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HIGHLIGHTED STUDENT RESEARCH

Are arthropod communities in grassland ecosystems affected by the abundance of an invasive plant?

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Abstract

Invasive plants cause changes to native plant communities and nutrient cycling, and by doing so, may alter the amount and quality of habitat available for animals at multiple trophic levels, including arthropods. Arthropods are generally abundant, diverse, and contribute to energy flow and nutrient cycling and are, therefore, an important group to study as a way of determining the effects of changes to ecosystem functioning. Spotted knapweed (*Centaurea stoebe* L.), a perennial forb native to Eastern Europe, is considered one of the most ecologically harmful invasive species in Western North America. Here, we test if spotted knapweed alters plant community, ground litter and ground temperature, and arthropod functional group structure and biomass in grassland habitats in British Columbia, Canada. Pitfall traps, installed at 20 sites that differed in spotted knapweed density, were sorted into herbivores, omnivores, predators, detritivores, and parasites. Decreases in herbivore and detritivore biomass was associated with increasing spotted knapweed density. The first two coordinates of a Principle Coordinates Analysis explained a cumulative 60% of the variation, and herbivores were separated from predators on both axes. The results suggest that spotted knapweed density may affect arthropod functional groups through changes in plant community composition, and surface soil temperatures. The results suggest that in terms of relative abundance and biomass, increasing knapweed density had positive effects on some arthropod functional groups, neutral effects on others, and negative effects on others. Thus, not all arthropod functional groups responded equally to knapweed invasion, and knapweed invasion does not necessarily decrease arthropod functional group diversity

Keywords Invasive species · Arthropod · Functional groups · Grassland

Introduction

Plant species invasions are a global conservation concern, leading to changes in native plant community composition and soil chemistry (Vitousek et al. 1996; Ehrenfeld 2003). A decrease in native plant diversity due to the colonization of invasive plants has resulted in a decrease in the diversity of native herbivore and omnivore arthropods (Vila et al. 2011; Litt et al. 2014). Arthropods contribute to ecosystem function in their roles as pollinators, foragers, soil engineers, and food for other organisms in the ecosystem (Tscharntke and Greiler 1995; Bourn and Thomas, 2002; Higgins and Lindgren 2006). Since arthropods make up the largest animal biomass and the majority of animal species and functional groups (herbivores, omnivores, predators, detritivores, and parasites) in terrestrial habitats, it is critical to understand how arthropods respond to increases in the density of non-native plants.

Trophic structure is the relationships between primary producers, herbivores, primary consumers, secondary consumers, tertiary consumers, and detritivores. A disturbance that removes a top predator can have large effects throughout the ecosystem (Schmitz et al. 2000; Shurin et al. 2002; Borer et al. 2006). Trophic structure is dynamic and is dependent on the availability of primary plant producers, the number and composition of species inhabiting the ecosystem, and feeding behavior of species (Leroux and Loreau 2015). These processes dictate how energy moves through a community and the amount of biomass at each trophic level

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This project explores the relationship between arthropods and a highly invasive plant. It contributes to a network exploring the restoration of disturbed areas using arthropods as bioindicators.

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(Trebilco et al. 2013). A better understanding of trophic structure with respect to ecosystems change as a result of non-native plant invasion will help managers respond to those changes.

Not all arthropod functional groups are expected to respond similarly to invasive plants. Tallamy et al. (2010) found that invasive plants, such as Norway maple and crepe myrtle, can potentially support generalist North American herbivore arthropod species in certain circumstances. Generalist herbivores are less diverse but far more abundant than specialist species (Tallamy 2004). Therefore, it is difficult to predict the response of herbivore and omnivore diversity to non-native plant invasion. Predator and parasite arthropod guilds can be adversely affected by changes in prey items or vegetation structure due to the colonization of invasive plants (Gratton and Denno 2005). This could lead to subsequent changes in ecosystem services due to the decrease of these arthropod groups. However, detritivore arthropod biomass might increase due to an alien plant invasion because increases in decaying ground litter associated with highly productive invasive plants with palatable high-nutrient leaf tissue could provide extra food for detritivores (Levin et al. 2006). It is expected that any changes to native arthropod diversity would lead to changes in guild dynamics regardless, which could result in a chain of effects throughout the ecosystem (Pearson 2009; Grant et al. 2017). For example, decreases in predators could relax the top–down control effect on their prey. Alternatively, herbivores could become less productive in highly invaded sites due to bottom-up control of limited native plant biomass for consumption with the introduction of plant competition depending on the preferences of generalists and the presence of obligate native host plants for specialists.

Centaurea stoebe L. subsp. micranthos (spotted knapweed) is a deeply tap-rooted perennial forb native to Eastern Europe that was first introduced into North America in the 1890s (Fraser and Carlyle 2011). It is considered one of the most ecologically harmful invasive plant species in Western North America (Hansen and Ortega 2009). How will spotted knapweed affect the relative composition of arthropod functional groups? Past studies suggest that arthropod functional groups may respond differentially to knapweed invasion. Research contributing to our understanding of invasive plants, such as spotted knapweed, is important in informing conservation management strategies essential in combatting the spread of invasive plants and the subsequent loss of biodiversity.

Our objective was to test the effect of spotted knapweed density on arthropod functional groups, including herbivores, omnivores, predators, detritivores and parasites, in semi-arid grasslands of southern central British Columbia, Canada. We hypothesize that herbivore and omnivore functional group biomass will decrease in the presence of spotted knapweed due to their inability to feed on non-native plants (Bernays and Graham 1988). If the ecosystem is food limited, this will lead indirectly to decreases in predator and parasite biomass due to changes in prey items. Detritivore biomass is hypothesized to increase, as was observed in the majority of studies reviewed by Litt et al. (2014), with increasing spotted knapweed density due to the increase in food availability and plant litter, with the colonization of spotted knapweed.

