

Litter accumulation drives grassland plant community composition and functional diversity via leaf traits

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Abstract Direct physical interference from litter is an important mechanism driving changes in the diversity and composition of plant communities dominated by perennial species. While the consequences of litter for species diversity and composition are well known, the mechanisms shaping how litter acts as a filter on leaf and shoot functional traits to alter community structure and functional diversity remain unclear. These questions were examined using a large field experiment in native mixed-grass prairie grasslands in the brown and dark brown soil zones in central Saskatchewan, Canada. Litter additions ranging from 0 to 2,290 g m⁻² were applied to plots in a response surface design, and responses including community structure, above-ground functional diversity, and community-weighted mean values for leaf functional traits were measured. Species richness, functional richness, and functional dispersion declined with increasing litter mass, but functional evenness increased. Community composition became

more variable because increased litter acted as a filter on the perennial species previously present in the plots; the remaining species in a given plot were the most litter-tolerant subset of the original community in the plot. Increased litter mass affected graminoid and forb species differently. Increased litter mass selected for graminoid species characterized by greater height, leaf area, specific leaf area (SLA), leaf thickness, and leaf tissue density. In contrast, increased litter selected for forb species characterized by larger, thicker leaves, lower SLA, and lower leaf tissue density. Forbs with cauline leaves were also selected for over acaulescent growth forms. Physical interference by litter likely reduces grassland diversity and alters species composition in diverse grassland communities by forcing convergence in community trait structure, but not convergence in species composition.

Keywords Community assembly · Leaf functional diversity · Litter accumulation · Plant functional traits

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Introduction

Litter is a key factor controlling grassland plant community structure and composition (e.g., Foster and Gross 1998; Jensen and Gutkunst 2003; Lamb 2008; Ruprecht et al. 2010a). Low amounts of litter can facilitate growth and seedling survival, while high litter accumulation can reduce grassland species diversity through mechanisms including shading, alteration of

germination cues, direct physical interference, sheltering seed predators, and encouraging pathogens (Carson and Peterson 1990; Deutsch et al. 2010a; Loydi et al. 2013; Ruprecht et al. 2010b; Xiong and Nilsson 1999). Few studies, however, have examined how functional diversity (i.e., the number of different plant strategies as defined by the range of plant trait values present within a local community) is influenced by litter accumulation (Pakeman 2011). In many perennial grasslands, patchy grazing can cause substantial small-scale variation in residual litter (Cid and Brizuela 1998; Willms et al. 1988); variation in the degree of direct physical interference from litter encountered by emerging leaves and stems is likely an important mechanism driving small-scale heterogeneity in plant community structure in these ecosystems. While much is known about litter impacts on seedlings (Loydi et al. 2013; Xiong and Nilsson 1999), much less is known about how litter acts as a physical environmental filter on perennial species emerging from rhizomes or perennating shoots. Given the dominance of long-lived perennial species in many dry grassland ecosystems (Coupland 1950; Lamb 2008), short-term effects of litter are likely to be driven by the responses of perennials renewing growth, rather than seed and seedling responses.

The mechanical constraints that leaf litter places on seedlings are well documented (e.g., Donath and Eckstein 2008; Hovstad and Ohlson 2008; Loydi et al. 2013; Xiong and Nilsson 1999). Building on those studies, it is expected that above-ground functional traits important in perennial plant responses to litter are likely to similarly include leaf area, specific leaf area (SLA, leaf area per unit leaf dry mass), leaf tissue density, leaf thickness, and plant height. Smaller leaves may be less likely to become trapped under a litter layer. Thick leaves and high leaf tissue density are associated with leaves that can withstand physical damage (Craine et al. 2001; Dijkstra and Lambers 1989; Grime et al. 1997; Reich et al. 1997). Taller plants with rigid leaves may be less affected by litter accumulation because they are able to push through litter. Consequent declines in species diversity and changes in functional diversity are expected to follow as species with leaf traits ill-suited to push through litter or unable to maintain photosynthesis while partially covered by litter are filtered from the community. Further, while the mechanical effects of litter on species diversity are well quantified, little is known about litter impacts on functional trait diversity in plant communities. Functional diversity is linked to a wide array of ecosystem

processes important in grasslands including primary productivity, nutrient cycling, energy cycling, site stability, and invasion resistance (e.g., Cadotte et al. 2011; Diaz and Cabido 2001; Pokorny et al. 2005).

Here, we examine how litter acts as an ecological filter to structure, species, and functional diversity in plant communities via leaf and shoot traits using a large-scale, field litter addition experiment. Specifically, we test how increased litter mass in a grassland plant community (1) structures species composition and diversity, (2) alters community-weighted mean leaf functional trait values and functional diversity, and (3) to identify the above-ground leaf traits most important in regulating species and functional diversity. We expect that increased litter will reduce species diversity and alter functional diversity in grasslands by filtering out species with leaf traits ill-suited to emergence from below a litter layer.

Materials and methods

Experimental design

Experiments were conducted in 2010–2011 and 2011–2012 on native Mixed-Grass Prairie in central Saskatchewan, Canada (Table 1). Two locations in the brown soil zone (Matador and Monet) and one location in the dark brown soil zone (King George) were utilized. Mixed-grass prairie is characterized by a mean annual temperature of ~ 3.5 °C and annual precipitation between 250 and 350 mm. Vegetation is dominated by grasses, with forbs contributing the majority of the species diversity (Coupland 1950). Soils at the sites are brown and dark brown Chernozems, or grassland soils with a well-developed A horizon with accumulated organic matter at least 10 cm thick. Dark brown soils have darker A horizons indicative of greater organic material and available nitrogen and are found in climate zones with higher precipitation and cooler average temperatures than the brown Chernozems (Campbell and Souster 1982; Soil Classification Working Group 1998). At each of the three locations, three study sites each containing 30 treatment plots were established in 2010–2011 for a total of nine study sites. Three new study sites in each of the three locations were established in 2011–2012 for a total of 18 study sites years. Each of the 18 study sites were in a different paddock with a unique grazing history. All study sites were grazed by cattle during the

