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ORIGINAL ARTICLE

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Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils

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Abstract Two important themes in ecology include the understanding of how interactions among species control ecosystem processes, and how habitats can be connected through transfers of nutrients and energy by mobile organisms. An impressive example of both is the large influx of nutrients and organic matter that anadromous salmon supply to inland aquatic and terrestrial ecosystems and the role of predation by brown bears (*Ursus arctos*) in transferring these marine-derived nutrients (MDN) from freshwater to riparian habitats. In spite of the recognition that salmon-bear interactions likely play an important role in controlling the flux of MDN from aquatic to riparian habitats, few studies have linked bear predation on salmon to processes such as nitrogen (N) or carbon (C) cycling. We combine landscape-level survey data and a replicated bear-exclosure experiment to test how bear foraging on salmon affects nitrous oxide (N_2O) flux, carbon dioxide (CO_2) flux, and nutrient concentrations of riparian soils. Our results show that bears feeding on salmon increased soil ammonium (NH_4^+) concentrations three-fold and N_2O flux by 32-fold. Soil CO_2 flux, nitrate (NO_3^-), and N transformation differences were negligible in areas where bears fed on salmon. Reference areas without concentrated bear activity showed no detectable change in soil N cycling after the arrival of salmon to streams. Exclosure experiments showed that bear effects on soil nutrient cycles were transient, and soil N processing returned to background conditions within 1 year after bears were removed from the system. These results suggest that recipient ecosystems do not show uniform responses to MDN inputs and highlight the importance of large mobile consumers in generating landscape heterogeneity in nutrient cycles.

Keywords Alaska · Marine-derived nutrients · N_2O · Denitrification · Exclusion

Introduction

Concern over disrupting critical links among species and associated ecosystem functions with the loss of biodiversity has become a basis for conservation efforts (Daily 1997). In particular, understanding how interacting species affect biogeochemical processes has implications for resource management, pollution control, and ecosystem restoration. Large vertebrates, though often considered unimportant to ecosystem processes compared to microbes and invertebrates, can have a significant influence on ecosystems through a variety of mechanisms. For example, in the Serengeti grasslands, grazing by ungulates maintains areas of high above-ground net primary productivity through deposition of nutrients in waste (excrement and urine), which in turn establishes a feedback where increased productivity leads to more grazing and thus increased nutrient cycling (McNaughton et al. 1988). Studies of both boreal and tropical systems have shown a different pattern, where selective browsing by vertebrate herbivores structures community composition by favoring species with more recalcitrant leaf material, thereby depressing rates of N cycling in soils (Feeley and Terborgh 2005; Pastor et al. 1993). Vertebrate effects on terrestrial

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ecosystem processes remain poorly understood, especially in terms of the potential magnitude and the spatial and temporal extent of effects on landscapes. Further, the degree to which large vertebrate carnivores directly influence biogeochemical cycles is nearly unexplored.

Landscape ecology and biogeochemistry have recently been integrated to enhance understanding of many ecosystem processes that must be considered within a spatial and temporal framework (McClain et al. 2003). This stems from the recognition that many ecologically important biogeochemical processes occur at the interface of ecosystems or habitat types (Hedin et al. 1998). Concurrent with investigations of spatial heterogeneity and ecosystem processes there has been a growing awareness of how disjunct ecosystems can be linked through inter-habitat movements of animals (Polis et al. 1997). Migrating salmon returning from the ocean to spawn in freshwater streams are a classic example of such biotic transfers and can be a substantial source of marine-derived nutrients (MDN) to aquatic and terrestrial ecosystems (Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). For example, sockeye salmon (*Oncorhynchus nerka*) returning to the Wood River System in Bristol Bay, Alaska import 12,700 kg P and 101,000 kg N annually (Moore and Schindler 2004). With the large population declines from historic levels in many parts of their range, the impact of lost salmon nutrients for maintaining ecosystem productivity and future salmon returns is of critical conservation concern for threatened populations of these commercially valuable species (Gresh et al. 2000).

Previous studies have used stable isotope and modeling approaches to identify salmon as a potentially important nutrient source in riparian areas (Bilby et al. 2003; Helfield and Naiman 2001, 2006). While previous research highlights the potential for substantial fluxes of nutrients from stream to riparian habitat, the role that soil microbial communities play in controlling MDN use by plants has been overlooked. Ammonium (NH_4^+) and nitrate (NO_3^-) are the primary plant-available N pools in most soils, yet represent only a small fraction of the total N (Chapin et al. 2002). Ammonia (NH_3) volatilization, NO_3^- leaching, and gaseous evasion (NO, N_2O, N_2) are important nitrogen loss pathways, which control inorganic N pools and are linked through the processes of mineralization, nitrification, and denitrification. Thus, the microbially mediated processes that control inorganic N supply (mineralization and nitrification) and losses (nitrification and denitrification) are the primary determinants of plant available N and should be considered when evaluating the dynamics and consequences of MDN in riparian areas.

In this paper, we combine multi-year landscape-level survey data and a replicated bear-exclosure experiment to investigate how brown bear foraging on salmon creates hotspots of N cycling in riparian soils. We also evaluate the extent to which these hotspots persist through time.

