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Herbivore species identity and composition affect soil enzymatic activity through altered plant composition in a coastal tallgrass prairie

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ABSTRACT

Although single herbivore species are known to affect soil microbial communities, the effects of herbivore species identity and community composition on soil microbes and their functioning are unknown. We tested the effects of single orthopteran species and species combinations on soil enzymatic activity with an enclosure experiment in a coastal tallgrass prairie. Species effects on soil enzymatic activity were non-additive: one particular mixed feeding species (*M. femurrubrum*) resulted in 65% higher BG enzyme activity and 35% higher total hydrolytic enzyme activity, whereas certain combinations containing this species had little to no effects. These results suggest that critical species or combinations of species that strongly affect plant functional composition may also have strong effects on soil enzymatic functioning and nutrient limitation.

Herbivores can have strong positive (Belovsky and Slade, 2000) and negative effects (Millett and Edmondson, 2015) on ecosystem processes, depending on nutrient availability, feeding preferences, and other species-specific attributes (Ritchie et al., 1998; Bardgett and Wardle, 2010). Herbivores may influence primary production (Dyer, 1993; Belovsky and Slade, 2000, 2002; de Mazancourt and Loreau, 2000; La Pierre et al., 2015), nutrient cycling (Lovett and Ruesink, 1995; Belovsky and Slade, 2000, 2002; Frost and Hunter, 2004; Fonte and Schowalter, 2005; Metcalfe et al., 2015), and decomposition (Wardle et al., 2002). Their cascading effects on ecosystem functioning likely occur when their feeding alters the quantity or quality of plant material and/or soluble organic material (e.g., frass or greenfall from messy feeding) entering the soil thereby altering microbial communities (Holland, 1995; Classen et al., 2007). Researchers examining how herbivores affect soil functioning typically manipulate only one species, and few have measured how insect herbivores affect microbial communities (Yang and Gratton, 2014), and thus the roles that herbivore species identity and composition play in soil microbial functioning is unknown (Bardgett and Wardle, 2003).

Competitive interactions between coexisting herbivore species often cause shifts in species' diets and behavior, and these interactions may result in very different outcomes on soil functioning than any one species alone (Bardgett and Wardle, 2003). Even if species interactions do not alter behaviors, the presence of competitors can result in a decrease in herbivore populations, diluting species-specific effects seen with one species alone. Here, we examined how species identity and community composition of ubiquitous grassland herbivores affect soil microbial enzyme activity and stoichiometry. We predicted that species would have differential effects on soil enzymatic functioning because of species-specific feeding preferences, and that combinations of species would exhibit non-additive effects on soil enzymatic functioning.

We varied orthopteran (i.e. grasshoppers and katydids) community composition in a coastal tallgrass prairie (University of Houston's Coastal Center, La Marque, Texas, USA; 29°23′N,

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Table 1
Orthopteran species used in this study. The top 4 species were focal species used in single species treatments, and all combination treatments; the bottom 4 species were only used in the 8 species combination (shown in Table 2).

Species	Family	Feeding guild
Conocephalus strictus	Tettigonidae	Grass-feeder (occasionally feeds on other insects)
Melanoplus femurrubrum	Acrididae	Mixed-feeder
Orchelimum vulgare	Tettigonidae	Mixed-feeder (occasionally feeds on other insects)
Orphulella speciosa	Acrididae	Grass-feeder
Hesperotettix speciosa	Acrididae	Forb feeder
Chortophaga austrailor	Acrididae	Grass-feeder
Melanoplus bispinosus	Acrididae	Mixed-feeder
Arphia simplex	Acrididae	Grass-feeder

Table 2
Experimental design: all treatment combinations that were sampled in this experiment are shown.

Treatment	Species	n
1 species	*C. strictus (10 individuals)*	6
	M. femurrubrum (12 individuals)	6
	O. vulgare (8 individuals)	6
	O. speciosa (12 individuals)	6
4 species	*C. strictus (3), M. femurrubrum (3), O. vulgare (2), O. speciosa (3)*	6
8 species	*C. strictus (1), M. femurrubrum (1), O. vulgare (1), O. speciosa (1), H. speciosa (1), C. austrailior (1), M. bivittatus (1), A. simplex (1)*	6
	Total number of enclosures	36

Table 3
GLM results showing treatment effects on 6 different enzymes, total enzyme activity, relative C:P acquisition, and plant biomass. * denotes significance at the 0.05 α level.

