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Soil nutrient additions increase invertebrate herbivore abundances, but not herbivory, across three grassland systems

Kimberly J. La Pierre[1,2] · Melinda D. Smith[3]

Abstract Resource availability may influence invertebrate communities, with important consequences for ecosystem function, such as biomass production. We assessed: (1) the effects of experimental soil nutrient additions on invertebrate abundances and feeding rates and (2) the resultant changes in the effects of invertebrates on aboveground plant biomass at three grassland sites spanning the North American Central Plains, across which plant tissue chemistry and biomass vary. Invertebrate communities and rates of herbivory were sampled within a long-term nutrient-addition experiment established at each site along the broad Central Plains precipitation gradient. Additionally, the effects of invertebrates on aboveground plant biomass were determined under ambient and elevated nutrient conditions. At the more mesic sites, invertebrate herbivore abundances increased and their per capita rate of herbivory decreased with nutrient additions. In contrast, at the semiarid site where plant biomass is low and plant nutrient concentrations are high, invertebrate herbivore abundances did not vary and per capita rates of herbivory increased with nutrient additions. No change in the effect of invertebrate herbivores on aboveground plant biomass was observed at any of the sites. In sum, nutrient additions induced shifts in both plant biomass and leaf nutrient content, which altered invertebrate abundances and feeding rate. However, due to the inverse relationship between changes in herbivore abundance and per capita rates of herbivory, nutrient additions did not alter the effect of invertebrates on aboveground biomass. Overall, we suggest that this inverse response of herbivore abundance and per capita feeding rate may buffer ecosystems against changes in invertebrate damage in response to fluctuations in nutrient levels.

Keywords Nitrogen · Per capita herbivory rate · Phosphorus · Plant tissue chemistry · Central Plains

Communicated by Andreas Prinzing.

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Introduction

It is well known that increased soil nutrient availability alters plant biomass production and tissue chemistry (Elser et al. 2000b; Cleland and Harpole 2010). Additionally, the invertebrate community is also affected by soil nutrient availability (Throop and Lerdau 2004; Cleland et al. 2006; Hartley et al. 2007; Schmitz 2008b; Cronin et al. 2010; Loaiza et al. 2011; Blue et al. 2011). Invertebrate herbivores may respond to changes in the quantity (i.e., biomass) of vegetation with soil nutrient alteration, due to limitation by the absolute amount of food available (Chase et al. 2000; Throop and Lerdau 2004; Schmitz 2008b; Borer et al. 2012) or alterations in predatory pressure in areas with higher vegetation density (Schmitz 2008a; Chen et al. 2010). Additionally, invertebrate herbivores may be influenced by shifts in plant tissue chemistry with nutrient

additions, as nutrient availability in their food source affects their ability to meet their nutritional needs (Sterner et al. 1992; Huxel 1999; Elser et al. 2000b; Forkner and Hunter 2000; Throop and Lerdau 2004; Berner et al. 2005; Hall 2009; Chen et al. 2010). Although sometimes set up as a dichotomy, plant biomass and tissue chemistry both likely have effects on invertebrate community composition and feeding rates. Understanding the relative strengths of these effects is a key question, the elucidation of which would improve our understanding of the determinants of food web structure and the interactive effects of top-down and bottom-up forces on primary producers.

Importantly, examining only herbivore abundances may mislead the interpretation of the role that herbivores play in an ecosystem due to shifts in herbivore feeding strategies at different levels of resource limitation. Invertebrate herbivores may control their own level of resource limitation by altering their feeding strategies between areas with high- and low-quality food to obtain the necessary nutrients, either consuming more low-quality food (compensatory feeding) in areas with low resource availability or consuming less high-quality food (selective feeding) in areas with high nutrient availability (Mattson 1980; Behmer and Joern 1993, 2008; Chambers et al. 1995; Oedekoven and Joern 2000; Denno and Fagan 2003; Berner et al. 2005; Fink and von Elert 2006; Loaiza et al. 2008; Schmitz 2008b). Therefore, examining per capita rates of herbivory in combination with abundance data can improve understanding of the effects of invertebrate herbivores on ecosystem function under altered nutrient conditions. For example, the per capita rate of herbivory may be lower in nutrient-rich areas, as each individual herbivore is under relative resource limitation, and therefore can feed less and still overcome the mismatch between their own body chemistry and that of their food source (Elser et al. 2000a; Schmitz 2008b). Thus, although the abundances of herbivores may increase with nutrient additions, the overall effect of herbivores on the plant community may remain constant due to the decrease in the per capita rate of herbivory. In contrast, if herbivore abundances increase without a simultaneous shift in herbivore feeding rates (or vice versa), then the total amount of plant material consumed by herbivores would vary with nutrient additions. Consequently, the different feeding strategies employed by invertebrate herbivores in response to nutrient additions can have major impacts on important ecosystem processes, such as aboveground biomass (Fagan et al. 2002; Schmitz 2008b; Hall 2009). Whether such shifts in per capita feeding by invertebrate herbivores occur in natural systems remains an open question.

Changes in the abundances of invertebrate herbivores due to changes in plant tissue chemistry or biomass may in turn alter invertebrate trophic structure by affecting the abundance and feeding guild composition of secondary consumers (Siemann 1998; Denno et al. 2002; Haddad et al. 2009; de Sassi et al. 2012). The abundance of invertebrate predators and parasitoids may be closely linked to changes in the abundance of their prey (Throop and Lerdau 2004; Borer et al. 2005). Additionally, shifts in the composition of invertebrate herbivores may have consequences for specialist secondary consumers (Duffy et al. 2007). These changes in invertebrate secondary consumers can also have important cascading consequences for ecosystem functions, such as nutrient cycling and biomass production.

Here we address the effects of soil nutrient availability on: (1) invertebrate abundances and community composition, (2) invertebrate feeding rates, and (3) invertebrate effects on aboveground plant biomass. We hypothesized that the initial composition of the invertebrate community as well as the effects of nutrient additions on plant tissue chemistry [leaf percent carbon (%C) and percent nitrogen (%N)] and quantity (aboveground biomass) likely have a large effect on invertebrate abundances and trophic structure, invertebrate feeding rates, and ultimately the effects of invertebrate herbivores on aboveground plant biomass. We tested this hypothesis at three US Central Plains grassland sites among which plant tissue chemistry and biomass differ: shortgrass steppe (SGS), mixed-grass prairie (MIX), and tallgrass prairie (TGP).

