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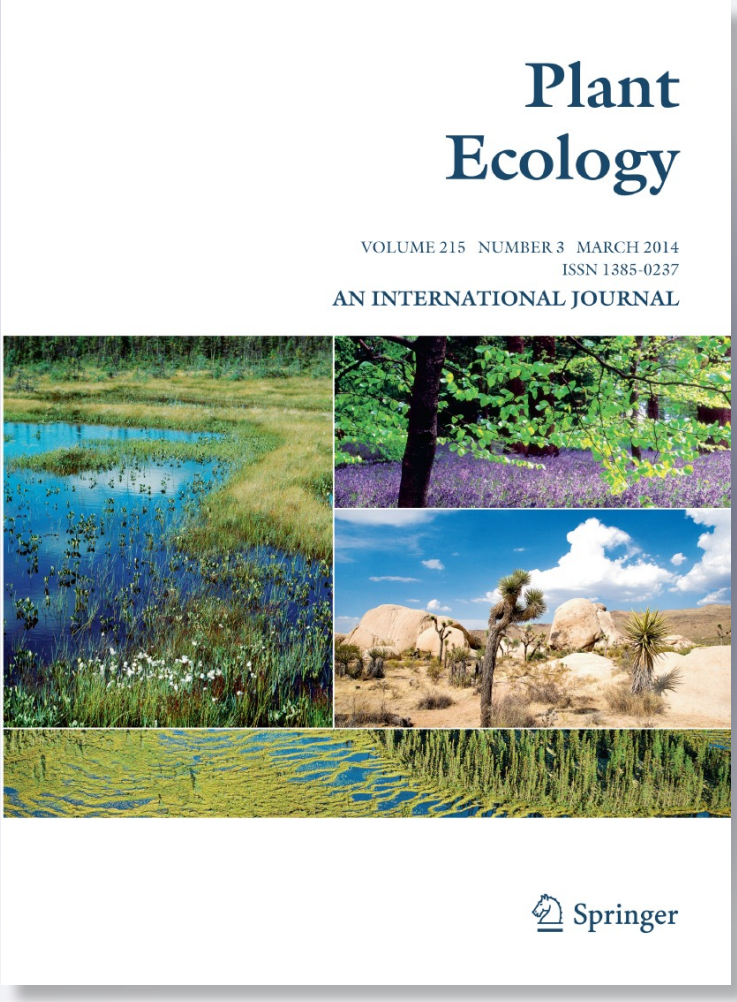

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Abstract Changes in the quantity and quality of plant litter occur in many ecosystems as they are invaded by exotic species, which impact soil nutrient cycling and plant community composition. Such changes in sagebrush-steppe communities are occurring with invasion of annual grasses (AG) into a perennial grass (PG) dominated system. We conducted a 5-year litter manipulation study located in the northern Great Basin, USA. Springtime litter was partially or completely removed in three communities with differing levels of invasion (invaded, mixed, and native) to determine how litter removal and litter biomass affected plant-available soil N and plant community composition. Litter biomass (prior to the removal treatment) was negatively correlated with plant-available N in the invaded community, but was positively correlated in the native community. Plant-available N had greater intra- and inter-annual fluctuations in the invaded compared to the mixed or native communities, but was not generally affected by removal treatments. Litter removal had negative effects on AG cover during a warm/dry year and negative effects on PG cover during a cool/wet year in the mixed community. Overall, the effectiveness of springtime litter manipulations on plant-available N were limited and weather dependent, and only removal treatments >75 % had effects on the plant community. Our study demonstrates how communities invaded by AGs have significantly increased temporal variability in nutrient cycling, which may decrease ecosystem stability. Further, we found that the ecological impacts from litter manipulation on sagebrush communities were dependent on the extent of AG invasion, the timing of removal, and seasonal precipitation.

Keywords *Bromus tectorum* · Climate · Plant-available nitrogen · Perennial bunchgrass · *Pseudoroegneria spicata* · Structural equation modeling

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Introduction

The role of plant litter on ecosystem processes is complex (Facelli and Pickett 1991a; Xiong and Nilsson 1999). Litter is initially produced either through senescence or mechanical breakage of live plant material, and then degraded and decomposed through abiotic and biotic agents (photodegradation, wind, herbivores, detritivores, and microbes). During the "afterlife" of plant material as litter, it exerts influences on the surrounding micro-environment by intercepting light, buffering soil temperatures, decreasing evaporative water loss, and providing substrate, which influences nutrient availability and seedling establishment (Facelli and Pickett 1991a, b; Xiong et al. 2008). The direction and amplitude of these influences are determined primarily by the quantity of litter and its physiochemical qualities (Castro-Díez et al. 2012; Cornwell et al. 2008; Ginter et al. 1979). Further, the overall impacts of litter on the micro-environment are tightly integrated with the macro-environment (e.g., soil properties, climate, and weather) and the regional biota, leading to complex interactions between litter and various ecosystem processes (Boeken and Orenstein 2001; Knapp and Seastedt 1986; Mayer et al. 2005; Sayer 2006). Accordingly, any changes that occur to litter (quantity or quality) through natural or anthropogenic disturbances could have cascading consequences to other trophic levels within the ecosystem.

Arid and semi-arid ecosystems in the western USA have experienced over a century of invasion by exotic annual grasses (AG) such as *Bromus tectorum* L., causing dramatic changes in the quantity, quality, distribution, and timing of litter inputs into these systems (Knapp 1996). With AG invasion, studies have reported increases in the amount of litter biomass with a more continuous fuel bed, which has been linked to increased fire frequency (Davies and Nafus 2013). This increase in fire frequency has numerous negative impacts on sagebrush-steppe communities, including decreased species biodiversity, increased soil erosion, and reduced forage for cattle and sheep (Knapp 1996). Invasion by AG is also associated with lower quality litter for microbial activity (e.g., higher carbon:nitrogen and lignin:nitrogen) leading to lower mineralization rates (Evans et al. 2001; Rimer 1998; Taylor et al. 1989).

