance between drainage-pairs and across the three trapping sessions. Finally, we multiplied all relative abundance estimates by the total number of trap occasions (intervals*total available traps for 2006-2009) to convert the relative abundance estimates to estimates of the total number of individual animals on a trapping grid.

We determined whether elk exclusion influenced small mammal species richness and diversity (Shannon's H' , calculated as $-\sum(pi \times \log pi)$, with pi as the proportion of unique captures for each species out of the total number of unique animals captured) by calculating paired differences in these variables for each drainage pair within each trapping period and year. For this analysis we only examined 2006 to 2009 data because deer mice and brush mice were only successfully differentiated after May 2006.

Red squirrel surveys

Red squirrels were abundant in the drainages (*personal observation*), but we did not capture them often in our traps. Thus, as an alternative method to estimate red squirrel relative abundance, in July of each summer from 2006 – 2009 we counted the number of middens along thirteen 100 m transects located along every other trap line on each trapping grid. Middens at our field site are a combination of stored food resources and collections of conifer litter that has accumulated from feeding (Uphoff 1990). A red squirrel may often have multiple smaller middens near its largest primary midden; therefore we only counted large primary middens. Furthermore, we only counted active middens where there was evidence of recent use (i.e. fresh cone parts). The number of active primary middens is a good index of relative abundance for red squirrels because they are often centrally located within an individual's territory, and the stored resources are critical for over-winter survival (Réale et al. 2003).

Microhabitat selection

In summer 2007 we estimated the percent cover of grasses, forbs, shrubs, woody debris, bare ground, and deciduous litter in a 5 m radius circle around a randomly chosen subset of trapping points where deer mice were either captured or not ($n = 99$ each), and also around 82 randomly selected trapping points where brush mice were either captured or not ($n = 41$ each). We chose deer and brush mice because we had a relatively large number of captures of each compared to the other species (*see Table 2*). Percent cover of deciduous litter is highly correlated with the number of maple and aspen stems (*unpublished data*), and thus represents an index of microhabitat that is dominated by these deciduous species. See Martin (1998) for further details regarding vegetation sampling design.

Statistical analyses

We used general linear models to test whether paired differences in relative abundance, richness, and diversity increased significantly between 2004 and 2009. Specifically we included relative abundance as the dependent variable and we treated drainage pair as a fixed factor, year as a covariate, and we included the interaction between year and pair to test whether the slopes for each drainage pair differed. We removed interaction terms from the model when they were not significant and when they were we conducted separate analyses by species pair to determine differences. To determine whether observed changes in paired differences were due more to changes occurring in exclosures or non-fenced control drainages (i.e. a positive change in paired differences could be due to either an increase in exclosures, a decrease in controls, or both), we regressed both exclosure and control relative abundance estimates against paired differences and examined the significance and coefficients of determination. We also used forward stepwise regression to determine which species or combination of species explained the most variation in species richness.

To determine whether the number of red squirrel middens changed in exclosures relative to non-fenced controls we used Generalized Estimating Equations (GEE) and we specified a poisson distribution with a log-link function (Torre et al. 2007) because the middens are repeated count data. We specified plot as the subjects variable, year as the within (repeated) subjects variable, midden number as the dependent variable, and treatment and year and their interaction as predictors. We used generalized linear models to look for individual treatment effects within each year.

Finally, in order to determine which microhabitat variables were selected by deer and brush mice, we used logistic regression (Hosmer and Lemeshow 2000, Manly et al. 2002) with

presence – absence data for each species as dependent variables, and arcsin square-root transformed vegetation variables as covariates. Elk exclusion treatment was also included as a categorical fixed factor to determine whether there was an effect of treatment on the selection of habitat variables (e.g. mice might select different habitat types inside vs. outside of the enclosures). We used a forward stepwise procedure (Sergio et al. 2003) with the enter value of 0.10 and removal value of 0.15 because the more traditional enter value of 0.05 may fail to identify important variables (Mickey and Greenland 1989, Hosmer and Lemeshow 2000). All statistical analyses were conducted using SPSS version 17 (SPSS, Chicago, Illinois, USA).

Results

Small mammal response

We captured 7 small mammal species and a total of 4,153 animals out of 109,400 trap nights between May 2004 and July 2009 (*Table 2*). Paired differences in the total relative abundance of all animals increased on enclosure drainages as compared to non-fenced control drainages between 2004 and 2009 ($F_{1, 14} = 12.11$, $R^2 = 0.54$, $P = 0.004$; Fig. 1A). Specifically, animals were more abundant on control drainages in the beginning and became more abundant on enclosures by the end (Fig. 1A). The increase in paired differences in total abundance on enclosures relative to controls was driven mostly by a decline on non-fenced control drainages. Specifically, control abundance explained 64.2% of the variation and was negatively associated with paired differences ($F_{1, 14} = 19.47$, $P = 0.001$) while enclosure abundance explained only 32.2% of the variation and was only marginally associated with paired differences ($F_{1, 14} = 3.65$, $P = 0.08$). Interestingly, changes in paired differences in total abundance between 2004 and 2009 were significantly related to paired differences in the relative abundance of voles ($F_{1, 14} =$

9.97, $R^2 = 0.50$, $P = 0.007$), and woodrats ($F_{1, 14} = 6.29$, $R^2 = 0.41$, $P = 0.025$), but not to any of the other small mammal species.

Paired differences in the relative abundance of voles within exclosures relative to non-fenced controls increased through time ($F_{1, 14} = 6.94$, $R^2 = 0.44$, $P = 0.02$). Paired differences in woodrat relative abundance, however, only increased on two out of the three drainage pairs (plot pair*year interaction, ($F_{2, 12} = 3.80$, $R^2 = 0.68$, $P = 0.05$). When we tested each drainage pair separately, woodrat relative abundance increased on both Buck Springs drainages ($F_{1, 4} = 58.2$, $R^2 = 0.94$, $P = 0.002$), and McClintock drainages ($F_{1, 4} = 8.33$, $R^2 = 0.68$, $P = 0.45$), but not on Dane ridge drainages ($F_{1, 4} = 0.24$, $P = 0.86$). For voles, the increase in paired differences in exclosures relative to non-fenced controls was driven mostly by increases in relative abundance inside the exclosures; paired differences were positively associated with exclosure relative abundances ($F_{1, 14} = 16.58$, $R^2 = 0.62$, $P = 0.001$), but not significantly associated with control relative abundances ($F_{1, 14} = 0.61$, $P = 0.45$). For woodrats, however, the increase in paired differences was mostly driven by declines in relative abundance in the non-fenced control drainages; control abundance was negatively associated with paired differences ($F_{1, 14} = 33.12$, $R^2 = 0.44$, $P < 0.001$). However, there was also a marginally significant plot pair*exclosure abundance interaction ($F_{2, 12} = 3.33$, $R^2 = 0.43$, $P = 0.071$), with a positive association between exclosure abundance and paired differences on Buck Springs drainages ($F_{1, 4} = 9.84$, $R^2 = 0.711$, $P = 0.035$), but not on either Dane drainages ($F_{1, 4} = 3.34$, $P = 0.142$), or McClintock drainages ($F_{1, 4} = 0.33$, $P = 0.59$).

We also found an increase in the relative abundance of both *Peromyscus* species combined on exclosures compared to non-fenced controls ($F_{1, 14} = 6.95$, $R^2 = 0.4$, $P = 0.02$; Fig. 1D). Similar to woodrats, this increase in paired differences was mostly explained by a decrease

in non-fenced control drainages. Exclosure abundance explained only 28.7% of the variation in paired differences and was only marginally related ($F_{1,14} = 3.64, P = 0.077$) while control abundance explained 76.8% of the variation in paired difference and was negatively associated with paired differences ($F_{1,14} = 40.13, P < 0.001$).

Paired differences in the relative abundance of deer mice showed no significant trends across years ($F_{1,8} = 0.99, P = 0.35$). Changes in brush mouse relative abundance across years depended on the particular drainage-pair (year*drainage pair: $F_{2,6} = 5.81, P = 0.039$). Paired differences in relative abundance declined on the McClintock drainages ($F_{1,2} = 14.26, P = 0.064$) indicating that brush mice shifted in abundance from exclosures to controls between 2006 and 2009 on McClintock drainages. Brush mouse relative abundance did not change in either of the other two drainage pairs (Buck Springs ridge: $F_{1,2} = 1.58, P = 0.34$; Dane ridge, $F_{1,2} = 3.02, P = 0.23$).

Chipmunks showed no change inside of the exclosures relative to the non-fenced control drainages between 2004 and 2009 (chipmunks, $F_{1,14} = 0.092, P = 0.77$, Fig. 1E), while paired difference in relative abundance for rock squirrels interacted with year (plot pair*year: $F_{2,12} = 3.46, P = 0.065$, Fig. 1F). Rock squirrel paired differences decreased on Buck Springs drainages ($F_{1,4} = 6.44, P = 0.064$), but showed no significant trends for either Dane drainages ($F_{1,4} = 2.67, P = 0.18$), or McClintock drainages ($F_{1,4} = 0.32, P = 0.60$). During this same time period we found a highly significant treatment * year interaction for red squirrel middens between 2006 and 2009 (Wald = 898.12, df = 3, $P < 0.001$), with significantly more middens on exclosures relative to control drainages in 2009 (Wald $\chi^2 = 8.09, df = 1, P = 0.004$; Fig. 2).

Species richness and diversity

Paired differences in small mammal species richness increased between 2006 and 2009 on enclosure drainages as compared to non-fenced control drainages ($F_{1,8} = 4.59$, $P = 0.065$; Fig. 3A). This change was driven by an increase in species richness in enclosures as paired differences was positively associated with enclosure richness ($F_{1,8} = 9.7$, $R^2 = 0.56$, $P = 0.014$), but not control richness ($F_{1,8} = 1.4$, $R^2 = 0.17$, $P = 0.27$). Also, forward stepwise regression showed that paired differences in species richness was significantly associated with paired differences in woodrats ($F_{1,10} = 5.45$, $R^2 = 0.59$, $P = 0.042$), which were the only species in the model. Finally, species diversity (Shannon's H) did not change between fenced and non-fenced control drainages during the same time period ($F_{1,8} = 2.15$, $P = 0.18$; Fig. 3B).

Microhabitat selection

Shrubs, woody debris, and deciduous cover were all important predictors of abundance for both species of *Peromyscus* (deer mice: $\chi^2 = 43.88$, $df = 3$, $R^2 = 0.27$, $P < 0.001$, brush mice: ($\chi^2 = 19.83$, $df = 3$, $R^2 = 0.29$, $P < 0.001$). Specifically, deer mice selected habitats high in shrub cover and woody debris (shrubs, $\beta = 1.39$, $Wald = 3.72$, $df = 1$, $P = 0.05$; woody debris, $\beta = 4.39$, $Wald = 15.41$, $df = 1$, $P < 0.001$), and avoided habitats high in deciduous litter ($\beta = -2.52$, $Wald = 17.18$, $df = 1$, $P < 0.001$). Interestingly, brush mice selected all three cover types (shrubs, $\beta = 2.6$, $Wald = 6.35$, $df = 1$, $P = 0.01$; woody debris, $\beta = 5.0$, $Wald = 8.11$, $df = 1$, $P = 0.004$, deciduous litter, $\beta = 2.21$, $Wald = 4.6$, $df = 1$, $P = 0.03$). Elk exclusion, however, did not influence selection for these three habitat variables ($P = 0.14$), and no interactions between treatment and the habitat variables were significant in any of the models.

Discussion

Experimental exclosures that protected vegetation from heavy herbivory by elk produced noticeable changes in the small mammal community over a relatively short six year time period (Fig. 1A). Voles, woodrats, and mice changed significantly inside of the exclosures relative to the non-fenced control drainages (Figs. 1B, 1C, 1D), while chipmunks and rock squirrels did not (Figs 1E, 1F). This indicates that the exclusion of elk influenced the quality of habitat inside the exclosures for some of the species of small mammal at our field site, but not for all.

Changes in small mammal communities may occur in areas where large mammalian herbivores are excluded because of asymmetrical competition. For example, pouched mouse (*Saccostomus mearnsi*) density doubled after only eight months of exclusion of large African ungulates (Keesing 1998, 2000). This increase in density inside of the ungulate exclosures was most likely due to an increase in food resources (Keesing 2000). Asymmetrical competition may also explain why voles at our field site exhibited such a marked increase inside of the exclosures in such a short time period (Fig. 1B). Voles are mainly herbivorous (Lin and Batzli 2001), and they have a significant amount of grass in their diet (Haken and Batzli 1996). Similarly, a significant proportion of the summer diet of elk is also grass (Kufeld 1973), and we found higher grass cover inside of the exclosures in 2009 compared to control drainages (*unpublished results*).

The observed increase in mice and woodrats was mainly driven by declines in relative abundance on control drainages through time rather than an increase in relative abundance on exclosure drainages. It is possible that habitat quality outside of the fence declined during the course of the study due to a recently documented decline in winter snow pack at this site (Martin 2007) associated with declines in food resources and protective cover. We found a decline in shrubs outside of the exclosures relative to the non-fenced control drainages (*unpublished*

results) that paralleled declines in the relative abundance of mice (two species of *Peromyscus*) (Fig. 1D), and logistic regression models showed that both species selected habitats high in shrub cover. This result suggests that at least for mice and woodrats, elk removal may have ameliorated the negative effects of habitat deterioration outside of the fences.

We also found that pretreatment differences were important in driving patterns of change in small mammal abundance and species composition. Voles, woodrats and mice were more numerous in non-fenced control drainages relative to exclosures during 2004 (Figs. 1B, C, D) and we found that when we excluded the pretreatment year from the analysis for voles and woodrats, trends were non-significant. This indicates that changes in these two species were relatively rapid between 2004 and 2005 perhaps due to a relatively rapid initial change in habitat quality.

Although no trends in American red squirrel relative abundance were apparent through trapping, individuals were relatively rarely trapped. Average midden differences, in contrast, increased through time and middens were significantly more numerous inside of exclosures in 2009 (Fig. 2). This increase in middens could reflect an increase in red squirrel density inside the exclosures. While it is likely that their main food supply of fir cones has not changed significantly with elk exclusion, other important food resources for red squirrels may be increasing inside the fences. For example, fungi sporocarps, a preferred food for red squirrels at this study site (Uphoff 1990), may be increasing inside the exclosures (*personal observation*) due to less soil compaction from ungulates. An increase in red squirrel middens, however, could also indicate an increase in the number of middens per squirrel. Because we counted large primary middens that were being actively used, however, this trend suggests increased red squirrel density inside of exclosures due to improved habitat quality.

Changes in the relative abundances of different species of small mammal paralleled an increase in species richness on enclosure versus non-fenced control drainages (Fig. 3A). Other studies have shown higher small mammal species richness inside of ungulate enclosures. For example, small mammal species richness and diversity was higher inside of cattle enclosures in arid farmland in South Africa, and these trends paralleled increased vegetation cover inside the fences (Eccard et al. 2000). These differences, however, were after ten years of exclusion of domestic livestock, and we witnessed rapid initial changes to the small mammal community after only a couple of years. With the exception of some work in Africa (Keesing 1998), these changes are likely more rapid than other studies of have shown.

Conclusion

Changes in small mammal community structure due to abundant Rocky Mountain elk are evident at our field site after only six years. These results demonstrate that large wild ungulates can structure ecologically important co-occurring animals in a relatively short time period. Furthermore, these findings are important because large native ungulate abundance is much higher now than historically in many parts of the United States (Alverson et al. 1988, McShea et al. 1997, Allombert et al. 2005). If abundant large herbivores generally have a negative impact on small mammals, then this trend could lead to impoverished small mammal communities in many regions. As small mammals can have significant impacts on communities in their own right (Brown and Heske 1990), high abundances of large wild herbivores may be currently impacting communities not only directly, but also through indirect effects mediated by changes in small mammal communities (Rooney and Waller 2003, Goheen et al. 2004). The importance of small-mammal mediated indirect effects, however, is still unclear.

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Table 1: The locations and names of the drainages used in the elk exclusion study.

Drainage classification and location					
Drainage Pair	Drainage Name	Treatment	Closest ridge	UTM location (Zone 12N)	Elevation (m)
1	14	Exclosure	Buck Springs	486213 E, 3806519 N	2367
1	8	Control	Buck Springs	486213 E, 3806519 N	2340
2	E4	Exclosure	Dane	484684 E, 3808369 N	2366
2	E3	Control	Dane	484684 E, 3808369 N	2397
3	12	Exclosure	McClintock	483153 E, 3808372 N	2356
3	11	Control	McClintock	483149 E, 3806524 N	2389

Table 2: Small mammal trapping summary results: 2004 to 2009. In addition, the two species of *Peromyscus* were only successfully differentiated in 2006. Between 2006 and 2009 we captured 1,505 individuals of *Peromyscus maniculatus* and 416 individuals of *Peromyscus boylii*. This table does not include shrews (*Sorex merriami*) or Northern pocket gophers (*Thomomys talpoides*) because we did not catch them frequently enough to include them in the analysis.

Genus	# Individuals	% of total	# of captures	% of total	Captures/individual
<i>Peromyscus</i>	2566	61.79	6947	68.48	2.71
<i>Tamias</i>	751	18.08	1467	14.46	1.95
<i>Neotoma</i>	342	8.24	758	7.47	2.22
<i>Microtus</i>	222	5.35	418	4.12	1.88
<i>Spermophilus</i>	165	3.97	356	3.51	2.16
<i>Tamiasciurus</i>	107	2.58	198	1.95	1.85

Figure legends

Figure 1: Paired differences (exclosure – control) in relative A) small mammal, B) vole, C) woodrat and D) all mice and E) chipmunk abundance for each paired drainage by year. The lines represent cases significant ordinary least squares regressions. Solid triangles, open circles, and solid circles represent Buck Springs, Dane Ridge, and McClintock Ridge drainages respectively. For woodrats and rock squirrels, the dotted, dashed, and solid lines represent OLS regressions for Buck Springs, Dane Ridge, and McClintock Ridge drainages respectively. Small arrows reveal where two points on the graph overlap.