Methods

Site description

Our study was conducted on four streams around Lake Nerka in the Wood River drainage, southwest Alaska (Fig. 1). The lakes and streams in this region support a large, commercially harvested stock of sockeye salmon,

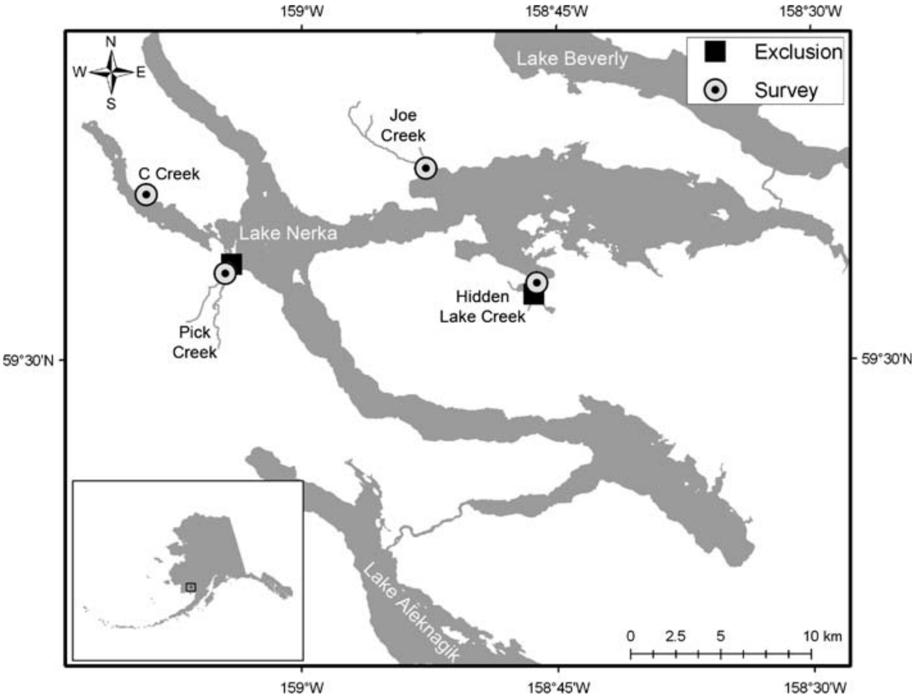

Fig. 1 Map of study sites in the Wood River System, southwest Alaska. *Dots* show locations of multi-stream survey sites (2003–2005) while *squares* are bear exclusion sites (2004–2005)

as well as much smaller populations of Chinook (*O. tshawytscha*), Chum (*O. keta*), Pink (*O. gorbuscha*), and Coho salmon (*O. kisutch*). Salmon typically enter spawning streams in July and August and within 6 weeks have completed their spawning activities and died. Thus, bear–salmon interactions on any stream are constrained to a short period of the year. Total returns of sockeye to the Wood River have averaged 2.7×10^6 individuals per year over the last 45 years (Schindler et al. 2005). Streams in our study were first or second-order with similar salmon density (Table 1). This region is also populated by brown bears (*Ursus arctos*). Long-term surveys of salmon abundance and bear predation in the Wood River System has shown that annual predation rates by bears on sockeye salmon range from 5 to 82% of spawning individuals (Winder et al. 2005). We studied riparian habitats of six sites on four streams to investigate the effect of salmon and bears on soil N cycling (Fig. 1, Table 2). The study was divided into two parts: (1) a multi-stream survey of paired reference and active bear sites sampled from 2003 to 2005, and (2) a bear exclusion experiment where bears were removed from two active foraging sites and rates of N cycle processes monitored.

Multi-stream survey

In August of 2003, after bears had begun foraging on salmon, we identified and sampled at three sites of intensive bear feeding activity (Lower Pick Creek, Upper Hidden Creek, and C Creek; see below for specific analyses). These sites were within 1–3 m of the stream bank, approximately 25–40 m^2 in area, and showed considerable visible evidence of bear activity (trampled vegetation, salmon carcasses, and scat). These 'bear areas' were paired with 'reference areas' showing no evidence of concentrated bear activity, typically immediately adjacent or across the stream. Although reference areas did not have obvious signs of bears feeding on salmon, bears forage continually along streams while salmon are spawning and are likely present throughout most of the riparian zone. Thus the reference sites were not bear-free, but rather areas without intense feeding activity. We focused on sites with concentrated bear feeding because these areas were most likely to show the maximum effects of MDN and bears on N cycling in riparian soils. Riparian soils were alluvial and rich in organic matter. Care was taken to ensure similar soils, vegetation, and physical structure among treatments.

The following season (July 2004, prior to the arrival of salmon), three additional sites (Joe Creek, Lower Hidden Creek, and Upper Pick Creek) were included with bear and reference areas chosen based on observations of bear activity in prior years. In both 2004 and 2005, sites were sampled once before salmon arrival (in late June or early July) and once during peak salmon abundance (in August). Thus, with the exception of 2003, sites were surveyed twice per season, immediately before salmon arrival and at peak spawning salmon abundance.

Table 1 Stream physical characteristics, annual salmon returns, and bear predation rates

Stream	Discharge[a] (m^3 s^{-1})	Depth[a] (m)	Width[a] (m)	Salmon density (run size)[b]			Predation rate[c]		
				2003	2004	2005	2003	2004	2005
Pick Creek	0.35	0.32	6.5	0.30 (4,001)	0.55 (7,502)	0.96 (13,057)	0.30	0.13	0.09
Hidden Lake Creek	0.19	0.14	5.1	0.19 (3,097)	0.66 (10,797)	0.32 (5,274)	0.36	0.13	0.17
C Creek	0.04	0.15	1.4	0.18 (128)	0.59 (417)	0.69 (493)	0.39	0.59	0.05
Joe Creek	0.97	0.21	6.7	NA	0.41 (4,401)	0.17 (1,845)	NA	0.07	0.18

[a] Average of all available measurements during the month of August

[b] Salmon density in fish m^{-2} of stream bed. Run size is total number of salmon observed in the stream (live + dead) on a standardized survey date

[c] Calculated as total number of salmon killed by bears divided by the run size. Rates are in-stream predation and are not specific to bear feeding sites in the riparian zone

Table 2 Bear and reference site names and study design

Stream	Site code	Treatments		
		2003	2004	2005
Pick Creek	UPC		Bear, reference	Bear, reference
	LPC	Bear, reference	Exclusion, reference	Exclusion, reference
Hidden Lake Creek	UHLC	Bear, reference	Exclusion, reference	Exclusion, reference
	LHLC		Bear, reference	Bear, reference
C Creek	CC	Bear, reference	Bear, reference	
Joe Creek	JC		Bear, reference	

U and *L* indicate site position as upper or lower. Sites within a stream were separated by a minimum of 1 km

Bear exclusion experiment

To examine the temporal persistence of nutrient cycling hotspots created by bear foraging, we excluded bears from areas with known high bear activity. In July of 2004, we excluded bears from our 2003 active bear areas at Lower Pick Creek and Upper Hidden Lake Creek and added bear and reference sites within the same drainages (Table 2, Fig. 1). We monitored exclusion and paired reference sites both before and after salmon entered the system in 2004 and 2005. The experiment was terminated in September 2005 because N cycling patterns had returned to the background rates observed in other riparian areas (see Results).