The role that litter plays in facilitating or inhibiting further invasion by AG into sagebrush-steppe communities is equivocal because results from litter manipulation studies are often contradictory (Evans and Young 1970; Evans et al. 2001; Gill and Burke 1999; Sperry et al. 2006). The ambiguity occurs, in part, because the quality and quantity of litter varies intra- and inter-annually in shrub-steppe ecosystems. For example, in spring, the residual litter that was originally deposited from the previous growing season is typically pressed flat to the ground, partially decomposed, and depleted of easily digestible compounds (Whalen and Sampedro 2009). This relatively low-quality litter in springtime often still contains a pool of organic nitrogen (N) that may be temporarily immobilized and unavailable for establishing seedlings, but may become available depending on other factors such as weather condition (Belnap and Phillips 2001; Scott and Binkley 1997; Stump and Binkley 1993). Precipitation and associated litter decomposition in sagebrush-steppe ecosystems primarily occur during winter. However, unusually dry winters combined with wet springs could influence the timing of decomposition, and thus the availability of soil N. In addition, the physical presence of a litter layer during springtime (albeit partially decomposed) affects soil temperature and moisture for germinating seedlings. Thus far, the majority of studies that manipulate litter biomass typically occur during fall, although the unique physiochemical properties of springtime litter may have different (yet important) influences on soil nutrient cycling and plant population dynamics. In particular, the quality and quantity of springtime litter may have a greater impact on AG compared to perennial grasses (PG) because AG do not have stored belowground resources, and are therefore, may be more reliant on current soil resources in springtime during their seedling stage (Booth et al. 2003).

Studies that examine the role of litter on ecosystem properties typically remove 100 % or add 2–3 times the existing litter layer (Dzwonko and Gawronski 2002; Patrick et al. 2008). While these extreme manipulations have yielded changes in nutrient availability, they may have a limited ecological relevance or management applicability. First, litter biomass may have large natural variation from year-to-year, but only large disturbance events such as fires completely eliminate the entire litter layer (Zavaleta et al. 2003). Second, complete removal of litter eliminates all chemical inputs that are unique to a species' aboveground litter quality (Dejong and Klinkhamer 1985).

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Third, while the addition of litter in large amounts tends to elicit soil and plant responses (Boeken and Orenstein 2001), these quantities are often impractical from a management perspective. Therefore, a series of partial removal treatments of litter would be more likely to identify any threshold values of litter cover that effectively inhibit or promote N cycling and vegetation production.

We conducted a study that repeatedly manipulated a gradient of partial litter removal treatments to understand the influence of litter on nutrient cycling and vegetation dynamics. We hypothesize that removal of springtime litter would decrease soil plant-available N during the subsequent summer and fall seasons due to a reduction in substrate for microbes, but the effects would be weather dependent (i.e., dependent on adequate precipitation). The reduction of plant-available N from litter removal would "trickle down" to the plant community, with greater effects in invaded communities and on AG than on PG. In addition, we conducted a post-hoc correlation analyses on the actual amount of litter biomass (both pre- and post-removal) to explore the importance of litter quantity in conjunction with litter source material on nutrient availability. We hypothesized that springtime litter biomass would be positively related to nutrient availability later into the growing season. In conducting this study, we aim to better understand the influences of litter on ecosystem processes in sagebrush-steppe communities, and how litter may promote or inhibit invasion by AG.

Methods

Study area

This study was located across southeastern Oregon within the High Desert and Humboldt Ecological Provinces in the northern Great Basin (43°24′–44°11′ N, 117°10′–119°43′W) (Davies et al. 2006). The primary native PG species were *Pseudoroegneria spicata* (Pursh) A. Love, *Achnatherum thurberianum* (Piper) Barkworth, *Poa secunda* J. Presl, and *Elymus elymoides* (Raf.) Swezey. The primary AG species was *B. tectorum*, with low amounts of *Eremopyrum triticeum* on some sites. The dominant native shrub species was *Artemisia tridentata* Nutt ssp. *wyomingensis* Beetle and Young. Climate typical of the northern Great Basin is characterized by warm, dry summers and cool, wet winters. During the five years of the study (2007–2011), the average air temperatures for each season were relatively close to the mean temperatures over the previous 18 years that data were collected at the nearby climate station, with the exception of unusually warm conditions in winter and spring 2010 (Online Resource 1; Fig. 1). Total precipitation was generally below average for each season of the study. Notably, there was relatively high precipitation during fall 2007, summer 2009, and spring 2011 compared to other seasons of the study (Online Resource 1; Fig. 1). Elevation of the study sites ranged between 780 and 1450-m above sea level. Bureau of Land Management records indicate no

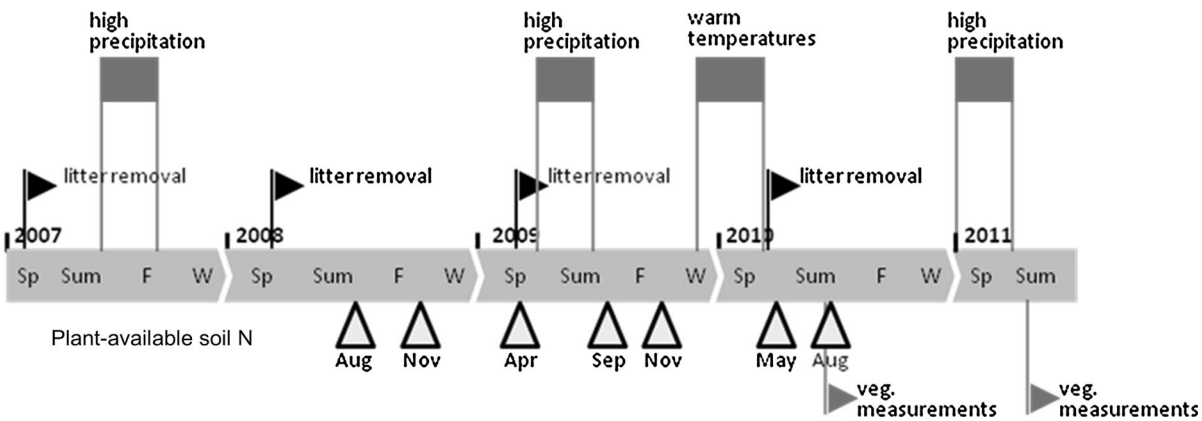

Fig. 1 A timeline showing the litter removal treatments during spring (*black flags*), seven measurements of nitrogen (N) availability (*light gray triangles* with month of sampling), and two vegetation measurements (*gray flags*). Periods of unusually high precipitation and warm temperatures are shown as *gray bars* above the timeline. The seasons spring (Sp), summer (Sum), fall (F), and winter (W) are embedded for each year within the timeline

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recorded fire history or other disturbances at any of the sites. Soils were also variable across the study sites and included Aridisols, Mollisols, and Andisols (Davies and Bates 2010).