Figure 2: Average difference (exclosures – controls) between red squirrel middens, 2006 through 2009 + SEM. Differences increased through time and there were significantly more red squirrel middens in exclosures compared to control drainages in 2009.

Figure 3: Paired differences in species richness (exclosure - control). 3A: paired differences in species richness increased in exclosures relative to non-fenced control drainages between June 2006 and July 2009, 3B: there was no significant change in species diversity (Shannon's H) inside of exclosures compared with non-fenced control drainages during the same time period. Solid triangles, open circles, and solid circles represent Buck Springs, Dane Ridge, and McClintock Ridge drainages respectively.

Figure 1

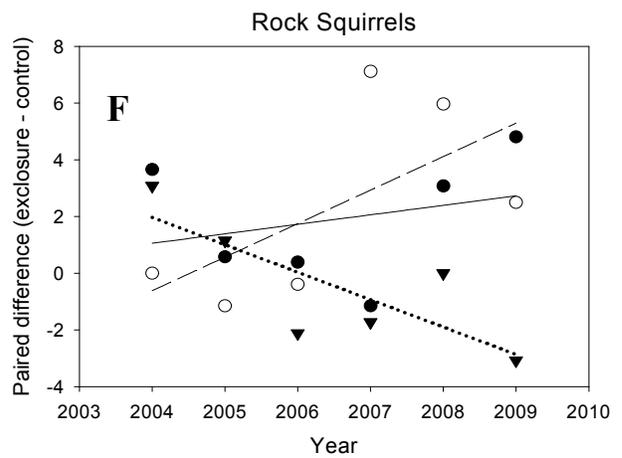
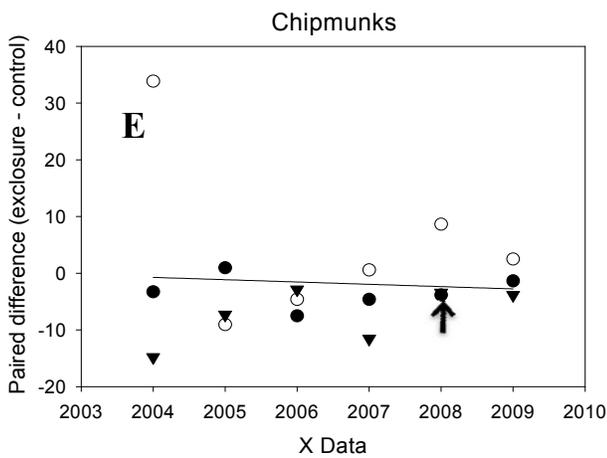
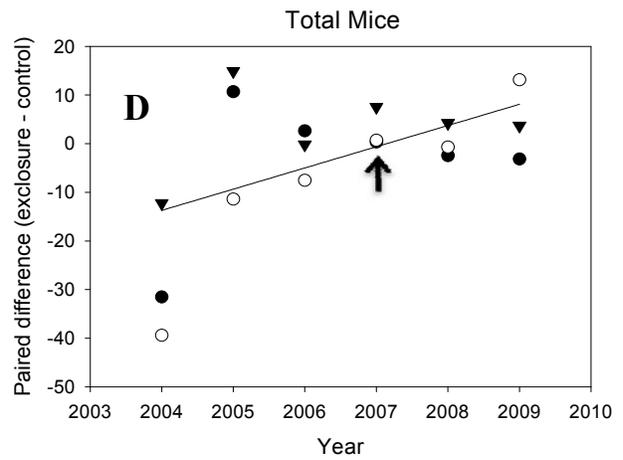
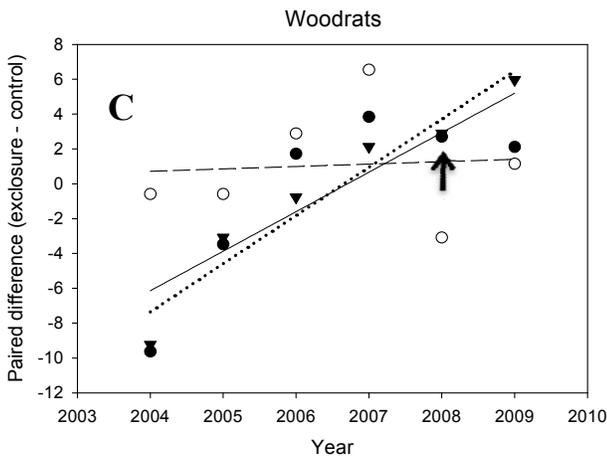
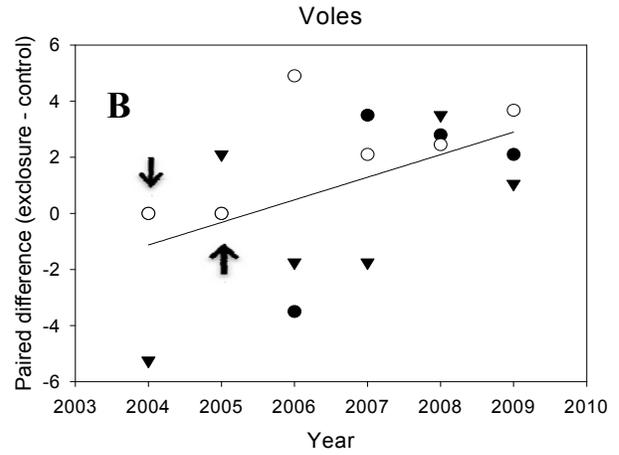
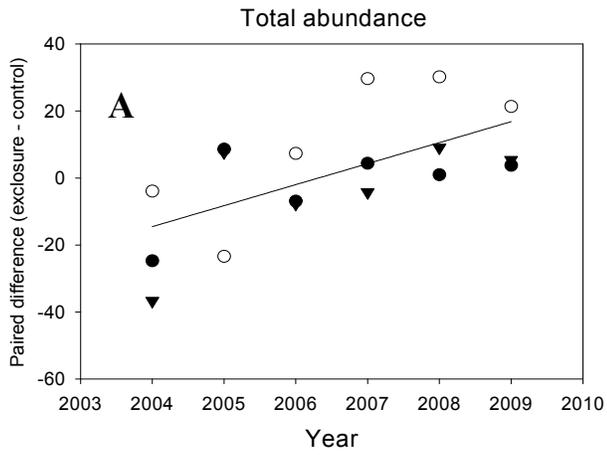


Figure 2

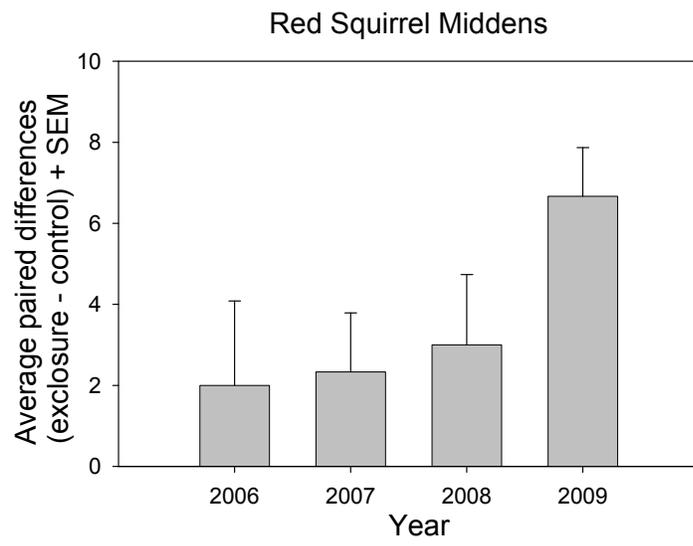
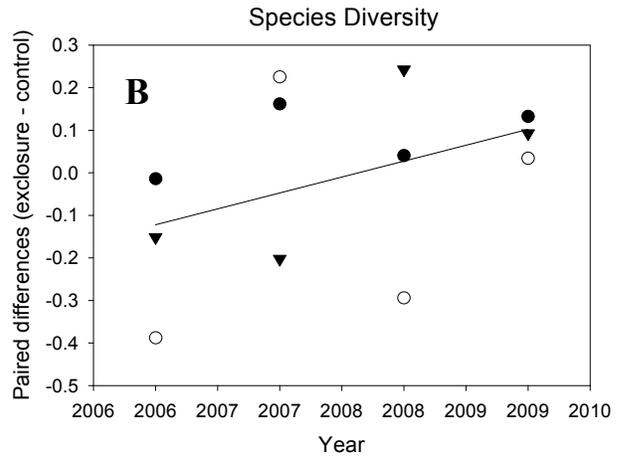
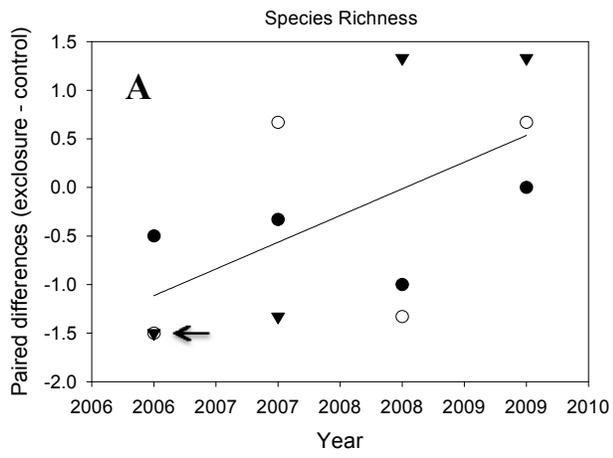


Figure 3



CHAPTER 3

LITTER MIXTURES HAVE SYNERGISTIC EFFECTS ON DECOMPOSITION DYNAMICS, NET NITROGEN MINERALIZATION, AND PLANT GROWTH

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Abstract

Litter from different plant species commonly vary in their decomposition rate and effects on ecosystem processes, such as N cycling. Yet how mixtures of litter from different species together influence the dynamics of decomposition and its byproducts is less understood. In particular, we know little about how litter mixtures influence soil nitrogen mineralization or plant growth. We measured the quality and decomposition rates of litter from single species and mixtures of litter from canyon maple (*Acer grandidentatum*), aspen (*Populus tremuloides*), and white fir (*Abies concolor*), trees that commonly co-occur in high elevation snow melt drainages in northern Arizona. We also conducted a greenhouse experiment where we tested whether soil amended with single species and mixed species litter influenced the emergence and growth of four co-occurring understory forb species. At the same time we assessed whether the single species litter and mixtures influenced net nitrogen mineralization in the soil. After 9 months of decomposition, the decay rate of litter mixtures was higher than predicted from the single species litter decay rates. The litter mixture also increased the nitrogen content and decay rate of aspen litter, decreased the nitrogen content of white fir litter (with no effect on decay rate), and had no effect on the nitrogen content of maple litter. In the greenhouse experiment, forb emergence was lower and total plant biomass higher with mixed litter than predicted from the single species litter treatments, and these effects were similar for all four species. Finally, the net mineralization of nitrogen was significantly higher in the mixture than predicted from the single species litter treatments, and net N mineralization was positively associated with mean plant biomass. These results indicate synergistic processes in diverse litter mixtures that enhance decomposition dynamics and plant performance.

Introduction

Organic matter decomposition is a fundamental ecosystem process. Decomposition represents the largest movement of carbon (C) from the terrestrial biosphere to the atmosphere (Aerts 1997; Schlesinger 1997; Meier and Bowman 2008; Hoorens et al. 2010), directly regulates soil C storage (Lal 2004), and recycles critical and often limiting plant nutrients (Schlesinger 1997; Chapin et al. 2002; Hättenschwiler et al. 2005; Cornwell et al. 2008; Hoorens et al. 2010). Early conceptual and analytical models suggested that decomposition of plant litter – the largest single source of organic matter in many ecosystems – is dominantly influenced by physical factors (*e.g.*, temperature, precipitation, soil type) and litter chemistry (*e.g.*, nutrient stoichiometry, N content, and the concentrations of lignocelluloses, secondary structural, metabolic, and defense compounds) (Melillo et al. 1982; McClaugherty et al. 1985; Hobbie 1996; Wardle and Lavelle 1997; Austin and Vitousek 2000; Austin and Vivanco 2006; Hobbie et al. 2006). However, recent research has shown that decomposition can be highly influenced by the community context in which the process occurs (Jonsson and Wardle 2008; Gessner et al. 2010; Laganière et al. 2010). For example, decomposition rates may be influenced by top-down factors including decomposer abundance and diversity (Jonsson and Malmqvist 2000; Heemsbergen et al. 2004; Hättenschwiler and Gasser 2005; Schädler and Brandl 2005), as well as bottom-up factors including plant litter diversity and species composition (Gartner and Cardon 2004; Hättenschwiler et al. 2005, Kominoski et al. 2007).

Data describing the effects of plant litter diversity on decomposition dynamics, however, show mixed results (Nilsson et al. 1999; Hoorens et al. 2003; Gartner and Cardon 2004; Hättenschwiler et al. 2005; Schindler and Gessner 2009). For example, litter diversity can have positive, negative, or neutral effects on important ecosystem processes such as decomposition

and nutrient cycling (Blair et al. 1990; McTiernan et al. 1997; Wardle et al. 1997; Hoorens et al. 2003; Chapman and Koch 2007; Lecerf et al. 2007; Hoorens et al. 2010). Moreover, the effects of diversity can be synergistic (i.e., when process rates are more rapid in mixture than would be predicted based on the process rates of individual component species) or antagonistic (i.e., when process rates are lower than the predicted level; Gartner and Cardon 2004). In either case, litter mixture responses are often “non-additive” meaning that the decomposition rates measured in litter mixture are not equal to the summed effects of individual component species (Gartner and Cardon 2004).

Non-additive effects may occur because of differences in the physical and chemical properties of mixtures versus component species (Schindler and Gessner 2009). For example, diverse litter mixtures can contain greater habitat heterogeneity than single litter types and this can favor higher decomposer richness and abundance (Kaneko and Salamanca 1999). Furthermore, increased decomposer diversity may increase the efficiency of decomposition and yield synergistic effects on process rates (Hansen and Coleman 1998). Also, mixtures that contain plants that vary in litter quality may increase the efficiency of decomposition by allowing the redistribution of nutrients among different litter types by decomposers or leaching (Schimel and Hättenschwiler 2007; Tiunov 2009). For example, fungi may more efficiently decompose nutrient poor litter if they can exploit nutrient-rich litter that is nearby (Gessner et al. 2010). Finally, litter mixtures may have antagonistic effects on process rates if inhibitory compounds solubilized from one litter decreases overall decomposer efficiency in mixed litter (McArthur et al. 1994).

All three proposed mechanisms require that mixtures influence the total efficiency of decomposition, meaning that net mass loss of the entire mixture is different from what would be

predicted from single species litter (Gartner and Cardon 2004). Yet this reveals little about whether mixtures affect the overall decomposition rate of all species within the mixture equally, or whether mixtures impact individual species within mixtures differentially (Hoorens et al. 2003). This lack of understanding can make it difficult to generalize about the importance of these different mechanisms. For example, the presence of high quality (high N) species in mixtures could commonly lead to increased decomposition rates of low quality species (low N) supporting the idea that nutrient redistribution is important. Conversely, low quality litter could decrease the decomposition rates of high quality species because of the presence of inhibitory compounds. Few studies, however, separate out individual species after decomposition has occurred likely due to the difficulties involved (Hoorens et al. 2003).

Non-additive effects observed in litter mixtures also might have “afterlife effects” that could influence important soil processes (Nilsson et al. 1999). For example, few studies have determined whether synergistic or antagonistic effects of litter mixtures translate to differences in soil nutrient cycling (Briones and Ineson 1996; Finzi and Canham 1998; Meier and Bowman 2008). Even fewer studies have assessed if or how litter mixture effects may feed back to influence plant emergence and growth (Chapman et al. 1988; Nilsson et al. 1999). Litter has been shown to have an overall negative effect on vegetation (Xiong and Nilsson 1999), but the vast majority of studies concentrate on single litter types. If litter mixtures can increase decomposition rates and also N mineralization, then plants could have higher growth rates when grown in mixtures as compared to individual litter types.

We sought to determine whether decomposition rates differed between mixtures versus individual litter types of three dominant canopy trees in northern Arizona, aspen (*Populus tremuloides*), canyon maple (*Acer grandidentatum*), and white fir (*Abies concolor*). Litter from

these three species commonly mix on the forest floor and together make up approximately 85% of the litter biomass deposited during peak leaf litterfall at our study sites in the high elevation snowmelt drainages (*see Chapter 4*). Moreover, aspen and canyon maple are both heavily browsed by ungulates (principally elk, *Cervus elaphus*) at this site (Martin 2007, *Chapter 4*), and this heavy herbivory appears partially responsible for the decline of these species at this site over the last twenty-five years (Martin 2007). This conclusion is bolstered by an elk enclosure study that was initiated in 2004 where we have seen dramatic changes in aspen and maple recruitment in drainages where elk are excluded compared to those where elk are present (Martin and Maron, *in review*). These observations and results strongly suggest that heavy browsing in this system has the potential to shift litter quality and quantity through changes in the abundance of deciduous versus coniferous species.

To examine how herbivore-driven changes in the relative abundance of single species of litter and litter mixtures might influence decomposition dynamics, we quantified: 1) decomposition rates and nutrient content of single species litter and litter mixtures in a field experiment, and 2) soil net N mineralization and plant growth in single species litter and litter mixtures in a greenhouse experiment.