Table 1 Summary of location characteristics (mean ± standard deviation) in control (no litter added) plots in each year

Location and Year	Litter mass	ANPP	Species richness	Evenness	Dominant species
King George 2011	30.57 ± 32.82	182.78 ± 37.21	11.5 ± 2.59	0.79 ± 0.06	<i>Carex spp.</i> , <i>Stipa curtiseta</i> , <i>Artemisia frigida</i> , <i>Koeleria macrantha</i>
King George 2012	20.22 ± 26.76	242.63 ± 49.55	7.17 ± 1.6	0.8 ± 0.06	<i>Stipa comata</i> , <i>Artemisia frigida</i> , <i>Agropyron smithii</i> , <i>Carex spp.</i>
Matador 2011	8.7 ± 7.43	139.46 ± 39.6	13.5 ± 4.85	0.86 ± 0.02	<i>Artemisia frigida</i> , <i>Koeleria macrantha</i> , <i>Stipa comata</i> , <i>Agropyron smithii</i> , <i>Carex spp.</i>
Matador 2012	9.57 ± 2.5	123.4 ± 14.73	15.83 ± 2.79	0.88 ± 0.03	<i>Selaginella densa</i> , <i>Carex spp.</i> , <i>Artemisia frigida</i> , <i>Phlox hoodii</i> , <i>Bouteloua gracilis</i>
Monet 2011	11.17 ± 4.9	181.37 ± 37.39	8.67 ± 1.21	0.8 ± 0.06	<i>Stipa comata</i> , <i>Carex spp.</i> , <i>Artemisia frigida</i> , <i>Achillea millefolium</i> , <i>Agropyron smithii</i>
Monet 2012	9.63 ± 6.87	180.4 ± 29.29	9.67 ± 2.5	0.85 ± 0.04	<i>Artemisia frigida</i> , <i>Agropyron smithii</i> , <i>Selaginella densa</i> , <i>Carex spp.</i> , <i>Koeleria macrantha</i>

Variables include litter mass (g m^{-2}), annual net primary productivity (ANPP g m^{-2}), Species richness (spp m^{-2}), species evenness, and a list of the most common plant species

June to September period in the summer prior to plot establishment; solar-powered electric fences were placed around every set of plots to prevent grazing by livestock during the study.

Each study site consisted of 30 treatment plots that were 3.16 m by 3.16 m in size (10 m^2) for a total of 270 treatment plots in each year. Within each study site, control plots received no litter while the remaining 28 plots received additional litter following a response surface design (Cottingham et al. 2005). In order to simulate the effects of litter carryover from the previous growing season, the litter treatment was applied to plots between 5 October and 21 October 2010 for the 2010–2011 sites and between 14 October and 20 October 2011 for the 2011–2012 sites. ‘Manipulation litter’ for these addition treatments was collected from a reference stand near each study site (within 50 m to 2 km of the treatment plots). The reference stands were the nearest locations to each study site within the same ecosite (i.e., similar plant community composition and topographic position) and either non-grazed or with negligible effects of grazing. Within each reference stand, 28 areas ranging in size from 0.5–40.0 m^2 were delineated and mowed to a 2.5-cm stubble height with a sickle mower in October (Figs. A1–A2). The mowed standing crop (including natural litter) from each of the 28 plots was collected and evenly distributed onto a randomly assigned treatment plot. These treatments resulted in litter additions within each site ranging from a low of 1 g m^{-2} fresh weight added to the lowest litter treatment to a maximum $2,290 \text{ g m}^{-2}$ added to the highest litter treatment. Plots were covered with 2.5-cm polypropylene netting to prevent the litter from being blown off the plots during the winter (Fig. A3). The netting was removed from the plots in mid-June of the first growing season.

In late June to early July 2011 and 2012, species composition was estimated in each of the treatment plots at each site by visually estimating the canopy cover of all plant species, litter, and bare soil in a 1 m by 1 m quadrat centered in the plot (Fig. A1). A single observer surveyed all plots. Litter mass in each plot was estimated by hand raking the litter from four, 0.5 by 0.5 m quadrats. Total litter in treatment plots thus includes the manipulation litter added to treatment plots as well as natural litter present in the plots prior to the beginning of the experiment. Litter samples were dried at 80 °C for 48 h and weighed.

Trait data collection

Leaf traits for the majority of species in this experiment including specific leaf area (SLA; leaf area per unit mass; $\text{cm}^2 \text{g}^{-1}$), leaf thickness, leaf weight, and leaf tissue density (leaf mass per volume ($\text{area} \times \text{avg. thickness}$); mg mm^{-3}) were assessed. Plants were collected for trait measurement from seven locations (Table A2). As it was not possible for us to directly assess all species, regional trait data (Kembel and Cahill 2011) were used for some species. While local data would be preferable, all analyses in this paper are based on community-level weighted means of trait values (Lavorel et al. 2008) and thus including as many species as possible from the community is an overriding concern. Table A1 lists the source of trait data for all species and lists the species observed in the treatment quadrats, but for which trait data were not obtained. Collections of plants for trait measurement were made in June and July; plants of the same species were separated by at least 6 m to ensure plants were not the same genetic individual. For each individual plant, 3 fully expanded leaves were collected from the plant, wrapped in a damp towel, and stored in a cooler throughout the day, and then stored at 4 °C in 70 % ethanol solution until analysis. The leaves were scanned for image analysis of the one-sided projected leaf area using WinFOLIA software at 400 dpi (Regent Instruments Inc.). Leaf thickness of field-moist leaves was measured to the nearest 0.1 mm using digital calipers at three locations per leaf; the leaves were then dried for 72 h at 70 °C and weighed. Plant height for each species was taken from Tannas (2004) and Moss (1983). If a range of height was given in the source, plant height was taken to be the midpoint of that range. Height measures were included so that the relative statures of species could be incorporated into the analyses. All leaf trait data collected from the study sites have been submitted to the TRY database (<http://www.try-db.org>).