Experimental design and procedures

We selected three plant community types based on the relative levels of AG invasion: (1) highly invaded communities with near monocultures of AG, (2) mixed communities of approximately 50:50 ratio of AG to PG, and (3) native PG communities with minimal AG invasion (0–4 % AG cover). Each community type was replicated three times for a total of nine sites (three sites per community). The sites averaged within 90 km of each other and were chosen to have similar attributes (e.g., slope, aspect, etc.). Shrub cover averaged 0–1, 5–10, and 5–15 % in the invaded, mixed, and native communities, respectively. Five blocks were established at each site in an area that was relatively uniform in production, land use, and community composition. Within each block, we established five plots that measured 2 × 2 m with a 1 m buffer between each plot. Each plot randomly received one of the five treatment levels of litter removal [unmanipulated (0), 25, 50, 75, and 100 percent removed by weight]. The control that we applied in this study was an "unmanipulated" control to identify any experimental artifacts from raking. In each plot, all litter (woody and non-woody) was removed by carefully raking all ground litter that was unattached to live or dead plant material. Due to the different qualities of woody and non-woody litter (and its potential impact on the response variables), we separated these two litter pools and weighed them separately, then removed an equal proportion of each litter type according to the treatment level, and then returned the remaining fraction of litter to the plots. Litter removal treatments were initiated in spring (April) 2007 and continued once each spring until 2010 (Fig. 1). The total quantities of litter biomass that were removed across all plots from the 25, 50, 75, and 100 % removal treatments were 39.8 ± 3.9, 67.2 ± 5.1, 72.5 ± 7.7, and 89.5 ± 9.7 g m^{-2}, respectively, (data not shown; removal treatment: $F_{3,164} = 19.92$, $P < 0.001$), and there were no significant interactions between removal and year or community type.

Soil plant-available nitrogen

Measurements of plant-available N allowed us to assess changes that were occurring in the N cycle with our litter manipulations and to quantify correlations/covariations with litter biomass and vegetation cover (Blank et al. 2007). Ion-exchange resin bags (14 × 14 mm) were used to assess nitrate (NO_3^--N) and ammonium (NH_4^+-N) availability in each of the plots. Resin bags simulate bioavailability in that they capture soil nutrients over time, including nitrate and ammonium, via diffusional transport around the buried bag. Factors such soil water content influence how far soil nutrients can diffuse. For example, nutrient transport to roots increases as soil water content increases, and similarly, more nutrients are captured in resin bags that are buried in soils with high water content. We added 10 g of ion exchange resin beads (Sigma-Aldrich) in each bag and tied off the top with a 27 cm nylon zip-tie that protruded from the soil when it was buried. Using a hori–hori knife, three square-shaped soil plugs were cut approximately 10 cm deep. At an angle, a slice was cut from the wall of each hole, making a shelf for the resin bag to sit on with undisturbed soil above it; the resin bags were placed on the shelf and the soil plugs were replaced back into each hole. The resin bags were removed prior to saturation of resin every 60–150 days (depending on accessibility to plots) from each plot and a new bag was deployed; the location of each bag within the plot was marked to avoid subsequent resin bags being placed in the same position. During the course of the study, resin bags were deployed to each site on seven sampling dates from March 2008 to August 2010 (Fig. 1), giving a total of 4725 resin capsules (3 capsules $plot^{-1}$ × 5 plots × 5 blocks × 9 sites × 7 sampling events). After recovery, each resin-bag was washed with deionized water and shipped to the USDA-Agricultural Research Service Soils Laboratory (Reno, Nevada) for analysis. Each resin bag was placed in a 50 mL polypropylene tube with 30 mL of 1.5 M KCl; the tubes were shaken to desorb NH_4^+-N, NO_2^--N, and NO_3^--N. Tubes were centrifuged at 3000×*g* for 5 min and then decanted into glass autosampler tubes. A Lachat® auto-analyzer was used to quantify NH_4^+-N and NO_2^--N + NO_3^--N (QuikChem). Standards were made using NIST-certified 1000 ppm. Raw NH_4^+-N and NO_3^--N data were then converted to a molar basis by dividing

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by the molecular weight of each moiety. To compare data among sampling times, converted data were divided by the number of days that the resins bags were in the soil, thus, the final data are expressed as μmol capsule^{-1} day^{-1}. Total mineral N was calculated by adding molar units of NH_4^+-N and NO_3^-N.

Vegetation sampling

We sampled the vegetation of each plot in August 3, 2010 and June 27, 2011 (Fig. 1). We visually estimated canopy cover (%) for each species within two randomly located 25 × 50 cm frames in each plot. Density of individuals (stems m^{-2}) was sampled by counting the number of grass tillers within each frame. Aboveground plant biomass (g m^{-2}) was harvested after each sampling, separated by species, dried at 60 °C for 48 h, and weighed. Cover, density and biomass measurements occurred on different areas of the plots in 2010 and 2011.

Data analysis

We used a three-factor, mixed-model analysis of variance (ANOVA) with repeated measures (SAS v9.3) to determine the effects of litter removal, community type, and time on plant-available N and vegetation cover, density and biomass over the course of the study. The between-subject fixed factors included removal treatment (25, 50, 75, or 100 %) and community type (invaded, mixed, or native), and the within-subject fixed factor was time (7 sampling events for plant-available N or 2 years for vegetation; Fig. 1). The sites (three per community), blocks (five per site) and plots (five per block) were random factors in each test; repeated measures occurred at the plot level.In addition, we conducted two-factor ANOVAs to determine effects of removal and community type on plant-available N for each of the sampling dates separately to better understand under which conditions litter removal may be especially important to plant-available N. The unmanipulated plots were not exposed to the same experimental artifacts as the treated plots, and were therefore not included in statistical analyses.