We first examined the responses of invertebrate feeding guilds to nutrient additions. We used structural equation modeling (SEM) to examine the potential direct and indirect effects of the observed invertebrate feeding guild responses to soil nutrient additions by incorporating leaf %C and %N and aboveground biomass into the model. In general, leaf %N and aboveground biomass both increase with nutrient additions at all three sites studied here (McCulley et al. 2009). Based on these plant responses, we predicted that invertebrate herbivores and secondary consumers would increase in abundance with soil nutrient additions. Second, we examined the relationship between nutrient additions and invertebrate herbivore feeding rates by linking the amount of leaf tissue removed by leaf-chewing herbivores to both the abundances of leaf-chewing herbivores and their per capita rates of herbivory. We predicted that the abundances of leaf-chewing herbivores would increase with nutrient additions, but that the per capita amount of leaf tissue removed by leaf-chewing herbivores would decrease with nutrient additions, thus resulting in no net change in the total amount of leaf tissue removed. This result would be indicative of selective feeding by invertebrate herbivores. Finally, we examined the effects of invertebrate herbivores on aboveground biomass and whether these effects varied with soil nutrient additions. We predicted that invertebrate herbivores would have a limited effect on aboveground biomass, and that their effect on aboveground biomass would not vary with nutrient additions, based on the predictions of

changes in invertebrate herbivore abundances and per capita rates of feeding described above.

Materials and methods

Study system

The grasslands of the US Central Great Plains span a broad west-east precipitation gradient (318–835 mm average annual precipitation), with the majority (~70 %) of the rainfall occurring during the growing season at all three sites (Risser et al. 1981; Lauenroth and Burke 2008). Aboveground biomass and leaf tissue C:N are strongly correlated with precipitation across this gradient, both increasing from west to east (Milchunas et al. 1988; Adler and Levine 2007). This study focused on three grassland sites, located within shortgrass steppe [Shortgrass Steppe Long-Term Ecological Research Station (LTER), north-central Colorado; SGS]; southern mixed-grass prairie (Saline Experimental Range, western Kansas; MIX); and tallgrass prairie (Konza Prairie LTER, northeastern Kansas; TGP).

The SGS site receives an average of 318 mm precipitation year^{-1} and the plant community is comprised of a few shortgrass, forb, and shrub species, with the C$_4$ grass *Bouteloua gracilis* and C$_3$ sedge *Carex eleocharis* accounting for the majority of the plant cover (Risser et al. 1981; Lauenroth and Burke 2008). Plant species in SGS tend to have traits associated with resource conservation, and thus have relatively low C:N and biomass (Risser et al. 1981; McCulley et al. 2009). The MIX site is centrally positioned between the shortgrass and TGPs, and receives approximately 603 mm of annual precipitation (Adler and Levine 2007). Because it is composed of both short and tall grasses, mixed-grass prairie community composition can vary greatly depending on weather conditions, with tall grasses tending to dominate in wet years and short grasses performing better in dry years (Risser et al. 1981). The TGP site receives an average of 835 mm precipitation year^{-1} and is dominated by C$_4$ grasses such as *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium* (Risser et al. 1981; Knapp et al. 1998). Plant species in TGP tend to have traits associated with fast resource uptake and growth, and thus have relatively high C:N and biomass (Risser et al. 1981; Knapp et al. 1998; McCulley et al. 2009). The TGP site studied here was burned in the spring once every 2 years in odd years (2009, 2011 in this experiment).

Experimental design

At each site plots were set up in a randomized block design ($n = 3$) with eight treatment combinations per block [control, N, phosphorus (P), potassium plus micronutrients

(K), NP, NK, PK, NPK]. Plots are 25 m^2 (5 m × 5 m) with 1-m-wide aisles between each plot and 2-m-wide aisles between blocks. Treatments involve the addition of relatively high levels of N, phosphorous, and potassium, each applied at a rate of 10 g m^{-2} year^{-1}. These relatively high rates of nutrient application, which are comparable to those of previous studies at these sites, were used to ensure alleviation of nutrient limitation. These nutrient additions occurred once yearly at the start of the growing season (mid-April) from 2008 to 2012. N was added as ammonium nitrate during the first year of treatment and as time-release urea for the remainder of the experiment. P was applied as calcium phosphate and K as potassium sulfate. The micronutrient treatment involved the addition of Scott's Micromax fertilizer, which contains calcium (6 g m^{-2}), magnesium (3 g m^{-2}), sulfur (12 g m^{-2}), boron (0.1 g m^{-2}), copper (1 g m^{-2}), iron (17 g m^{-2}), manganese (2.5 g m^{-2}), molybdenum (0.05 g m^{-2}), and zinc (1 g m^{-2}). The micronutrient treatment was only applied during the first year of the experiment (2008) to prevent the build up of these elements in the soil, some of which are toxic to plants at high levels.

Beginning in May 2012, we examined the effects of invertebrate herbivores on aboveground biomass using cage exclosures within each plot at each site to exclude invertebrate herbivores. The exclosures were 0.25 m × 0.25 m at the base and 1 m tall at the TGP and MIX sites and 0.25 m tall at the SGS site. Each exclosure consisted of a wooden frame surrounded on all sides and the top by aluminum window screening with 18 × 16 mesh and 0.3 mm wire diameter. The screening was buried to a depth of 5 cm on all sides to prevent access by invertebrates and all invertebrates were removed from the caged vegetation at the time of construction. Additionally, cages were monitored throughout the growing season for the presence of invertebrates that may have been missed during cage construction. Throughout the growing season, only one beetle (MIX) and two cicadas (TGP; likely emerged from the soil after cage construction) were found in these subsequent cage checks. Caging controls were also erected within each plot to mimic the effects of the cages on light and water availability, but allow access by invertebrate herbivores. The caging controls were constructed in the same manner as the exclosures, but with several large holes cut into the sides to allow access by invertebrates. The caging controls were erected over vegetation that was similar in species composition and abundances as the exclosures based on qualitative assessment at the time the cages were erected.

Data collection

Invertebrate communities were sampled from within a permanently marked 1-m^2 subunit within each 5 × 5-m plot

at peak invertebrate abundance at each site (mid-July) from 2009 to 2011. Invertebrates were sampled using a modified leaf blower with a vacuum attachment on warm, cloudless days close to solar noon. Orthopterans that hopped away from the vacuum sampler and out of the plots were identified to family and counted by sight. Collected invertebrates were frozen, identified to family, and counted and weighed. The feeding guild of each family collected (leaf-chewing herbivore, sap-sucking herbivore, gall-forming herbivore, leaf-mining herbivore, pollen/nectar-eating herbivore, fungivore, detritivore, predator, and parasitoid) was also determined (see ESM Appendix 1 for classifications).

