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# Introduced ungulate herbivore alters soil processes after fire

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**Abstract** Ungulate herbivory can have profound effects on ecosystem processes by altering organic inputs of leaves and roots as well as changing soil physical and chemical properties. These effects may be especially important when the herbivore is an introduced species. Utilizing large mammal exclosures to prevent access by introduced elk at multiple sites along a fire chronosequence, we examined the effects of elk herbivory and fire on soil microbial activity and nutrient availability. Using time since fire as a co-variate and herbivore exclosures, paired with areas outside of the exclosures, we hypothesized that reductions in plant biomass due to herbivory would reduce organic inputs to soils and impact soil microbial activities and nutrient storage. We found three major patterns: (1) when elk were excluded, surface

mineral soils had higher soil organic carbon (C), total nitrogen (N), microbial N pools, and increased extracellular enzyme activity of a C-acquiring enzyme across a gradient of time since fire. (2) When introduced elk are present, the activity of some extracellular enzymes as well as  $\text{NO}_3^-$  availability are enhanced in the soil but the post-fire patterns described above with respect to nutrient accrual over time are delayed. (3) Herbivory by an introduced ungulate upsets the trajectory of ecosystem “recovery” after wildfire and delays soil C and N dynamics by an estimated 14.5–21 years, respectively. These results suggest that introduced, browsing herbivores significantly decelerate ecosystem processes but herbivory by exotics may also result in unpredictability in specific soil responses.

**Keywords** Aspen · Decelerated nutrient cycles · Elk · Fire · Introduced herbivores · *Populus*

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## Introduction

Ungulate herbivores can alter ecosystems by changing both abiotic and biotic factors that regulate nutrient cycles. Abiotic factors such as soil water availability, pH, temperature, aeration and bulk density as well as soil chemistry can be directly or indirectly altered by ungulates via the mechanisms of trampling, inputs of urine or feces or shifts in the plant community (Pastor et al. 1993; Pastor and Cohen 1997; Ritchie et al. 1998;

Stark et al. 2002; Pastor and Danell 2003; Côte et al. 2004; Sankaran and Augustine 2004; Harrison and Bardgett 2008). Moreover, changes to biotic components such as rates of herbivory can result in compensatory growth by browsed plants (Augustine and McNaughton 1998; Frank et al. 2002) and altered C allocation patterns affecting above- and below-ground growth as well as root exudation patterns (Bardgett et al. 1998; Bardgett and Wardle 2003; Hamilton et al. 2008). For example, changes in the composition and abundance of plant communities due to selective herbivory of high nutrient-containing plant species increases the abundance of species with low nutrient content and alters the quantity and quality of organic inputs to the soil, which can affect nutrient cycles (Pastor et al. 1993; Ritchie et al. 1998; Harrison and Bardgett 2004). The effects of ungulate herbivores can be positive, neutral or negative across habitat types, grazing/browsing pressures and landscape scale (Pastor et al. 1993; Frank and Groffman 1998; Ritchie et al. 1998; Augustine and Frank 2001; Singer and Schoenecker 2003; Binkley et al. 2003; Schoenecker et al. 2004; Harrison and Bardgett 2004, 2008). For example, the effects of grazers in grassland ecosystems can result in very different patterns of productivity and nutrient cycling than browsing by herbivores in forested ecosystems. Ungulate herbivory in grasslands has been shown to commonly stimulate soil microbial communities and enhance rates of nutrient cycling, while browsing in forests often results in negative impacts on the microbial community and rates of nutrient cycling (see review in Harrison and Bardgett 2008).

When ungulate herbivores are introduced to an ecosystem, the effects can be strong, although highly idiosyncratic, with browsing significantly altering plant density and community composition (Smale et al. 1995; Veblen et al. 1989; Relva and Veblen 1998; Vázquez 2002; Husheer et al. 2003; Potvin et al. 2003; Relva et al. this issue; Martin et al. this issue, Wallem et al. this issue) as well as the composition and abundance of animal associated communities (Wardle et al. 2001; Allombert et al. 2005a, b). The role of introduced wild ungulates on ecosystem processes, such as nutrient cycles, is poorly understood but the dramatic shifts recorded in plant communities suggest that their effects may be large. Wardle et al. (2001) found that introduced red deer (*Cervus elaphus scoticus*) across 30 sites in New Zealand have

significant effects on the diversity and abundance of native plant communities as well as associated litter-dwelling, meso- and macrofauna communities in soil. However, introduced red deer had idiosyncratic effects on soil C storage or N dynamics (Wardle et al. 2001). In aquatic ecosystems, herbivory by introduced Nutria (grazing herbivore; *Myocastor coypus*) in wetlands reduces plant biomass (above- and belowground) and soil elevation, which can contribute to marsh loss (Ford and Grace 1998). Similarly, the introduction of beaver (*Castor canadensis*) in Chile has resulted in great shifts in riparian plant communities (Wallem et al. this issue), reduces macroinvertebrate richness and diversity by 50% but results in a 3–5-fold increase in secondary production in streams relative to areas that have not been impacted by beaver (Anderson and Rosemond 2007). Such results suggest that much more study and experimentation is required across species and ecosystems to determine both the extent and mechanisms of the effects of introduced herbivores on ecosystem processes as well as how introduced herbivores interact with other disturbance regimes (sensu Relva et al. 2008).