We used Pearson's correlation coefficients to correlate litter biomass and plant-available N (alpha = 0.01 for significance). For values of litter biomass, we used data from the original total biomass prior to the removal treatments, and also of the total litter biomass that remained on the plots after removal (pre-removal and post-removal, respectively). For values of plant-available N, we used data from each of the sampling dates that occurred several months before, during or after each of the three spring litter removal treatments. Litter biomass data from 2007 were not used for analyses because corresponding values of plant-available N were not available until the first sampling event in August 2008. The goal of the correlation analyses was to investigate overall trends, differences, and strengths of relationships among communities and litter types.

The influence of springtime litter biomass on vegetation dynamics could either be "direct" (through impacts on micro-climate) or "indirect," through its influence on plant-available N (which in turn impacts plant production) (see Fig. 2a for a conceptual model). We used a structural equation model to determine the total (direct plus indirect) effect of litter biomass on grass production in each of the three community types with the maximum likelihood as the estimation method (AMOS v.18). We separated litter into its woody and non-woody 2010 biomass components, plant-available N into nitrate and ammonium from the 2010 springtime sampling (May 2010), and vegetation into AG and PG biomass from 2010. Litter biomass was considered exogenous and plant-available N and grass biomass were endogenous variables. The goal of our structural equation model was to confirm a specific hypothesized set of relationships, so we did not alter or remove non-significant paths from the models.

Results

Litter removal treatment

Plant-available N was generally influenced most by time, and exhibited greater temporal fluctuations in the invaded compared to the native or mixed communities (Fig. 3), leading to a community × time interaction (Table 1). There were no overall effects of the removal treatments on plant-available N, however, there was a significant increase in total mineral N and nitrate with removal in all three communities during the November 2009 measurement only (nitrate: $F_{3,11} = 5.84$, $P < 0.001$; Fig. 4).

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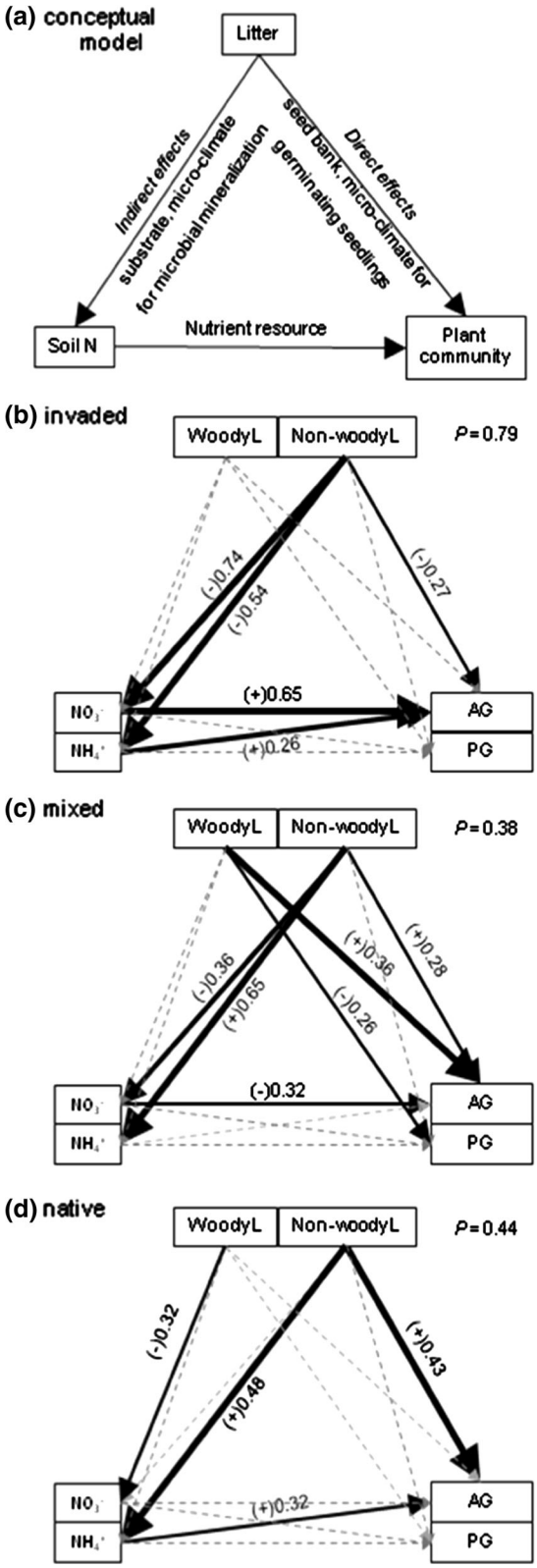

◀ **Fig. 2** *Top panel* (**a**) A conceptual model describing the relationship between plant litter and the plant community. Plant litter can influence the plant community *directly* as ground cover, which impacts the seed bank, as well as micro-climate conditions for germination and establishment of young seedlings. Plant litter can also affect the plant community *indirectly* by providing substrate or adjusting micro-climate conditions for microbial decomposition, which convert organic nitrogen (N) to plant-available inorganic nitrogen in soils. Bottom three panels (**b**–**d**): Comparison of three structural equation models from (**b**) invaded, (**c**) mixed, and (**d**) native communities describing the effects of 2010 woody and non-woody litter (L) biomass on nitrate (NO_3^-) and ammonium (NH_4^+) availability in spring 2010, and on annual (AG) and perennial (PG) grass biomass in 2010. Non-significant *P* values (>0.05) on each panel indicate that the data did not significantly diverge from the model. Solid lines indicate significant relationships ($P < 0.05$); with thicker lines indicating lower *P*-values