Plant species composition was measured from 2009 to 2011 within the same permanently marked 1-m^2 subunit as the invertebrate sampling twice per growing season, once at the beginning (SGS, late May; MIX and TGP, early June) to determine the abundance of early season forbs and C_3 grasses, and once at the end (SGS, early August; MIX and TGP, early September) to determine the abundance of late season forbs and C_4 grasses. Percent areal cover was determined for each species to the nearest 1 %. Aboveground standing crop was sampled once per growing season, at peak biomass (SGS, early August; MIX and TGP, early September) from 2009 to 2011. Two 0.1-m^2 quadrats were sampled in each plot by clipping all aboveground biomass at ground level and the location of the quadrats was changed each year to prevent resampling. Previous year's biomass (litter) was separated from current year's biomass.

Leaf tissue %C and %N were assessed for the most common plant species at each site. The plant species analyzed were *Andropogon gerardii* (grass), *Sorghastrum nutans* (grass), *Schizachyrium scoparius* (grass), *Dichanthelium oligosanthes* (grass), *Ambrosia psilostachya* (forb), and *Solidago missouriensis* (forb) in TGP; *S. scoparius, Sporobolous asper* (grass), *A. psilostachya*, and *Psoralea tenuiflora* (legume) in MIX; and *Bouteloua gracilis* (grass), *Carex eleocharis* (sedge), and *Sphaeralcea coccinea* (forb) in SGS. These species can be found in every plot within each respective site. On average, the species measured made up 84.9 % of the relative plant cover in each plot. Leaf tissue was collected from three randomly selected individuals of each species within each of the plots twice during the 2011 growing season (June, August). The center-most fully emerged leaf of each individual was collected, dried, and ground. Ground leaf material from the three plant individuals collected for each species within each plot was combined in equal proportions and run on an elemental analyzer (Costech ESC 4010 Elemental Combustion System; Costech Analytical Technologies, Valencia, CA) to determine %C and %N for each species in each plot. An aggregate measure of leaf %C and %N was derived from the species' measures as follows:

$$\%_A = \Sigma(\text{cover}_n \times \%_n),$$

where $\%_A$ is the aggregate %C or %N value of all species in the plot, cover$_n$ is the relative cover of plant species n in the plot, and $\%_n$ is the %C or %N value of plant species n.

The proportion of tissue removed by chewing herbivores was visually estimated to the nearest 10 % for each plant individual collected for the tissue chemistry analysis (three individuals per plot in June and August 2011). The proportion of tissue removed was calibrated using grid estimates of tissue removed vs. overall leaf area for a subset of the individuals sampled. Although tissue may have been lost to greenfall or holes chewed by herbivores may have been expanded as the leaf grew, these effects were assumed to be minimal. The proportion tissue removed was converted into a measure of the amount of tissue removed for each individual as follows:

$$g = (m * r)/(1-r),$$

where g is the amount of tissue removed (in grams), m is the measured total biomass of the individual (i.e., mass of tissue remaining after herbivory), and r is the proportion of the tissue removed by leaf-chewing herbivores. The total amount of leaf tissue removed in each plot was then calculated as the community aggregate amount of leaf tissue removed, as described above for leaf tissue chemistry. The amount of leaf tissue removed in each plot was averaged across the two sampling dates (June, August 2011). Although this methodology does not capture herbivory by sucking or belowground invertebrates, it allows for the direct measurement of plant tissue lost to herbivory and can therefore inform our understanding of the indirect effects of nutrient availability on feeding strategies of invertebrate herbivores.

The amount of tissue removed by leaf-chewing herbivores was combined with the abundance data of leaf-chewing herbivores collected during the 2011 growing season to determine per capita rates of leaf tissue damage (hereafter, "per capita rate of herbivory"). The total herbivore damage in each plot was calculated as the aggregate amount of tissue removed, as described above. The per capita rate of herbivory (i.e., the amount of damage done by one individual invertebrate herbivore) was estimated as the total herbivore damage divided by the number of leaf-chewing herbivores sampled in the plot.

Aboveground biomass was determined within the exclosures and caging controls by clipping all standing biomass at ground level in August 2012. Biomass was separated into current year's growth (live and recently senesced material) and previous year's growth (litter), dried, and weighed.

Statistical analysis

No difference in invertebrate biomass was observed across the three sites based on a repeated-measures

ANOVA (rmANOVA) with site as a fixed factor and year as a repeated factor ($F_{1,2} = 1.228$, $p = 0.449$), therefore all remaining analyses were based on abundance data. A distance-based permutational multivariate ANOVA (PERMANOVA) tests for significant differences between groups of samples in a distance matrix (Anderson 2001). This method allows for the use of non-normally distributed data and the use of any distance measure, making it a valuable method for analyzing ecological data (Anderson 2001, 2006). We used a distance-based PERMANOVA to test for variation in the baseline (i.e., control plots only) composition of invertebrate feeding guilds among sites and years. The PERMANOVA was performed using Bray-Curtis resemblance matrixes, an appropriate distance metric for relative abundance data (Anderson 2005), with site and year as fixed factors. The differences in invertebrate feeding guild composition among sites and years were visualized using multidimensional scaling. The difference in the abundance of each feeding guild through space and time was determined using rmANOVAs with site and year as fixed factors and year as a repeated factor.

SEM was used to examine the indirect effects of soil nutrient-addition treatments on invertebrate feeding guilds through their direct effects on aboveground biomass and community aggregate leaf %C and %N. Invertebrate abundance data from all 3 years of the study were included in the model, as invertebrate abundances within each plot were assumed to be independent from year to year (Borer et al. 2012). Leaf-mining and pollen/nectar-eating herbivores, fungivores, and detritivores were not included in the SEM analysis due to their low abundances within each site and year. Each site was modeled separately, as only one site of each ecosystem type was used, and a maximum-likelihood approach was used to parameterize each model. Covariance between community aggregate leaf %C, community aggregate %N, and aboveground biomass was included in the models.