Aspen ecosystems in northern Arizona provide a good model system in which to study the effects of an introduced herbivore (Rocky Mountain elk; *Cervus elaphus*) on soil processes after disturbance, such as fire (DeByle and Winokur 1985; Romme et al. 1995). Aspen (*Populus tremuloides* Michx.) is a resilient tree species that can survive fire, by re-sprouting from roots, and recolonize after wildfires, which contributes to the long-term persistence of aspen across landscapes (Mitton and Grant 1996). Vigorously growing clonal re-sprouts (i.e., ramets) are a common and important food resource for mammalian herbivores such as elk (Kilpatrick et al. 2003), and in northern Arizona up to 90% of these ramets can be eliminated by elk in the first year of growth (Bailey and Whitham 2002). While the interacting effects of fire and elk on associated communities and even ecosystem processes have been well described in the native range of elk (Singer and Hartner 1996; Augustine and McNaughton 1998), little is appreciated on the effects of both fire and herbivory on soil processes in areas where elk have been introduced.

In 1913 Rocky Mountain elk were introduced to northern Arizona. Since then, elk populations have been managed for large herds for hunting and have reached population densities as high as 35,000

individuals ([www.azgfd.gov](http://www.azgfd.gov), Hoffmeister 1986; Rolf 2001; Hoffmeister 1986), At these densities elk are acting as an important agent of selection that is contributing to the decline of several native plant species (Maschinski 2001), including aspen (Rolf 2001; Bailey et al. 2007). In an effort to remedy the compounding negative effects of elk grazing at high densities and catastrophic fire following historical fire suppression, over 45 ha of elk exclosures were established by the U.S. Forest Service (Rolf 2001) following major fires to allow aspen forests as well as understory plant communities to re-establish (Rambo and Faeth 1999; Kay and Bartos 2000; Rolf 2001). Utilizing elk exclosures across six sites along an 18 year old fire chronosequence, we tested the hypothesis that herbivory by introduced elk reduces the activity of soil microorganisms and soil nutrient pools, due to altered inputs of plant biomass.

## Materials and methods

### Study sites

Quaking aspen (*Populus tremuloides* Michx.) is able to grow at a wide range of elevations throughout North America, making it the most extensively distributed deciduous tree species in the United States, as well as a foundation species with large ecological impacts (DeByle and Winokur 1985; Ellison et al. 2005). We utilized a series of regenerating aspen stands, that varied in time since wildfire and in exposure to an introduced herbivore (with elk exclosures), to experimentally test the independent and combined importance of these two ecological factors on multiple soil properties and processes. Rocky Mountain elk are a large species of elk that were introduced in 1913 to the San Francisco Peaks (Hoffmeister 1986; Rolf 2001). While there was a native species of elk in Arizona (Merriam's elk; *Cervus elaphus merriami*), it was a dwarf species whose range was restricted to the White Mountains of eastern Arizona and western New Mexico. Population sizes of this native elk species were thought to be small (although densities are unknown) and this elk species has been extinct since the late nineteenth century (Hoffmeister 1986). The introduction of Rocky Mountain elk therefore represents a significant disturbance to aspen ecosystems in northern Arizona

as there was no large herbivore in these forests until ~100 years ago.

We used six study sites located on the north side of the San Francisco Peaks mountain range in the Coconino and Kaibab National Forests, near Flagstaff, AZ, USA, that were all burned by naturally occurring, lightning-initiated wildfires from 1986–2004. These high severity crown fires created large gaps in the otherwise closed canopy mixed-conifer (i.e., *Pinus ponderosa*) forest, allowing for the rapid regeneration of aspen trees. After each individual fire occurred, the U.S. Forest Service erected 2 m high elk exclosures, ranging in size from 0.8 to 9.9 ha, to allow regeneration of aspen in the absence of elk (Rolf 2001). An elk exclosure at each site allowed us to examine the effects of herbivory along a fire chronosequence by comparing soil properties from paired samples inside (in the absence of elk) and outside the exclosure (with elk herbivory) across a natural experiment (i.e., an 18 year fire chronosequence). Specific information for each site is shown in Table 1.

The soils at all six sites were derived from basalt and andesite parent materials and are relatively coarse-textured (Table 1). All sites are dominated by *Populus tremuloides*, with a patchy understory of grasses (including *Poa compressa*, *Bromus catharticus*, *B. tectorum*) and herbs (including *Senecio spartioides*, *Penstemon barbatus*, *Artemisia ludoviciana*), and much exposed bare soil. High densities of elk outside of all of the exclosures have resulted in >90% reduction in aspen populations (Bailey and Whitham 2002), leaving small, heavily browsed clumps of shrubby aspen (<0.25 m tall) interspersed with many of the same species of grasses and herbs (Fig. 1).