Species and functional diversity metrics

Plant community diversity was measured as total species richness and the Evar evenness index (Smith and Wilson 1996). Four measures of above-ground functional diversity (functional richness, evenness, divergence, and dispersion) were used (Laliberte and Legendre 2010; Mouillot et al. 2013; Villéger et al.

2008). It is important to investigate multiple measures of functional diversity as each of the indices measures different aspects of the community and the community response to external environmental conditions (Laliberte and Legendre 2010; Mouillot et al. 2013; Pakeman 2011). Functional richness is a measure of the proportion of possible functional space as defined by the measured traits that is occupied by the species in the community. Functional evenness describes the distribution of species abundance within the functional space, particularly how regularly or evenly abundance is distributed within the functional space. Functional divergence is a measure of how much of the community is made up with species that have unusual or extreme trait values relative to the community mean. Functional dispersion is a measure of the deviation of the community as weighted by species abundance from mean trait values assuming equal species abundances. Functional diversity indices were calculated using the dbFD function from the FD library in the R statistical package (Laliberte and Legendre 2010; R Development Core Team 2012). Indices were calculated using the abundance of all species in the community and trait values including leaf area, leaf thickness, SLA, leaf tissue density, growth form (forb or graminoid), and plant height. The dbFD function can accommodate categorical variables and missing values; thus all species in the community were categorized as graminoids or forbs allowing species otherwise missing trait values to be included in this analysis. The “lingoes” correction (Lingoes 1971) was used because the species by species distance matrix was not Euclidian. Functional richness, evenness, and dispersion cannot be calculated for communities with less than three functionally identical species (Laliberte and Legendre 2010); thus two data points with only two species present each were eliminated from subsequent analyses of those variables. Functional richness, functional divergence, and functional dispersion all positively correlated with species richness while functional evenness was not correlated with species richness (Fig. A2).

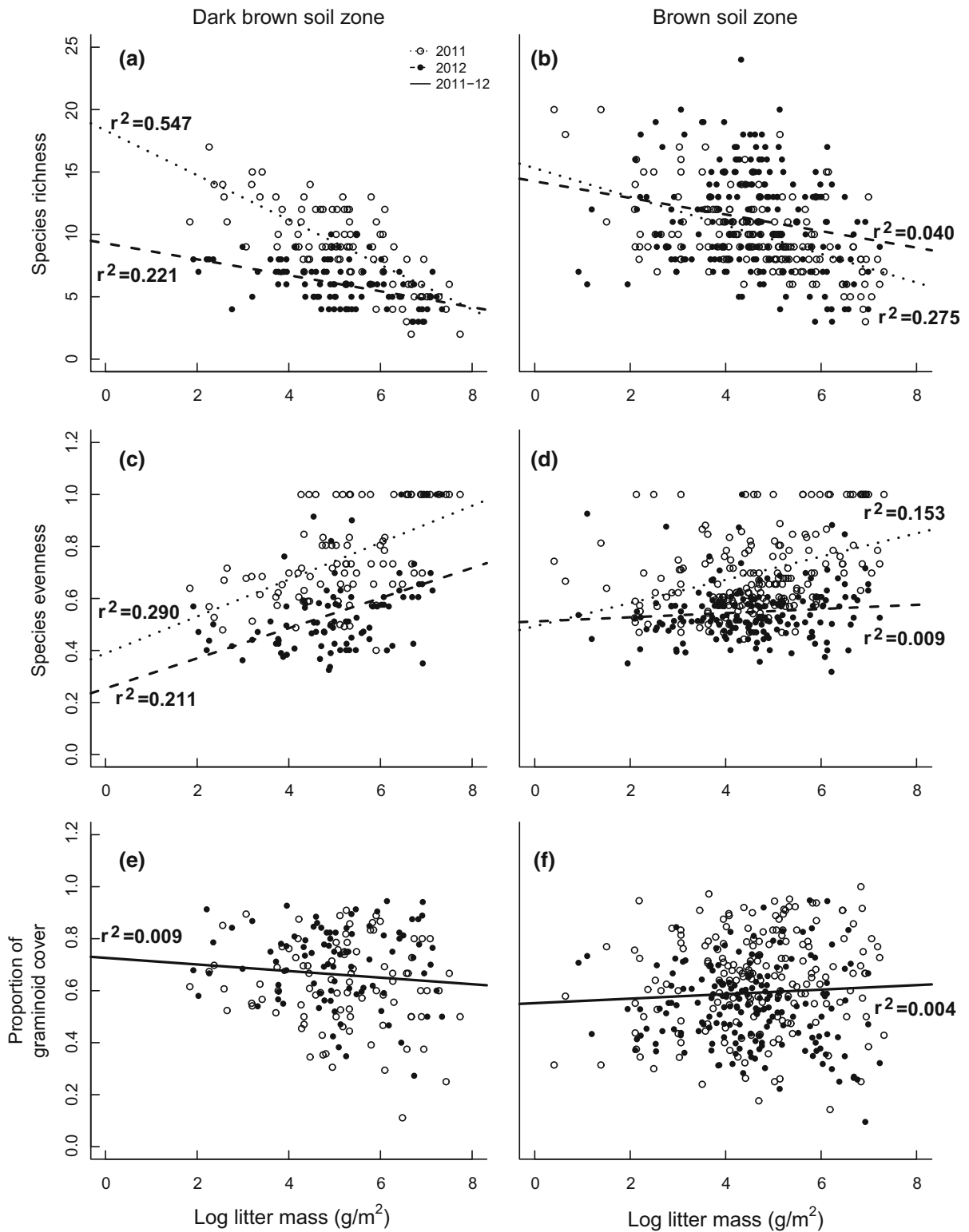
Statistical methods

The effects of litter mass on plant community response variables (species richness and species evenness), functional diversity (functional richness, evenness, divergence, and dispersion), and plant traits