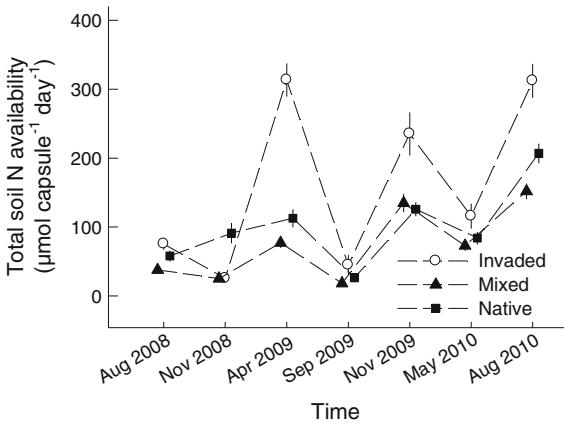

Fig. 3 Mean (±SE) values of total soil nitrogen (N) availability (µmol capsule^{-1} day^{-1}) from seven sampling dates from summer 2008 to winter 2010 in three plant communities that were comprised of invasive annual grasses, primarily *Bromus tectorum* (*dashed open circle*, Invaded), native species, primarily *Pseudoroegneria spicata*, and other perennial bunch grasses (*dashed filled square*, Native), and a mix of invasive and native species (*dashed filled triangle*, Mixed). Data points are averaged across all removal treatments because there were no overall differences in soil N availability across all sampling dates from the removal treatments. Significant effects and interactions among the communities and time follow ANOVA results in Table 1

Biomass, density, and cover of AG and PG differed among communities and years, with all communities having consistently higher values in 2011 compared to 2010 (Table 2). There were no main effects of litter removal on vegetation; however, both AG and PG grass cover were influenced by the interaction of removal × community × year (Table 2). This three-

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Table 1 Seasonal and annual variation in soil nitrogen availability in three shrub-steppe community types with differing levels of annual grass invasion

	Total nitrogen		Ammonium		Nitrate	
	F	*P*	*F*	*P*	*F*	*P*
Removal (*R*)	0.00	0.999	0.57	0.635	1.81	0.148
Community (*C*)	0.65	0.553	0.25	0.784	0.73	0.518
Time (*T*)	7.94	0.217	**38.16**	**<0.001**	**210.69**	**<0.001**
$R \times C$	0.19	0.980	0.16	0.987	0.44	0.850
$R \times T$	0.00	0.969	0.75	0.756	0.47	0.972
$C \times T$	**11.41**	**<0.001**	**8.47**	**<0.001**	**12.88**	**<0.001**
$R \times C \times T$	0.40	0.999	0.51	0.993	0.36	0.999

Results from repeated measures ANOVA (*F* and *P* values) testing for the effects of litter removal (*R*) (25, 50, 75, or 100 % removed), plant community type (*C*) (invaded, mixed, and native) and time (*T*) (seven sampling dates from 2008 to 2010) on availability of total soil nitrogen, ammonium and nitrate (μmol capsule^{-1} day^{-1}). Total nitrogen was calculated as the sum of ammonium and nitrate. Significant effects ($P < 0.05$) are in bold text

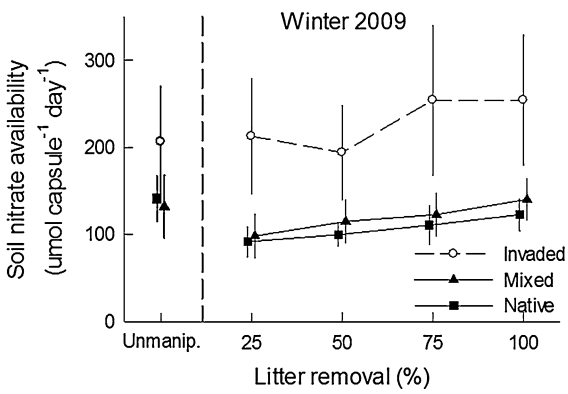

Fig. 4 The effect (mean ± SE) of litter removal (25, 50, 75, or 100 % removed) on nitrate availability (μmol capsule^{-1} day^{-1}) from three plant communities that were comprised of invasive grasses, primarily *Bromus tectorum* (*dashed open circle*, Invaded), native species, primarily *Pseudoroegneria spicata,* and other perennial bunch grasses (*dashed filled square*, Native), and a mix of invasive and native species (*dashed filled triangle*, Mixed) during Winter 2009. An unmanipulated plot (unmanip.) was used to assess experimental artifacts of the removal treatment

way interaction appeared to be the result of a stronger effect of removal in the mixed compared to invaded or native communities, with removal having negative effects on AG cover in 2010 and on PG cover in 2011. These effects of removal caused the ratio of AG to PG (AG:PG) in the mixed community to decrease with removal in 2010 and increase in 2011, leading to a significant interactive effect of removal × year on AG:PG (Fig. 5; AG:PG cover: $F_{3,56} = 4.46$, $P = 0.007$; biomass: $F_{3,56} = 3.99$, $P = 0.012$; density: $F_{3,56} = 2.66$, $P = 0.057$).

Pearson's correlation coefficients and structural equation modeling

In general, there were more and stronger significant relationships (both positive and negative) between plant-available N and the pre-removal litter biomass compared to the post-removal biomass in all communities (Online Resource 2). Specifically, there were 14 significant relationships with pre-removal biomass compared to 4 with post-removal biomass. Also, there were more relationships between plant-available N and non-woody compared to woody litter biomass across communities (data not shown). In the invaded community, plant-available N and litter biomass tended to have negative relationships (i.e., decreasing plant-available N with the increasing litter biomass), with particularly strong relationships (highest r^2 values) during spring 2010 (Online Resource 2).

Our structural equation models consistently demonstrated a good fit to the data in all three communities as indicated by non-significant *P* values (Fig. 2b–d). The three community types had unique relationships among litter, nutrients, and vegetation, with the majority of relationships occurring with non-woody (but not woody) litter. In the invaded community (Fig. 2b), non-woody litter biomass had a negative effect on AG biomass, which primarily occurred indirectly through the negative effect of litter on plant-available ammonium and nitrate. In the native community (Fig. 2d), there were positive (mostly direct) effects of non-woody litter on AG biomass. In the mixed community (Fig. 2c), plant-available nitrate was negatively related to AG

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Table 2 Effects of litter biomass removal on annual and perennial grasses in three shrub-steppe communities with differing levels of invasion after a dry year (2010) and wet year (2011)