Methods

Study site

Our study sites consisted of a series of parallel snow melt drainages that flow into steeper north-facing canyons along the Mogollon Rim in north-central Arizona (34° 24' N, 111° 09' W). The canopy vegetation in these drainage bottoms is primarily composed of aspen (*Populus tremuloides*), canyon maple (*Acer grandidentatum*), and white fir (*Abies concolor*), although several other coniferous and deciduous species occur at lower densities in these drainages

(Martin 1998, 2007). The overall study area, which is located within Coconino National Forest, is at an elevation of about 2350 m above sea level, and is characterized by a cool and subhumid climate (Hart et al. 2006). Annual temperature varies between a high of 17.2° C and a low of -0.3° C elevation. Mean annual precipitation is 494.28 mm, and mean annual snow depth is 1.09 m with the majority of snow falling between November-April. The site experiences a short dry season from May – June that is followed by a wetter period in July that begins with the onset of the summer monsoonal rains (Bailey and Covington 2002, Hart et al. 2006). The soils are moderately well drained, are derived from limestone and calcareous sandstone with influence from basalt, and are classified as a complex of fine-silty, mixed, superactive, frigid Typic Cumulic Haplustolls (USDA 2008).

Decomposition experiment

We conducted a litterbag experiment to examine both species-specific decomposition rates of the three dominant species (maple, aspen, and white fir) as well as the effects of litter mixtures on mass loss. In early November 2008 (during peak litterfall), we collected fresh dry leaf litter from each of the three species near the study drainages. We collected litter from white fir by placing a tarp under ~10 trees and gently shaking the tree until the litter fell. However, we arrived in northern Arizona ~ 1 week after a hard frost caused the majority of aspen and maple leaves to fall (US Forest Service, *personal communication*). Therefore, we collected litter from directly beneath ~ 10 trees of each of these species. We separated the litter, pooled the samples within species and air-dried the litter. We constructed 100 cm² litter bags made of fiberglass window-screen (0.1 mm mesh size) and filled individual bags with 6 g of dried litter per species. The litter at the time of filling the bags was dry and homogeneous, and thus wet/dry weight conversions were unnecessary to measure. In addition, a subsample of undecomposed (initial)

litter from each of the three species was kept and returned to the University of Montana for total C and N analysis using a CHN elemental analyzer (Model EA1110, CE Instruments, Hindley Green, U.K.).

Most studies examining differences in mass loss between specific litter types and mixtures have used equal masses in mixed and individual litter bags, with equal proportions of component species (Gartner and Cardon 2004). The effect of mixed litter versus individual species effects on decomposition rates is usually determined by comparing mass loss rates in mixtures to predicted litter mass loss rates of individual species (Bardgett and Shine 1999) because it is logistically challenging to separate individual species from decomposing mixtures (for examples where this was done successfully, see: Hättenschwiler and Jørgensen 2010, Hoorens et al. 2010). Using equal litter masses in mixed and individual litterbags facilitates this comparison. However, our goal was to compare litter decomposition rates of individual species in mixtures to those of single species decomposed in isolation. Thus, we decided to hold litter mass constant within species instead of holding total litter bag mass constant: single species litterbags contained a total of 6 g of single species litter, our mixed species litter bags contained 6 g of each of the three species.

To minimize potential micro-environmental effects on decomposition, we conducted the litter decomposition experiment in a single study drainage that was generally representative of the canopy vegetation in the snowmelt drainages along the Mogollon Rim. Within this area we designated 15 randomly selected plots along a 60 m long, 10 m wide transect, with each plot separated by a minimum of 2 m. Prior to deploying the constructed litterbags, we cleared an area of litter and woody debris from the soil surface. Then, within each plot we deployed 5 identical litter bags containing aspen, maple, fir or a mixture of these species (15 plots x 4 treatments x 5

bags each treatment = 300 total bags) on 4 November 2008. Litter bags were attached to the ground with wooden stakes. For the single-species litter treatments, this translated to 30 g of litter of each species in each plot which is within the range of natural variation of litter biomass located on an equal area of ground during the peak in litterfall (E. Parsons, *unpublished data*).

We retrieved all of the bags on 21 July 2009 (after 259 days) and dried them in a drying oven at 62°C to constant weight. We then removed dirt, rocks, and any non-litter vegetation from the bag. Because the different litter types were easily distinguishable (even small pieces), we separated and then weighed the litter by species to the nearest 0.5 g. Litter that was too small to identify was negligible and was divided and added equally among the three species (Hättenschwiler and Jørgensen 2010). Finally, we analyzed a subsample of the litter (n = 4 for each species) for total C and N content using a CHN elemental analyzer (Model EA1110, CE Instruments, Hindley Green, U.K.).

Greenhouse experiment

We also conducted a greenhouse experiment to assess the effects of physical and chemical differences in individual decomposing litter types and mixtures on native understory plant emergence and subsequent growth. In October 2007 we collected seeds from two understory forbs that are common at the site (*Hymenoxys hoopesii* [owl's-claws], and *Penstemon virgatus* [upright blue beardtongue]), and two relatively uncommon species (*Mentha arvensis* [American wild mint] and *Aquilegia chrysantha* [golden columbine]). These four species occur at different elevations along a moisture gradient within drainages (data not shown), and thus represent a diversity of plants that may be influenced by tree species litter inputs. The seeds were air dried and stored in paper envelopes in a dry location until the start of the experiment. Concurrent with seed collections, we also collected litter by placing plastic sheets underneath 10

trees of each species and gently shaking the trees to release standing senesced litter. Collected litter was pooled by species, air dried and stored in paper bags until the start of the experiment.

We grew seeds in 2.4 L plastic pots (19 cm diameter and 22 cm depth) using four litter addition treatments: maple, aspen, white fir, a mixture of all three; a no litter treatment as an experimental control. The experimental design consisted of 10 replicates of each treatment (4 species \times 5 treatments (including controls) \times 10 replicates = 200 total pots). We filled the bottom half of each pot with sterile sand (20/30 grit silica sand, Lane, Montana), and the top half with a 50/50 mixture by volume of sand and potting soil (*Miracle Gro*, 21-14-7 NPK, The Scotts Company LLC), and 100 g native soil collected from the study sites to provide a native soil microbiota inoculum. We chose this soil mix to facilitate harvest of the roots of the four native plant species at the end of the experiment. In addition, we added 10 g of senesced leaf litter to each pot that was mixed in the top layer of sand and soil (except in the controls). This mass was chosen because it represents an average amount of litter present on a similar area of ground at the study sites as determined by leaf litterfall traps from a different experiment (E. Parsons, *unpublished results*). Litter was crushed and passed through a 4.75 mm sieve so that individual litter pieces were approximately 1 – 5 mm in diameter. Finally, we randomly assigned the location of each pot in the greenhouse in order to account for potential micro-environmental variability.

On 10 February 2008, we placed 10 seeds of one of the four target species in each pot (according to forb species treatment) and allowed these seeds to germinate. We watered the pots daily using a fine mist until the soil was saturated. After four weeks (when all germination was complete), we counted the number of seedlings that had emerged so that we could determine litter treatment effects on percent emergence. For the growth experiment we wanted only one

seedling per pot so we excavated all seedlings within a pot and randomly transplanted one of them back into the center. A few pots contained no seedlings, so one seedling was transplanted into the pot center from another pot (with excess seedlings) belonging to the same species and treatment. Since seedlings in each pot germinated within a few days of each other, culled and uncultured seedlings were roughly equal in height (E. Parsons, *unpublished results*). Pots were saturated with water daily and plants were grown on a 12 hours of light and 12 hours of dark schedule, which roughly mimicked growing conditions during the growing season in the summer in the mountains of Arizona. When plants began to produce flowers in late July, we harvested all plants, separated all sand and dirt from the roots, dried them to constant weight in drying ovens at 62°C, and then weighed the root and shoot biomass to the nearest 0.01 g.

We used a set of Mixed Bed Exchange Resin bags (H^+/OH^- , Mallinckrodt Baker Inc., Phillipsburg, New Jersey, USA) to determine whether litter treatment influenced net soil N mineralization. Ten g nylon resin bags were buried 10 cm below the soil surface in 10 pots of each treatment without plants (5 treatments \times 10 = 50 total pots) at the beginning of the experiment on 10 February 2008 and removed at the end of the experiment on 31 July 2008 (173 days later). Following removal, resin capsules were brushed to remove dirt and debris, and extracted in 2N KCl. Briefly, resin capsules were placed in a 50 ml centrifuge tube with 10 ml KCl, and tubes were shaken on a shaker table for one h. The process was repeated two more times, and the resulting 30 ml KCl solution was centrifuged at 3,000 RPM for 5 minutes, decanted into scintillation vials and frozen until analysis. Total extracted ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were analyzed on a Flow Injection Analyzer at the UC Davis Analytical Laboratory (Davis, California, USA).

Statistical Analyses

To determine whether mass loss rates of the mixture were different than what would be predicted based on the individual litter treatments, we first averaged the individual litter mass of the five bags containing the same litter type within each plot. We then summed the remaining mass of the fir, aspen, and maple treatments and calculated the decomposition rate constants (*k-values*) for both the “expected” and “observed” mixture treatments. Decomposition rate constants were estimated using the single negative exponential decay model (Olson 1963; Wieder and Lang 1982): $L_t = L_0 e^{-kt}$, where L_0 is the litter mass before decomposition, L_t is the litter mass after decomposition at time t (years), and k is the fraction of mass remaining at time t (Schlesinger 1997; Chapin et al. 2002). In this particular analysis, t was equal to 0.7096, or 259 days of decomposition/365 days. A matched-pair t-test was used to determine whether decomposition rate constants differed between expected and observed groups because we were comparing paired data from two groups. Also, to determine whether decomposition constants within species were significantly different between mixtures and individual litter treatments we similarly calculated decomposition rate constants and we used matched-pair t tests (with Bonferonni correction) within species. To determine whether litter decay rates and initial and final litter C/N ratio were different between the three species we used ANOVA with species as a fixed factor and decay rates or C/N ratio as dependent variables.

We used ANOVA to determine whether emergence and biomass differed by litter treatment or forb species. In these models, emergence and total plant biomass were dependent variables, and species, litter treatment and their interaction were independent predictors. When we found significant species*litter treatment or biomass interactions we tested individual forb species with separate ANOVAs. We similarly used ANOVA to test for litter treatment effects on

total net N mineralization with N (mg/L) as the dependent variable and litter treatment as a fixed factor. We used Tukey HSD (Honestly Significant Difference) post-hoc tests to look for significant differences between groups. We also calculated expected emergence and biomass for each forb species for the mixture treatment by summing the total biomass values for each individual litter treatment and dividing by three (Bardgett and Shine 1999, Gartner and Cardon 2004). We compared expected and observed emergence with matched-pair t-tests.

Finally, we determined the relationship between net N mineralization and mean plant biomass using ANCOVA. In this model, mean biomass was the dependent variable and net N mineralization was used as a covariate. Species and litter treatment were fixed factors. We first tested for all two-way interactions between the fixed factors and the independent variables, and non-significant terms were removed from the models. We calculated expected net N mineralization by summing the net N mineralization for all individual litter treatments and dividing by three (Gartner and Cardon 2004). In all analyses, variables were log transformed (or arcsin square-root transformed for percentages) when necessary in order to meet the assumptions of normality and homogeneity of variances, and all analyses were conducted using SPSS version 17 (SPSS, Chicago, Illinois, USA).

Results

Decomposition experiment

The observed average mass loss rate of the mixture was higher than the expected rate predicted from the single-species litter treatments ($t_{14} = 3.16$, $P = 0.007$). However, this increase was relatively small; the decomposition constant k of the mixture was 13% lower than it was for k predicted from the individual litter types (mean $k = -0.32$ expected, -0.36 observed). This difference was driven by a higher decomposition rate of aspen litter in the mixture compared to

the individual litter treatment ($t_{14} = 10.99$, $P < 0.001$, Fig. 1A). In mixture, the mean aspen decomposition rate constant decreased by 47% in mixture compared to when it was decomposed alone (mean $k = -0.38$ alone, -0.56 mixture). However, mass loss did not differ between the mixture and the single species litter treatments for maple ($t_{14} = -0.94$, $P = 0.36$) or white fir ($t_{14} = -0.50$, $P = 0.62$).

Litter decomposition rates differed among the three canopy tree species in the individual litter treatments ($F_{2,42} = 98.08$, $P < 0.001$, Table 1). Maple litter mass loss was most rapid, followed by aspen and then white fir (Tukey test, $P < 0.01$ in all comparisons), and the difference between white fir and maple was the largest; the average decomposition constant for maple was 183% smaller than white fir and 19% smaller than aspen. The decomposition rate constant of aspen was 138% smaller than white fir. Litter decomposition rates also varied by species within the mixtures ($F_{2,42} = 313.81$, $P < 0.001$, Tukey test, $P < 0.001$ in all comparisons), but the order of lowest to highest k values shifted from (maple < aspen < white fir) to (aspen < maple < white fir). Specifically, the decomposition rate constant of aspen was 30% smaller than maple and 259% lower than white fir, while maple was 177% smaller than white fir (Fig. 1A).

The C/N ratio of the three canopy tree species differed before decomposition ($F_{2,9} = 15.31$, $P < 0.01$) with maple having a significantly lower C/N ratio than both aspen and white fir (Tukey test, $P < 0.05$; Table 1). At the end of the decomposition experiment, the C/N ratio differed between individual and mixture treatments for both aspen and white fir (aspen: $t_6 = 3.97$, $P < 0.01$, fir: $t_6 = -3.88$, $P < 0.01$, Fig. 1B); the C/N ratio of aspen was 41% lower in the mixture compared to the individual litter treatment due to an 88% increase in nitrogen content in the mixture ($t_6 = -2.66$, $P = 0.03$). However, the C/N ratio of white fir was 21% higher in mixture due to a 22% decrease in the nitrogen content ($t_6 = 1.96$, $P = 0.09$).

Greenhouse experiment

The effect of the litter additions on emergence varied among the four forb species (species*litter interaction, $F_{12, 180} = 2.48$, $P < 0.01$, Table 2). For both *Hymenoxys* and *Aquilegia*, litter treatment did not affect percent emergence (*Hymenoxys*, $F_{4, 45} = 0.91$, $P = 0.47$; *Aquilegia*, $F_{4, 45} = 1.22$, $P = 0.31$) whereas litter treatment influenced the emergence of *Mentha* and *Penstemon* (*Mentha*, $F_{4, 45} = 12.35$, $P < 0.001$; *Penstemon*, $F_{4, 45} = 7.88$, $P < 0.001$, Table 2). *Mentha* emergence was strongly inhibited by litter (Tukey test $P < 0.05$). Compared to the no-litter control, the maple and mixed litter treatments reduced emergence of *Mentha* by 70% and 66% respectively, while the white fir and aspen treatments reduced emergence by 58% and 36% respectively. *Penstemon* emergence, however, was only inhibited by the maple and mixed litter treatments (Tukey test $P < 0.05$). Compared to the no-litter control, emergence was reduced by 70% in the maple treatment and by 55% in the mixed litter treatment. Finally, for all four forb species, the observed percent emergence in the mixture treatment was smaller than the expected values calculated from the individual litter treatments ($t_3 = 4.2$, $P = 0.03$, Fig. 3A).

Single species litter strongly influenced the final biomass of forbs, though the effects varied by species (species*litter interaction, $F_{12, 145} = 4.27$, $P < 0.001$, Fig. 2). At the end of the experiment, the total biomass of *Mentha*, *Penstemon*, and *Aquilegia* were significantly influenced by the single species litter treatment (*Mentha*, $F_{4, 42} = 87.1$, $P < 0.001$; *Penstemon* $F_{4, 45} = 19.27$, $P < 0.001$; *Aquilegia*, $F_{4, 15} = 40.21$, $P < 0.001$): litter additions reduced biomass of all three species relative to the no-litter controls. For *Mentha*, the total biomass in aspen, fir, and maple litter treatments was 93%, 88%, and 29% lower, respectively, than *Mentha* biomass in the controls. Total *Penstemon* biomass was reduced by 63%, 69%, and 44% in the aspen, fir and maple litter treatments respectively, total *Aquilegia* biomass was 75%, 79%, and 43% lower,

respectively, than biomass in the controls. However, for all three species, total plant biomass was not significantly reduced in mixed litter compared with controls ($P > 0.05$ in all comparisons, Fig. 2). *Hymenoxys* did not respond as strongly to litter as the other three species. The total biomass of *Hymenoxys* was significantly influenced by the litter treatment ($F_{4,44} = 2.68$, $P < 0.05$), but only because of a difference between the fir and mixture treatments ($P < 0.05$). Finally, for all four forb species, the observed total biomass in the mixed-litter treatment was much larger than the predicted values calculated from the single species litter treatments ($t_3 = -5.35$, $P = 0.01$, Fig. 3B).

Litter treatments also had significant effects on net inorganic N ($\text{NH}_4 + \text{NO}_3^-$) mineralized over the duration of the experiment ($F_{4,45} = 40.32$, $P < 0.001$, Fig. 4), and the observed differences in net mineralized N were driven entirely by differences in nitrate ($F_{4,45} = 45.6$, $P < 0.001$). Relative to the no-litter control, net N mineralization was 74% and 71% lower with white fir and aspen litter, respectively (Tukey test, $P < 0.001$ for both comparisons). However, net N mineralized did not differ between the maple and mixed litter treatments, and the control (Tukey test, $P > 0.05$). Furthermore, observed net N mineralization was 170% higher than would have been predicted based on single-species litter treatment effects on net N mineralization. Finally, the initial C/N ratio of added litter was not significantly associated with net mineralized N ($F_{1,3} = 1.17$, $P = 0.36$), but net mineralized N was positively associated with mean plant biomass at the end of the experiment ($\beta = 0.02$, $R^2 = 0.68$, $F_{1,18} = 38.47$, $P < 0.001$).

Discussion

Litter mixtures and decomposition dynamics

We found non-additive effects on the decomposition rate of a mixture of litter from three dominant and co-occurring canopy trees during a nine-month long field incubation experiment.