Bears were excluded using solar-powered electric fencing (Electro-Braid, Nova Scotia, Canada). Fences were 1.2 m in height with three strands of electrified webbing spaced roughly 0.3 m apart. Thus, smaller animals were able to access the sites freely. Fenced areas were approximately 80 m^2 and encompassed the full area sampled in the previous year. Fences were checked approximately weekly and found intact except on two occasions at the Lower Pick Creek site. In both instances there were no signs of bears having entered the site.

N_2O and CO_2 flux estimates

To quantify soil ecosystem responses to seasonal salmon availability and associated bear foraging activities, we measured nitrous oxide (N_2O) and carbon dioxide (CO_2) flux from soils using established methods (Keller and Reiners 1994; Matson et al. 1990). In short, for each sampling period, four circular polyvinyl-chloride (PVC) bases 0.25 m in diameter and 0.1 m in height were inserted into the soil at each site with minimal disturbance. Bases were placed randomly within the sites. The surface area within the chambers was roughly 1% of the total site area, which is typical spatial coverage for N trace gas studies (Erickson et al. 2001; Keller and Reiners 1994; Matson et al. 1990). After a minimum 15-min equilibration, flux measurements were initiated by capping the PVC bases with acrylontrile-butadiene-styrene (ABS) covers (0.1 m height) fitted with gas-tight septa (Matson et al. 1990). Headspace gas samples (15 ml) were recovered from each chamber at 15-min intervals for 45 min (0, 15, 30, and 45 min) in disposable 20-ml syringes fitted with gas-tight stopcocks. PVC bases were removed after sampling to avoid attracting bears.

Gas samples were transferred to 10-ml borosilicate vials within 12 h of collection for subsequent analysis. Vials were fitted with heavy black butyl stoppers (Geo-Microbial Technologies, Ochelata, OK, USA) and flushed with pure N_2 gas in the lab. Prior to injecting samples in the field, vials were evacuated to approximately 95 kPa. Samples were analyzed at Stanford University or the University of Washington for N_2O concentration by gas chromatography and referenced to certified gas standards (Scott Specialty Gases, Longmont, CO, USA). Effects of storing samples in vials were corrected for by injecting N_2O standards into vials under field conditions and analyzing them in parallel with samples. The flux of N_2O from soils was calculated by least-squares linear regression of N_2O concentration over time and corrected for ambient air temperature and chamber volume. The minimum detectable flux was approximately 0.02 mg N_2O–N m^{-2} d^{-1}.

In 2003 and 2004, CO_2 flux from soils was determined in a manner similar to N_2O. Chamber headspace samples were analyzed for CO_2 concentration using a gas chromatograph equipped with a flame ionization detector and in-line methanizer. Flux measurements were calculated by linear regression as above. In 2005, CO_2 flux was measured in the field immediately after N_2O flux measurements using a portable, continuous-flow infrared gas analyzer (IRGA; LI-COR Biosciences). An ABS cover was fitted with a 1 l min^{-1}air pump that continuously recirculated headspace air though the IRGA. The flux measurement lasted a minimum of 4 min per chamber over which time CO_2 concentration was sampled at 5-s intervals. Fluxes were calculated in mg CO_2–C m^{-2} h^{-1} by least-squares regression of the most linear segment that included at least 25 observations.

Soil nutrient concentration and N transformations

Soil inorganic N concentrations (NH_4^+ and NO_3^-) and N transformation rates (net mineralization and nitrification) were measured on 2–6 soil cores per site from within or adjacent to the area covered by the gas flux chambers. Soils were collected to a depth of 0.1 m and 260 cm^3 in volume using a standard bulb corer and were hand-sieved to 2 mm within 12–18 h of collection. Fifty to 100 g of soil (wet weight) was dried at 105°C to constant mass to determine water content.

To determine initial NH_4^+ and NO_3^- concentrations, subsamples (10–12 g wet weight) of sieved soils were immediately extracted in 100 ml of 2 M potassium chloride (KCl) (Hart et al. 1994). Soil extracts were shaken in KCl for 60 s then left to settle for 18–24 h before being filtered through Whatman #1 paper filters pre-leached with 90 ml KCl. Filtered extracts were frozen and later analyzed colorimetrically with an Alpkem Flow Solution IV (OI Analytical, College Station, TX, USA). A second 10–12 g soil subsample was incubated aerobically in the dark for 14–28 days at 12–16°C (conditions similar to ambient soils temperatures) prior to extraction with KCl as above. Net mineralization was calculated as the change in inorganic N concentration (NH_4^+ + NO_3^-) divided by incubation duration, while net nitrification was calculated as the change in NO_3^- concentration over the incubation. Linear regression of net mineralization and nitrification rates versus length of incubation showed that differences in incubation duration did not bias estimates of N transformations (mineralization $r^2 = 0.003$, $P > 0.5$; nitrification $r^2 = 0.005$, $P > 0.5$).

Statistical analyses

Our study design resulted in data collected at sites in four stream drainages, across 3 years (not all streams were surveyed each year), with each site having paired bear and reference sites ($n = 30$ site–year combinations, Table 2). Gas flux data were averaged within each site and date using a random effects model that weighted individual chamber measurements ($n = 4$) based on the coefficient of determination and standard error of the regression coefficients of N_2O and CO_2 evolution through time (Shadish and Haddock 1994). Soil nutrient data were averaged among soil cores within each site and date.