Table 2 Tests of the effects (*F* and *p* values) of litter mass, soil type (brown soil zone vs. dark brown soil zone), year, and interactions on species richness, species evenness, functional diversity, and community-weighted mean values for leaf area, specific leaf area (SLA), leaf thickness, leaf tissue density, and plant height

Variable	Litter mass	Soil type	Year	Litter mass: soil type	Litter mass: year	Soil type: year	Litter mass: soil type: year
df*	1, 518	1, 14	1, 14	1, 518	1, 518	1, 14	1, 518
Species richness	287.25 <i>p</i> < 0.001	3.56 <i>p</i> = 0.080	0.06 <i>p</i> = 0.812	0.27 <i>p</i> = 0.604	1.56 <i>p</i> = 0.212	2.77 <i>p</i> = 0.118	20.18 <i>p</i> < 0.001
Species evenness	107.41 <i>p</i> < 0.001	0.02 <i>p</i> = 0.898	34.62 <i>p</i> < 0.001	22.36 <i>p</i> < 0.001	23.19 <i>p</i> < 0.001	0.25 <i>p</i> = 0.624	0.97 <i>p</i> = 0.326
Prop. graminoid cover	0.17 <i>p</i> = 0.679	1.94 <i>p</i> = 0.186	0.76 <i>p</i> = 0.397	4.07 <i>p</i> = 0.044	0.00 <i>p</i> = 0.974	3.46 <i>p</i> = 0.084	1.01 <i>p</i> = 0.314
Functional richness	16.51 <i>p</i> < 0.001	1.39 <i>p</i> = 0.258	0.14 <i>p</i> = 0.716	5.49 <i>p</i> = 0.019	0.24 <i>p</i> = 0.622	1.74 <i>p</i> = 0.208	0.50 <i>p</i> = 0.479
Functional evenness	72.85 <i>p</i> < 0.001	0.75 <i>p</i> = 0.401	43.46 <i>p</i> < 0.001	11.02 <i>p</i> = 0.001	5.97 <i>p</i> = 0.015	0.23 <i>p</i> = 0.642	3.44 <i>p</i> = 0.064
Functional divergence	0.32 <i>p</i> = 0.574	0.58 <i>p</i> = 0.460	0.09 <i>p</i> = 0.767	2.19 <i>p</i> = 0.139	0.39 <i>p</i> = 0.533	5.48 <i>p</i> = 0.034	0.32 <i>p</i> = 0.573
Functional dispersion	37.70 <i>p</i> < 0.001	1.78 <i>p</i> = 0.203	0.51 <i>p</i> = 0.487	0.79 <i>p</i> = 0.375	6.43 <i>p</i> = 0.011	0.09 <i>p</i> = 0.763	0.41 <i>p</i> = 0.524
Graminoid leaf area	1.81 <i>p</i> = 0.179	0.61 <i>p</i> = 0.447	1.98 = 0.181	7.27 <i>p</i> = 0.007	0.56 <i>p</i> = 0.452	0.71 <i>p</i> = 0.413	1.25 <i>p</i> = 0.264
Forb leaf area	23.90 <i>p</i> < 0.001	0.00 <i>p</i> = 0.971	0.74 <i>p</i> = 0.403	4.60 <i>p</i> = 0.032	0.07 <i>p</i> = 0.791	1.58 <i>p</i> = 0.229	2.54 <i>p</i> = 0.112
Graminoid SLA	14.26 <i>p</i> < 0.001	0.00 <i>p</i> = 0.972	0.32 <i>p</i> = 0.581	0.21 <i>p</i> = 0.650	1.48 <i>p</i> = 0.223	4.68 <i>p</i> = 0.048	0.20 <i>p</i> = 0.65
Forb SLA	25.78 <i>p</i> < 0.001	2.27 <i>p</i> = 0.15	7.85 <i>p</i> = 0.014	11.57 <i>p</i> = 0.001	3.20 <i>p</i> = 0.074	8.21 <i>p</i> = 0.012	0.00 <i>p</i> = 0.953
Graminoid leaf thick	14.26 <i>p</i> < 0.001	0.00 <i>p</i> = 0.972	0.32 <i>p</i> = 0.581	0.21 <i>p</i> = 0.650	1.49 <i>p</i> = 0.223	4.68 <i>p</i> = 0.048	0.20 <i>p</i> = 0.652
Forb leaf thick	8.58 <i>p</i> = 0.004	0.99 <i>p</i> = 0.337	0.23 <i>p</i> = 0.636	1.08 <i>p</i> = 0.299	2.32 <i>p</i> = 0.129	2.09 <i>p</i> = 0.170	1.63 <i>p</i> = 0.201
Graminoid leaf density	1.62 <i>p</i> = 0.204	2.49 <i>p</i> = 0.137	3.97 <i>p</i> = 0.066	10.63 <i>p</i> = 0.001	3.53 <i>p</i> = 0.061	0.28 <i>p</i> = 0.606	7.91 <i>p</i> = 0.005
Forb leaf density	56.16 <i>p</i> < 0.001	8.79 <i>p</i> = 0.010	2.89 <i>p</i> = 0.111	9.00 <i>p</i> = 0.003	0.31 <i>p</i> = 0.575	3.41 <i>p</i> = 0.086	0.28 <i>p</i> = 0.595
Graminoid height	12.37 <i>p</i> = 0.001	0.04 <i>p</i> = 0.848	1.13 <i>p</i> = 0.305	2.55 <i>p</i> = 0.111	0.00 <i>p</i> = 0.982	3.08 <i>p</i> = 0.101	0.085 <i>p</i> = 0.770
Forb height	4.15 <i>p</i> = 0.042	0.26 <i>p</i> = 0.615	0.03 <i>p</i> = 0.855	0.88 <i>p</i> = 0.349	0.88 <i>p</i> = 0.347	2.49 <i>p</i> = 0.137	3.75 <i>p</i> = 0.053