A mixture of aspen, maple, and white fir litter decomposed more rapidly together than expected based on single-species decomposition rates. Previous studies showed similar synergistic effects of litter mixtures on decomposition (McArthur et al. 1994; McTiernan et al. 1997; Conn and Dighton 2000; Gartner and Cardon 2004; Hättenschwiler et al. 2005; Gessner et al. 2010). However, we found that the litter mixture had a positive synergistic effect on the decomposition rate of only one of the component species (Fig. 1A). The complementary resource use hypothesis predicts that when chemically and/or structurally divergent leaf species are present in a mixture, decomposers should be able to optimize their nutrient acquisition, and a more efficient use of resources should increase overall decomposition rates for all species (Gessner et al. 2010). We used litter from three species that varied in decay rate and litter quality characteristics (Table 1), but we found that litter mixtures only stimulated decomposition of aspen litter and had no significant effects on maple and white fir (Fig. 1A). Thus, the complementary resource use hypothesis is not supported in that not all species in the mixture were equally affected.

Synergistic effects of litter mixtures on decomposition rates may be caused by a transfer of nutrient resources from nutrient-rich litter to nutrient-poor litter (Gartner and Cardon 2004; Hoorens et al. 2010). This transfer can be active whereby fungi growing in nutrient poor litter gain limiting nutrients through their hyphal network from nutrient rich litter that is nearby, or passive whereby soluble nutrients are leached from high to low quality litter (Gessner et al. 2010). If this mechanism were operating in our decomposition experiment, we would expect the high quality litter (maple) N content to decrease through time, and the lower quality litter (aspen or white fir) N content to increase through time. Using four subsamples from both the individual and mixture treatments, we estimated net change in nitrogen and carbon in the litter of all three species by incorporating both mass and percent N and C in initial and final samples. We found

that for maple, nitrogen was immobilized within litter overall in the single species litter treatments, but released from litter overall in the mixture (single species = 8.1 mg N, mixture = -10.1 mg N). The opposite, however, was true for aspen; N was released overall in the aspen litter treatment, but immobilized overall in the mixture (individual = -48.1 mg N, mixture = 4.6 mg N). Also, carbon loss in aspen was much higher in the mixture than the single species litter treatments (319.8 mg more C lost in mixture). Therefore, it is possible that decomposer-mediated (or passive) N transfer from maple to aspen increased aspen litter quality and subsequent carbon loss. These results are corroborated by other studies that have found increased decay rates of lower quality litters when decomposed near higher quality litters (Briones and Ineson 1996, McTiernan et al. 1997).

Litter mixtures and forb emergence

We found that litter additions had an overall inhibitory effect on *Mentha* and *Penstemon* emergence; the no-litter control had the highest emergence, while the lowest emergence was in the maple and mixture treatments (Table 2). This was not the case for both *Hymenoxys* and *Aquilegia*, however, as emergence in these two species did not differ between any of the litter treatments and the control. Moreover, across all four forb species, emergence in the mixture was lower than expected as compared to the individual litter treatments (Fig. 3A). What could have led to the negative effects of the litter mixture treatment on emergence? Plant germination is affected by a variety of abiotic factors, the most important of which include light quality, water and temperature (Bewley 1997; Penfield and King 2009; Nambara et al. 2010). These factors can act as signals that influence plant hormones that break dormancy and initiate germination (Nambara et al. 2010). Our litter treatments likely did not differentially influence light quality or water because litter was mixed with the soil, and pots were saturated with water daily. Also, the

mixture treatment contained equal litter mass as the other litter treatments, and so structural effects of the litter on physical properties, such as soil moisture or temperature should have been equal, or nearly equal across treatments and not magnified in the mixture. Therefore, the negative effects of the litter mixture on emergence are probably not due to treatment differences in these physical factors.

Emergence in the litter mixture could have been reduced by other factors, however, including changes in soil nitrate or CO₂ concentration, or plant secondary chemicals (DeJong and Klinkhamer 1985; Facelli and Pickett 1991; Alboresi et al. 2005; Nambara et al. 2010). Nitrate and other nitrogenous compounds can act as a signal for germination (Nambara et al. 2010), and we found increased net N mineralization due to higher mineralized nitrate in the mixture treatment than the aspen and fir treatments (Fig. 4). As well, litter mixtures can increase the activity of decomposers (Gessner et al. 2010), and increased decomposer activity can lead to immobilization of N, depletion of O₂, and toxicity of CO₂ in the soil (DeJong and Klinkhamer 1985; Facelli and Pickett 1991), which could have negatively affected germination. Finally, phytotoxins present in litter could have had allelopathic effects on germination (Rice 1979; Jefferson and Pennacchio 2003; Orr 2005), though it is unclear why these effects would be magnified in the litter mixture. In any case, to our knowledge this is the first example of non-additive effects of litter mixtures on emergence, and future studies are needed to determine the mechanisms as well as whether these litter-diversity effects can occur in the field.

Litter mixtures, plant growth and net N mineralization

As opposed to the negative effects of mixed litter additions on plant emergence, we found that the litter mixture had positive effects on plant growth (Fig. 3B). In all four understory forb species, observed biomass in the mixture was significantly larger than the predicted biomass

from the summed effects of the single species litter treatments (Fig. 3B). The effect was strongest in *Mentha* with biomass in the mixture almost 330% larger than the predicted level, and weakest in *Hymenoxys* with biomass in the mixture 65% larger than the predicted level. This increased growth in the mixture treatment was likely due to a synergistic effect of the litter mixture on mineralized nitrogen (Fig. 4). Observed net N mineralization in the mixture was ~160% higher than that predicted from the single species litter treatments, and this closely matched the observed mean increase in biomass across the four forb species, which was ~150% larger than the predicted level. These results together imply that diverse litter mixtures may have important positive indirect effects on subsequent plant performance through non-additive effects on decomposition dynamics.

We also found that the biomass of all four understory forbs in the mixture treatment was no different from that in the no-litter control (Fig. 2). This result is important because many studies that have examined single species litter impacts on plant performance have found evidence that litter often has a negative impact on plant performance (Facelli and Pickett 1991, Facelli 1994, Boserup and Reader 1995, Xiong and Nilsson 1997, 1999, Molofsky et al. 2000). Since forested ecosystems often contain multiple plant species, and thus mixtures of plant litter may be more the norm than the exception (Hoorens et al. 2010), the negative impacts on plant growth observed in many experiments could be reduced in more litter-diverse environments.

The increase in net N mineralization in the greenhouse study in the mixed litter treatments could have been due to higher decomposition rates of the mixed litter as we observed increased decay rates of aspen litter in the mixtures in the field decomposition experiment (Fig. 1A). If so, more rapid rates of N mineralization may have stimulated plant growth by augmenting N stocks to growing plants. Nitrogen is commonly limiting to plant growth in many

areas, especially in developmentally young ecosystems (Vitousek and Howarth 1991), and this result implies that litter diversity may play an important role in influencing N cycling and productivity in these and other ecosystems (Gessner et al. 2010).

Finally, the abundance of the two deciduous species used in this study (aspen and maple) is declining at our study sites in Arizona likely due to a combination of elk browsing and climate change (Martin 2007). Elk abundance in northern Arizona has been stable or declining over the course of this study, but multiple ungulate exclosures erected in 2004 have yielded a rapid increase in the density and growth of both aspen and maple trees inside the fences (Martin and Maron, *in review*, *Chapter 4*). Furthermore, this heavy herbivory is likely to shift the quantity and quality of litter inputs on the forest floor (Bailey et al. 2007). Recently, we found that elk browsing at this site has influenced the quantity of aspen and maple litter being deposited each year during the peak in litterfall (but not white fir), and this has likely affected the diversity of litter mixtures present on the forest floor (*Chapter 4*). Thus, herbivore-mediated effects on N dynamics and indirect effects on plants are possible at this site. However, whether herbivore-induced changes in litter mixtures influence N cycling and productivity is currently unknown and deserves future research.

Conclusion

Our study adds to the growing number of studies describing non-additive effects of litter mixtures on decomposition dynamics. We found synergistic effects on the decomposition rate of one of the three species in mixture and non-additive effects on final nitrogen content of two of the three litter species. More litter mixture studies that separate out individual species after decomposition are needed in order to determine whether litter mixtures more commonly influence decomposition dynamics of all component species or whether only individual species

within mixtures are affected. Also, we found in a greenhouse experiment that litter mixtures had antagonistic effects on emergence and synergistic effects on nitrogen mineralization and growth. Together, these results indicate that the non-additive effects on decomposition dynamics that many studies have observed may in fact have important feedback effects on plants.

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Figure legends

Figure 1: Mean (+SE) A) decomposition rate constants (k) of litter; B) mean C/N ratios of litter at the end of the decomposition experiment for maple, aspen and white fir. Black bars denote values from individual species decomposed alone and gray bars denote values from litter mixtures. Asterisks indicate significant differences ($P < 0.05$) within species between single and mixed litter treatments using matched pair-t tests with Bonferonni correction.

Figure 2: Mean (+SE) biomass of the four understory forbs at the end of the experiment for: A) *Mentha arvensis*, B) *Penstemon virgatus*, C) *Hymenoxys hoopesii*, and D) *Aquilegia chrysantha* in the five treatments: fir, aspen, maple, mixed litter, and a no-litter control. Letters indicate significant differences among treatments (Tukey HSD post-hoc test).

Figure 3: A) predicted (black bars) and observed (gray bars) plant emergence; and B) plant biomass in the mixed litter treatment. Black bars represent the actual values observed in response to the mixed litter treatment while gray bars represent the average of the summed contributions of the three individual litter treatments. Men = *Mentha*, Pen = *Penstemon*, Hym = *Hymenoxys*, and Aqu = *Aquilegia*.

Figure 4: Net inorganic N (ammonium + nitrate) mineralized in the five treatments (fir, aspen, maple, a mixture of all three, and a no-litter control) over the course of the greenhouse experiment. Values represent means \pm SE.

Table 1

Mean percent C, N, C/N ratio, and decomposition rate constant (k), of maple, aspen, and white fir litter from the single species litter treatments used in the decomposition experiment. Numbers represent values (mean \pm SE in parentheses) obtained from analysis of freshly collected (undecomposed) litter samples, and letters represent significant differences between species as determined by a Tukey HSD post-hoc test.

Species	Percent carbon	Percent nitrogen	C/N ratio	Decomposition rate k
Maple	45.44 <i>a</i> (0.14)	1.51 <i>a</i> (0.07)	30.27 <i>a</i> (1.29)	-0.45 <i>a</i> (0.02)
Aspen	47.88 <i>b</i> (0.28)	0.78 <i>b</i> (0.14)	67.40 <i>b</i> (11.62)	-0.38 <i>b</i> (0.02)
White fir	49.06 <i>b</i> (0.43)	0.72 <i>b</i> (0.06)	70.07 <i>b</i> (6.06)	-0.16 <i>c</i> (0.01)

Table 2

Mean (\pm SE) percent emergence of the four species of understory forbs in response to litter treatments (maple, aspen, white fir, mixture of all three and a no-litter control) in the greenhouse experiment. Letters in bold and italics represent significant differences based on Tukey HSD post-hoc tests (N=10 for all treatments) for comparisons between litter treatments. Separate Tukey tests were conducted for each species of understory forb.

<i>Treatment</i>	<i>Mentha</i>	<i>Hymenoxys</i>	<i>Penstemon</i>	<i>Aquilegia</i>
Maple	0.19 \pm 0.05 <i>a</i>	0.10 \pm 0.03 <i>a</i>	0.15 \pm 0.06 <i>a</i>	0.04 \pm 0.03 <i>a</i>
Aspen	0.41 \pm 0.05 <i>b</i>	0.14 \pm 0.04 <i>a</i>	0.47 \pm 0.05 <i>bc</i>	0.04 \pm 0.02 <i>a</i>
White fir	0.27 \pm 0.04 <i>ab</i>	0.15 \pm 0.04 <i>a</i>	0.38 \pm 0.06 <i>bc</i>	0.02 \pm 0.01 <i>a</i>
Mixture	0.22 \pm 0.04 <i>ab</i>	0.08 \pm 0.03 <i>a</i>	0.23 \pm 0.04 <i>ab</i>	0.02 \pm 0.01 <i>a</i>
No litter	0.64 \pm 0.05 <i>c</i>	0.18 \pm 0.04 <i>a</i>	0.51 \pm 0.08 <i>c</i>	0.07 \pm 0.02 <i>a</i>

Figure 1

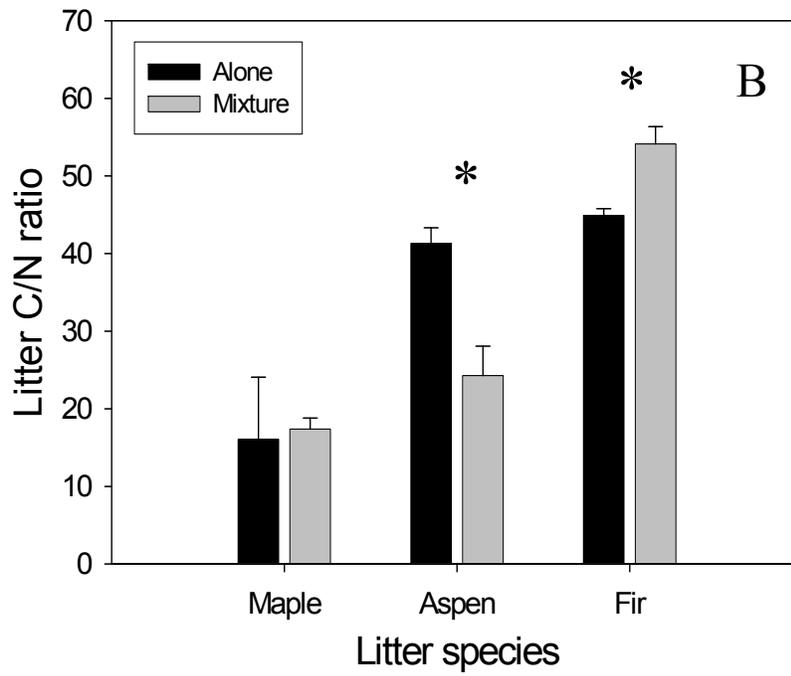
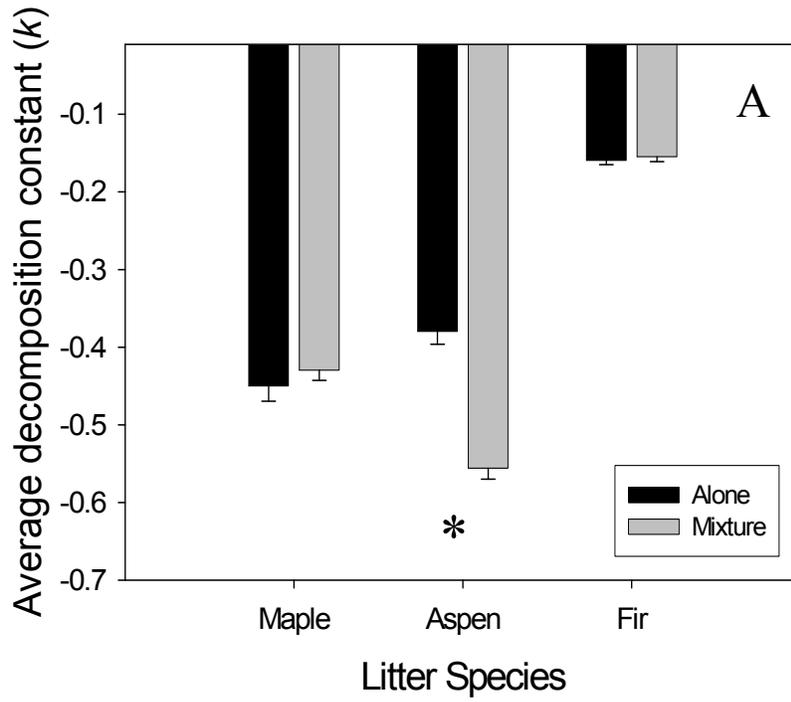