Multi-stream survey comparisons of gas flux, soil N pools, and N transformation rates were analyzed by two-way ANOVA with each site and year combination as replicates. Bear versus reference areas, and before versus after salmon, were treated as factors (Systat 10.0, Systat Software Inc., 2004). Post-hoc tests comparing bear and salmon combinations were made using Tukey's HSD. For the bear exclusion experiment, comparisons between reference and bear exclusion sites were made for each sampling date using two-sample *t*-tests with individual flux chambers or soil cores as replicates. All data were checked for normality and when necessary log-transformed ($\log_{10}[X + 1]$).

Results

Multi-stream survey

Analysis of 30 site–date combinations showed that the presence of salmon and localized bear foraging activities interacted to significantly enhance N_2O flux from riparian soils (Fig. 2a–b; two-way ANOVA, $P < 0.01$; see Electronic Supplementary Material for ANOVA tables). Post-hoc tests showed that in years where sites were sampled prior to the seasonal arrival of salmon there was no difference between bear and reference areas, with N_2O emissions near detection limits (Fig. 2a; Tukey's HSD $P > 0.05$). After salmon arrival, soil N_2O emissions showed a large and statistically significant increase in sites with concentrated bear feeding activity but not in nearby reference sites on salmon streams (Fig. 2b; $P < 0.05$). Mean N_2O flux in bear sites was 3.1 mg N_2O–N m^{-2} d^{-1} with some individual chambers >7 mg N_2O–N m^{-2} d^{-1}, rates on par with fertilized agricultural fields (Stehfest and Bouwman 2006). Before

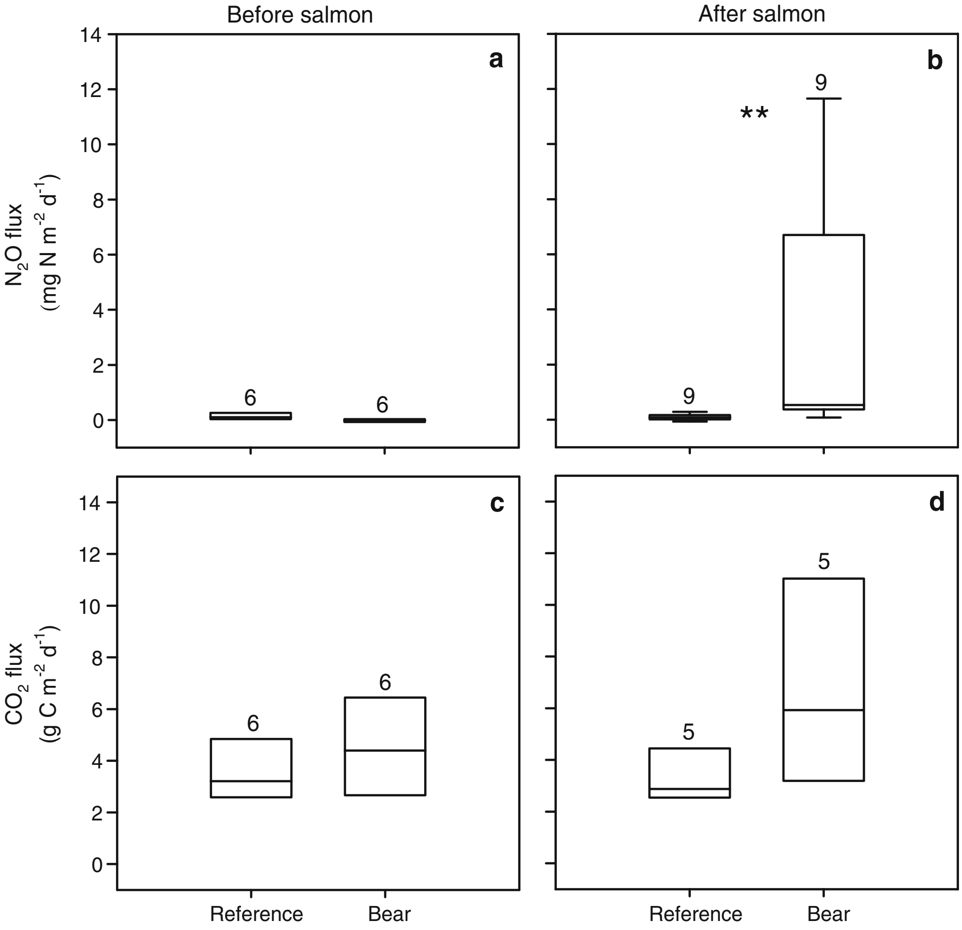

Fig. 2 Box-plots of N_2O and CO_2 fluxes from riparian soils among bear and reference sites, before (*left panels*) and after the seasonal entry of salmon to streams (*right panels*). *Numbers* indicate the number of site-date combinations within each group (n). Each site-date combination is the average of four individual flux measurements weighted based on the standard error of the slope coefficient as well as the r^2 of the linear regression using a random effects model. *Asterisks* indicate significant bear-salmon interaction on N_2O flux ($P < 0.01$). CO_2 flux did not differ significantly among groups

salmon and in reference areas, average N_2O fluxes ranged from undetectable to 0.18 mg N_2O–N m^{-2} d^{-1} (mean = 0.10). There was a significant treatment effect on soil CO_2 emissions with bear areas having higher soil CO_2 flux than reference sites both before and after salmon ($P < 0.05$), and no seasonal change associated with the arrival of salmon (Fig. 2c–d).

Soil nutrient concentrations (NH_4^+ and NO_3^-) and N transformations (net mineralization and nitrification) showed no significant difference between bear and reference areas when sampled prior to the arrival of salmon (Fig. 3a–b; $P > 0.05$). After salmon and in the presence of bears, soil NH_4^+ concentration increased with a significant interaction effect of salmon and bears ($P = 0.05$); reference areas without bears did not respond to salmon (Fig. 3a). Nitrate concentrations tended to be elevated in bear areas after salmon arrival, however, results were not statistically significant (Fig. 3b; $P > 0.05$). N transformations were not statistically different among groups although there was a trend toward higher net N mineralization in bear areas after salmon (Fig. 3c–d; $P > 0.05$).