* denominator degrees of freedom for functional richness, evenness, and divergence were 516 as these indices could not be calculated for two plots that had less than three functionally singular species



◀ **Fig. 1** Effect of increasing litter mass on species richness, species evenness, and the proportion of graminoid cover in communities in the brown and dark brown soil zones. Open circles indicate data collected in 2011 and closed circles 2012. *Solid lines* indicate relationships between litter and traits that were the same between years (no year interactions); in the case of a significant year interaction, the *dotted line* indicates the 2011 relationship and the *dashed line* 2012

(individual leaf area, SLA, leaf tissue density, leaf thickness, and plant height) were examined using linear mixed effects models. Graminoids and forbs differed in their average trait values (Fig. A3) and were thus expected to differ in their response to litter. Therefore, the effects of litter mass on individual plant traits were examined separately for each life-form. In each model, the fixed effects included log litter mass, soil zone (dark brown or brown), year, and all two- and three-way interactions. Site was used as a random factor to account for the aggregation of the litter mass treatments within sites. All mixed models were fit using the R statistical software (Ver. 3.0.2) and the lme function from the nlme package (Pinheiro et al. 2012; R Development Core Team 2012). Changes in species

composition with litter mass were examined using a non-metric multidimensional scaling (NMDS) percent cover for all species observed in the study. Due to the species compositional differences between the soil zones, each zone was analyzed separately. Two-dimensional NMDS analyses using Bray-Curtis distances were done with the metaMDS function in the vegan package (Oksanen et al. 2011; R Development Core Team 2012). The final NMDS solutions had stress of 0.236 and 0.221 for the brown and dark brown zones, respectively.

Results

Increasing litter mass had strong effects on plant community species diversity, functional diversity, and community-weighted mean leaf functional trait values; many of these effects were modulated by environmental conditions, as significant interactions between litter, year, and soil zone were common (Table 2). Species richness declined with increasing litter across all sites (Fig. 1a, b) with the strongest effect in 2011 in the dark brown soil zone (Fig. 1b).

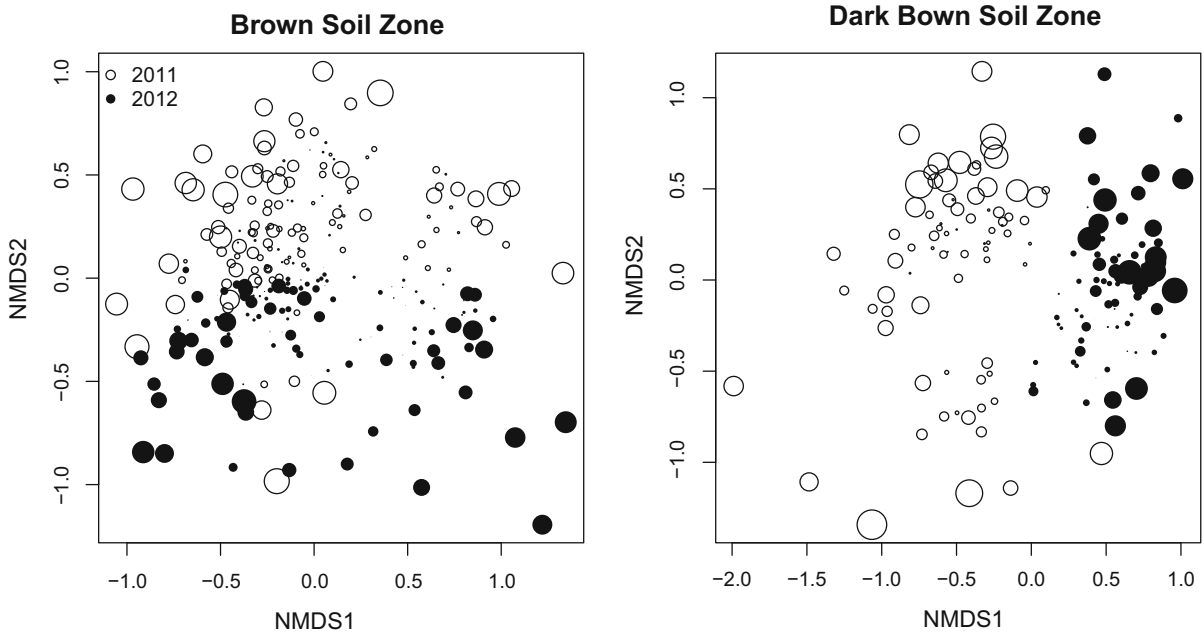
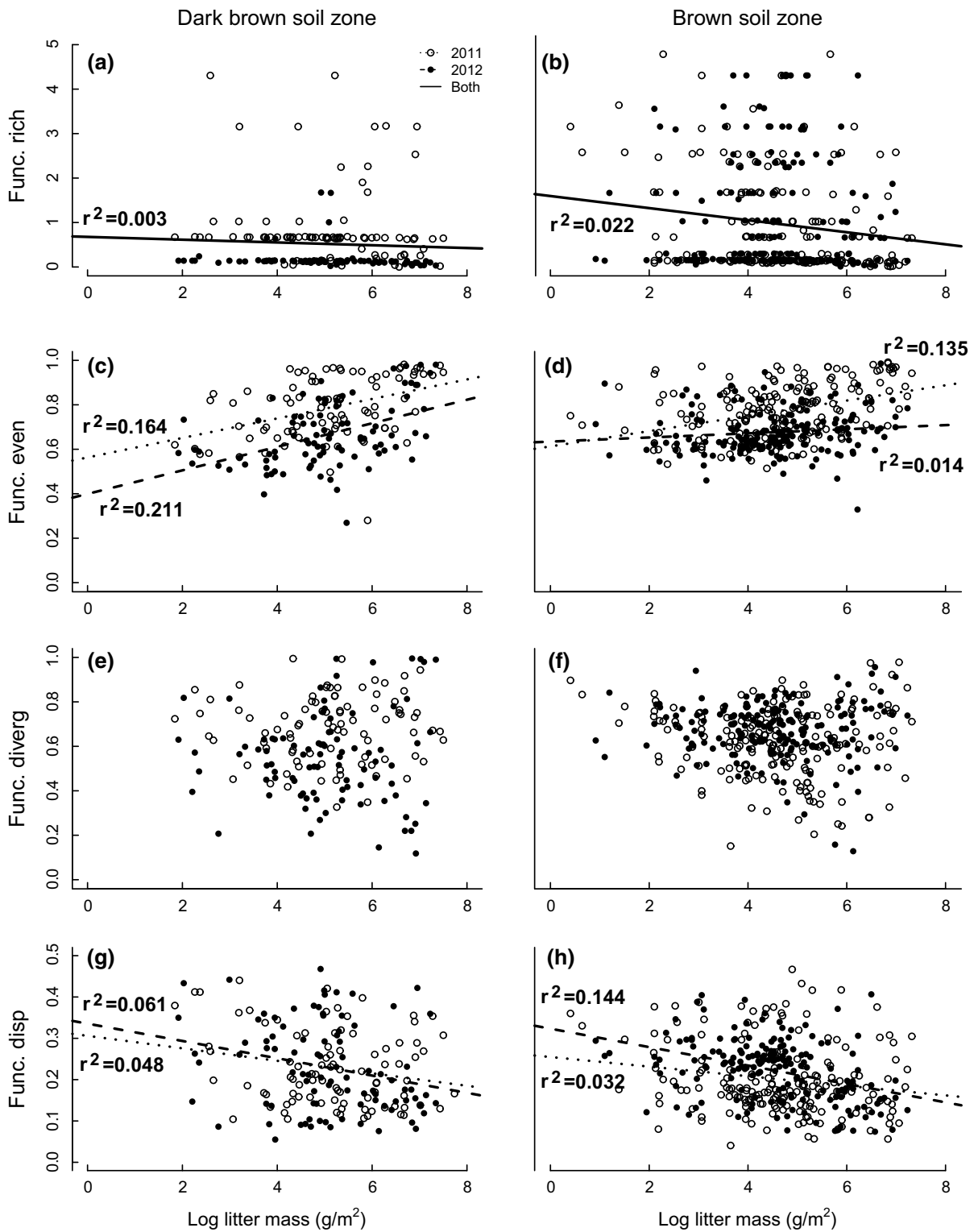