Figure 2

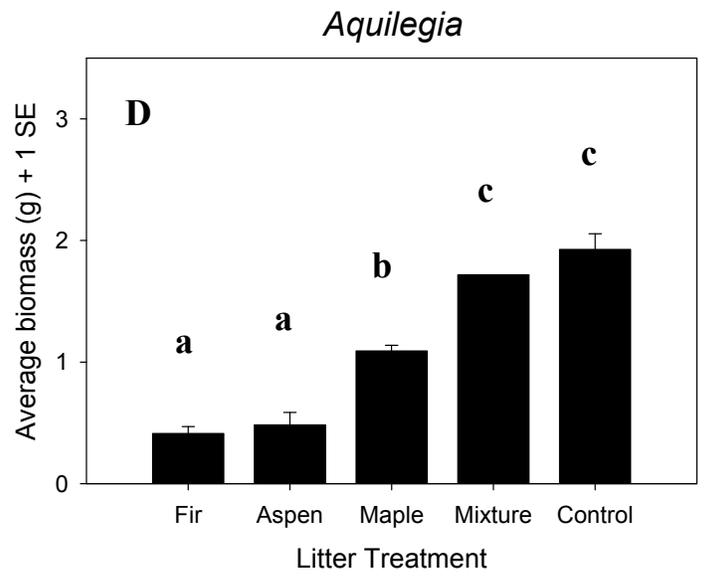
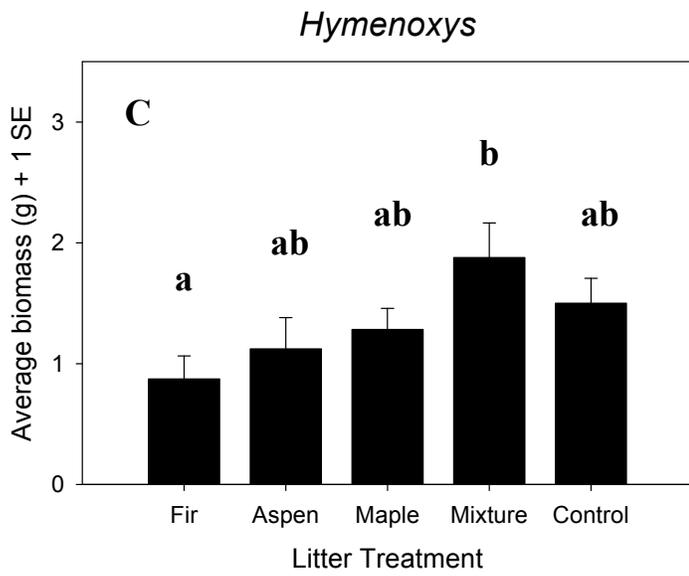
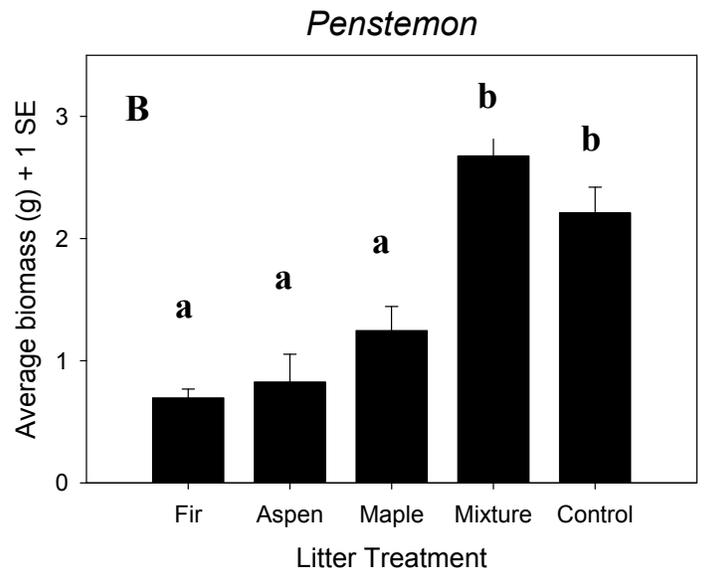
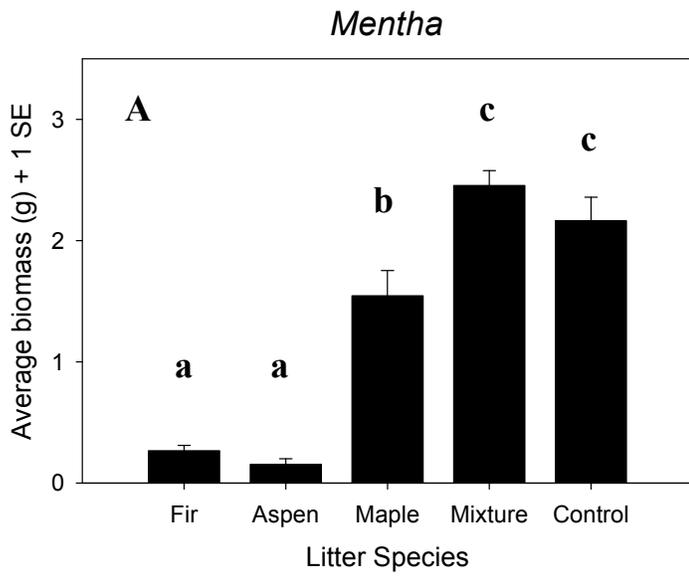


Figure 3

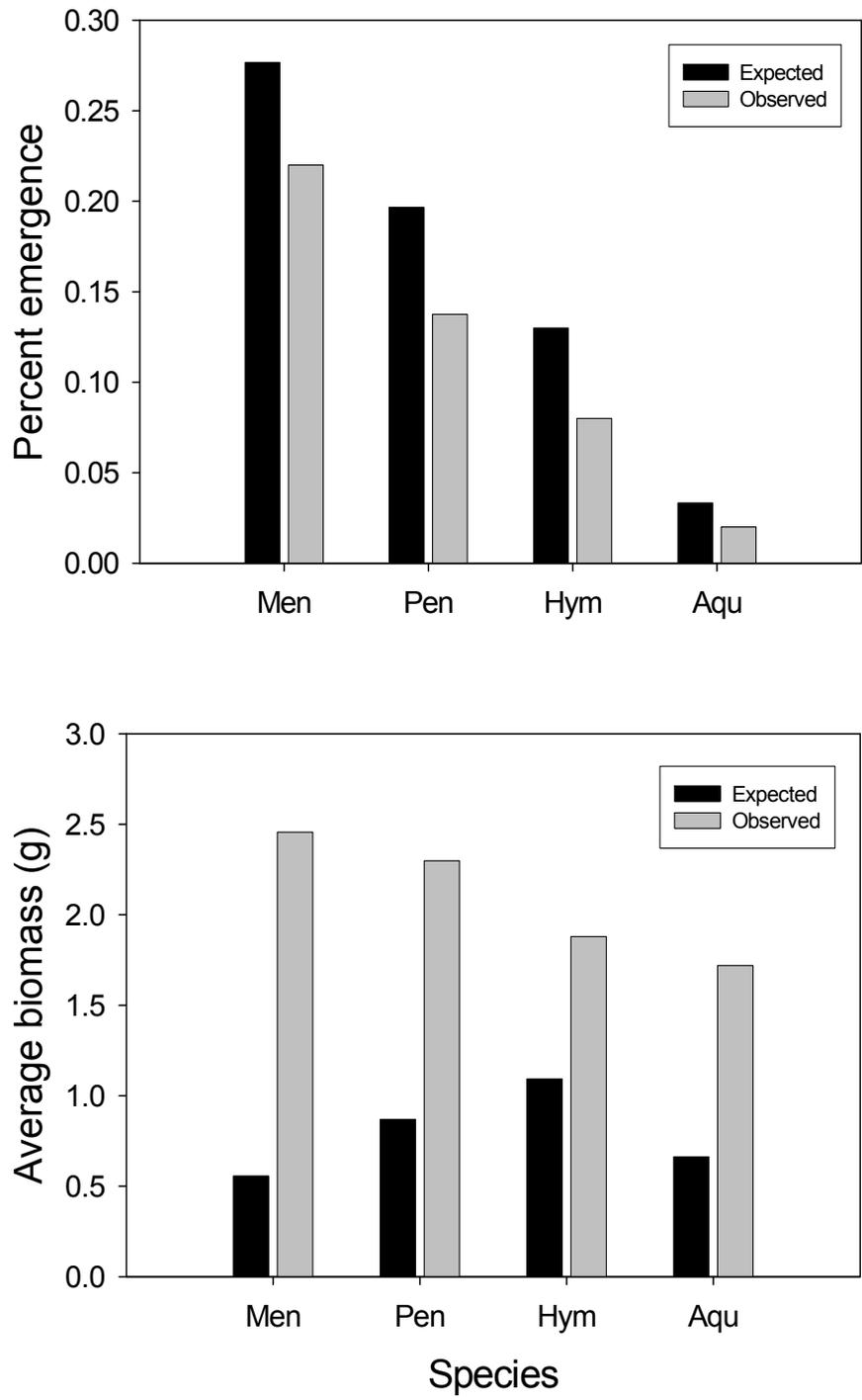
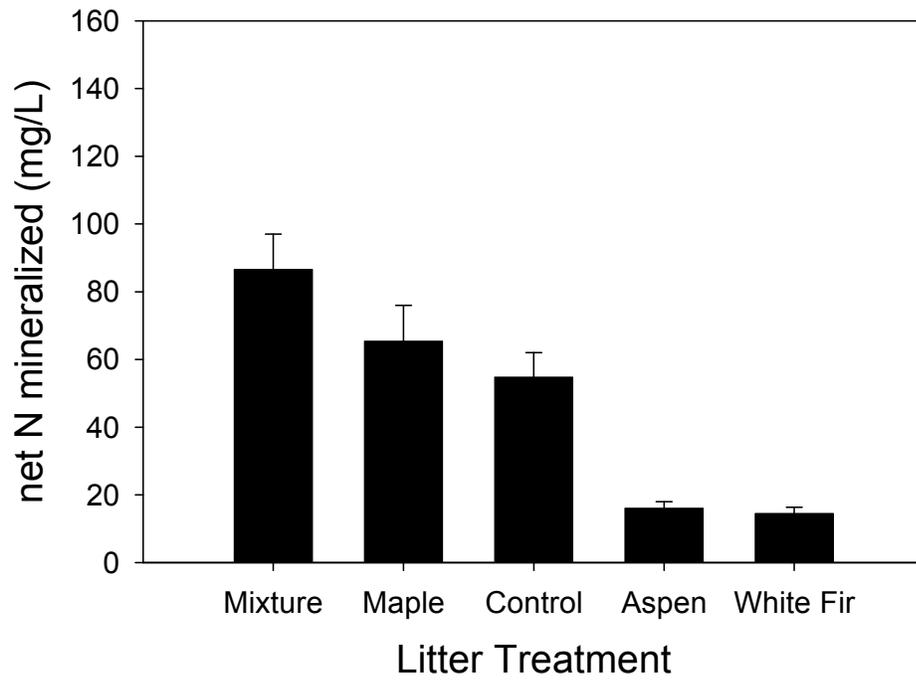


Figure 4



CHAPTER 4
ELK INFLUENCE NITROGEN INPUTS VIA IMPACTS ON LITTER QUALITY AND
QUANTITY AND NITROGEN-FIXING FORB ABUNDANCE

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Abstract

Large herbivores are major drivers of plant community structure in many terrestrial systems, but effects on ecosystem processes are less clear. One way large herbivores may influence ecosystem properties is through modification of plant-soil feedbacks. By selectively foraging on nitrogen-rich plants, large herbivores are thought to favor species with nitrogen-poor, slowly decomposing litter, and this is hypothesized to slow down rates of N cycling. A large number of studies have shown rapid recruitment of both deciduous and nitrogen-fixing species when large herbivores are excluded, but relatively few large-scale experimental studies exist that quantify short-term impacts on N cycling. By excluding Rocky Mountain elk at large scales, we determined their effects on the recruitment of deciduous and evergreen trees and how this influenced litter inputs, C/N ratios of litter, and litter decomposition rates. We also examined whether litter from the dominant tree species influenced nitrogen mineralization, and we quantified the effects of elk exclusion on forb community composition, richness, and diversity. Five years of elk exclusion resulted in a large increase in the abundance of recruits of two deciduous tree species and small increases in the recruits of two of the four conifers. Deciduous litter had higher initial N content and more rapid rates of decomposition than conifer litter, but litter identity did not influence soil net nitrogen mineralization. Elk exclusion did not alter the richness or total abundance of understory forbs but the abundance of nitrogen-fixing legumes and one N-fixing tree was greatly enhanced by elk exclusion. Our results suggest that large herbivores can have strong and rapid impacts on plant community structure but that subsequent effects on ecosystem processes appear to develop more slowly.

Introduction

Herbivores can influence plant community structure by impacting plant survival, reproduction, and competitive interactions (Huntly 1991, Horsley et al. 2003, Gomez 2005). The effects of herbivores on ecosystem processes are less clear. Herbivores can increase, decrease, or have no effect on process rates such as nutrient cycling (Pastor et al. 1988, McNaughton et al. 1997, Singer and Schoenecker 2002). Also, studies have found both higher and lower quantities of extractable N, C, and P in soils inside of herbivore exclosures as compared to areas where herbivores have access (Frank and Evans 1997, Wardle et al. 2001, Singer and Schoenecker 2002, Augustine et al. 2003). The net effects of herbivores on ecosystem processes are likely due to a variety of factors related to herbivore identity and pressure as well as the biotic and abiotic properties of the ecosystem (McNaughton et al. 1997, Augustine and McNaughton 1998, de Mazancourt and Loreau 2000, Bardgett and Wardle 2003, Bakker et al. 2004, Côté et al. 2004, Danell et al. 2006).

One way herbivores are thought to influence rates of N cycling is by changing the quantity and quality of organic matter inputs in ecosystems (Bardgett et al. 1998, Sirotiak and Huntly 2000, Bardgett and Wardle 2003, Wardle et al. 2004). On a short timescale, herbivores may accelerate N cycling by turning lower quality plant material into higher quality organic matter that is rapidly decomposable. For example, ungulate urine and feces can stimulate N mineralization rates and enrich N availability at small local sites (McNaughton 1976, McNaughton et al. 1997). Herbivores are also thought to decelerate N cycling over the longer term by shifting plant species composition from highly palatable and rapidly decomposing species towards less palatable and more slowly decomposing species (Pastor et al. 1988, McInnes et al. 1992, Pastor et al. 1993, Kielland and Bryant 1998, Ritchie et al. 1998, Bardgett

and Wardle 2003). Herbivores may accomplish this by preferentially browsing on high quality plants such as deciduous and N-fixing species (Kielland and Bryant 1998, Pastor et al. 1998) and lowering their abundance. Litter from these preferred species tends to have lower C: N ratios, lower chemical defenses and fewer tough structural components than less preferred species such as conifers. Thus, decreases in high quality species could cause a shift in forest structure towards dominance of low quality species, with more nutrients tied up in slowly decomposing litter and this could slow down nutrient turn-over rates (Singer and Schoenecker 2002).

The importance of this process, however, likely depends on how strongly herbivores suppress the recruitment of preferred species as well as the length of time it takes for herbivores to influence succession (Pastor and Naiman 1992, Davidson 1993, McShea et al. 1997, Danell et al. 2006). Moreover, few large-scale experimental studies have simultaneously investigated how quickly plant communities respond to the elimination of browsing pressure and whether the rapid recruitment of high quality species can immediately impact N cycling. This is surprising given the increasing number of studies that document large impacts of browsing on deciduous and N-fixing species (Ritchie and Tilman 1995, Knops et al. 2000, Sirotiak and Huntly 2000, Bailey and Whitham 2002, Beschta 2005, Hebblewhite et al. 2005, Kaye et al. 2005, Bailey et al. 2007, Beschta and Ripple 2010, Kauffman et al. 2010).

Another way in which large herbivores could affect nutrient cycling rates is by changing the composition of litter mixtures on the forest floor. Mixtures of litter from different species commonly increase rates of decomposition and mineralization more than predicted for the rates for each species alone (Gartner and Cardon 2004, Hattenschwiler et al. 2005, Lecerf et al. 2011). These synergistic effects are hypothesized to occur 1) because of a greater presence of microhabitat niches available for decomposers in chemically and physically heterogeneous

mixtures and 2) through passive or decomposer-mediated nutrient redistribution from high to low quality litter which speeds up decomposition of the lower quality litter (Gartner and Cardon 2004). High densities of large herbivores can decrease plant species diversity (Horsley et al. 2003) and homogenize plant communities (Rooney 2009), and thus it is possible that herbivory could affect the diversity of litter mixing on the forest floor, and by doing so affect decomposition and N cycling. However, it is also possible that short-term changes in plant litter quantity and quality may have no immediate effect on nutrient cycles because of microbial immobilization in some cases (Knops et al. 2002).

We used a replicated large-scale ungulate exclusion experiment that was initiated in 2004 in the mountains of north-central Arizona to study the cumulative effects of elk (*Cervus elaphus*) browsing on plants and ecosystem processes. First, we quantified the extent to which elk selectively forage on deciduous versus coniferous tree species. Second, we examined how the recruitment of deciduous and coniferous saplings was affected by elk herbivory, how elk altered litter quality and quantity, and subsequently how this affected rates of litter decomposition. Third, we examined whether differences in decomposition rates of deciduous versus coniferous litter and a mixture translated into meaningful differences in N mineralization. Finally, we quantified differences between exclosures and paired non-fenced areas in forb diversity and abundance, particularly focusing on the abundance of N-fixing legumes and *Robinia neomexicana*, an N-fixing tree.

Methods

Study site

Our study area lies at an elevation of 2350 m in north-central Arizona (34° 24' N, 111° 09' W), and is characterized by a cool and subhumid climate (Hart et al. 2006). Annual

temperature varies between a high of 17.2° C and -0.3° C (Blue Ridge Ranger Station weather station), mean annual precipitation is 494.28 mm, and mean annual snow depth is 1.09 m with the majority of snow falling between November and April. The middle of the summer is characterized by a long dry period (May – July) that is followed by a wetter period that begins with the onset of the summer monsoonal rains (Bailey and Covington 2002, Hart et al. 2006).

Study sites consisted of a series of parallel snow melt drainages that occur along the Mogollon Rim in Coconino National Forest in north-central Arizona (34° 24' N, 111° 09' W). These drainages flow into steeper north-facing canyons. The canopy vegetation in these drainage bottoms is primarily composed of aspen (*Populus tremuloides*), canyon maple (*Acer grandidentatum*), and white fir (*Abies concolor*), although several other coniferous and deciduous species occur at lower densities, including Douglas fir (*Pseudotsuga menziesii*), white pine (*Pinus flexilis*), Ponderosa pine (*Pinus ponderosa*), Gambel's Oak (*Quercus gambelii*), and New Mexico Locust (*Robinia neomexicana*) (Martin 1998, 2007). Aspen and canyon maple are both browsed by ungulates (principally elk; Martin 2007, *unpublished results*), and this heavy herbivory appears partially responsible for the decline of these species at this site over the last twenty-five years (Martin 2007).

We identified three pairs of drainages (6 total), each separated by ~ 200 m, with canyons containing pairs of drainages separated by ~ 2 km. We randomly assigned one drainage of each pair to receive an ungulate exclusion treatment. This consisted of erecting 2.5 m tall game fence around perimeters of drainages (total area enclosed for each replicate drainage = 10 ha) that was attached to metal fence posts 0.3 m above ground level to allow predator access. Fences had two strands of high tension wire above them to bring the fence to a final height of 3 m. Fences were constructed during fall and winter 2004, and paired control drainages were left unfenced. The

fences excluded elk (*Cervus elaphus*), and suppressed but did not completely exclude mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*). Evidence of black bears (*Ursus americanus*), coyotes (*Canis latrans*), and mountain lions (*Puma concolor*) was seen both inside and outside the fences each year.