	Annual grass biomass		Annual grass density		Annual grass cover		Perennial grass biomass		Perennial grass density		Perennial grass cover	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Removal (*R*)	1.97	0.181	1.33	0.265	0.97	0.412	0.94	0.423	0.91	0.437	0.38	0.766
Community (*C*)	**45.84**	**<0.001**	**38.94**	**<0.001**	**31.54**	**<0.001**	**10.83**	**0.003**	**33.38**	**<0.001**	**33.34**	**<0.001**
Years (*Y*)	**101.81**	**<0.001**	**24.42**	**<0.001**	**37.50**	**<0.001**	**46.08**	**<0.001**	**25.29**	**<0.001**	**13.63**	**<0.001**
$R \times C$	1.18	0.319	0.88	0.451	0.63	0.598	0.27	0.846	0.13	0.943	0.35	0.789
$R \times Y$	2.53	0.061	2.38	0.074	1.85	0.143	2.08	0.107	1.15	0.333	1.37	0.255
$C \times Y$	**66.90**	**<0.001**	**35.85**	**<0.001**	**17.29**	**<0.001**	2.55	0.113	**4.80**	**0.031**	0.58	0.449
$R \times C \times Y$	1.57	0.158	**3.09**	**0.030**	**2.98**	**0.034**	2.68	0.051	1.92	0.131	**2.97**	**0.035**

Results from a three-factor ANOVA (*F* and *P* values) testing for the effects of litter removal (*R*) (25, 50, 75, or 100 % removed), plant community type (*C*) (invaded, mixed, and native) and year (*Y*) (2010, 2011) on the biomass (g m^{-2}), density (stems m^{-2}), and cover (%) of annual and perennial grasses. Significant effects ($P < 0.05$) are in bold text

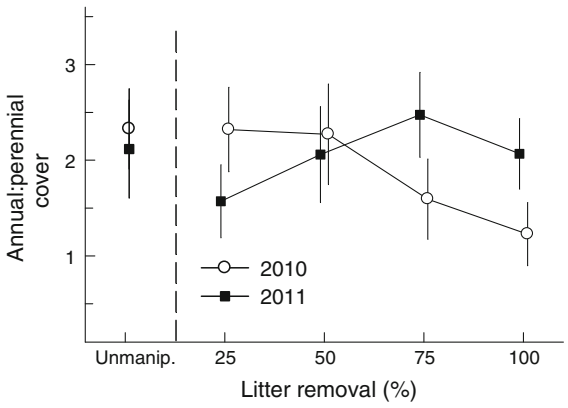

Fig. 5 The effect (mean ± SE) of litter removal (25, 50, 75, or 100 % removed) on the ratio of annual to perennial cover in a warm and dry year (*dashed open circle* 2010) compared to a cool and wet year (*dashed filled square* 2011) in plant communities that were comprised of a mix of native and invasive species. An unmanipulated plot (unmanip.) was used to assess experimental artifacts of the removal treatment

biomass, but non-woody litter negatively affected nitrate, so the net effect was minimal on AG biomass. Unlike the invaded or native communities, woody litter had significant effects only in the mixed community (Fig. 2c) by having a positive relationship with AG biomass and a negative relationship with PG biomass.

Discussion

Context-dependent effects of litter on soil nutrient availability and vegetation are very common in litter manipulations studies, making broad generalizations difficult to synthesize (Xiong and Nilsson 1999). Nevertheless, it is critical to have a comprehensive understanding of the litter cycle because it is directly linked to the nutrient, water and carbon cycles, energy flow, and microbial, detritivore, herbivore, and plant communities (Facelli and Pickett 1991a).

Litter and plant-available nitrogen

There were minimal effects of litter removal on soil plant-available N across all sampling dates over the study period, which generally supported results of previous studies (Sayer and Tanner 2010; Villalobos-Vega et al. 2011). Springtime litter had the potential to influence nutrient availability from its impact on micro-climate (i.e., from its physical presence) and its chemical composition (i.e., from residual organic N). However, despite these potential physiochemical contributions of springtime litter on plant-available N, the impacts were small, likely due to complete (or near complete) decomposition that occurs during the fall and winter seasons. Nevertheless, our results do not suggest that litter quantity is inconsequential to ecosystem processes, but that the weather during the litter removal treatments was an interacting element affecting plant-available N. For example, in winter 2009, plant-available N *increased* linearly with removal of litter in all three communities (Fig. 4), contrary to other sampling events. This impact of removal occurred after the wettest summer of the study (by threefold the average summer precipitation).

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Increased light penetration and soil temperatures from litter removal coupled with moist soils provided more favorable condition for microbial activity, leading to increased plant-available N (Fierer and Schimel 2002; Wang et al. 2011). In drier years, removal of springtime litter may have also increased soil temperatures, but without adequate moisture, microbial activity was apparently unaffected (Eviner et al. 2006).

Despite few overall effects of litter removal on plant-available N, there were notable correlative relationships between litter biomass and plant-available N. However, contrary to our hypothesis, springtime litter biomass after each of the removal treatments (post-removal litter) had relatively weak relationships with plant-available N, particularly compared to litter biomass prior to removal (pre-removal). The quantity and quality of pre-removal litter biomass in spring is largely influenced by the amount of litter accumulated in the fall and the rates of litter decomposition during winter, which were not measured directly in the current study. Nevertheless, the continued relationships between the pre-removal litter biomass and plant-available N indicate legacy effects of the previous year's litter cycle on soil properties that could continue for up to one year. These legacy effects could explain why our removal treatment did not exert stronger influences on plant-available N. It appears that the long residence of the litter on the ground allowed sufficient time for its physiochemical influences to persist even after our removals, demonstrating a long afterlife effect of plants on their habitats (Wardle et al. 1997).

Annual grasses have different seasonal phenology than native PGs and shrubs, and thus may affect the mineralization of N over the season differently than in native communities (Jackson et al. 1988). We observed much greater temporal fluctuations in plant-available N in the invaded communities than in the mixed or native communities (Fig. 3). Semi-arid climates have high seasonal variation in temperature and precipitation, leading to naturally high levels of temporal variation in soil N mineralization rates (Parker et al. 1984). Additional variation in soil nutrient dynamics from invasion by AG could decrease ecosystem stability, and drive the system to a new stable state (Scheffer et al. 2001).