Fig. 2 Two-dimensional NMDS ordinations of species composition in communities in the brown and dark brown soil zones. Increasing symbol size indicates increasing mass of added litter. In both soil types, plots with small amounts of added litter are

clustered near the center, indicating similar species composition. Divergence with increasing mass of litter is indicated by the concentration of large symbols around the margins of the plots



◀ **Fig. 3** Effect of increasing litter mass on functional richness (proportion of total functional space occupied by the species in the community), functional evenness (distribution of species abundance within functional space), functional divergence (a measure of the relative abundance of species with unusual or extreme trait values), and functional dispersion (deviation of the community trait values as weighted by species abundance from trait values assuming equal species abundances) in communities in the brown and dark brown soil zones. *Open circles* indicate data collected in 2011 and *closed circles* 2012. *Solid lines* indicate relationships between litter and traits that were the same between years (no year interactions); in the case of a significant year interaction, the *dotted line* indicates the 2011 relationship and the *dashed line* 2012

Species evenness increased with litter in the dark brown soil zone in both years (Fig. 1c) and in 2011 in the brown (Fig. 1d). Litter had weak effects on the abundance of graminoids relative to forbs (Fig. 1e, f).

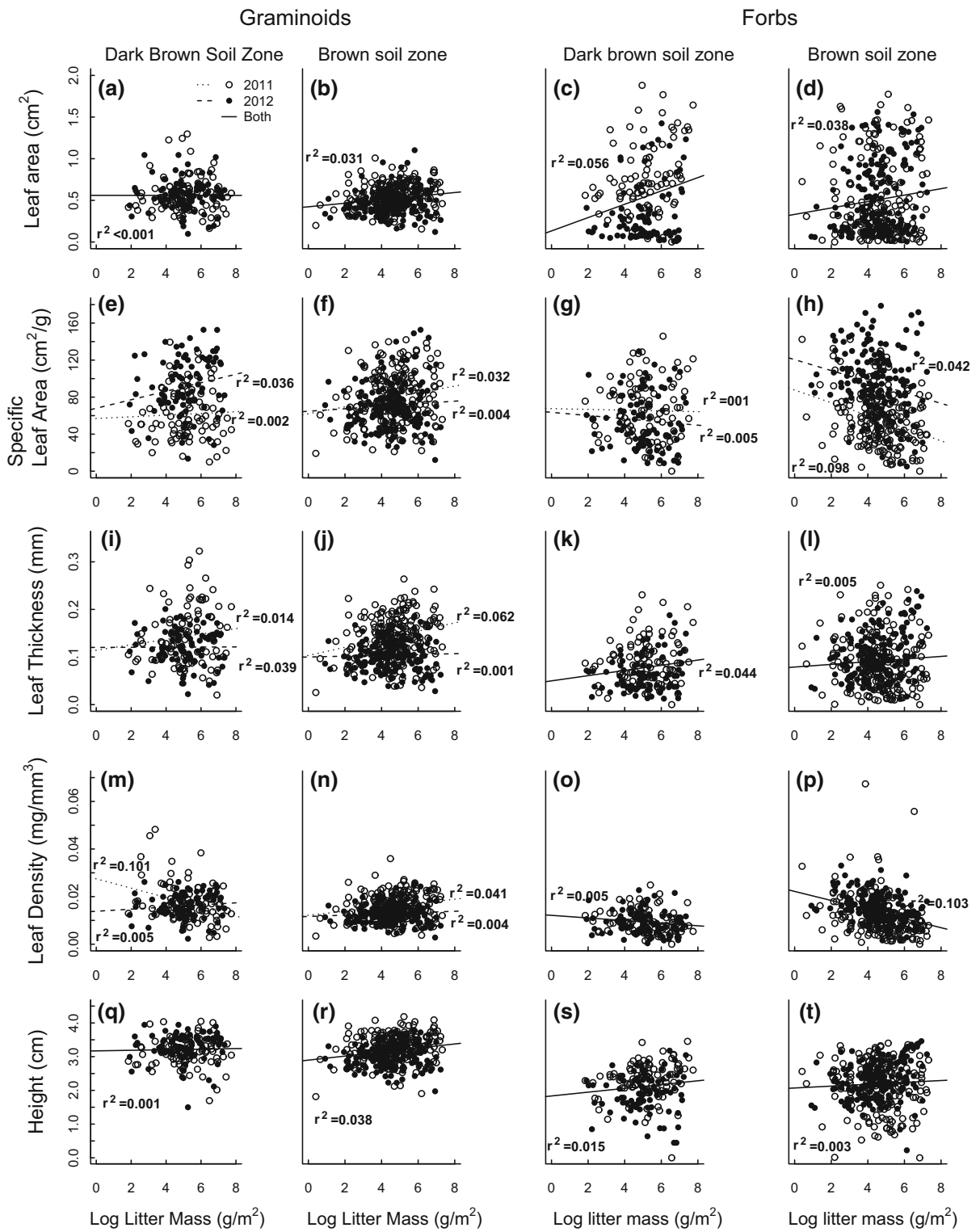
The plant community composition ordination demonstrated that litter addition resulted in highly divergent community composition, as plots with low levels of litter clustered to the center of the ordination diagrams while high-litter plots were distributed around the margins (Fig. 2). This demonstrates that the decreases in species diversity with increasing litter did not reflect convergence to a single high-litter community. Rather, increased litter caused highly divergent community composition between sites, with the high-litter communities at each site dominated by a different set of species.