Tree recruitment and browsing

To quantify how cessation of elk browsing influenced the regeneration of forest trees we used a random stratified sampling design. On each experimental drainage we established 10 sampling subplots stratified across each of five strata that included the bottom, lower third, middle, upper third, and ridge of each drainage. Thus, each drainage had a total of 50 sampling subplots. Stratification of subplots was important because soil moisture and the composition of both trees and herbs changes along the gradient (Martin 1998). Subplots consisted of a 5 m radius circle with a permanent marker at the center (see Martin 1998 for more details regarding sampling design).

In each sampling subplot we identified and counted the number of recruits and saplings of each species each year starting in 2005. We focused on recruits and small trees (saplings) because we expected that the majority of the response of the trees to fencing would occur in the understory where small recruits and saplings would respond to release from herbivore pressure. Maple, aspen, and locust, the dominant deciduous species at our site, reproduce asexually by sending up clonal sprouts (ramets) from either shallow underground roots or rooting stems (Phillips and Ehleringer 1995, Springer et al. 2009). Therefore, to quantify the response of the deciduous species we counted the number of ramets and seedlings that were less than 8 cm diameter at breast height (dbh), which included all new growth since 2005. The conifers at our site, however, grow slowly compared with the deciduous species and reproduce only from seed.

Because we expected that a release from browsing could affect both the abundance of seedlings and the growth of saplings we counted the number of seedlings and saplings also that were < 8 cm diameter at breast height (dbh). In addition to quantifying tree recruitment and abundance yearly, we also recorded the number of stems of each species in the understory that showed signs of fresh browsing by ungulates. Browsing sign was easy to spot on all species because of the presence of terminal branches without leaves, and discoloration in the remaining leaves and stem (Keigley and Frisina 1998).

Litter quantity

We hypothesized that elk browsing was eliminating the recruitment of the deciduous species at our site (Martin 2007). Therefore we expected that the exclusion of ungulates would lead to a rapid increase in the number of deciduous recruits (ramets and seedlings) and thus an increase in the quantity of deciduous leaf litter added to exclosure drainages. To estimate leaf litter quantity we individually marked stems of aspen and maple starting in 2005, with unique metal identification tags. We randomly chose and tagged 3 ramets of each species found in each of the sampling subplots and measured their height. In each subsequent year after 2005, we measured the height of all tagged individuals that could be found and 3 additional ramets that were randomly selected and tagged. In cases where fewer than 3 ramets were available in a 5 m sampling subplot, as many ramets were tagged as possible. In addition we haphazardly selected 80 ramets total of maple and aspen in 2008 inside one of the exclosures. We selected ramets that varied in height and that occurred across the moisture gradient from drainage bottoms to the ridges. We then counted the number of leaves on all selected ramets and used regression of height against LN-transformed leaf number to predict leaf number from height. The coefficients

of determination were both relatively high (0.77 for maple, $F_{1, 78} = 254.9$, $P < 0.001$, and 0.83 for aspen $F_{1, 78} = 373.9$, $P < 0.001$).

Next we estimated the total number of leaves added to each drainage by each of the five cohorts between 2005 and 2009. It was important to quantify leaf addition for all cohorts and all years because there was new recruitment each year and recruits generally increased in height annually. To do this, we first estimated survival probabilities for each cohort, year, and drainage by determining the proportion of ramets within a cohort that were alive in each successive time period. Survival of a 2005 cohort of maple ramets, for example, ranged from a low of 0% surviving in a non-fenced drainage to a high of 40% surviving in a paired enclosure in 2009. Ramet mortality was caused by browsing, snow burial, and wind. If a tag was missing and never found, the individual ramet was coded as dead. We then multiplied survival (5 cohorts tagged, 2005-2009) of each cohort by the mean number of stems (all ramets plus seedlings) to estimate the number remaining from each cohort through time. We multiplied the estimated number of stems by mean height in each cohort during each time period and then calculated leaf number for that height from the regression equations (above). Finally, we summed the number of leaves contributed by each cohort during each time period. This approach allowed us to incorporate survival, growth, and recruitment into our calculations of leaf additions. Also, the greatest abundance of both aspen and maple occur in the lower halves of the drainages; for example, in 2009, 86% of all aspen stems and 92% of all maple stems occurred in the lower three strata. Therefore, we restricted our leaf addition analysis to the lower three strata.

Litter quality and decomposition

To quantify differences in litter quality and decomposition rate by species, we collected freshly senesced litter from 10 trees of maple, aspen, and white fir (the three dominant tree

species) near the experimental drainages. We placed a tarp underneath each tree in late October 2007 and shook the trees gently until litter fell. Litter from the trees was then pooled by species, air dried, and then 6 g of each was put into 10 cm² nylon bags with 1 mm mesh size. We then randomly selected 10 locations on each drainage and at each location we staked five identical bags of each of aspen and maple to the forest floor so that we could determine mass loss five different times (6 drainages x 2 species x 10 locations x 5 bags each = 600 bags). These bags were harvested 3 times a year in 2008 (May, July, and November), and twice in 2009 (May, and July). The litter was dried at 60 °C to constant weight, and dirt, rocks, and non-litter plant material was removed from the bags and the litter was weighed to the nearest 0.01 g. This experiment allowed us to test whether the treatment (elk enclosure) influenced litter decomposition rates. We examined enclosure effects on decomposition rates because we hypothesized that elk would alter the decomposition environment (i.e. abiotic factors or decomposer communities that affect N cycling), and we used maple and aspen because we expected that their relatively faster decomposition rates (i.e. deciduous litter tends to decompose more rapidly than conifer litter) would make them more sensitive to changes in the decomposition environment.

We also placed an additional 50 bags of white fir litter on one enclosure drainage (same 10 locations as above x 5 bags each location = 50 bags) in order to look for decomposition rate differences by species. For litter quality we randomly selected 4 of these 10 locations, and litter from one bag of aspen, maple, and fir from each sampling period (3 species x 4 sites x 5 sampling periods = 60 bags) was ground to a fine powder. We then used a CHN elemental analyzer (*CE instruments model EA1110*) to determine the percentage carbon and nitrogen content of the litter subsamples.

Net N mineralization

In fall 2008 we collected freshly fallen litter on the ground that had been there < 1 week from trees near the study area. We pooled the litter by species and air dried it. We cleared an area of litter and woody debris in one study drainage that was generally representative of the canopy vegetation in the snowmelt drainages along the Mogollon Rim. By conducting this study within one area it allowed us to minimize micro-environmental effects on decomposition processes. Within this area we designated 15 randomly selected plots (along a 60 m long, 10 m wide transect), with each plot separated by a minimum of 2 m. The transect ran down the length of the drainage and was parallel to the drainage axis. Within each plot we deployed 5 identical litter bags containing 6 g of aspen, maple, white fir, or nothing (a no-litter control). In addition, we deployed a mixture treatment containing an equal 6 g of each species placed together so that the different litter types could intermingle. Our litter mixture treatment allowed us to test the hypothesis that the mixture increased net N mineralization in the soil. This number of litter bags translated to ~ 32 g of litter of each species at each location which is within the natural range of variation of litter biomass found in a similar area at this site (E. Parsons, *unpublished data*). In total we had 375 total litter bags (15 plots x 5 treatments x 5 bags of each type = 375 bags). Litter bags were attached to the ground with wooden stakes.

We used Mixed Bed Exchange Resin (H^+/OH^- , Mallinckrodt Baker Inc., Phillipsburg, N.J., USA) to determine whether litter identity influenced soil nitrogen mineralization. We created 10 g nylon bags of resin and we buried each bag 10 cm below the soil surface under each litter treatment location at the start of the experiment. While placing the capsules, we excavated the soil carefully in order to minimize disturbance. We excavated the resin capsules in July 2009 (after 9 months) and stored them in a freezer prior to analysis. We then removed dirt from their

exterior and we placed them in large centrifuge tubes filled with 10 ml of 2N KCL. These were placed on a shaker table and gently agitated for one hour. We then poured off the KCL and repeated this process two additional times, each time using a fresh aliquot of KCL. We centrifuged the reserved 30 ml of extracted KCL at 30 RPM for 5 minutes, then decanted the solution into scintillation vials and placed them in the freezer. In addition we analyzed blanks (unused capsules) and tested these in the same manner as above. We sent the samples to the U.C. Davis Analytical Laboratory (Davis, California, USA) for analysis of NH_4^+ and NO_3^- . The blanks returned nitrogen values that were not significantly different from zero, so the values did not need to be corrected.

Forb composition, abundance and diversity

To quantify the effect of elk on the composition and abundance of understory forbs, we sampled plants in mid-summer 2009 by placing a 1 m² quadrat (divided with string into 25 equal sized squares) at the center of each sampling subplot. We identified each species present, and the relative cover by counting the number of times any part of an individual of each species occurred in each of the 25 squares.

Statistical Analyses

We first averaged the proportion of browsed individuals (# browsed / total number) of either deciduous (aspen + maple + oak + locust) or evergreen species (white fir + white pine + Douglas fir + Ponderosa pine) by strata for 2009. We then used ANOVA with proportion browsed as the dependent variable, and treatment, strata and their interaction as predictors. For recruitment we similarly averaged the number of individual stems of each species in 2009 (ramets + seedlings/saplings < 8 cm dbh for deciduous species, saplings < 8 cm dbh for conifers)

by strata and we used ANOVA with stem number as the dependent variable, and treatment and strata, and their interaction as predictors.

To see if species, treatment, or time influenced litter addition and decomposition rates we used repeated measures ANOVA. For the litter addition experiment we specified litter quantity (number of leaves) across time (5 levels, 2005-2009) as within-subjects variables, and treatment, species (aspen and maple) and their interaction as between-subjects factors. Litter quantity was the mean number of leaves added to drainages across all strata by species and year.

Decomposition rate constants were estimated using the single negative exponential decay model (Olson 1963; Wieder and Lang 1982): $L_t = L_0 e^{-kt}$, where L_0 is the litter mass before decomposition, L_t is the litter mass after decomposition at time t (years), and k is the fraction of mass remaining at time t (Schlesinger 1997; Chapin et al. 2002). K -values were averaged by species, drainage, and sampling period and were the within-subjects factor across time (5 sampling occasions). We specified treatment, species, and their interactions as between-subjects factors. For the litter quality analysis we used univariate ANOVA to look for initial differences in litter quality between species with C/N ratio as the dependent variable and species as the fixed factor. To look for differences in litter quality through time we used repeated measures ANOVA with C/N ratio averaged by species across 5 sampling periods as the within-subjects variables and species as the between subjects factor. We used Mauchly's W to test the sphericity assumption with all repeated measures models and when this was violated ($P < 0.05$) we report the corrected Greenhouse-Geisser values. For the field mineralization experiment we averaged total N mineralized ($\text{NH}_4^+ + \text{NO}_3^-$) first within site and then by treatment. We used ANOVA with total N mineralized as the dependent variable and treatment as a fixed factor.

To determine whether litter gained or lost N during the course of the long-term decomposition study we first calculated mean litter mass remaining by time period and species. Then we multiplied mean litter mass remaining by percent N as determined from the mean percent N of the subsamples (above) used in the litter quality analysis.

We used Shannon's H' to determine whether elk affected understory forb diversity. We first calculated the number of times each species appeared in the smaller 4 cm² squares. Shannon's H was calculated as $-\sum(pi \times \log pi)$; with pi as the proportion of times each species appeared out of the total number of plants counted in the quadrat. We then averaged diversity within strata and used ANOVA to test for differences by treatment with Shannon's H as the dependent variable and treatment, strata, and their interactions as predictors. We similarly tested for an effect of the elk exclusion treatment on forb species richness by using species richness as the dependent variable, and treatment, strata and their interaction as factors. We also used ANOVA to determine whether the treatment influenced the cover of nitrogen fixing forbs. To do this we first averaged cover within species, plot and strata and specified cover as the dependent variable and treatment as a fixed factor.

In all analyses, variables were log-transformed (or arcsin square-root transformed for proportions) when necessary in order to meet the assumptions of normality and homogeneity of variances. Furthermore, when interactions were non-significant they were removed from the model. When interactions were significant we conducted separate ANOVAs to determine within-group differences. All analyses were conducted using SPSS version 17 (SPSS, Chicago, Illinois, USA), except for the non-linear regressions which were conducted using SigmaPlot version 7 (Systat Software Inc, San Jose, California, USA).

Results

Elk browsing

The number of browsed deciduous recruits (which included aspen, maple, locust and oak) was approximately 10 times lower inside exclosures (treatment: $F_{1,24} = 17.98$, $P < 0.001$, strata: $F_{4,24} = 0.2$, $P = 0.94$). On average, 30.3% of deciduous stems were browsed on control drainages compared to an average of 2.4% inside exclosures (Fig. 1A). The number of browsed conifers (white fir, Douglas fir, white pine and Ponderosa pine) was also reduced in the exclosures (treatment: $F_{1,24} = 4.5$, $P = 0.044$, strata: $F_{4,24} = 0.39$, $P = 0.82$), with 2.7% of conifers exhibiting signs of browsing in control drainages compared to 0.5% inside exclosures. Deciduous trees were more highly browsed than evergreen trees in control drainages (plant type: $F_{1,24} = 18.29$, $P < 0.001$; strata: $F_{4,24} = 0.19$, $P = 0.94$; Fig. 1B).

Recruitment

Aspen ramets were much more abundant inside exclosures than in non-fenced controls and the effect of the treatment was dependent on location (strata) within the drainage (treatment*strata $F_{4,20} = 5.27$, $P = 0.005$). Specifically, aspen recruits were 13.5 times more numerous in the drainage bottoms and 9.5 times more numerous in the lower third of the drainages on exclosures compared with control drainages (bottom: $F_{1,4} = 21.09$, $P = 0.01$, lower third: $F_{1,4} = 6.77$, $P = 0.06$). However, aspen ramets did not differ between treatments in the middle, upper third, or ridge sections of the drainages (middle: $F_{1,4} = 0.48$, $P = 0.53$, upper third: $F_{1,4} = 1.43$, $P = 0.30$, ridge: $F_{1,4} = 2.24$, $P = 0.21$). Moreover, increased aspen recruits in the bottom and lower third of the drainages paralleled a higher number of adult aspens (stems > 8 cm dbh) in the lower two strata as compared to the upper three ($F_{1,9} = 4.74$, $P = 0.058$). Maple stems were 3 times more numerous in exclosures than controls with the majority of maple stems

in exclosures (91%) occurring in the bottom to middle sections of the drainage (treatment: $F_{1,24} = 7.43$, $P = 0.012$; strata: $F_{4,24} = 4.17$, $P = 0.011$). Finally, the two most abundant conifer species did not differ in abundance between treatments (white fir, treatment: $F_{1,24} = 0.004$, $P = 0.95$; strata: $F_{4,24} = 0.94$, $P = 0.46$, Ponderosa pine, treatment: $F_{1,24} = 1.05$, $P = 0.32$; strata: $F_{4,24} = 2.5$, $P = 0.07$). Two less abundant conifer species, however, showed increased abundance on exclosures: Douglas fir stems were 1.8 times more abundant (treatment: $F_{1,24} = 7.43$, $P = 0.012$; strata: $F_{4,24} = 1.2$, $P = 0.36$) and white pine stems were 2.6 times more abundant (treatment: $F_{1,24} = 5.86$, $P = 0.023$, strata: $F_{4,24} = 0.32$, $P = 0.86$) in exclosures compared to controls.

Litter quantity

The quantity of litter deposited into drainages from recruits depended on species, treatment, and year (year*treatment*species: $F_{2.1,16.5} = 10.01$, $P = 0.001$). Aspen litter was more abundant in exclosure drainages, but this effect differed by year (treatment*year: $F_{4,16} = 4.03$, $P < 0.001$). Early on, just after the experiment was initiated in 2005, aspen litter did not differ by treatment ($F_{1,4} = 0.14$, $P = 0.72$). But by 2009, aspen litter was increased by 10 times on exclosure drainages compared to controls ($F_{1,4} = 27.97$, $P = 0.006$, Fig. 2A). Maple litter was also more abundant in exclosures and this depended on year as well (treatment*year: $F_{4,16} = 7.53$, $P = 0.001$). In 2005 and 2006, maple litter did not differ by treatment (2005: $F_{1,4} = 0.16$, $P = 0.71$; 2006: $F_{1,4} = 0.69$, $P = 0.45$), but by 2007 maple litter had increased by 183% in exclosures ($F_{1,4} = 312.4$, $P < 0.001$), and by 2008 and 2009 a maple litter deposition increased 232% and 184% respectively (2008: $F_{1,4} = 9.05$, $P = 0.04$, 2009: $F_{1,4} = 4.76$, $P = 0.09$, Fig. 2B).

Decomposition rates, litter quality and mineralization

Before the decomposition experiment, the initial C/N ratio of freshly collected litter from aspen, maple, and fir differed ($F_{2,9} = 24.96$, $P < 0.001$). A Tukey test revealed no difference in

C/N ratio between aspen and white fir ($P > 0.05$), but the C/N ratio of maple was 50% higher than white fir and 35% higher than aspen ($P < 0.05$). The C/N ratio also decreased through time, but the effect depended on species (time*species: $F_{8, 36} = 2.6$, $P = 0.02$, Fig. 4A). The litter C/N ratio did not differ by species after 7 or 9 months (7: $F_{2, 9} = 1.2$, $P = 0.35$, 9: $F_{2, 9} = 2.97$, $P = 0.1$), but after a full year maple litter had a lower C/N ratio than either aspen or white fir litter ($F_{2, 9} = 11.93$, $P = 0.003$). After 20 months of decomposition, however, the C/N ratio again did not differ by species ($F_{2, 9} = 1.3$, $P = 0.32$). Also, the change in C/N ratio over time was due almost entirely to an increase in litter N content in the 3 species. Percent N increased 137% in maple ($P = 0.001$), 71% in aspen ($P < 0.001$), and 57% in fir ($P = 0.002$) compared to initial values by the end of the experiment. Initially, N content differed by species ($F_{2, 9} = 24.32$, $P < 0.001$) with maple having significantly lower N content than either aspen ($P = 0.001$) or white fir ($P < 0.001$), but by the end of the experiment N content did not differ by species ($F_{2, 9} = 0.08$, $P = 0.017$).