There were also large differences among the plant communities in how the quantity of litter biomass related to plant-available N. In general, as litter biomass increased, available N decreased in the invaded community, but not in the mixed or native communities. These differing trends were likely driven by differences in functional plant traits (Castro-Díez et al. 2012; Cornwell et al. 2008; Godoy et al. 2010; Hobbie 1992), which in turn affected the litter quality and microbial community (Hawkes et al. 2005). Invasion by *Bromus tectorum*, one of the most widespread AG species in semi-arid land of the western USA, has been shown to decrease N mineralization through the addition of low-quality litter (Evans et al. 2001; Rimer 1998; Taylor et al. 1989), which could explain the negative relationships that we observed of litter biomass with plant-available N in heavily invaded communities.

Litter and vegetation

Removal of the litter layer during springtime had a greater influence on vegetation patterns than on plant-available N, as observed in other studies also (Pan et al. 2011), but is not ubiquitous across all studies in grassland or shrub-steppe communities (Hayes and Holl 2003; Patrick et al. 2008). In our study, the influences from 4-year litter manipulations on grass production and community composition were highly dependent on weather and on community type (Dzwonko and Gawronski 2002; Ogle et al. 2003; Suding and Goldberg 1999). Among the three community types, the strongest influences of litter removal primarily occurred in the mixed community, but not heavily invaded or native community. Within the mixed community, during the relatively warm and dry year of 2010, removal of 75 % or more litter had negative effects on AG cover, similar to studies in grasslands (Pan et al. 2011; Wang et al. 2011; Wolkovich et al. 2009). This suggests that litter removal could be more important for controlling AG during dry years, which are expected to increase in frequency with climate change (Chambers and Pellant 2008). In contrast, 2011 was a cool and wet year compared to 2010 (spring temperatures was about 15 °C cooler and with twice as much precipitation), and the same removal treatments (75 % or more) had strong negative effects on PG, although the reason is less clear. Also during 2011, there were no removal treatments, meaning that the impacts on vegetation were not related to short-term changes in micro-

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climate, but instead appeared to be legacy effects due to slower responses of PG from the previous years' growing conditions and litter manipulations. While few studies have reported post-manipulation effects of litter (Wolkovich et al. 2009), they could be related here to longer-term influences on macro-detritivore and the microbial community (Mayer et al. 2005).

Our structural equation model illustrates how litter biomass can influence vegetation either directly (through changes in micro-climate), or indirectly through its effects on plant-available N (Fig. 2); each of our three plant community types responded quite differently to litter biomass manipulation. In the invaded community, there was a negative effect of AG litter on AG biomass, which was primarily mediated through a negative effect of AG litter on plant-available N. While this negative relationship is supported by other studies (Amatangelo et al. 2008), it is also contrary to other reports in the literature that indicate a positive feedback between non-native litter and non-native species abundance (Wolkovich et al. 2009). The native and mixed communities had nearly opposite trends compared to the invaded community, with litter from PG and shrubs having positive influences on AG. These positive impacts of PG and shrub litter on AG biomass could contribute to an increased rate of invasion by AG into native sagebrush communities. These data reveal how litter source (and corresponding quality) is critical in determining the direction and magnitude of its impact on plant community composition (Quested and Eriksson 2006).

Our unique design of partial removal treatments showed that a minimum quantity of litter removal was necessary (75 %) to elicit any responses in community composition, whereas removal of springtime litter had limited, weather-dependent effects on plant-available N. Litter source material and litter biomass were important drivers of community composition, with litter from invaded communities having negative impacts on AG production. These relationships between litter, nutrients, vegetation, and weather have many ecological and management implications. First, our results indicate that removal of any residual organic N in springtime litter does not explicitly reduce the pool of plant-available N in the soil, suggesting that decomposition processes occurring during fall and winter effectively mobilize and transfer that majority of N out of the litter layer. Second, in recent years there has been a growing interest in how the functional traits of plants carry over to their litter after death, which impacts their decomposability and associated nutrient cycling (Freschet et al. 2012). We demonstrate how litter from the previous year can have legacy effects for at least one year post-removal on both plant-available N and community composition. Moreover, the legacy effects of litter appeared to be dependent largely on seasonal precipitation, highlighting the complex relationship between litter and the climate. Also, highly invaded communities were negatively impacted by their own litter indirectly through their negative impacts on soil nutrients. This confirms that management of invaded systems can be accomplished through management of soil nutrients, but only in specific community types. In contrast, litter from non-invaded communities appeared to facilitate AG production, which could quicken a rapid replacement of "desired" species with invasives (Sheley et al. 2010). Our study supports the importance of litter source, but also incorporates the influences of litter quantity and weather, thus providing a framework to account for multiple factors in developing a comprehensive assessment of the role of litter on ecosystem processes.

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References

Amatangelo KL, Dukes JS, Field CB (2008) Responses of a California annual grassland to litter manipulation. J Veg Sci 19:605–612

Belnap J, Phillips SL (2001) Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. Ecol Appl 11:1261–1275

Blank RR, Chambers J, Roundy B, Whittaker A (2007) Nutrient availability in rangeland soils: influence of prescribed burning, herbaceous vegetation removal, overseeding with *Bromus Tectorum*, season, and elevation. Rangel Ecol Manage 60:644–655

Boeken B, Orenstein D (2001) The effect of plant litter on ecosystem properties in a Mediterranean semi-arid shrubland. J Veg Sci 12:825–832

Booth MS, Caldwell MM, Stark JM (2003) Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. J Ecol 91:36–48

Author's personal copy

Castro-Díez P, Fierro-Brunnenmeister N, González-Munoz N, Gallardo A (2012) Effects of exotic and native tree leaf litter on soil properties of two contrasting sites in the Iberian Peninsula. Plant Soil 350:179–191

Chambers JC, Pellant M (2008) Climate change impacts on northwestern and intermountain United States rangelands. Rangelands 30:29–33

Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Perez-Harguindeguy N, Quested HM, Santiago LS, Wardle DA, Wright IJ, Aerts R, Allison SD, Bodegom PV, Brovkin V, Chatain A, Callaghan TV, Diaz S, Garnier E, Gurvich DE, Kazakou E, Klein JA, Read J (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol Lett 11:1065–1071

Davies KW, Bates JD (2010) Vegetation characteristics of mountain and Wyoming big sagebrush plant communities in the northern Great Basin. Rangel Ecol Manage 63:461–466

Davies KW, Nafus AM (2013) Exotic annual grass invasion alters fuel amounts, continuity and moisture content. Int J Wildland Fire 22:353–358