### Soil analyses

We collected mineral soil samples (0–15 cm depth) in July 2005 for microbial and soil nutrient analyses. In order to control for differences in the spatial extent of the experiment (i.e., there is more habitat and thus more environmental heterogeneity outside of the exclosure than inside of the exclosure), the locations of soil cores taken at each site were from one randomly selected side of each fenced exclosure and included five replicates within the exclosure, matched with five replicates outside of each elk exclosure. No sampling (either inside or outside of the fence) was

**Table 1** Site characteristics of aspen-dominated forests in Northern Arizona, USA

Site	Date of fire	Latitude/longitude	Elevation (m)	Avg. precip <sup>a</sup> (cm)	Soil type <sup>a</sup>	Sand/silt/clay (%)
Hochderfer B	1987	23°17.92'N 45°57.15'W	2439	60–68	Udic Argiboroll	58/37/5
Hochderfer C	1989	23°14.31'N 46°57.15'W	2448	50–60	Typic Argiboroll	54/39/7
760	1997	23°19.98'N 46°41.13'W	2443	50–60	Typic Argiboroll	40/49/11
Pumpkin	2001	23°49.69'N 52°10.45'W	2521	50–60	Mollic Eutoboralfs	58/32/10
151A	2003	18°39.28'N 45°04.27'W	2469	50–60	Lithic Eutoboralf	49/37.5/8.5
151B	2003	18°39.28'N 45°04.27'W	2469	50–60	Lithic Eutoboralf	52/40/8

<sup>a</sup> Data collected from the U.S. Forest Service Terrestrial Ecosystem Survey of Coconino and Kaibab National Forests

**Fig. 1** Photographs illustrating the effects of introduced elk on aspen (*Populus tremuloides*) establishment in northern Arizona. The regenerating aspen are enclosed behind a fence protecting them from herbivory (Photos by Thomas C. Whitham)



conducted within 2 m of the fence to avoid edge effects. Soils were collected using an Oak-Field soil sampler (2 cm in diameter). Soils were transported to the laboratory in a cooler, stored at 4°C until processed (less than 24 h) and sieved to 2 mm before any analyses. We quantified soil texture, pH, organic C and total N from soils within each treatment at all sites. Soil texture was determined using the hydrometer method on fresh soils; all samples were homogenized and pooled per treatment and per site (Gee and Baker 1986). The pH of each soil was determined from pooled (as in the soil texture analysis), air-dried soils in 0.01 M CaCl<sub>2</sub> with a pH meter (Hendershot et al. 1993; Orion 720A series, Thermo Fisher Scientific, Inc., Waltham, MA, USA). We quantified soil organic C and total N of air-dried soil after the samples were ground with a pestle and mortar to a fine powder; the samples were run on a Thermo-Finnigan Delta<sup>plus</sup> Advantage gas isotope-ratio mass spectrometer interfaced with a Costech Analytical ECS4010 elemental analyzer (Thermo Fisher Scientific, Inc. Waltham, MA, USA).

To determine microbial biomass N pools a ~25 g field-moist sub-sample from each soil sample was extracted with 50 ml 0.5 M K<sub>2</sub>SO<sub>4</sub>, shaken for 1 h on a mechanical shaker, gravity-filtered with Whatman filter paper no. 1 (filter paper leached with deionized water and K<sub>2</sub>SO<sub>4</sub>), and stored in a freezer until analyzed chemically. Another ~25 g field moist, sieved sub-sample was exposed to chloroform for 5 days in a glass vacuum desiccator with 30 ml ethanol-free chloroform (Haubensak et al. 2002). After the fumigation period, the samples were extracted with 50 ml of 0.5 M K<sub>2</sub>SO<sub>4</sub> in the same manner as above. Microbial biomass N (expressed as N in fumigated soil extract–un-fumigated soil extract) was determined on the thawed extracts with a micro-Kjeldahl digestion followed by colorimetric analysis on a Lachat AE-auto analyzer using the salicylate method (Lachat Industries, Inc., Loveland, CO, USA). A sub-sample of field moist soil was oven dried (48 h at 105°C) to determine the soil gravimetric water content. All microbial biomass N values are expressed on an oven-dry mass basis.