We developed a priori structural equation models with which to test the hypothesized relationships between the predictor and response variables. Our aim was to identify the indirect effects of soil nutrient availability on invertebrate herbivores and secondary consumers, therefore we included hypothesized paths from resource availability (N, P, and K) to aboveground biomass (a proxy for plant quantity) and community aggregate leaf %C and %N (proxies for plant quality), from aboveground biomass and community aggregate leaf %C and %N to herbivore feeding guild abundances, and from herbivore feeding guild abundances to secondary consumer feeding guild abundances. Direct paths from resource availability to herbivores and secondary consumers were not included in the models, as the nutrient treatments here involved

the direct application of nutrients at the soil level and these nutrients were not directly consumed by invertebrates. Similarly, direct paths from aboveground biomass and community aggregate leaf %C and %N to secondary consumers were not included in the models, as secondary consumers do not directly consume plant material. Although variance in community aggregate leaf %C or %N may affect invertebrate herbivore abundances, prior analyses found no relationship between these two variables (La Pierre, unpublished data), therefore variance in community aggregate leaf %C or %N was not included in the SEM.

Two different types of models were tested for each site: a bottom-up model, and a top-down model. The bottom-up model included paths leading from variables at lower trophic levels to variables at higher trophic levels (i.e., resources → plants → herbivores → secondary consumers). The top-down model included paths leading from variables at higher trophic levels to variables at lower trophic levels (i.e., secondary consumers → herbivores → plants), with the exception of the paths between aboveground biomass, community aggregate leaf %C and %N, and nutrients, as the experimentally applied nutrient treatments were expected to override all top-down effects on soil nutrient availability. Top-down pressure from vertebrate herbivores, omnivores, and predators was not included in any of the models; however, previous vertebrate removal experiments at each site have shown these effects to be minimal (Borer et al. 2014; La Pierre et al. 2015; La Pierre unpublished data). The bottom-up and top-down models were compared for each site using second-order bias-corrected Akaike's information criteria (AICc) (Burnham 2004). At all sites, the bottom-up model had a lower AICc value (better fit), therefore the bottom-up model was retained for all analyses presented here.

The effects of nutrient additions on aboveground plant biomass, community aggregate leaf %N, and invertebrate feeding rate (abundance of leaf-chewing herbivores, the per capita rate of herbivory by leaf-chewing herbivores, and the amount of leaf tissue removed by leaf-chewing herbivores) were examined using separate three-way ANOVAs for each site with N, P, and K treatments as fixed factors. As data on the amount of leaf tissue removed were only measured in 2011, only 2011 data were used for this analysis, despite the collection of leaf-chewing herbivore abundance data in all years of the study.

The effect of invertebrate herbivores on aboveground biomass was determined by comparing aboveground biomass between the exclosures and the caging controls within each plot using a nested ANOVA, with the exclosure treatment nested within the nutrient-addition treatments.
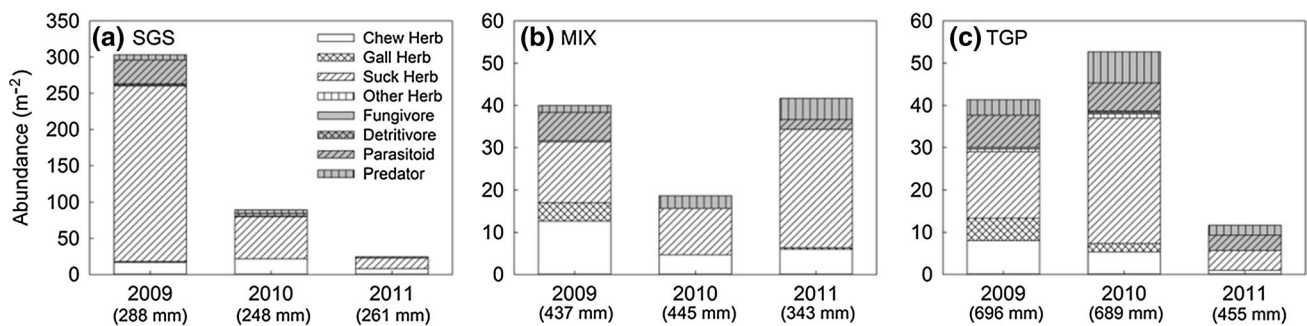
Fig. 1 Abundances of invertebrates by feeding guild vary through time and across three grassland sites spanning the broad precipitation gradient of the US Central Plains: **a** shortgrass steppe (*SGS*), **b** mixed-grass prairie (*MIX*), **c** tallgrass prairie (*TGP*). Herbivores are shown in *white*, while other feeding guilds are shown in *grey*. Growing season precipitation (mm) is indicated *in parentheses* below the year at each site. Note the difference in scale between the *x*-axes

The PERMANOVA analysis was performed in PRIMER version 6.1.13 (Plymouth Marine Laboratory, UK). All other analyses were performed in SAS version 9.3 (SAS Institute, Cary, NC).

Results

Natural variation in invertebrate abundances and trophic structure through space and time

The PERMANOVA revealed that the compositions of invertebrate feeding guilds within the control plots (i.e., no nutrients added) significantly differed among the three grassland sites and over the 3-year study period (Appendixes 2 and 3; Fig. 1). Leaf-chewing herbivores were more abundant in SGS than MIX and TGP, but composed a smaller fraction of the invertebrate community at SGS than TGP or MIX (Appendix 3). Additionally, chewing herbivores were more abundant in 2009 and 2010 than in 2011 at all sites (Appendix 3). A significant site × year interaction was observed for sap-sucking herbivores (Appendix 3), with higher abundances of sap-sucking herbivore in SGS in 2009 and 2010 than any other year or site. Parasitoid abundances were higher in 2009 than 2010 or 2011 (Appendix 2). No other feeding guilds varied significantly across the three sites or over time (Appendix 2).

Indirect effects of nutrient additions on invertebrate communities

In TGP, a weak covariance was detected between community aggregate leaf %N and aboveground biomass ($R^2 = 0.249$; $p < 0.001$) and community aggregate leaf %C and %N ($R^2 = 0.153$; $p = 0.001$). No covariance was observed between community aggregate leaf %C and aboveground biomass ($R^2 = 0.037$; $p = 0.107$). N additions increased aboveground biomass and community aggregate leaf %N (Fig. 2; Table 1). Community aggregate leaf %N, in turn, had a positive effect on leaf-chewing and sap-sucking herbivores (Fig. 2; Table 1). All herbivore feeding guilds had a strong positive effect on parasitoid abundance and sap-sucking herbivores had a positive effect on predator abundance, while leaf-chewing herbivores had a negative effect on predator abundances (Fig. 2; Table 1). Overall, soil N availability indirectly affected the invertebrate community by increasing community aggregate leaf %N (Table 2).