Davies KW, Bates JD, Miller RF (2006) Vegetation characteristics across part of the Wyoming big sagebrush alliance. Rangel Ecol Manage 59:567–575

Dejong TJ, Klinkhamer PGL (1985) The negative effects of litter of parent plants of *Cirsium vulgare* on their offspring: autotoxicity or immobilization? Oecologia 65:153–160

Dzwonko Z, Gawronski S (2002) Influence of litter and weather on seedling recruitment in a mixed oak-pine woodland. Ann Bot 90:245–251

Evans RA, Young JA (1970) Plant litter and establishment of alien annual weed species in rangeland communities. Weed Sci 18:697–703

Evans RD, Rimer R, Sperry L, Belnap J (2001) Exotic plant invasion alters nitrogen dynamics in an arid grassland. Ecol Appl 11:1301–1310

Eviner VT, Chapin FS, Vaughn CE (2006) Seasonal variations in plant species effects on soil N and P dynamics. Ecology 87:974–986

Facelli JM, Pickett STA (1991a) Plant litter: its dynamics and effects on plant community structure. Bot Rev 57:1–32

Facelli JM, Pickett STA (1991b) Plant litter: light interception and effects on an old-field plant community. Ecology 72:1024–1031

Fierer N, Schimel JP (2002) Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. Soil Biol Biochem 34:777–787

Freschet GT, Aerts R, Cornelissen JHC (2012) A plant economics spectrum of litter decomposability. Funct Ecol 26:56–65

Gill RA, Burke IC (1999) Ecosystem consequences of plant life form changes at three sites in the semiarid United States. Oecologia 121:551–563

Ginter DL, McLeod KW, Sherrod C (1979) Water stress in longleaf pine induced by litter removal. For Ecol Manage 2:13–20

Godoy O, Castro-Díez P, Van Logtestijn RSP, Cornelissen JHC, Valladares F (2010) Leaf litter traits of invasive species slow down decomposition compared to Spanish natives: a broad phylogenetic comparison. Oecologia 162:781–790

Hawkes CV, Wren IF, Herman DJ, Firestone MK (2005) Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecol Lett 8:976–985

Hayes GF, Holl KD (2003) Site-specific responses of native and exotic species to disturbances in a mesic grassland community. Appl Veg Sci 6:235–244

Hobbie SE (1992) Effects of plant species on nutrient cycling. Trends Ecol Evol 7:336–339

Jackson L, Strauss R, Firestone M, Bartolome J (1988) Plant and soil nitrogen dynamics in California annual grassland. Plant Soil 110:9–17

Knapp PA (1996) Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert: history, persistence, and influences to human activities. Glob Environ Change 6:37–52

Knapp AK, Seastedt TR (1986) Detritus accumulation limits productivity of tallgrass prairie. Bioscience 36:662–668

Mayer PM, Tunnell SJ, Engle DM, Jorgensen EE, Nunn P (2005) Invasive grass alters litter decomposition by influencing macrodetritivores. Ecosystems 8:200–209

Ogle SM, Reiners WA, Gerow KG (2003) Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairie. Am Midl Nat 149:46–58

Pan JJ, Ammerman D, Mitchell RJ (2011) Nutrient amendments in a temperate grassland have greater negative impacts on early season and exotic plant species. Plant Ecol 212:853–864

Parker LW, Santos PF, Phillips J, Whitford WG (1984) Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan desert annual, *Lepidium lasiocarpum*. Ecol Monogr 54:339–360

Patrick LB, Fraser LH, Kershner MW (2008) Large-scale manipulation of plant litter and fertilizer in a managed successional temperate grassland. Plant Ecol 197:183–195

Quested H, Eriksson O (2006) Litter species composition influences the performance of seedlings of grassland herbs. Funct Ecol 20:522–532

Rimer RL (1998) The influence of plant invasion and surface disturbance on nitrogen cycling in a cold desert ecosystem. University of Arkansas, Fayetteville

Sayer EJ (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol Rev 81:1–31

Sayer EJ, Tanner EVJ (2010) Experimental investigation of the importance of litterfall in lowland semi-evergreen tropical forest nutrient cycling. J Ecol 98:1052–1062

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Scott NA, Binkley D (1997) Foliage litter quality and annual net N mineralization: comparison across North American forest sites. Oecologia 111:151–159

Sheley R, James J, Smith B, Vasquez E (2010) Applying ecologically based invasive-plant management. Rangel Ecol Manage 63:605–613

Sperry LJ, Belnap J, Evans RD (2006) *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. Ecology 87:603–615

Stump LM, Binkley D (1993) Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Can J For Res 23:492–502

Suding KN, Goldberg DE (1999) Variation in the effects of vegetation and litter on recruitment across productivity gradients. J Ecol 87:436–449

Author's personal copy

Taylor BR, Parkinson D, Parsons WFJ (1989) Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70:97–104

Villalobos-Vega R, Goldstein G, Haridasan M, Franco AC, Miralles-Wilhelm F, Scholz FG, Bucci SJ (2011) Leaf litter manipulations alter soil physicochemical properties and tree growth in a Neotropical savanna. Plant Soil 346:385–397

Wang J, Zhao ML, Willms WD, Han GD, Wang ZW, Bai YF (2011) Can plant litter affect net primary production of a typical steppe in Inner Mongolia? J Veg Sci 22:367–376

Wardle DA, Bonner KI, Nicholson KS (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79:247–258

Whalen JK, Sampedro L (2009) Soil Ecology and Management. CAB International, Cambridge

Wolkovich EM, Bolger DT, Cottingham KL (2009) Invasive grass litter facilitates native shrubs through abiotic effects. J Veg Sci 20:1121–1132

Xiong SJ, Nilsson C (1999) The effects of plant litter on vegetation: a meta-analysis. J Ecol 87:984–994

Xiong YM, Xia HX, Li ZA, Cai XA, Fu SL (2008) Impacts of litter and understory removal on soil properties in a subtropical *Acacia mangium* plantation in China. Plant Soil 304:179–188

Zavaleta ES, Shaw MR, Chiariello NR, Thomas BD, Cleland EE, Field CB, Mooney HA (2003) Grassland responses to three years of elevated temperature, CO_2, precipitation, and N deposition. Ecol Monogr 73:585–604