There were strong effects of litter on many aspects of above-ground functional diversity and community-weighted mean trait values (Table 2). Increasing litter mass caused declines in functional richness (Fig. 3a, b), increases in functional evenness (Fig. 3c, d), and declines in functional dispersion (Fig. 3g, h). Functional divergence was unaffected by litter mass (Fig. 3e, f). Similarly, complex interactions between litter mass, soil zone, and year were found for all plant traits (Table 2). Leaf area increased with increasing litter mass, with a stronger response by forbs than graminoids (Figs. 4 a–d). Graminoid SLA increased with litter mass (Fig. 4e, f), while forb SLA decreased as litter mass increased; forb SLA declines were stronger in the brown than the dark brown soil zone (Fig. 4g, h). Changes in SLA with increasing litter mass were stronger in 2012 than in 2011 (Fig. 4 e–h). Graminoid leaf thickness increased with litter mass in 2011, but remained constant in 2012 (Fig. 4i, j), while

forb leaf thickness had smaller increases with litter that did not differ between years (Fig. 4k, l). Graminoid leaf tissue density declined with increasing litter mass in the dark brown soil zone in 2011 (Fig. 4m), but increased in 2012 and in both years in the brown soil zone (Fig. 4m, n). Forb leaf tissue density declines with increasing litter mass were consistent between years, but stronger in the brown than the dark brown soil zone (Fig. 4o, p). Graminoid height consistently increased with increasing litter mass across both soil zones and years (Fig. 4q, r); forb height similarly increased with increasing litter mass with the exception of the brown soil zone in 2012 (Fig. 4s, t).

Discussion

As reported in many other studies, increasing litter mass reduced species richness and increased species evenness in this grassland community (Amatangelo et al. 2008; Carson and Peterson 1990; Foster and Gross 1998; Lamb 2008; Stirling and Wilsey 2001; Weiher and Keddy 1999; Wilsey and Stirling 2007; Xiong and Nilsson 1999). Here, we demonstrate that these changes in species richness are closely linked to declines in functional richness and functional dispersion. Similarly, increases in species evenness with increasing litter mass were associated with increased functional evenness. Only one previous study has explored the relationships between litter accumulation and functional diversity. Pakeman (2011) found hump-shaped litter effects on species diversity, but no relationship between litter mass and functional richness, functional diversity, or functional dispersion across a range of Scottish plant communities, and a negative functional evenness–litter relationship. Pakeman's (2011) observations were made across a gradient from fallow agricultural fields to pastures, shrubland, and forest communities, while we applied experimental litter manipulations to narrower range of grassland communities. The responses observed in the present study likely capture the direct filtering effect of recent litterfall on established perennials, while the patterns in Pakeman's (2011) work also include longer-term processes of litter turnover and species establishment. Variation in grazing intensity can rapidly lead to the development of thick litter layers in these grasslands at scales similar to the sampling in this study (Cid and Brizuela 1998; Willms et al. 1988).



◀ **Fig. 4** Relationships between individual plant traits (community-level weighted averages) and litter mass for grass and forb species in the brown and dark brown soil zones. *Open circles* indicate data collected in 2011 and *closed circles* 2012. *Solid lines* indicate relationships between litter and traits that were the same between years (no year interactions); in the case of a significant year interaction, the *dotted line* indicates the 2011 relationship and the *dashed line* 2012. Transformed values ($\ln + 1$) are plotted for leaf area, leaf thickness, and height

Understanding the short-term effects of litter on the functional diversity of grassland communities is therefore crucial to interpreting the long-term effects of litter accumulation on patterns of grassland plant community structure through cycles of disturbance and recovery (e.g., Guedo and Lamb 2013; Lamb 2008).