In MIX, a weak covariance was detected between community aggregate leaf %C and %N ($R^2 = 0.264$; $p < 0.001$). No covariance was observed between community aggregate leaf %C and aboveground biomass ($R^2 = 0.013$; $p = 0.344$) or community aggregate leaf %N and aboveground biomass ($R^2 = 0.001$; $p = 0.817$). N and P additions had a positive effect on aboveground biomass and N additions had a positive effect on community aggregate leaf %N (Fig. 2; Table 1), with a stronger biomass effect than leaf %N effect. Aboveground biomass had a positive effect on leaf-chewing herbivore abundance (Fig. 2; Table 1). Additionally, all herbivore feeding guilds had a positive effect on parasitoid abundances and sap-sucking herbivores had a negative effect on predator abundance (Fig. 2; Table 1). Overall, N and P additions had an indirect effect on leaf-chewing herbivore abundances by increasing aboveground biomass and community aggregate leaf %N (Table 2).

In SGS, a weak covariance was detected between community aggregate leaf %C and %N ($R^2 = 0.324$; $p < 0.001$). No covariance was observed between community aggregate leaf %C and aboveground biomass ($R^2 = 0.027$; $p = 0.172$) or community aggregate leaf %N and aboveground biomass ($R^2 = 0.005$; $p = 0.566$). The structural equation model for SGS did not fit the data well ($p < 0.05$), indicating that soil nutrient availability was not related to aboveground biomass or community aggregate leaf %C and %N, or invertebrate herbivore or secondary consumer abundances.

Fig. 2 Soil nutrient additions directly affect plant tissue chemistry ▶ and biomass, which in turn alter the abundances of several invertebrate feeding guilds at two of three grassland sites spanning the US Central Plains. Shown are structural equation models for the three sites. *Dashed paths* are not significant, *solid paths* are significant at $p \leq 0.10$, and *bold paths* are significant at $p \leq 0.05$. *Minus signs* indicate negative effects, and for simplicity are only shown for significant paths. Covariances between community aggregate leaf % carbon (%C), community aggregate leaf % nitrogen (%N), and aboveground plant biomass were included in all models; however, these are not shown here for simplicity (see text for details). *P* Phosphorus, *K* potassium plus micronutrients

(a) Tallgrass Prairie
$X^2=30.34$, df=25, p=0.212, AGFI=0.821

(b) Mixed-Grass Prairie
$X^2=32.09$, df=25, p=0.155, AGFI=0.832

(c) Shortgrass Steppe
$X^2=42.32$, df=25, p=0.017, AGFI=0.760

## Effects of nutrient additions on the feeding rate of chewing herbivores

In TGP, N additions resulted in an increase in aboveground biomass and community aggregate leaf %N (Fig. 3c, f; Appendix 4). N additions resulted in an increase in the number of leaf-chewing herbivores (Fig. 3i; Appendix 4). Additionally, N additions resulted in a decrease in the per capita rate of herbivory by leaf-chewing invertebrates in TGP (Fig. 3l; Appendix 4). Therefore, no change in the total amount of leaf tissue removed by chewing herbivores was observed (Fig. 3o; Appendix 4).

In MIX, P additions resulted in an increase in aboveground biomass (Fig. 3b, e; Appendix 4). A similar trend for changes in community aggregate leaf %N and rates of herbivory as was observed in TGP was also observed in MIX, but was not significant (Fig. 3; Appendix 4).

In SGS, no change was observed in aboveground biomass with nutrient additions (Fig. 3a; Appendix 4). However, community aggregate leaf %N did increase with N additions at the site (Fig. 3d; Appendix 4). No change was observed in the number of chewing herbivores with nutrient additions; however, the per capita rate of herbivory by leaf-chewing invertebrates increased with N and P additions in SGS (Fig. 3a, d; Appendix 4). As a result, the total amount of leaf tissue removed by chewing herbivores increased with N and P additions (Fig. 3g; Appendix 4). However, even in these nutrient-addition plots, the per capita rates of herbivory and the total amount of leaf tissue removed were much lower in SGS than in TGP.

Effect of invertebrate removal on aboveground biomass

In TGP and MIX, removal of invertebrates resulted in an increase in aboveground biomass (Fig. 4; Appendix 5). No effect of invertebrate removals were observed in SGS. Additionally, the effects of invertebrate removals on aboveground biomass did not covary with nutrient additions at any site.
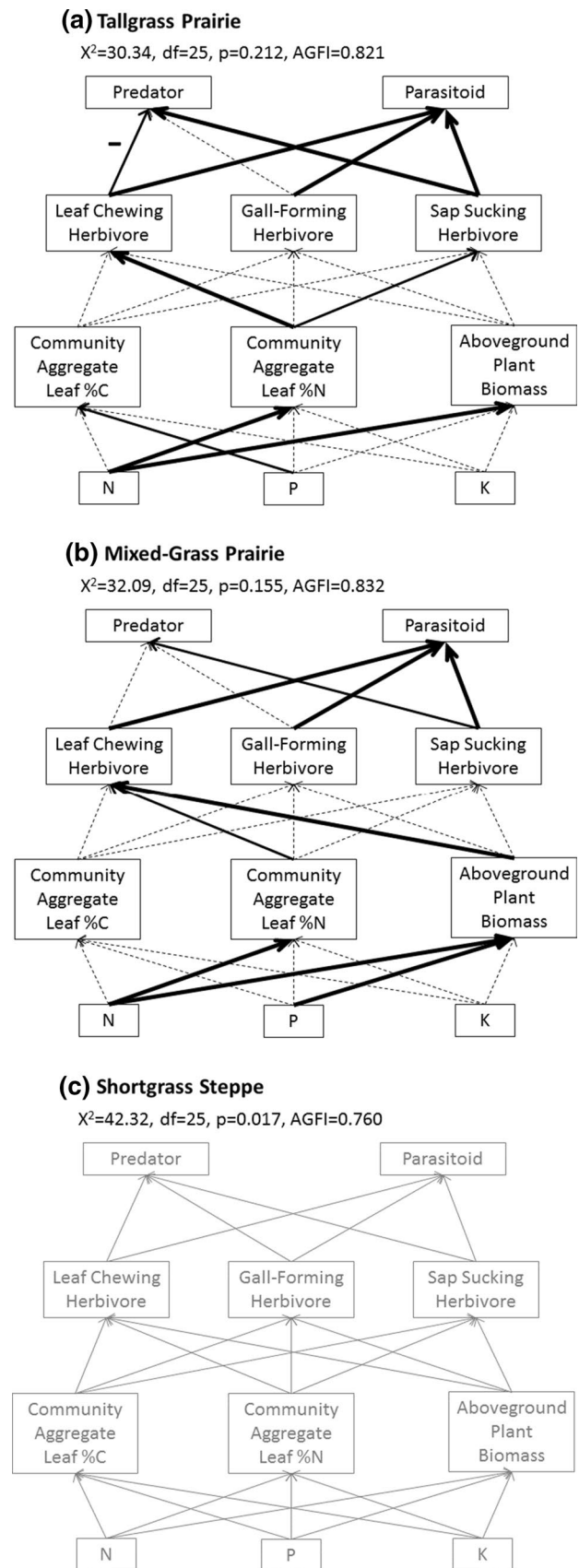
Table 1 Soil nutrient additions alter plant tissue chemistry and biomass, which in turn affect the abundance of several invertebrate feeding guilds at two of three grassland sites spanning the precipitation gradient of the US Central Great Plains