We quantified potential soil microbial extracellular enzyme activity from each soil (*sensu* Saiya-Cork et al. 2002; Waldrop et al. 2004). Immediately after sieving, the activity of five enzymes were assessed for all soil samples (1.0 g of soil in 50 mmol/L sodium acetate buffer:  $\alpha$ -1,4-glucosidase (EC 3.2.1.20),  $\beta$ -1,4-glucosidase (EC .2.1.21), phenol oxidase (EC 1.10.3.2), peroxidase (EC 1.11.1.7), acid phosphatase (EC 3.1.3.2). Both  $\alpha$ -glucosidase and  $\beta$ -glucosidase are C acquiring enzymes that degrade starches, phosphatase is a phosphorus (P) acquiring enzyme, while phenol oxidase and peroxidase are enzymes that degrade lignin and polyphenolic compounds in soil (Tabatabai and Dick 2002; Hendel et al. 2005). We analyzed eight analytical replicates per sample. The incubation times for each enzyme were as follows: acid phosphatase 0.5 h,  $\beta$ -glucosidase and  $\alpha$ -glucosidase 2 h, phenol oxidase and peroxidase 24 h. The substrate Methylumbelliferyl (MUB) was used for fluorometric analysis of  $\alpha$ -glucosidase,  $\beta$ -glucosidase, and acid phosphatase (SpectraMax Gemini EM fluorimeter, Molecular Devices Corp., Sunnyvale CA). Colorimetric analysis and the substrate L-3, 4-dihydroxyphenylalanine (L-DOPA) was used to quantify phenol oxidase and peroxidase in duplicate plates with and without the addition of 0.3%  $\text{H}_2\text{O}_2$  (SpectraMax Plus<sup>384</sup> spectrophotometer, Molecular Devices Corp., Sunnyvale, CA, USA). Phenol oxidase activity was indicated by L-DOPA metabolism without  $\text{H}_2\text{O}_2$ , and peroxidase activity was measured as the difference between L-DOPA metabolism with and without  $\text{H}_2\text{O}_2$ .

We used the ion exchange resin (IER) bag method (Hart and Firestone 1989) to assess the availability of inorganic N across the treatments. We buried eight ion-exchange resin bags, inside and outside of each enclosure at each site (paired across enclosures, as above). Approximately 25 g of mixed-bed ion-exchange resin (J.T. Baker, Phillipsburg, NJ, USA; Hart et al. 1994) was placed into nylon stocking bags and buried at a depth of 15 cm, installed at an angle to minimize soil disturbance on top of each bag. The resin bags were incubated *in situ* for 3 months. After incubation, the resin bags were collected into individual paper-sacks, air-dried and then extracted with 100 ml 2 M KCl. The filtered extracts were then frozen until analysis of ammonium and nitrate on a Lachat AE flow-injection auto-analyzer (Hart et al. 1994; Lachat Industries, Inc., Loveland, CO, USA). A subsample of air-dried, un-incubated resin was

oven dried (70°C for 48 h) to allow the final data to be expressed on an oven-dry mass basis.

### Statistical analyses

We assessed variation in soil texture and pH across herbivore treatment only (inside or outside of the enclosure) on the pooled samples (pooled across sites) using analysis of variance (ANOVA). We used analysis of co-variance (ANCOVA) to assess the effects of herbivore treatment (i.e., inside or outside of the enclosure) on soil organic C, total N, soil microbial N, potential microbial enzyme activity, and soil nitrogen availability, using the fire chronosequence (i.e., time [year] since fire) as the co-variate. Using linear regression models we examined the length of time that would potentially take for the same amount of soil organic C and total N to accumulate outside of the enclosure as was inside the enclosures after 18 years. This comparison was only made for organic C and total N as these are more stable nutrient pools than microbial biomass pools, potential enzyme activity or N availability with resins. Data for all response variables were square-root transformed to meet assumptions of normality when necessary. All statistical analyses were performed using JMP IN 5.1 (SAS Institute Cary, NC, USA).