While the effects of litter on functional richness and evenness are clearly interpreted in relation to species diversity effects, the decline in functional dispersion with increasing litter mass is less easily interpreted. This is the first time the relationship between functional dispersion and litter has been investigated. Functional dispersion is a measure of the deviation of the community abundance-weighted trait values from mean trait values assuming equal species abundances (Laliberte and Legendre 2010). The increase in species evenness with litter accumulation provides a partial explanation (Fig. 1c, d), as higher evenness should result in community-weighted trait values closer to the mean assuming equal species abundance. There was a weak positive correlation ($r = 0.177$) between species richness and functional dispersion (Fig. A5) indicating that further explanation is required. We propose that the mechanism underlying the functional dispersion effect is likely driven by species losses in the high-litter communities leading to a convergence of traits among the few species able to persist. Even though the high-litter communities had highly divergent species composition (Fig. 2), the consistent effects of litter on leaf traits (Fig. 4) indicate that the remaining species were generally similar in their trait values.

The pattern of trait convergence but compositional divergence observed in this study demonstrates the importance of the site and plot-level species pool in modulating short-term litter effects. Specifically, given the strong negative effects of litter on the germination of many species (Loydi et al. 2013; Xiong and Nilsson 1999), past events (i.e., competition, dispersal, nutrient or moisture driven environmental

filtering) that define the pool of perennial species in the community determine the identity of the species with litter-tolerant traits that come to dominate the community. Ultimately, these consistent filtering effects of litter mass on species with particular traits can explain longer-term patterns of species abundance change associated with the history of litter buildup and removal by fire in similar grasslands (Guedo and Lamb 2013).

Traits favoring graminoids under high-litter mass included high leaf area, SLA, leaf thickness, density of leaf tissues, and plant height. The large graminoid leaf areas largely resulted from the production of very long, stiff leaves that extended through the litter layer. Graminoid species with larger, thicker leaves of lower density were most abundant under high-litter mass. These traits are associated with a strategy of leaves penetrating vertically through litter. This strategy is illustrated by *Pascopyrum smithii* (Rydb.) Love (Western wheatgrass), a rhizomatous perennial grass. Western wheatgrass was common at the study sites, comprising $13\% \pm 12$ (mean \pm standard deviation) of the total live plant cover in control plots. This species more than doubled in abundance, increasing to $27\% \pm 24$ in plots in which the mass of litter was $>1,000 \text{ g m}^{-2}$. Conversely, the low-growing graminoid *Bouteloua gracilis* (Willd ex. Kunth) Lag. Ex Griffiths (Blue grama) was eliminated from the higher litter mass treatments, likely because it produces short and flexible basal leaves that can rarely emerge through the litter.

Traits favoring forbs under high-litter mass included high leaf area, lower SLA, higher leaf thickness, but lower leaf tissue density. Responses of forbs to increased litter mass were more complex than the graminoids and were partially driven by growth form. As with graminoids, forb species with larger, thicker leaves increased under high mass of litter. Unlike graminoids, however, there was a strong decline in leaf tissue density and specific leaf area of forbs with increasing mass of litter. Thus, many forb species in this community with thick, basal leaves that are unable to extend through and above the litter layer were filtered out. Forb species with an erect or twining growth habit such as *Vicia americana*, Muhl. Ex Willd. (American vetch) increased nearly 6-fold under the greater mass of litter. Anecdotal observations in plots suggest that internode elongation enabled these plants to penetrate the litter and expand leaves above.

In addition to the mechanical effects of litter discussed above, interactions between litter, soil moisture, and soil nutrients may also have played a role. The effects of moderate increases in litter on soil moisture and annual net primary productivity are well documented, as are the effects of nutrient availability on functional diversity (e.g., Cadotte et al. 2011; Deutsch et al. 2010b; Diaz and Cabido 2001; Willms et al. 1986, 1993). Some of these effects are likely reflected in the complex interactions between the environment (soil type and between-year precipitation changes) and many plant traits in this study. Increased mass of litter, for example, decreased the cover of graminoids relative to forbs in the dark brown soil zone, but graminoids increased in the brown soil zone. Different species pools between the two soil types may explain some of these differences. Plant communities in the dark brown soil zone generally have greater productivity and are likely to contain more forb species (Coupland 1950; Coupland and Brayshaw 1953) such as *V. americana* that are well adapted to high mass of litter. Further, the brown soil zone is more arid (Acton et al. 1998; Ellis et al. 1970); the increased soil moisture associated with higher litter mass (Deutsch et al. 2010b; Hooper et al. 2005; Loreau and de Mazancourt 2013; Willms et al. 1986, 1993) may have stimulated growth of graminoids, altering the graminoid-forb ratio. Between-year effects were likely driven by changing precipitation patterns. The Monet site, for example, was dry in 2011 and average in 2012; Matador was average in 2011 and dry in 2012; and King George was average in 2011 and wet in 2012. In addition, the patterns of precipitation were not the same between years and among sites. In 2011, precipitation was received throughout the growing season, while in 2012 precipitation was concentrated in the early part of the growing season. Finally, the winter of 2010–2011 had substantial snow cover but 2011–2012 was snow-free; snow-free conditions and exposure of plants to low temperatures can influence species composition (Gross and Romo 2010). Year-to-year variation in environmental conditions and plant community composition is common in these grassland ecosystems; these responses demonstrate how interactions between environmental variability and a consistent plant community response to litter can create strong heterogeneity in plant community structure at the landscape scale.

Conclusions

In this study, apparent physical interference from litter controlled plant community functional diversity and trait structure. Increasing litter mass caused rapid declines in plant diversity and a convergence in trait structure toward dominance by taller graminoids with increased leaf area, SLA, thickness, and density of leaf tissues. By contrast, selection of forbs by litter was more influenced by growth form, with species with well-developed stems and cauline leaves favored over rosette plants. This convergence of community trait structure was not driven by convergence in species composition, as increased litter selected a subset of species from the pre-treatment flora of each plot. The extent to which these interactions between historical factors such as grazing history and chance events as well as deterministic selection by litter accumulation drive grassland diversity at medium to large scales remains to be determined.

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