	N	P	K	%C	%N	AB	Chew	Gall	Suck
TGP									
%C	0.080	−0.201†	0.140						
%N	0.725†	−0.131	0.062						
AB	0.522†	0.151	0.024						
Chew	0.352†	−0.060	0.047	0.148	0.378†	0.128			
Gall	0.155†	−0.010	0.026	0.121	0.081	0.165			
Suck	0.203†	−0.025	0.019	0.019	0.232†	0.063			
Pred	0.022	0.002	0.001	−0.004	0.015	0.021	−0.203†	0.157	0.340†
Para	0.225†	−0.031	0.028	0.079	0.230†	0.100	0.314†	0.205†	0.409†
MIX									
%C	0.084	0.106	−0.009						
%N	0.311†	0.092	−0.154						
AB	0.309†	0.368†	0.163						
Chew	0.187†	0.155†	0.030	−0.142	0.240†	0.402†			
Gall	0.033	0.016	−0.018	0.148	0.085	−0.021			
Suck	0.087	0.046	−0.014	−0.093	0.205	0.101			
Pred	0.029	0.020	0.001	−0.046	0.053	0.054	0.074	−0.102	0.216†
Para	0.083†	0.056	−0.006	0.022	0.153†	0.107	0.229†	0.529†	0.258†
SGS model not significant									

Shown are standardized total effect sizes for structural equation models

TGP Tallgrass prairie, *MIX* mixed-grass prairie, *SGS* shortgrass steppe, *N* nitrogen, *P* phosphorus, *K* potassium plus micronutrients, *%C* community aggregate leaf % carbon, *%N* community aggregate leaf % N, *AB* aboveground biomass, *Chew* chewing herbivores, *Gall* gall-forming herbivores, *Suck* sap-sucking herbivores, *Pred* predators, *Para* parasitoids

† $p \leq 0.10$

Table 2 Soil nutrient additions indirectly alter the abundance of invertebrate feeding guilds at two of three grassland sites spanning the precipitation gradient of the US Central Plains (SGS, MIX, TGP)

	N	P	K	%C	%N	AB
TGP						
Chew	0.352†	−0.060	0.047			
Gall	0.155†	−0.010	0.026			
Suck	0.203†	−0.025	0.019			
Pred	0.022	0.002	0.001	−0.005	0.015	0.021
Para	0.225†	−0.031	0.028	0.079	0.230†	0.100
MIX						
Chew	0.187†	0.155†	0.030			
Gall	0.033	0.016	−0.018			
Suck	0.087	0.046	−0.014			
Pred	0.029	0.020	0.001	−0.046	0.053	0.054
Para	0.083†	0.056	−0.006	0.022	0.153†	0.107
SGS model not significant						

Shown are standardized indirect effect sizes for structural equation models. For abbreviations, see Table 1