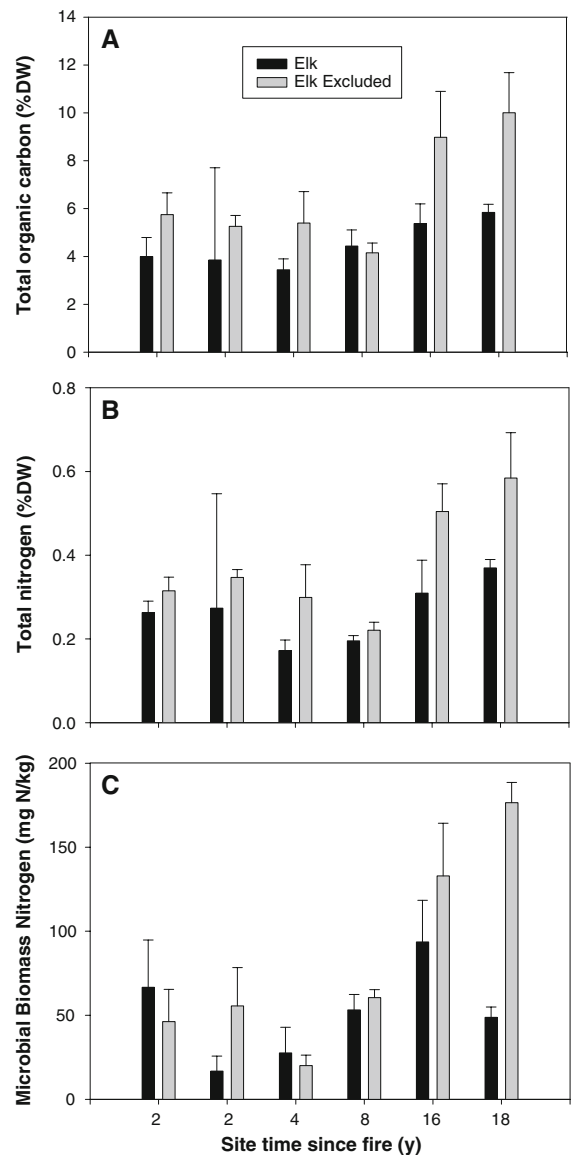
### Results

Overall, we found that herbivory by introduced elk (across sites) had no effect on soil texture (percent sand;  $F_{(1,10)} = 1.05$ ,  $P = 0.33$ ) and soil pH ( $F_{(1,10)} = 2.59$ ,  $P = 0.14$ ). However, elk herbivory had significant effects on both microbial activities and nutrient dynamics in soils and this effect often varied across time since fire. Herbivory by elk and the covariate (time since fire) both had significant impacts on soil organic C, total N, but there were no interactions between these factors (Fig. 2; Table 2). These results indicate that the co-variate (time since fire) accounts for some of the variation in soil C and N but there is still residual variation attributable to herbivory. Twenty percent of the variance in soil organic C and 17% of the variance in soil total N is related to the time since the site was burned. Across all sites, herbivory by elk reduces both soil organic C

and total N by 28 and 32%, respectively. With the linear regression models outside of the exclosures, we found that it would take an additional 14.5 and 21 years to accumulate the same concentration of organic C and total N, respectively, when elk are absent ( $C = 3.25 + 0.176[\text{time since fire}]$ ,  $N = 0.204 + 0.008[\text{time since fire}]$ ). Herbivory by elk also tends to alter the trajectory of microbial N pools over time. We found significant covariate (time since fire) and herbivore treatment effects on microbial N pools, but no significant interaction of time since fire and elk herbivory (Fig. 2; Table 2). Over the 18 year fire chronosequence, elk tended to reduce microbial N pools over time.

Time since fire and elk herbivory both altered extra-cellular soil enzyme activity (Fig. 3; Table 2). Only the C acquiring enzymes (i.e.,  $\alpha$ - and  $\beta$ -glucosidase) demonstrated significant herbivore treatment effects (with no significant effects of the co-variate or interactions between herbivory and time since fire), however the direction of the response between these soil enzymes was variable. Potential  $\alpha$ -glucosidase activity was significantly (43%) higher outside of the exclosures, while  $\beta$ -glucosidase activities were 37% higher in the absence of elk herbivory. In contrast, with potential phosphatase activity, much of the variation in activity was explained by the co-variate (time since fire), but this response significantly interacts with herbivory (i.e., a significant time since fire and herbivory interaction). The lignin and polyphenol degrading enzymes were highly variable, with phenol-oxidase demonstrating no differences in potential activity across the fire chronosequence or with herbivory. Potential peroxidase activity demonstrated significant interactive effects only, indicating that there were no general treatment effects, as the response was dependent upon the co-variate of time since fire.

We found that mineralized N was related to the effects of fire and herbivory, however, fire and herbivory affected inorganic N pools differently (Fig. 4; Table 2). There were no effects of the co-variate, time since fire, on nitrate ( $\text{NO}_3^-$ ), nor was there an interactive effect. On average, elk herbivory increased  $\text{NO}_3^-$  pool sizes by 38%. In contrast, time since fire had a strong effect on soil available ammonium ( $\text{NH}_4^+$ ) over time, with the co-variate explaining most of the variation in soil  $\text{NH}_4^+$ ; there were no effects of elk herbivory or interaction effects. The co-variate, time since fire, and herbivory both



**Fig. 2** Soil organic carbon (C), total nitrogen (N) and microbial biomass N pool sizes vary by herbivore treatment across the fire chronosequence. The panels show the mean soil organic carbon (a), soil total N (b), microbial biomass N (c), for each site within each herbivore treatment (i.e., inside and outside the exclosures). Each bar represents the mean and the vertical lines show one standard error; black bars are outside the exclosures (i.e., in the presence of elk herbivory) and gray bars are inside the exclosures (i.e., in the absence of elk herbivory)

account for significant variation in total inorganic nitrogen (TIN; ammonium + nitrate) with no interactive effects. When the herbivore effect is averaged across both treatments, TIN tends to decline along the

**Table 2** Results from Analysis of Co-Variance (ANCOVA) for multiple soil response variables, using post-fire age chronosequence (Fire) as the co-variate and herbivore (Herb) treatment (inside or outside the elk exclosures) as fixed factors