Bear exclusion experiment

Bear exclusion showed effects on soil N cycling properties consistent with survey results. Before the exclusion of bears (August 2003, when bears were actively feeding on salmon at these sites), N_2O flux was significantly higher in bear areas on both Pick Creek (site code LPC) and Hidden Lake creeks (UHLC) (Figs. 4a, 5a; $P < 0.01$ and $P < 0.05$, respectively). Exclusion fences were erected in June of 2004 and both the LPC and UHLC exclusion sites had returned to reference conditions upon the first resampling in early July of the same year (11 months after initial sampling). N_2O fluxes remained at reference levels through the rest of the experiment.

Upon initiation of the bear exclosure experiment, we established new active bear sites to monitor in conjunction with the exclusion sites (site codes UPC & LHLC). Sites were selected based on observations of bear activity in previous years. Our initial sampling occurred before the arrival of salmon (July 2004) and showed no differences between treatment (bear or exclusion) and reference areas for all metrics of N cycling (Figs. 4, 5). Unfortunately, bear activity was generally low in 2004 (Table 1) and not in the areas we predicted. Thus, we did not observe increased rates of N cycling after salmon entered the system as expected. In 2005, bears did concentrate their feeding activities in our predicted areas and as a result we observed a significant increase in N_2O flux from the Hidden Lake Creek active bear site (LHLC; Fig. 5b; $P < 0.05$). Pick Creek (UPC) however did not have significant differences in N_2O flux after salmon (Fig. 4b).

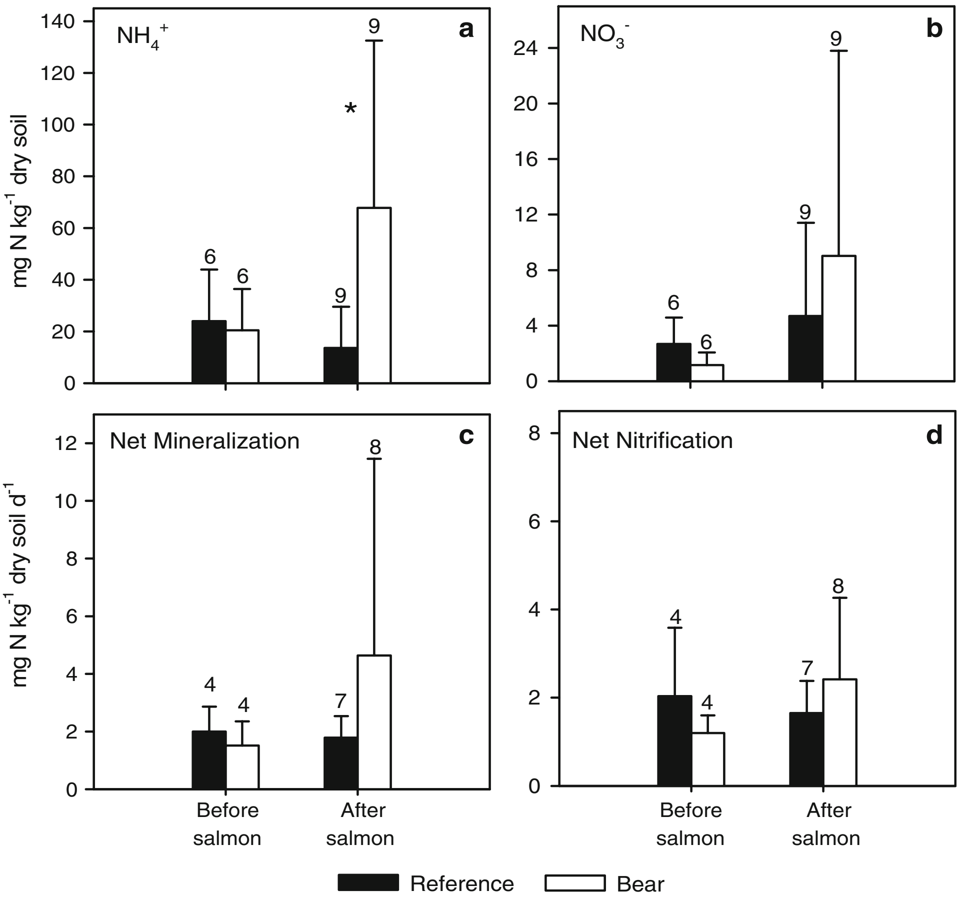

Fig. 3 Average soil inorganic N concentration and N transformations from landscape survey sites before and after salmon entered the system. *Numbers* indicate site-date combinations within each group (*n*). Two-way ANOVA showed significant bear–salmon interaction on NH_4^+ concentration ($P = 0.05$). Nitrate (NO_3^-) concentration, net mineralization, and net nitrification did not show significant differences among groups. *Error bars* are 1 SD

Soil respiration also showed a tendency to decline following bear exclusion. CO_2 flux was initially higher in the Pick Creek exclusion area compared to the reference area (LPC; Fig. 4c; $P < 0.05$) when sampled after salmon and before the exclusion was initiated. Fluxes declined to at or below reference levels within 11 months of our initial after-salmon measurements and remained at reference levels throughout the exclusion experiment. This was not the case on Hidden Lake Creek (UHLC) where there was no difference in rates of CO_2 flux initially (Fig. 5c). The active bear sites at both Pick Creek and Hidden Lake Creeks (UPC & LHLC) showed significant increases in soil CO_2 flux after salmon in 2005 (Figs. 4d, 5d; $P < 0.05$ and $P < 0.01$, respectively).

Pre-exclusion soil NH_4^+ concentration was significantly higher in the Hidden Lake Creek exclusion site versus the reference site (Fig. 5e; $P < 0.01$), but no significant difference was observed between the Pick Creek exclusions and reference sites. After exclusion, Hidden Lake Creek NH_4^+ concentration decreased to reference levels by the following spring, 11 months after sampling (Fig. 5e). As with N_2O and CO_2 flux, soil NH_4^+ concentration in the active bears sites (UPC & LHLC) increased significantly after the arrival of salmon in 2005 (Figs. 4f, 5f; $P < 0.05$ and $P < 0.01$). Nitrate concentrations were not affected by bears and salmon before or during the exclusion experiment (data not shown). N transformation data for exclusion sites were limited due to lost samples and are therefore not shown.