Enzyme	df	F	p
ln (AP)	5,35	3.043	0.024*
ln (NAG)	5,34	0.567	0.725
ln (BG)	5,28	3.195	0.025*
ln (CHB)	5,33	0.691	0.635
ln (POX)	5,34	0.788	0.567
ln (PER)	5,35	2.317	0.068
ln (Total)	5,25	2.897	0.040*
ln (BG): ln (AP)	5,28	2.876	0.037*
Grass biomass	5,35	2.644	0.043*
Herb biomass	5,35	1.318	0.283
Shrub biomass	5,35	2.806	0.034*
Total biomass	5,35	3.409	0.015*

95°02′W) with small field mesocosms (basal area: 0.25 m^2, mesh size: 18 × 14 holes/inch^2). Soils at these sites are Vertisols of the Lake Charles series (fine, smectitic, hyperthermic Typic Hapluderts). The plant community is dominated by graminoids with 3 species making up over 90% of plant biomass (*Tridens longspicia*; *Paspalum plicatulum*, and *Andropogon gerardii*), but some shrub species can become abundant (*Berchemia scandens*, *Rubus argutus*, and *Myrica cerifera*). Treatments represented 6 herbivore communities (n = 6): 4 single species (2 grass feeders and 2 mixed grass and herb feeders); these 4 species combined; and an 8 species community that included 4 additional species, representing a more diverse community (Table 1). We stocked nymphal orthopterans (May 28th, 2012) at roughly equal biomass across treatments using the average adult biomass for each species (~1.2 g dry weight orthopteran/enclosure). We censused enclosures weekly, and added individuals as needed to maintain stocking biomass. Non-target organisms were removed throughout the experiment, which ended when most individuals were adults (7 weeks). All vegetation was clipped from each enclosure, sorted to species, dried and weighed. Soils were sampled from the center of each plot (0–10 cm) and stored at −20° C. We assessed hydrolytic enzyme activity (cellobiohydrolase (CBH), acid phosphatase (AP), N-acetyl-β-glucosaminidase (NAG), and β-glucosidase (BG)) and ligninolytic enzymes (phenol oxidase (POX) and peroxidase (PER)) following DeForest (2009). Total hydrolytic functioning was measured as the sum of all hydrolytic enzymes, and we calculated enzyme stoichiometry (Sinsabaugh et al., 2008). Differences in enzyme activity, stoichiometry, and plant biomass were analyzed with univariate general linear models with treatment as the factor ($\alpha = 0.05$). We determined if changes in microbial enzyme activity were related to plant biomass shifts resulting from orthopteran communities using regression; such analyses that examine links between soil enzymes and plant biomass are common in the literature (e.g., Dornbush, 2007; Sanaullah et al., 2011). Because multiple non-independent measurements of plant biomass were tested, we used Bonferroni corrections for these regressions ($\alpha = 0.017$). All analyses were conducted in SYSTAT 13.

Although this experiment only took place over two months, orthopteran community composition had strong effects on soil enzymatic activity: orthopterans affected AP and BG activity, as well as total hydrolytic enzyme activity and the relative acquisition of C:P (estimated by ln(BG):ln(AP); Table 3; Fig. 1), but did not affect NAG, CHB, POX and PER enzyme activity ($p > 0.05$). We propose several mechanisms by which orthopterans could affect soil functioning over this time scale. First, in laboratory feeding trials and our field experiments, we see evidence that many orthopterans are "messy feeders", potentially leading to high quality green litter inputs as other researchers do (Gandar, 1982). Certain orthopteran species and combinations had strong effects on soil enzymatic activity, and we propose that some of these effects may be occurring via changes in plant community composition. At this site, decomposition is relatively rapid since temperature and moisture levels are high, and some shrubs are evergreens and constantly shedding leaves; while the graminoids slowly shed leaves throughout the summer. Although the majority of the biomass was still alive at the time of plant harvest, rapid decomposition of senesced leaves, combined with greenfall from messy feeding or species-specific frass inputs could operate to affect soil functioning at this time scale.