	Whole model	Fire	Herb	Fire X herb interaction
Soil C and N data <sup>a</sup>				
Organic carbon	<b>7.67</b> (<0.001)	<b>15.04</b> (<0.001)	<b>7.49</b> (<0.001)	0.48 (0.49)
Total nitrogen	<b>7.25</b> (<0.001)	<b>13.15</b> (<0.001)	<b>7.71</b> (<0.001)	0.89 (0.35)
Soil microbial data <sup>b</sup>				
Microbial biomass N	<b>9.06</b> (<0.001)	<b>26.72</b> (<0.001)	<b>6.52</b> (0.01)	2.47 (0.12)
$\alpha$ -glucosidase	<b>4.39</b> (0.008)	3.37 (0.07)	<b>9.59</b> (0.003)	0.21 (0.65)
$\beta$ -glucosidase	<b>5.58</b> (0.002)	1.95 (0.17)	<b>14.24</b> (<0.001)	0.55 (0.46)
Acid phosphatase	<b>5.91</b> (0.001)	<b>4.57</b> (0.04)	1.64 (0.20)	<b>11.50</b> (0.001)
Phenol-oxidase	<b>3.53</b> (0.02)	2.01 (0.16)	2.64 (0.11)	<b>5.95</b> (0.02)
Resin data				
NH <sub>4</sub> <sup>+</sup>	<b>4.39</b> (0.006)	<b>11.99</b> (<0.001)	0.16 (0.69)	1.11 (0.295)
NO <sub>3</sub> <sup>-</sup>	<b>3.00</b> (0.03)	1.97 (0.16)	<b>7.03</b> (0.009)	0.16 (0.69)
Total inorganic N	<b>4.66</b> (0.005)	<b>10.35</b> (0.002)	<b>3.77</b> (0.05)	0.16 (0.69)

F-ratios are listed followed by p-values (in parentheses). Values in bold represent significant effects at the  $\alpha = 0.05$  level

<sup>a</sup> Soil C:N ratios had a non-significant whole model effect and were therefore not included in this table

<sup>b</sup> Peroxidase enzyme activity had a non-significant whole model effect and was therefore not included in this table

18 year fire chronosequence, with ~10% of the variance related to the time when the site was burned. However, across time since fire, elk herbivory enhances TIN by 22% relative to soils inside of the exclosure (protected from elk).

## Discussion

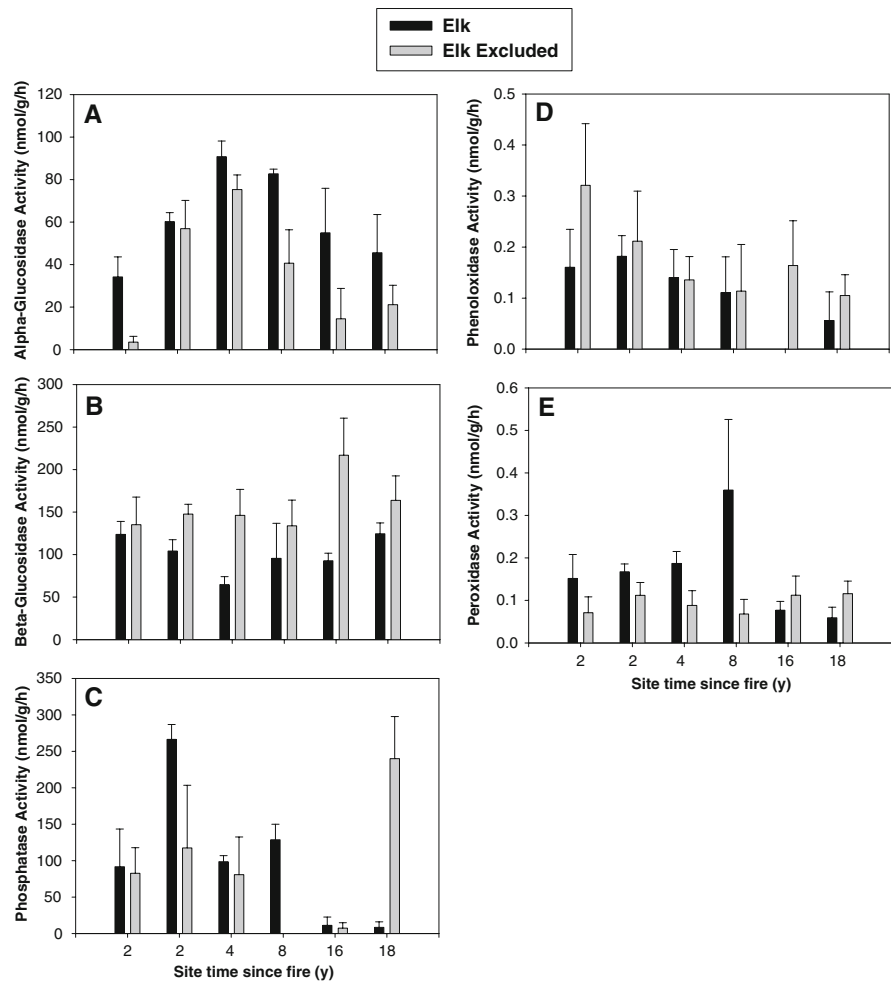
Overall, three main patterns emerge from these data: (1) In the absence of elk herbivory, aspen forest soils tend to increase in soil organic C, total N, microbial N pools and some extra-cellular enzyme activity (one of the C-acquiring enzymes- $\beta$ -glucosidase) in the years following fire; (2) When elk are present, the soils demonstrate more idiosyncratic responses such as, altered enzyme dynamics (of some enzymes), higher soil NO<sub>3</sub><sup>-</sup>, and the patterns described above (with respect to time) are often disrupted; (3) The presence of elk, slows organic C and total N accumulation after fire by an estimated 14.5–21 years, respectively, relative to the exclosures without elk. Taken together, these data suggest that herbivory by this introduced species can disrupt and alter patterns of soil recovery after fire that may have long-term consequences for ecosystem productivity.