† $p \leq 0.10$

Discussion

Resource availability is thought to affect invertebrate abundances and feeding rates (Throop and Lerdau 2004; Schmitz 2008b; Cronin et al. 2010). However, the relative roles of alterations in plant biomass or tissue chemistry with nutrient additions in driving these changes in the aboveground invertebrate community remain unknown. To address this question, we examined the effects of soil nutrient additions on the aboveground invertebrate
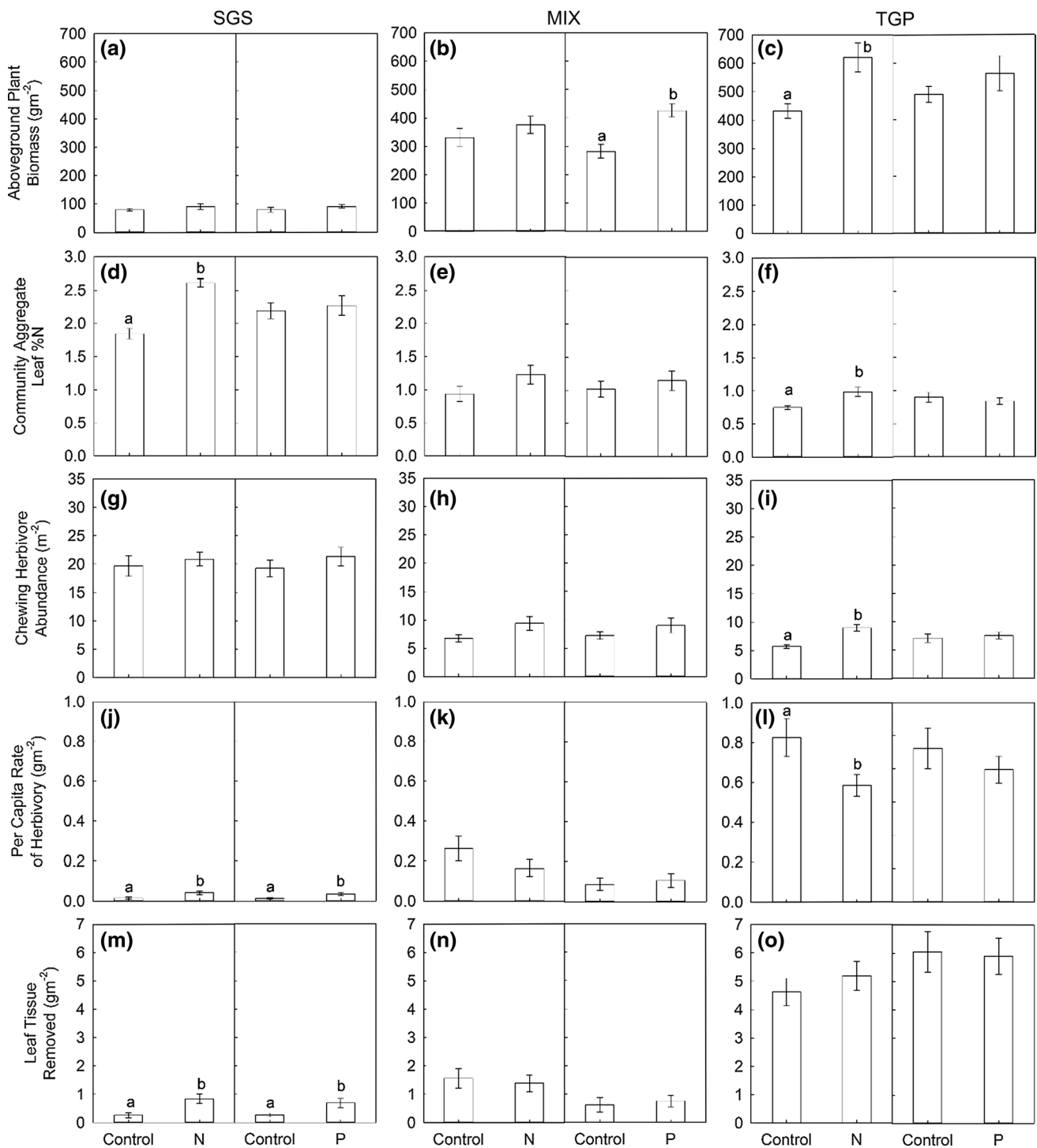
Fig. 3 Soil nutrient additions directly alter plant biomass and tissue chemistry, and indirectly alter herbivore abundances and feeding rates at three grassland sites spanning the broad precipitation gradient of the US Central Plains (SGS, MIX, TGP). Shown are the effects of N and P additions on aboveground plant biomass (**a–c**), community aggregate leaf %N (**d–f**), chewing herbivore abundance (**g–i**), per capita rate of herbivory (**j–l**) by chewing herbivores, and leaf tissue removed by chewing herbivores (**m–o**). Although the effects of N, P, and K were measured in all combinations, only the direct effects of N and P are shown here as there were no significant effects of K alone and no interactive effects among the three nutrients added (Appendix 4). Shown are means ± SEs. *Different letters* indicate significant differences between treatments. For abbreviations, see Figs. 1 and 2
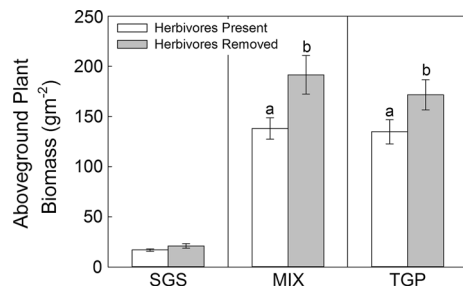
Fig. 4 Removal of invertebrate herbivores increases aboveground plant biomass at two of three sites spanning the broad precipitation gradient of the US Central Plains (TGP, MIX, SGS). *Different letters* indicate significant differences between treatments. Shown are means ± SEs. For abbreviations, see Fig. 1

community at three sites spanning the US Central Great Plains.

We observed a shift in the composition of aboveground invertebrate communities with nutrient additions at two of the three sites studied here, TGP and MIX, corresponding to the two more mesic sites along the Great Plains' precipitation gradient (Fig. 2; Table 1). Because this study spanned multiple invertebrate herbivore generations, we could not determine whether this difference was due to a change in the population dynamics within a plot (i.e., altered birth and/or death rates) or movement of herbivores into the nutrient-addition plots. However, the mechanisms behind the shift in invertebrate abundances with nutrient additions may be similar in either case. At both the TGP and MIX sites, the invertebrate functional group that responded most strongly to nutrient additions was leaf-chewing herbivores, although gall-forming and sapsucking herbivores also increased with N additions at TGP. This result may be due to the different digestive capacity of these invertebrate groups, with gall-forming and sapsucking herbivores better able to extract nutrients from plant tissue with low nutrient content (Mattson 1980). Interestingly, the invertebrate response to P was strong in MIX, but not in TGP. This may be due to differences in plant %P or invertebrate P requirements at the two sites, and deserves further investigation.

The changes in herbivore abundance with nutrient additions in TGP and MIX, in turn, affected parasitoid abundances (Fig. 2; Table 1); the latter were positively correlated with the abundances of all three herbivore feeding guilds included in the SEM model. Additionally, predator abundance increased with increasing sapsucking herbivore abundance at both sites and decreased with increasing leaf-chewing herbivore abundance at TGP. However, the indirect effects of nutrient additions decreased in magnitude up the food chain, with the greatest effect of nutrient additions on aboveground biomass,

a weaker effect on herbivore abundances, and the weakest effect on parasitoid abundances (Table 1). The dampened responses of herbivores and secondary consumers to nutrient additions may be the result of changes in plant allocation to defenses or herbivore feeding rate, stoichiometry, or abundances (Mattson 1980; Siemann 1998; Throop and Lerdau 2004; Agrawal and Fishbein 2006; Haddad et al. 2009).

Based on the SEM analysis, we found that the aboveground invertebrate community responded to increases in community aggregate leaf %N with N additions at both TGP and MIX (Fig. 2; Table 2). This is indicative of invertebrate herbivores cuing in on increased food quality within the N-added plots, as has been documented many times under lab conditions (Mattson 1980; Behmer and Joern 1993; Chambers et al. 1995; Oedekoven and Joern 2000; Fagan et al. 2002; Berner et al. 2005; Fink and von Elert 2006). In addition, leaf-chewing herbivores responded to increased aboveground plant biomass with N and P additions in MIX (Fig. 2; Table 2). The relationship between the abundance of leaf-chewing herbivores and aboveground biomass may be due to a variety of factors. An increase in aboveground biomass may correspond to an increase in the absolute amount of food available, thereby reducing competition among herbivores (Chase et al. 2000; Throop and Lerdau 2004; Schmitz 2008b; Borer et al. 2012). Additionally, increased aboveground biomass may reduce competition for non-food resources, such as available habitat space (Schmitz 2008b). Finally, areas with higher aboveground biomass may provide more protection from predators by providing dense vegetation within which to hide (Throop and Lerdau 2004; Schmitz 2008a; Chen et al. 2010). Further study to tease apart the mechanisms behind the relationships between leaf tissue chemistry, aboveground biomass, and leaf-chewing herbivore abundances in TGP and MIX is warranted.