Discussion

Our results show that bears feeding on salmon in riparian zones can alter N cycling processes in soils. After examining active bear middens and reference areas without concentrated bear activity in four drainages across 3 years, we found that bears feeding on salmon significantly increased N_2O flux and soil NH_4^+ concentration in highly localized areas. N_2O is the product

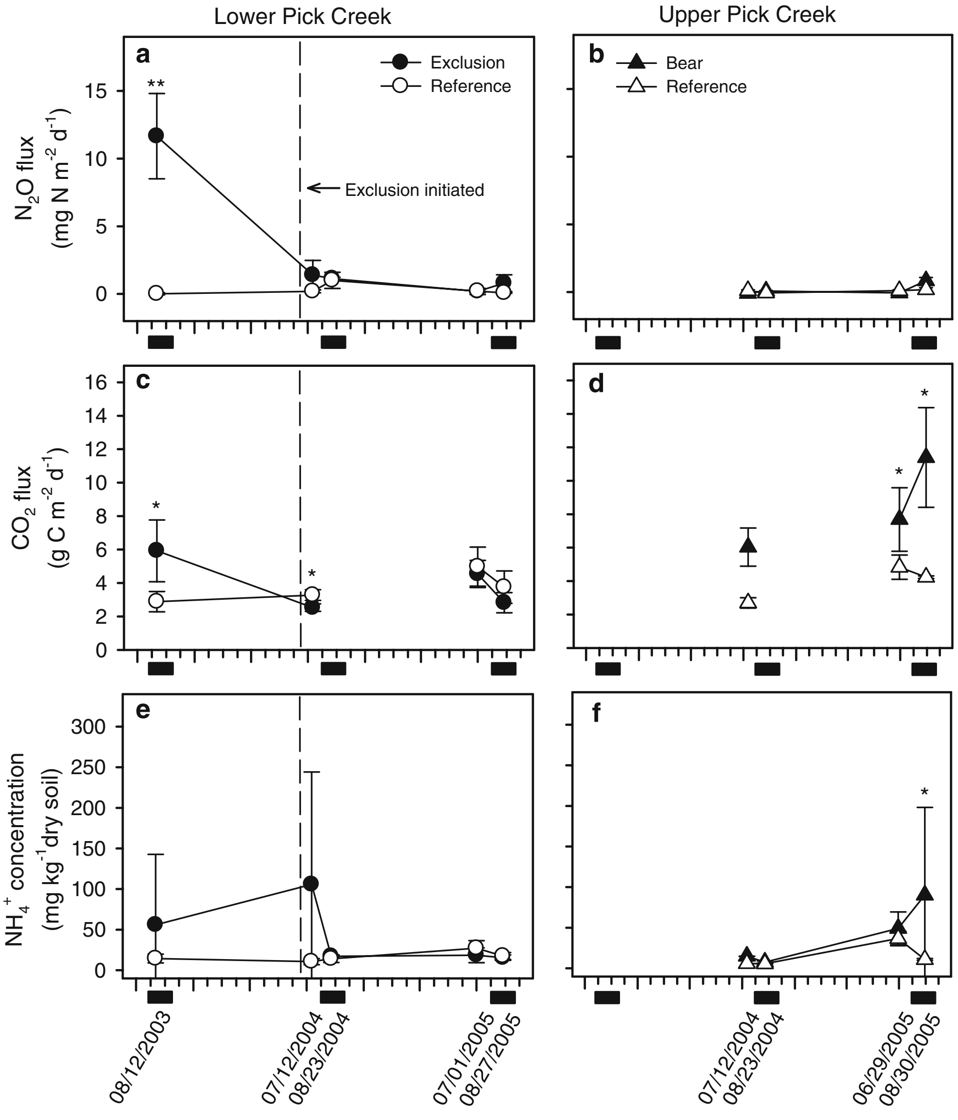

Fig. 4 Time series of N_2O flux, CO_2 flux, and soil NH_4^+ concentration for bear exclusion experiments on Pick Creek. *Circles* indicate the exclusion–reference site pairs, while *triangles* represent the unexcluded bear–reference site pairs. *Filled symbols* are bear areas (active or excluded) and *open symbols* are the reference areas. Exclusions were initiated in June of 2004 (*vertical line*). Bears were actively feeding on salmon during the August 2003 sampling. *Bars* at the bottom of each panel indicate when spawning salmon were present in the streams. Data are mean ± 1 SD. Number of flux or soil nutrient measurements (n) was four in all cases except for NH_4^+ concentration on 7/1/2005 where $n = 2$ and CO_2 flux at the Upper Pick Creek sites on 7/12/2004 where $n = 3$. *Asterisks* indicate significant differences between bear or exclusion areas and the paired reference areas