We found that in the absence of elk herbivory, aspen soils gradually increase in soil organic C, total

N and microbial biomass pools and the activity of a C-acquiring extracellular enzyme ( $\beta$ -glucosidase) in the first 18 years after fire, confirming patterns recorded in other soil studies after fire (White et al. 2004). For example, similar to our results, soil microbial activity tends to increase over both short time scales (1 month to 1 year post-fire), as well as after 13 years; (Vázquez et al. 1993; Acea and Carballas 1996; Prieto-Fernández et al. 1998). Thirteen years after wildfire in which soils were sampled regularly, Prieto-Fernández et al. (1998) found that microbial biomass and extractable C gradually increased over time, while extractable N gradually declined over time. While many studies have shown differences in soil properties pre- and post-fire, fewer have shown how soils recover along a fire chronosequence (see Binkley et al. 2003; Treseder et al. 2004; White et al. 2004). Of those, mixed, context- and species-specific results have been found. For example, microbial activities may increase over time, (Acea and Carballas 1996) but soil organic C and total N have been shown to change in both positive and negative directions over time (Choromanska and DeLuca 2002). Over an 87-year post-fire and disturbance chronosequence, soil C and N steadily declined over time but only up to 20 years post-fire; beyond that C and mineralized N steadily increased due to feedbacks from maturing vegetation (White et al.



**Fig. 3** Potential extra-cellular enzyme activity of  $\alpha$ -glucosidase (a),  $\beta$ -glucosidase (b), phosphatase (c), phenoloxidase (d) and peroxidase (e) varies by herbivory treatment across the fire chronosequence. *Black bars* indicate the mean enzyme activity for each site outside the exclosures (i.e., in the presence of elk), while *gray bars* are the mean values for each site inside the exclosures (i.e., in the absence of elk herbivory)

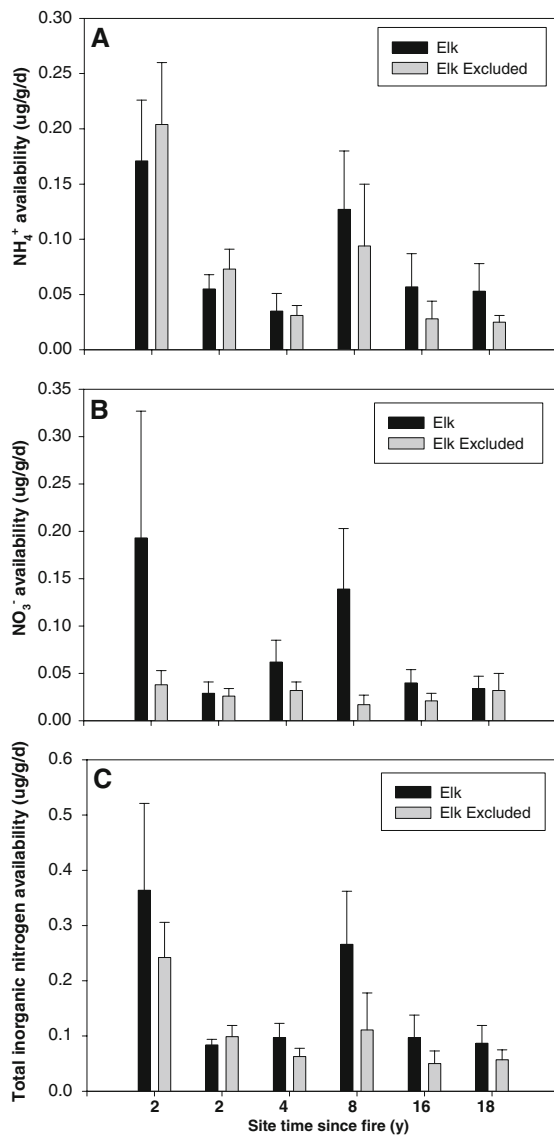


2004). Our study demonstrates that over time, soil organic C and total N, pools of microbial N, and some extracellular enzyme activities all increase, presumably due to gradual accumulations of organic matter from re-vegetation following fire. Herbivory by ungulates are likely to interact with these patterns over time to alter soil responses.