In addition to shifts in the abundance of leaf-chewing herbivores in TGP and MIX, we found that feeding rates of leaf-chewing herbivores changed as well. The per capita rate of herbivory (i.e., the amount of leaf tissue removed per individual) significantly decreased with N additions in TGP, with a similar but not significant trend in MIX (Fig. 3). The decrease in the per capita rate of herbivory with N additions in TGP and MIX may have been driven by an increase in leaf tissue %N. Because community aggregate leaf tissue %N was higher in the N-addition plots, it is possible that with N additions the leaf-chewing herbivores could consume less plant material and still meet their nutritional needs (Mattson 1980; Behmer and Joern 1993; Joern and Behmer 1998; Berner et al. 2005). The congregation of leaf-chewing herbivores in N-addition plots and the lower per capita rate of herbivory are an indication of selective feeding at these sites.

In addition to examining the effects of nutrient additions on the invertebrate community, we also examined the effects of removing invertebrate herbivores on aboveground biomass both with and without nutrient additions. We found that the removal of invertebrate herbivores from both TGP and MIX communities resulted in an increase in aboveground biomass (Fig. 4) and that this effect did not vary with nutrient additions. This is consistent with the previous result that the total amount of leaf tissue removed by leaf-chewing herbivores does not vary with nutrient additions due to the inverse relationship between the increase in herbivore abundance and the decrease in the per capita feeding rate with N additions. Because of the opposing shifts in invertebrate herbivore abundance (increasing) and per capita feeding rates (decreasing) in response to N additions at the mesic sites studied here, the effect of invertebrate herbivores on aboveground biomass did not vary with nutrient additions. This result emphasizes the need to study both herbivore abundances and their feeding responses to resource availability in tandem (Throop and Lerdau 2004; Schmitz 2008b).

In contrast to the TGP and MIX sites, at the SGS site studied here nutrient additions did not result in a change in invertebrate herbivore or secondary consumer abundances (Table 1). Additionally, although the abundance of leaf-chewing herbivores did not vary with nutrient additions, the per capita rate of herbivory increased with N and P additions (Fig. 2). As a result, the total amount of leaf tissue removed by chewing herbivores increased with N and P additions in SGS (Fig. 2). Yet ultimately, the removal of invertebrate herbivores did not affect aboveground biomass in SGS (Fig. 4), perhaps because the amount of leaf tissue removed in any nutrient treatment was relatively small. Overall, leaf-chewing herbivores at the SGS site appeared to feed in a compensatory manner, as compared to leaf-chewing herbivores in the TGP and MIX sites, which fed in a selective manner.

Because this study did not have replication at the site level, it is difficult to assess why the responses in the SGS site were different from those in the more mesic TGP and MIX sites. However, the SGS site is known to be distinct from the TGP and MIX sites in both its plant and invertebrate communities in ways that invite some speculation (Knapp et al. 1998; Lauenroth and Burke 2008). The initial composition of the SGS invertebrate community differed greatly from that observed in MIX or TGP (Fig. 1). The abundance of aboveground invertebrates was much higher in SGS than in TGP or MIX in all 3 years of collection. However, we found that the biomass of invertebrates was consistent across all sites studied here, therefore the biomass of individual invertebrates at SGS must be lower than at the TGP and MIX sites. Additionally, the proportional abundance of

sap-sucking herbivores (primarily in the Cicadellidae family) was higher in SGS than in either TGP or MIX, nearly an order of magnitude greater in a higher than average precipitation year (2009). This different invertebrate community at SGS may have different nutritional requirements (Throop and Lerdau 2004; Lauenroth and Burke 2008) and therefore differ in its responses to nutrients compared to the invertebrate communities in the other two sites. Finally, belowground herbivory has been shown to have a stronger effect than aboveground herbivory at SGS (Milchunas et al. 1990; Coffin et al. 1998), therefore further research into the belowground response to nutrient additions is warranted.

In addition to differences in the invertebrate community, the plant community in SGS also differs from that of either TGP or MIX (Lauenroth and Burke 2008; McCulley et al. 2009). Having evolved in a low-precipitation environment, SGS plants tend to be lower in biomass and higher in nutrient content than TGP and MIX plants (Coley et al. 1985; Chapin et al. 1993). Although aboveground biomass did increase with nutrient additions in SGS, it may not have had as strong an effect on habitat availability or protection from predators for invertebrate herbivores, as the canopy remained relatively open even after nutrient additions at this site (La Pierre, personal observation). Additionally, as leaf tissue %N in SGS is already high compared to that in TGP or MIX, N may not be a limiting resource for leaf-chewing herbivores at that site. Thus, the compensatory feeding with N and P additions at SGS indicate that the addition of these nutrients resulted in a decrease in the availability of a resource other than N that is limiting leaf-chewing herbivores at this site (Throop and Lerdau 2004; Behmer 2009). Overall, more research is needed to identify the mechanisms underlying the response of the invertebrate community at SGS to nutrient additions.

As shown here, invertebrate herbivores can have a relatively strong effect on aboveground biomass in grassland systems (Fagan et al. 2002; Schmitz 2003; Whiles and Charlton 2006; Hall et al. 2009). Although this effect might be expected to vary with nutrient additions due to changes observed in invertebrate herbivore abundances (Mattson 1980; Huxel 1999; Throop and Lerdau 2004; Loaiza et al. 2011; Borer et al. 2012), we did not find that to be the case in this study. Rather, a shift in the feeding rate of invertebrate herbivores ameliorated the effect of increased invertebrate herbivore abundance on aboveground biomass in response to nutrient additions, particularly in more mesic grasslands. Thus, the patterns observed here suggest that invertebrate effects on ecosystem processes in response to altered nutrient availability, either natural or anthropogenically induced, may be lower than expected from data on invertebrate abundances alone. Further research aimed

at identifying the mechanisms underlying these responses, particularly with respect to invertebrate community composition/behavioral shifts and plant defense allocation, including how these may vary among ecosystems, is needed to assess the generality of herbivore community responses to increased resource availability.

Author contribution statement K. J. L. and M. D. S. conceived and designed the experiments. K. J. L. performed the experiments and analyzed the data. K. J. L. wrote the manuscript with editorial input from M. D. S.

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