N release from decomposing litter differed by species during the long-term decomposition experiment (Fig. 3). After 625 days of incubation in the field, aspen litter lost 59.33% of its nitrogen (Fig. 3A). This pattern was different for maple, however, as maple litter immobilized N in the beginning and released N at the end; N content was 46% higher after 260 days, but after 625 days N content was 6.9% lower than initial values. Finally, white fir lost N initially – after 260 days N content declined by 14.7%, but after 625 days white fir was immobilizing N and N content was increased by 4.3% over starting values.

The decomposition rates of aspen, maple, and white fir differed after 7 months of incubation in the field ($F_{2, 27} = 202.34$, $P < 0.001$, Tukey tests $P < 0.001$ in all comparisons). Aspen lost the most mass with only 33.33% remaining; maple had only 50.8% remaining, while

white fir lost the least mass with 81.3% of its initial mass remaining (Fig. 4B). These differences between species remained significant through all collection periods ($F_{2, 22} = 174.64, P < 0.001$), and at the end of the experiment after nearly 21 months of decomposition aspen had only 24% of its initial mass remaining, and maple and fir had 36% and 66% respectively. The decomposition rate of maple and aspen also differed by elk exclusion treatment (treatment: $F_{1, 9} = 6.56, P = 0.03$, Fig. 5). The difference in decomposition rate constant overall amounted to roughly a 4% predicted increase in k or a 10.4% predicted increase in percent mass loss overall in the enclosures compared to the controls. When either species was examined in isolation, however, treatment was not significant (Maple: $F_{1, 4} = 4.54, P = 0.1$, Fig. 5A; Aspen: $F_{1, 4} = 1.96, P = 0.23$, Fig. 5B). Finally, net N mineralization in the soil beneath the litter bags (ammonium and nitrate) was not influenced by litter treatment (ammonium: $F_{4, 73} = 1.34, P = 0.26$, nitrate: $F_{4, 73} = 0.23, P = 0.92$).

Forbs and shrubs: richness, diversity, and cover

Elk exclusion had no significant effects on either forb richness or diversity (richness: $F_{1, 24} = 1.22, P = 0.28$, Fig. 5A, diversity: $F_{1, 24} = 1.49, P = 0.24$, Fig. 6B). As well, the total cumulative cover of grasses and forbs was not influenced by the elk exclusion, although plant cover was marginally higher on enclosure drainages (treatment: $F_{1, 24} = 3.02, P = 0.095$, strata: $F_{4, 24} = 2.29, P = 0.09$) with higher plant cover in the lower third of the drainages ($F_{1, 4} = 7, P = 0.057$). Shrub species richness and diversity were not significantly different by treatment (richness: $F_{1, 24} = 0.83, P = 0.37$; diversity $F_{1, 24} = 0.66, P = 0.43$), and total cover of all shrubs did not differ by treatment ($F_{1, 24} = 0.04, P = 0.84$). However, two shrubs were only found outside the enclosures, curl-leaf mahogany (*Cercocarpus ledifolius*), and Rocky mountain blueberry (*Vaccinium oreophilum*).

Nitrogen fixers

Nitrogen fixers which included Arizona pea (*Lathyrus leucanthus*), American Vetch (*Vicia americana*), Hill's Lupine (*Lupinus hillii*), Pine Thermopsis (*Thermopsis pinetorum*), Wood's Clover (*Trifolium pinetorum*), and Wright's Deervetch (*Lotus wrightii*) as a group were more abundant in exclosures than non-fenced control drainages ($F_{1,24} = 9.13$, $P = 0.006$, Fig. 7). In addition, New Mexico locust stems (recruits and ramets < 8 cm dbh) were 2.4 times greater in exclosures than in non-fenced controls (treatment: $F_{1,24} = 6.53$, $P = 0.017$, strata: $F_{4,24} = 1.75$, $P = 0.17$), and this was not dependent on strata (Treatment*Strata: $F_{4,20} = 0.40$, $P = 0.80$).

Discussion

The effects of Rocky Mountain elk in the mountains of northern Arizona most closely fit the criteria of having a decelerating effect on N cycling according to the model proposed by Wardle et al. (2004). Elk preferred to browse high quality deciduous species over lower quality evergreen species (Fig. 1B), and we found rapid recruitment and increased litter deposition of both aspen and maple inside the exclosures (Fig. 2A, B) but no change in the recruitment of white fir, the dominant conifer. As well, aspen and maple decomposed more rapidly than white fir, and aspen litter released a significant proportion of its initial N during decomposition (Fig. 3A) while the N content did not change predictably for maple or white fir (Fig. 3B, C). Therefore, short-term changes in aspen recruitment and subsequent litter deposition have the potential to influence N dynamics in this system. The strong effects of elk on aspen are not surprising as aspen is an important food source for large herbivores (Kay 1990, Romme et al. 1995, Kay 1997), and elk browsing in other parts of northern Arizona can eliminate 60 to 90% of aspen recruits (Bailey and Whitham 2002, Bailey et al. 2007).

However, we found no detectable effect of litter identity or a mixture on net N mineralization despite widely differing quality of the three litter types. There are a number of reasons why we may not have detected changes in soil net N mineralization in our litter-mineralization experiment. First, litter decomposition often occurs over long time periods (years to decades, Parton et al. 2007), and our litter-mineralization experiment was short in duration (~ 7 months) and thus only a small proportion of the deployed litter decomposed. Also, differences in plant quality may be slow to influence the release of nitrogen because of a bottleneck where nutrients are immobilized by microbes (Knops et al. 2002). We found that while aspen litter lost on average 76% of its mass and released 60% of its N over the course of the long-term decomposition experiment, both maple and white fir N content did not change in any predictable way despite 64% mass loss in maple, and 34% mass loss in white fir. This strong immobilization of nutrients within the decomposing litter could explain the lack of an effect on net N mineralization in soil underneath maple and white fir litter.

Importantly, we found that aspen and maple litter decomposed more rapidly on exclosure drainages as compared to non-fenced control drainages during the course of the long-term decomposition experiment (Fig. 5A, B). Litter decomposition rates can be influenced by physical properties including soil moisture and temperature, soil N content, and differences in soil micro and macro-fauna (Hobbie 1996, Chapin et al. 2002, Fierer et al. 2005, Davidson and Janssens 2006). Deciduous litter can increase soil moisture content and can have a moderating effect on soil temperature fluctuations (Facelli and Pickett 1991), and we found increasing deposition of deciduous litter on exclosure drainages. Therefore it is possible that the higher decomposition rates we observed in the exclosures could be due to higher soil moisture availability or changes in soil temperature.

It is equally possible that elk are influencing N cycling through other pathways at this site. Ungulates deposit urine and feces, and a considerable amount of N can be volatilized or lost during leaching from these deposits (Mossier et al. 1992, Frank and Zhang, 1997). In addition, ungulates can move N (e.g. scat or urine) from one location to another through daily or seasonal movement patterns, and elk in this area often move to lower elevations during accumulation of winter snowfall (Sweeney and Steinhoff 1976, Kauffman et al. 2010). Finally, herbaceous vegetation can play a significant role in N dynamics because of relatively higher nutrient content and faster turnover rates than woody vegetation (Gilliam 2007, Nilsson and Wardle 2005). We found that the height of understory forbs and grasses was significantly reduced outside the fences as compared to inside (E. Parsons, *unpublished results*), indicating that elk likely reduced the biomass of understory herbaceous vegetation and grasses. All three of these factors, 1) increased N loss from ungulate scat and urine and trampling, 2) net transport of N by ungulates and 3) reduced understory forb and grass NPP could have led to different soil N and a different decomposition environment inside the exclosures.

Finally, we found that exclusion of elk led to a large increase in the abundances of two N-fixing leguminous forbs and a leguminous tree. The tree, New Mexico locust, also experiences high levels of herbivory at our site and has relatively high tissue N content compared to aspen and maple (2 times the mean amount of N compared to maple and 1.5 times that of aspen). Because these three species fix nitrogen, their increase inside of the exclosures suggests an additional nitrogen input into the system that may influence N cycling. A growing number of studies show that plants with high tissue N concentrations are preferred by herbivores and these plants increase in size or abundance when herbivores are excluded (Mattson 1980, Ritchie and Tilman 1995, Ritchie et al. 1998, Knops et al. 2000, Sirotiak and Huntly 2000). Therefore, the

strong negative effects of large herbivores on N fixing plants may be a common mechanism by which large herbivores decelerate N cycles in N-limited ecosystems (Mattson 1980, Vitousek and Howarth 1991).

Overall, this work demonstrates that Rocky Mountain elk can cause rapid shifts in the functional composition of vegetation, and also large shifts in the quantity and quality of litter inputs into soil (Bardgett and Wardle 2003, Bailey et al. 2007). Because we found a rapid increase in both high quality deciduous litter and in the cover of N-fixers as well as increased decomposition rates of maple and aspen on exclosure drainages, our results most closely match the deceleration model of herbivore effects on ecosystems.

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Figure Legends

Figure 1: Mean percent (\pm SEM) of A) deciduous stems (aspen, maple, locust and oak) showing evidence of ungulate browsing on exclosure and control drainages, and B) deciduous versus evergreen stems showing signs of ungulate browsing on control drainages, 2009.

Figure 2: Estimated mean (\pm SEM) number of senesced leaves of A) aspen recruits and B) maple recruits deposited as litter in 5 m radius subplots on exclosure and control drainages, 2005-2009.

Figure 3: Nitrogen release of aspen (A), maple (B), and white fir (C) litter during long-term decomposition. Number of days of decomposition, x-axis; total N released from litter (mg/g), y-axis.

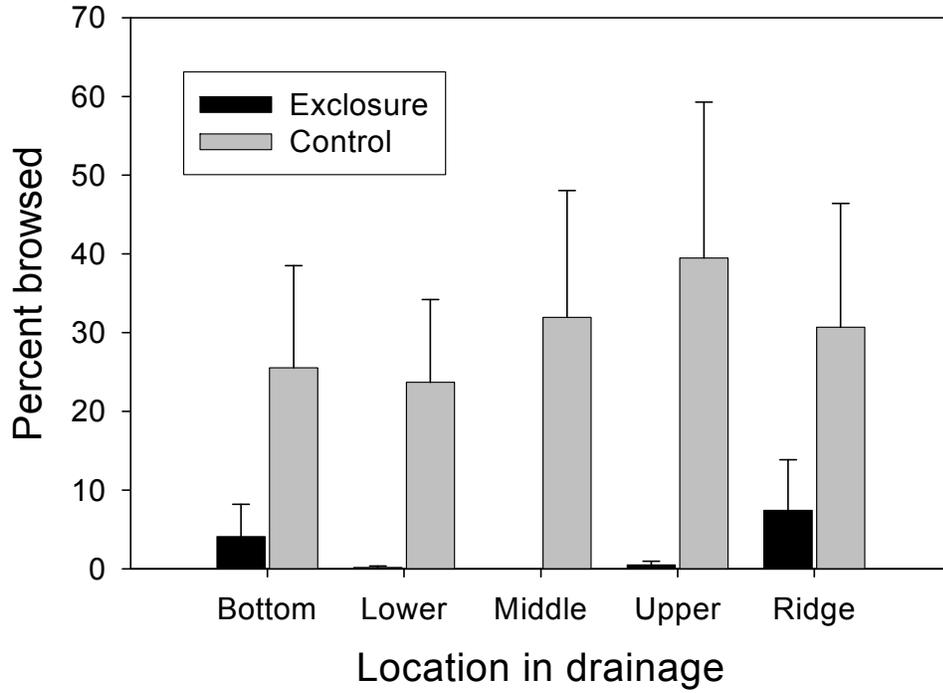
Figure 4: A) Mean (\pm SEM) C/N ratio of aspen, maple, and white fir litter during five sampling periods (2008-2009) and B) Mean (\pm SEM) decomposition rate constant (k) of aspen, maple, and white fir during the same five sampling periods.

Figure 5: Mean (\pm SE) paired differences (exclosure – control) decomposition rate constant (k) in A) aspen, and B) maple, decomposed in both exclosure (fenced) and control (non-fenced) drainages across five sampling periods (2008-2009). X axis categories are number of days of incubation in the field.

Figure 6: Mean (\pm SEM) A) forb species richness and B) diversity (Shannon's H) on exclosure versus control drainages by location (strata) in drainage, 2009.

Figure 7: Mean (\pm SEM) cover of nitrogen fixing forbs in exclosure versus control drainages.

Figure 1
A



B

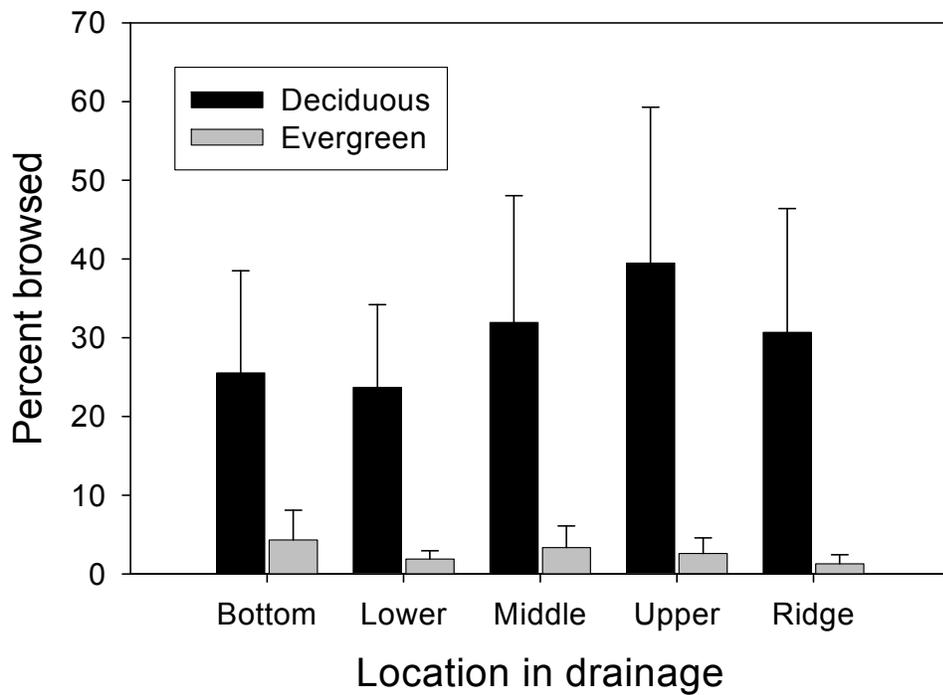
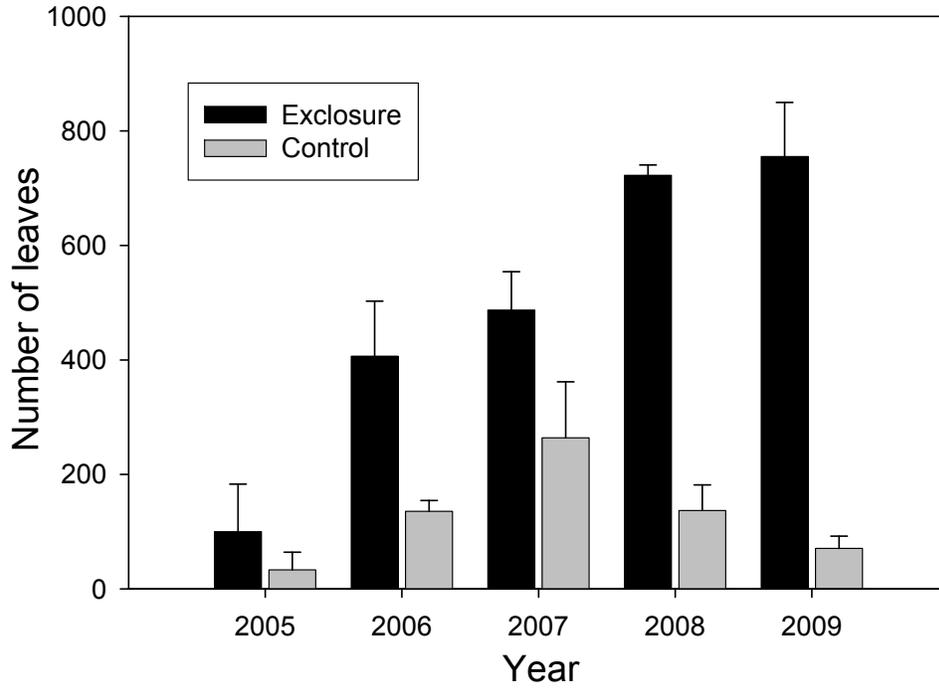