#### Herbivory effects

The effects of non-livestock ungulate herbivory, whether the herbivore is native or introduced, on soil processes are varied. Herbivory that occurs in grasslands often has “accelerating” effects on soil nutrient processes. Compensatory growth by plants is often stimulated after herbivory, which alters C allocation patterns, including root growth and root exudation which can then alter microbial and

mesofaunal communities and their activities (Bardgett et al. 1998; Frank et al. 2000; Hamilton and Frank 2001; Hamilton et al. 2008; Harrison and Bardgett 2008). In contrast, browsing by herbivores in forests or woodlands often has neutral or “decelerating” effects on nutrient processes (Pastor et al. 1993; Ritchie et al. 1998; Harrison and Bardgett 2008). For example, ungulates can disturb and compact soil, and excrete waste as they browse. While deposition of waste may increase soil N by increasing the amount of soluble N for plant use, the foraging ranges of plant browsers may lead to a net export of N due to excretion in areas apart from where the browsing took place (Schoenecker et al. 2004). Herbivory may also decelerate nutrient cycles due to shifts in plant communities by selective herbivory to less palatable woody species with lower N content and higher concentrations of lignin or polyphenols in their litter (Pastor et al. 1993;



**Fig. 4** Soil nutrient availability, as determined by the ion exchange resin bag method, varies by fire chronosequence and herbivore treatment. Soil ammonium (a), nitrate (b) and total inorganic nitrogen (c)

Ritchie et al. 1998; Harrison and Bardgett 2004). For example, in birch forests, browsing by deer has been found to reduce rates of net N mineralization and microbial C and N pools by reducing the growth and abundance of birch trees.

Browsing by introduced herbivores may have even larger effects on soil nutrient processes as their effects on plant abundance and/or community composition can be dramatic. In forest ecosystems of the western U. S., Binkley et al. (2003) found that elk browsing in

aspen stands increased bulk density, resulted in increases in soil pH (0.7 units), but had no overall effect on available soil nutrients (soil total organic C and total N). Our results in aspen forests where elk are introduced, demonstrated the opposite effect in that we found no difference in soil pH but decreased soil microbial activities (i.e., potential enzyme function of some extracellular enzymes), reduced microbial biomass N and reduced C storage through time. When focusing on mineralized N ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ), anecdotal evidence indicates that where elk are native in aspen ecosystems, elk have been shown to have no effect on N availability relative to aspen stands inside elk exclosures (evaluated with in-field resin bags after 35 years of exclosure; Binkley et al. 2003; Singer and Schoenecker 2003; Schoenecker et al. 2004). In contrast, we found that in aspen forests where elk are introduced, N availability overall was 22% higher outside of the exclosures (in the presence of elk) relative to inside of the exclosures. There are at least two possible hypotheses for this increase outside of the exclosures, when total N is generally lower in the presence of elk. First, increased microbial turnover and nitrifier activity could result in the warmer and drier soil outside of the exclosure. Increased immobilization inside of the exclosures (i.e., higher microbial N pools) support this contention. Second, this measured increase in  $\text{NO}_3^-$  could be due to the fact that there is considerably less biomass outside of the exclosures, due to consumption by elk, which reduces plant uptake or reduces the interception of water by plants and increases rates of leaching and resin interception of  $\text{NO}_3^-$ . While the issues of herbivore density and previous site history are important, these data overall suggest that introduced herbivores may have quite different effects on soil processes relative to forest stands where herbivores are native.

**Conclusions**

We conclude that herbivory by an introduced ungulate can significantly delay C and N dynamics after fire by an estimated 14.5–21 years (relative to non-browsed exclosures). Combined, these results generally support the “deceleration” model of Ritchie et al. (1998) but they also suggest that species interactions have been altered which contribute to shifts in ecosystem processes in aspen forests. Introduced elk in northern

Arizona appear to alter the trajectory of soil recovery after fire by virtually eliminating the dominant plant species in the community (Fig. 1). While we do not know if our results are from direct or indirect effects of elk browsing on soil properties (or both), they suggest that the effect of introduced elk can be significant. Such dramatic and rapid shifts in the dominant vegetation have long-term consequences for soil microbial communities and the ecosystem processes they mediate with the net result of decelerating nutrient cycles. At these sites we document that elk have significant effects on the activities of soil microbial communities affecting patterns of microbial immobilization and potential extra-cellular enzyme activity in idiosyncratic ways. Similarly, elk herbivory significantly alters patterns of nutrient availability and nutrient storage in the soils. Relative to sites where elk are native, these data suggest that introduced herbivores significantly increase the variability in soil processes after a disturbance such as fire which may have longterm consequences for aspen forest regeneration and productivity. These data also highlight the fact that there are few comparative studies examining the role of introduced herbivores on ecosystem processes or studies comparing response variables to the herbivores in both their native and introduced ecosystems (*sensu* Hierro et al. 2009), which suggests that future research priorities should focus on these effects.

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