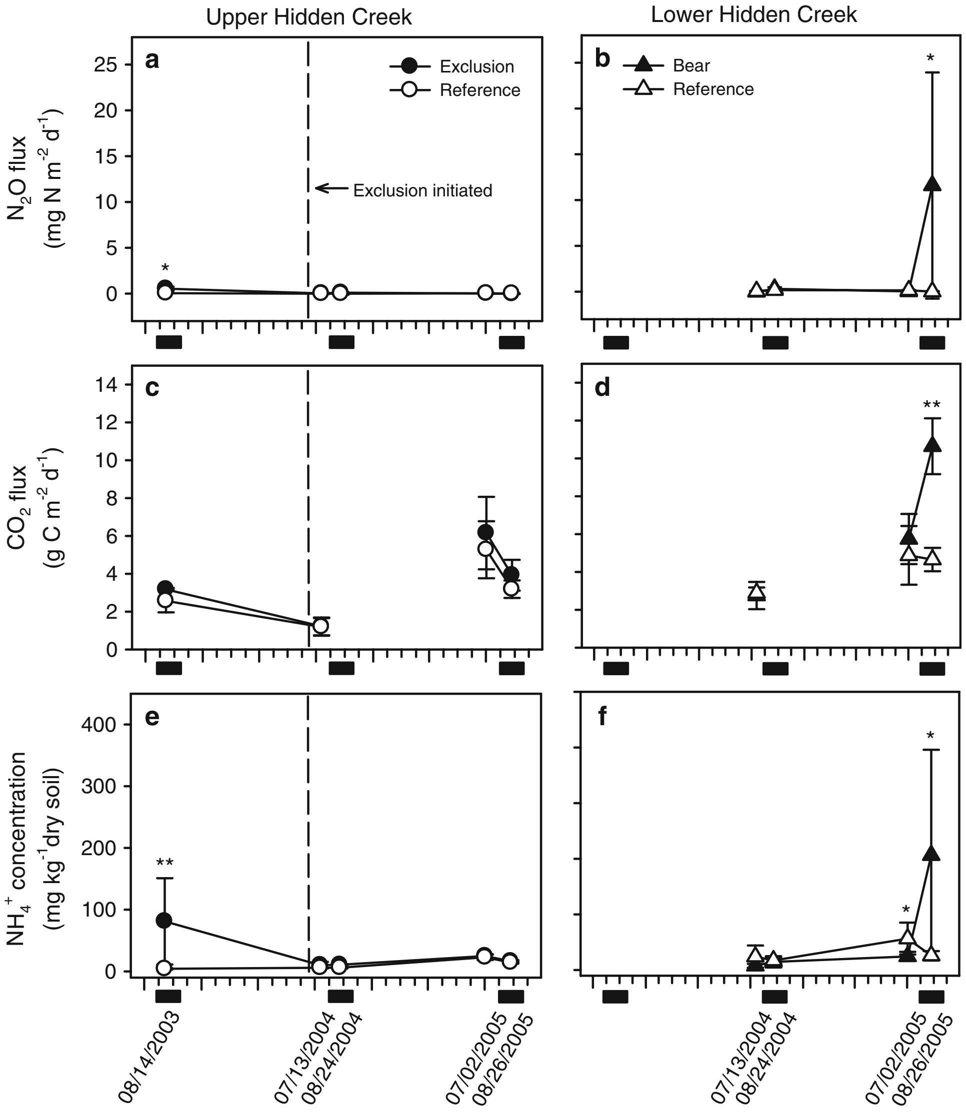

Fig. 5 Time series of N_2O flux, CO_2 flux, and soil NH_4^+ concentration for bear exclusion experiments on Hidden Lake Creek. See Fig. 4 for description of symbols. Number of flux or soil nutrient measurements (*n*) was four in all cases except for NH_4^+ concentration on 7/13/04, 8/24/2004, and 7/2/2005 where $n = 2$, 2, and 3, respectively

of both nitrification and dentrification and the rate of N_2O flux is reflective of the overall N cycling in soils (Davidson et al. 2000). The exclusion of bears from their preferred foraging sites also demonstrated that bear-induced hotspots of soil NH_4^+, CO_2 flux, and N_2O flux were transient and returned to background levels within 1 year after bear exclusion. Elevated N cycling parameters observed with bears and salmon were not detectable the following spring in either the multi-stream survey or bear exclosure experiments.

Bears feeding on salmon elevates total inorganic N pools ($NH_4^+ + NO_3^-$) three-fold and gaseous N_2O losses 32-fold over reference areas, with positive N mineralization and nitrification in reference sites and areas with high bear activity (i.e., middens). Total inorganic N pools in bear middens averaged 79.8 mg kg^{-1} dry soil and were three to ten times higher than other Alaskan riparian soils (Giblin et al. 1991), which is likely because of the large percentage of N-fixing alder in these watersheds and the presence of bears and salmon (Helfield and Naiman 2006). Reference areas on salmon streams showed little change in trace gas flux or soil N pools after the arrival of salmon in spite of high spawning densities and significantly elevated dissolved nutrients in stream water (Moore et al. 2007; O'Keefe and Edwards 2002).

Multiple mechanisms exist by which bears and salmon can alter soil N cycling dynamics. The most obvious is the highly concentrated N inputs via deposition of salmon carcasses, as well as defecation and urination by bears. It is well recognized that application of N to soils in a variety of forms will increase inorganic N pools and N losses via trace gases (Eichner 1990). Other mechanisms include the trampling of vegetation by bears, which could reduce N demand by plants allowing microbes to better compete for N. Direct disturbance by bears may also influence N cycling by aerating soils and raising soil temperature similar to conventional tillage in agro-ecosystems (Tardiff and Stanford 1998).

Nitrogen losses from the ecosystem other than trace gases (N_2O and N_2) may also be influenced by bear activity. Losses from ammonia (NH_3) volatilization and NO_3^- leaching may increase in response to inputs of MDN (Gende et al. 2007). Similarly, disturbance by bears could accelerate both gaseous losses and leaching. Fellman et al. (2008) recently demonstrated that a significant pulse of salmon-derived dissolved organic matter is mobilized from riparian area to streams during storm events. Given that there is no apparent legacy effect of MDN input on soil N pools the spring following deposition, it is possible that a significant proportion of MDN transferred to riparian areas by bears is hydrologically mobilized back to streams during typical fall rains or spring thaw. Together, trace gas and hydrologic flushing combine to make the bear-salmon nutrient subsidy relatively ephemeral with respect to plants incorporating these sources of nutrients into biomass.

Several factors including CO_2 flux, NO_3^- concentration, net N mineralization, and net nitrification did not change with bears and salmon at the site scale. We expected significantly elevated soil CO_2 flux in bear areas after salmon due to accelerated microbial processing of soil organic matter with the addition of MDN and labile carbon. Although apparent in the active bear sites at Pick Creek (2003, 2005) and Hidden Lake Creek (2005), the multi-stream survey indicated a trend for elevated CO_2 flux but the results were not conclusive. CO_2 in soils is the product of both autotrophic and heterotrophic respiration. MDN in riparian areas increases short-term rates of N cycling, however it appears this is not directly translated to significant increases in microbial activity, microbial biomass, or root respiration by plants. This is consistent with a more detailed study from a central Alaskan boreal forest, which demonstrated longer-term N additions to soils resulted in changes in fungal community composition but not microbial biomass or soil CO_2 flux (Allison et al. 2008).