Figure 2
A



B

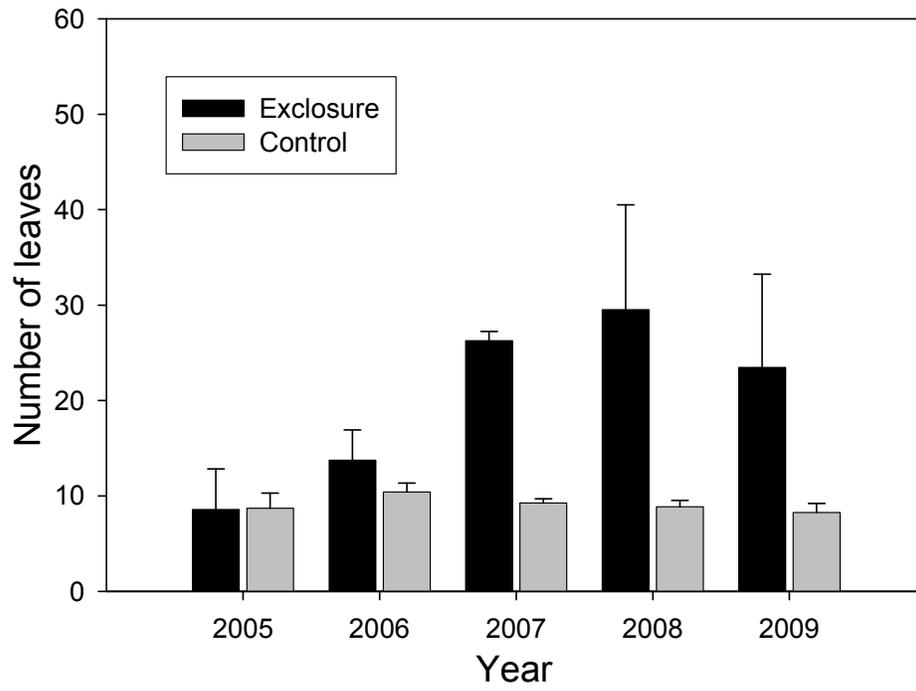


Figure 3

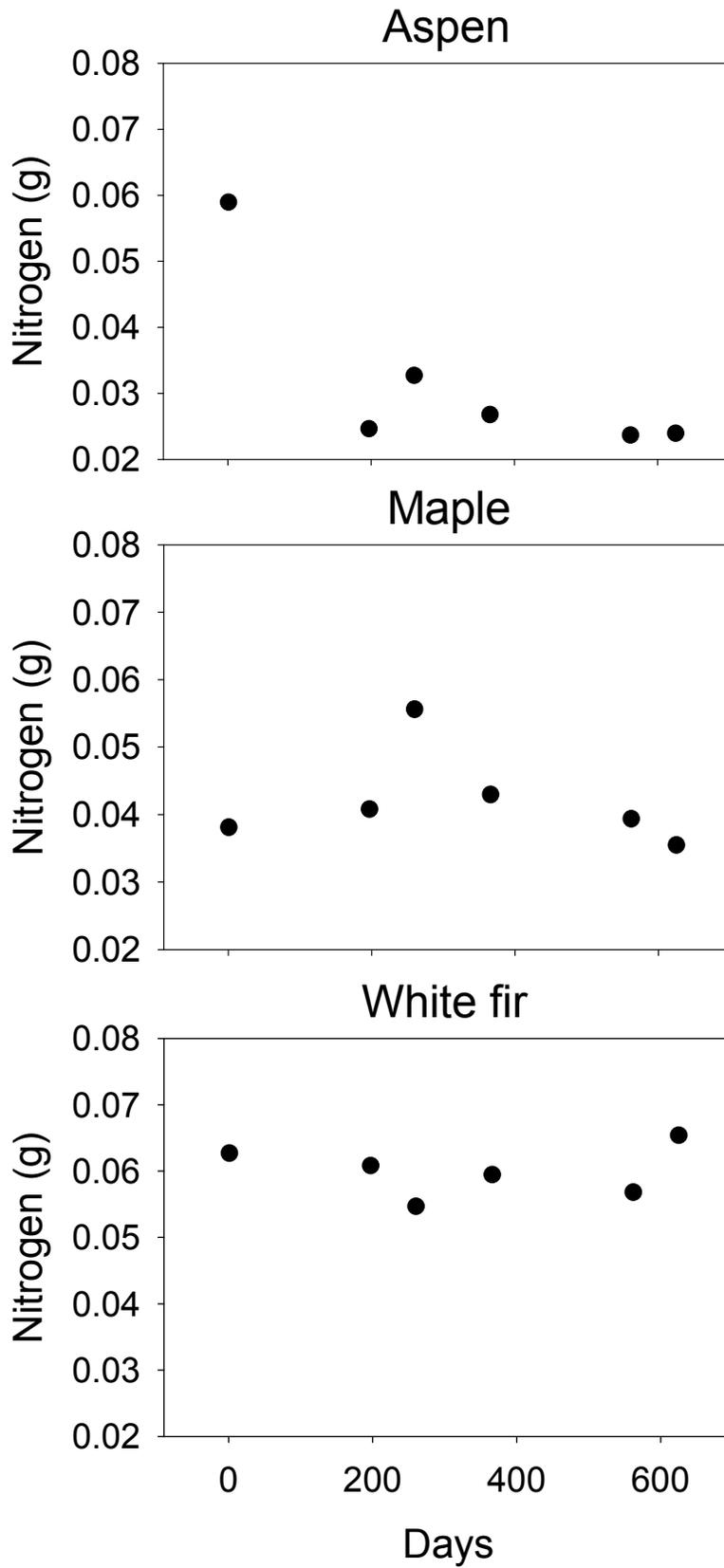
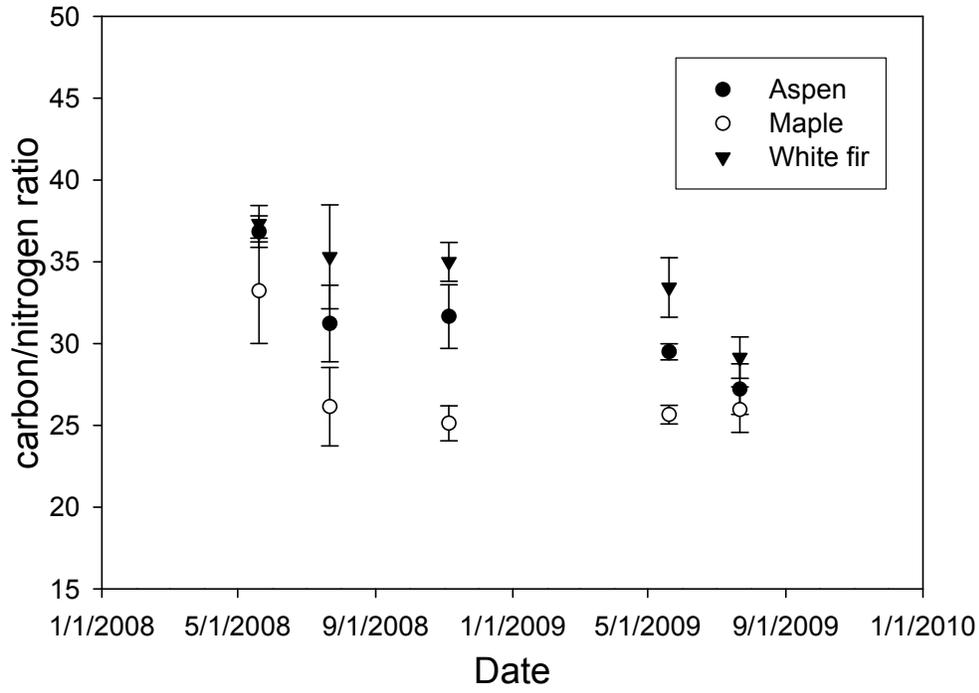


Figure 4
A



B

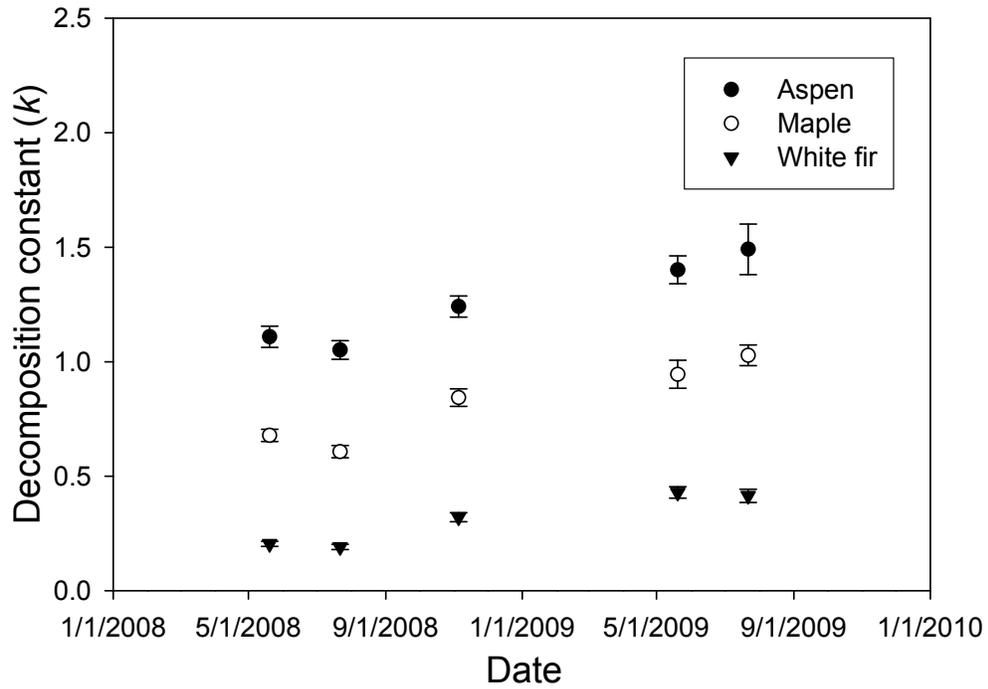
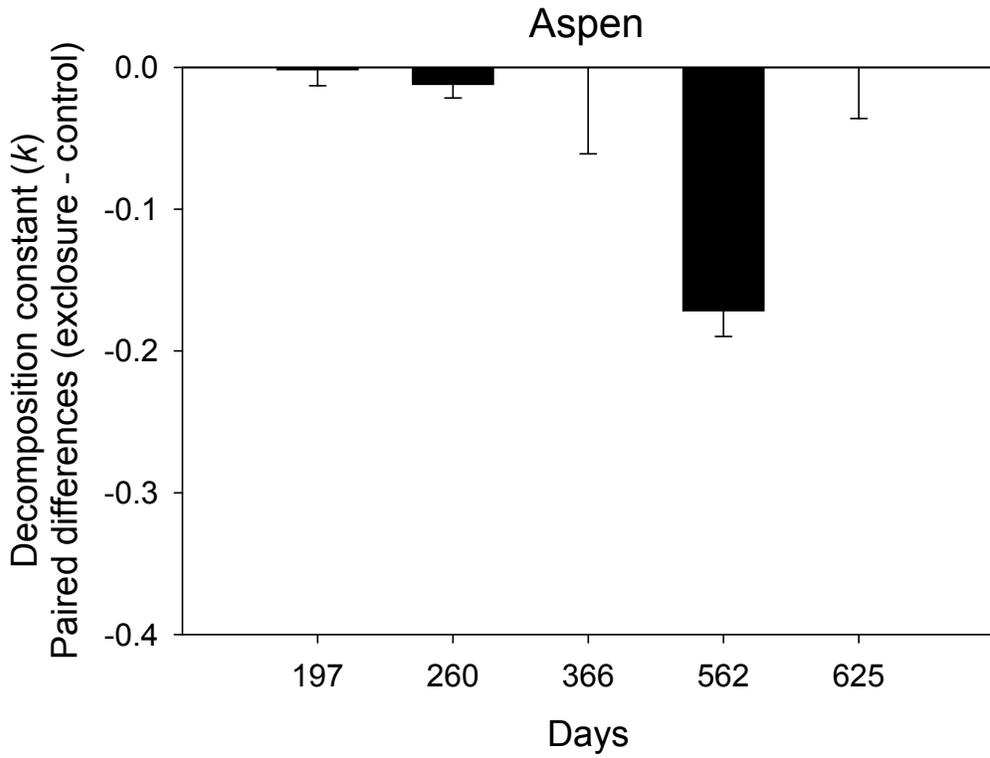


Figure 5
A



B

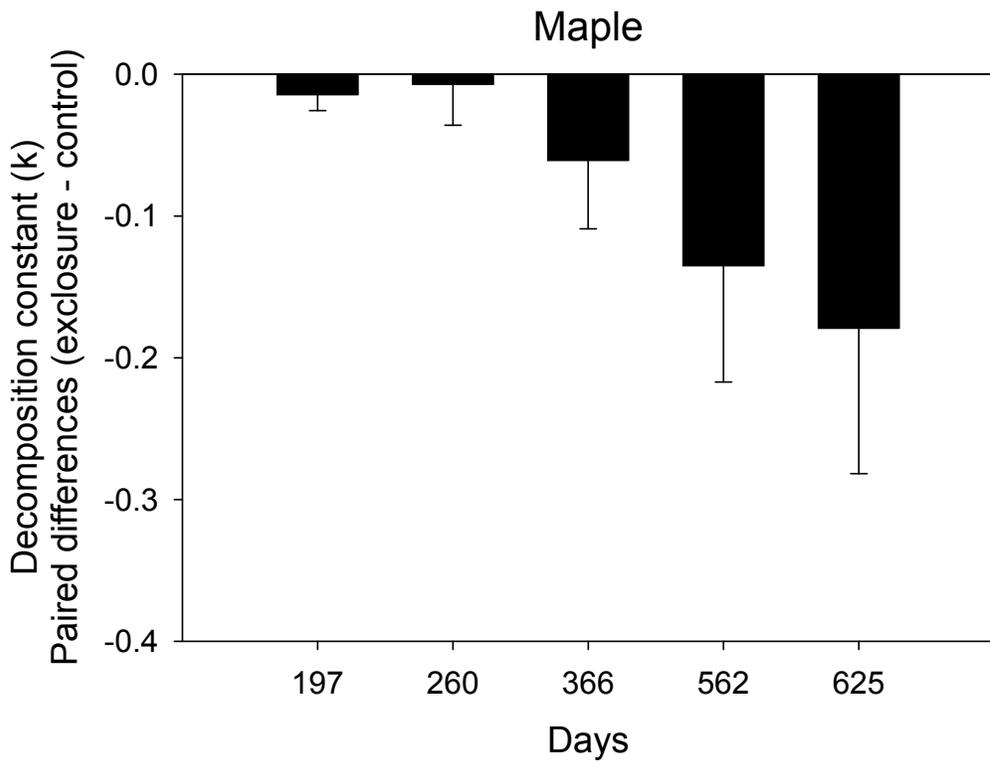
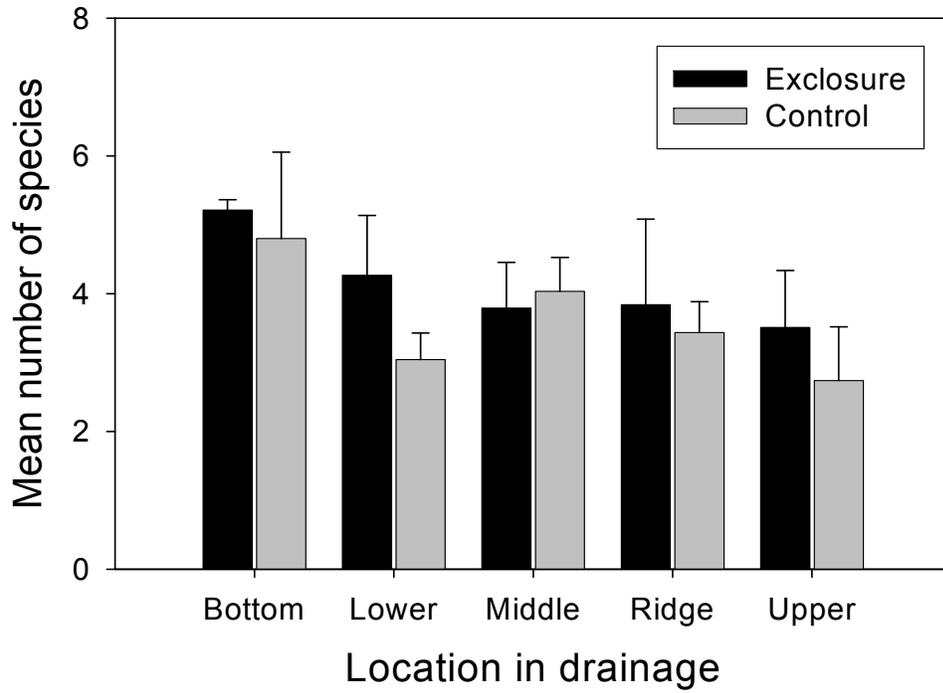


Figure 6

A



B

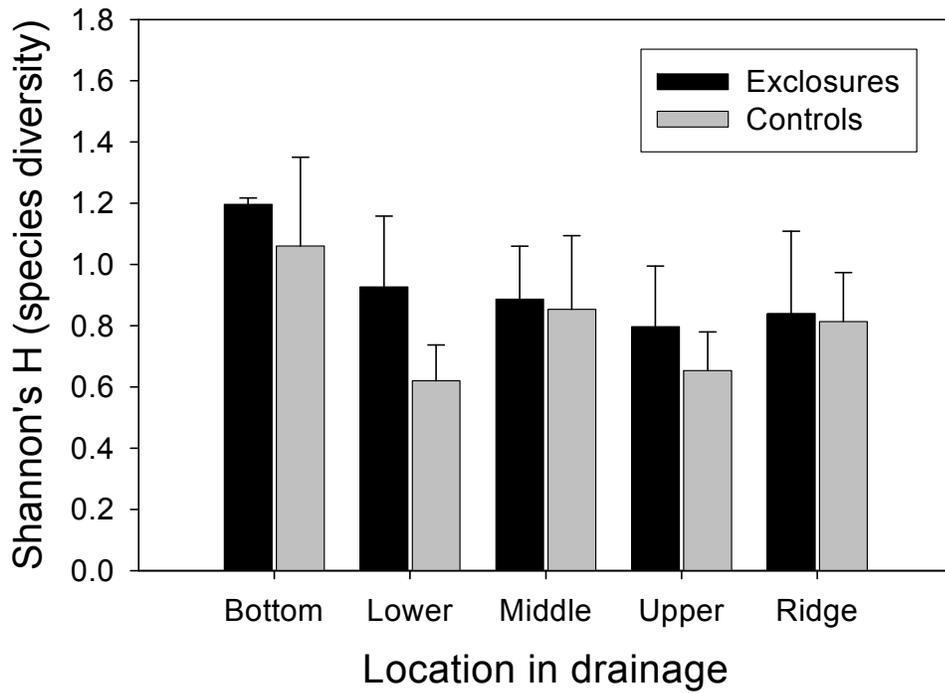


Figure 7