Previous work shows that interior Alaska riparian soils experience net immobilization of N (i.e., negative net N mineralization) during the growing season as plants and microbes compete for resources (Giblin et al. 1991). Our sites showed positive net N mineralization suggesting greater overall N availability than interior areas. Site-level fluxes of N_2O and CO_2 were positively related to soil inorganic N concentration (see supplemental material), but were unrelated to rates of net N mineralization and net nitrification. This suggests a tendency for greater gross N mineralization and nitrification in sites with high N_2O fluxes (i.e., bear sites after salmon) and immobilization of N by microbial communities. With N immobilization, some of the MDN transferred to riparian areas can be retained in soils and later released in plant available forms (Drake et al. 2006). Without a clearer indication of retention within the ecosystem over the winter months and the degree to which N is the limiting resource for plant growth, it remains unclear to what extent primary productivity is being supported by MDN. It is important to note that salmon are rich in phosphorus, potassium, and calcium, and these nutrients may play a role in supporting terrestrial productivity.

To date, only two studies have evaluated the effects of MDN on soil inorganic N (Drake et al. 2005; Gende et al. 2007), both with experiments that simulated carcass deposition in riparian habitats. Both studies demonstrated that soil NH_4^+ was significantly higher within days after salmon addition and that NO_3^- concentrations peaked several weeks after soil NH_4^+ concentrations. Given our experiments occurred at the peak of salmon spawning with the majority of salmon/MDN deposition having occurred within days to weeks of sampling, it is possible that NO_3^- concentrations would have been significantly higher in bear areas had sampling been repeated 4–6 weeks later. In general, the observed changes in soil inorganic N pools from this study, which experienced multiple effects of bears such as carcass deposition, bear excreta, and trampling, were similar in magnitude to changes observed from previous carcass addition experiments, which did not include the direct effects of bears (Drake et al. 2005; Gende et al. 2007). This suggests that the single greatest factor creating N cycling hotspots is the deposition of carcasses by bears, and not the effect of bears themselves.

The bulk of N transferred to riparian areas is via salmon carcass deposition which must first be decomposed then mineralized by microbes before it is available to plants (Helfield and Naiman 2006). In contrast, MDN transferred to riparian areas through consumption by bears is mostly deposited as urea in urine, which is mineralized to NH_4^+ on the order of hours to days (Bol et al. 2004; Hilderbrand et al. 1999). We could not control for how recently active bear areas had been used as well as the relative proportion MDN deposited as excreta versus carcasses. These factors likely contributed to the high variability amongst sites and years observed in our study. Soil N pools in previous bear areas consistently returned to reference conditions by the following season indicating little annual carry-over in the inorganic N pool, a result consistent with earlier studies (Drake et al. 2005; Gende et al. 2007).

Bears feeding on salmon are not the only mechanism to transfer MDN to riparian areas. Scavengers including birds and small mammals also have the potential to move MDN out of streams (Merz and Moyle 2006), a process also facilitated by bear predation (Gende et al. 2004). Floods can move carcasses into riparian areas, but peak flows in our system are in spring before salmon arrive and after most carcasses from the previous season have been mineralized or deposited in downstream basins. O'Keefe and Edwards (2002) showed that riparian forests in the Wood River System are connected to streams through hyporheic flow and elevated nutrients in stream water after salmon are removed by sorption or uptake in highly localized sites (within 1 m) at the stream-soil interface. MDN can also be transferred to riparian areas through emergent and scavenging insects (Francis et al. 2006; Meehan et al. 2005). The minimal change in soil N cycling of reference areas before versus after salmon spawning suggests that these mechanisms collectively linked salmon spawning in streams to riparian soils only weakly at our sites, even in streams which have consistently high salmon densities.

The spatial extent of bear-salmon induced biogeochemical hotspots remains largely unknown. To fully elucidate the watershed scale effect of bears on soil N cycling would require detailed observation of bear activity combined with measurement of soil N cycling metrics at relatively high temporal resolution. Our study of discrete patches highly influenced by bears does demonstrate that: (1) bear activity and MDN inputs to riparian areas increase inorganic N pools and N cycling as evidenced by N_2O flux; and (2) the changes do not persist from one season to the next.

Our study highlights previously identified limitations when attempting to estimate MDN inputs to terrestrial systems using $\delta^{15}N$ alone (Gende et al. 2002). Typically in $\delta^{15}N$ based studies, N isotopic signatures in terrestrial organisms (trees, herbaceous plants, insects) collected near salmon spawning reaches are more enriched in $\delta^{15}N$ than signatures in comparable reference areas without salmon (Ben-David et al. 1998; Helfield and Naiman 2001; Hocking and Reimchen 2006). N transformation processes in soils, however, can have strong and highly variable isotopic effects. Nitrification and denitrification will fractionate (preferentially favor the light isotope) by 15–35‰ and ~30‰, respectively (Hogberg 1997), far exceeding the $\delta^{15}N$ range observed in comparative studies. The result that N_2O flux, the product of both nitrification and denitrification, increases by over an order of magnitude with high MDN inputs reveals a positive feedback on soil $\delta^{15}N$ and plants utilizing this resource. MDN inputs will elevate soil $\delta^{15}N$ both by contributing an enriched N source and by stimulating in situ fractionation processes that preferentially remove the light isotope (^{14}N). Without accounting for these fractionation biases, estimates of MDN in terrestrial vegetation based on $\delta^{15}N$ and the simple two-source mixing model will overestimate the importance of salmon in riparian habitats (Gende et al. 2002; Morris et al. 2005). The extent of this overestimation is not well understood at present.

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