Methods

Study area

In May 2017, arthropod-sampling sites were established in the upper grasslands of Lac Du Bois (LDB) (Fig. 1), a 15,000-ha grassland area located Northwest of Kamloops, British Columbia (BC), Canada (50° 39′ 59″ N, 120° 19′ 09″ W). LDB is a protected bunchgrass and shrub–steppe ecosystem that occurs in the rain shadow of the BC Coast Mountains. The park and surrounding region is characterized as semi-arid, with annual precipitation of 277.6 mm, (including 63.5 cm of snowfall). Average annual daily temperature for the region is 9.3 °C (Environment Canada 2010). Dominant grasses in the region include bluebunch wheatgrass (*Pseudoroegneria spicata*) and rough fescue (*Festuca scabrella*). Common shrubs include big sagebrush (*Artemisia tridentata*), rabbit brush (*Ericameria nauseosa*), prickly rose (*Rosa acicularis*) and grey horsebrush (*Tetradymia canescens*) (Lee et al. 2014). LDB is a multi-use area managed for recreation, wildlife, and livestock grazing at low to moderate stocking rates (Evans 2011; Schmidt et al. 2012; Bassett and Fraser 2015). The continuous use of the grasslands by recreational users and ranchers leaves the area susceptible to the introduction of invasive plants through hitchhiking seeds attached to clothing, boots, vehicle tires, and other means. This makes it an important study area due to the numerous invasive plants currently in the park and the potential for further human seed dispersal of invasive species.

Site selection

Twenty 40-m diameter sampling sites were located in the LDB grasslands with varying densities of spotted knapweed: ‘None’ (0–1 stems m^{-2}), ‘Low’ (2–44 stems m^{-2}), ‘Medium’ (45–69 stems m^{-2}), and ‘High’ ($>$ 70 stems m^{-2}) (Fig. 1). The sites were all located within <2 km^2 to ensure that they shared similar ecosystem properties to allow observed differences to be more meaningful (Bode and Maciejewski 2014).

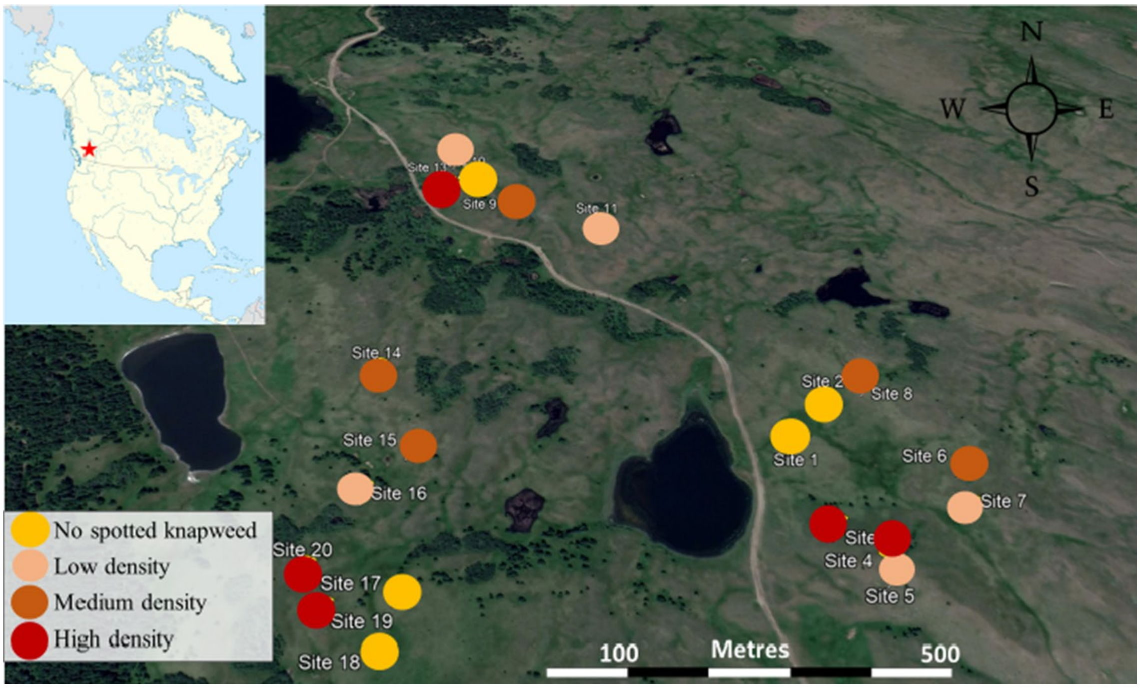

Fig. 1 Location of sampling sites in the upper grasslands of Lac du Bois Grasslands protected area, Northwest of Kamloops, British Columbia, Canada

Sampling protocol

In the center of each sampling site, four pitfall traps were set up in a square arrangement, each 2 m apart. Pitfall traps are small epigeal arthropod collection traps that consist of a collection cup (11.5 cm diameter, 7.5 cm depth) dug into the earth flush with ground level (Bassett and Fraser 2015). The collection cups were filled with 87% denatured ethanol solution to preserve the specimens. Plywood cover boards (30 cm × 35 cm) were placed above each pitfall trap to reduce ethanol evaporation. Spotted knapweed seedlings emerge in early May (Schirman 1981). All pitfall traps were opened for a period of 5 days each on the last week of May, June, July, and August 2017.

Soil temperature data loggers (DS1921G-F#5 Thermochron, iButtonLink LLC, Whitewater, Wisconsin, USA) were installed at 5-cm depth in the center of each site. Spotted knapweed has been observed to increase soil temperature and surface water runoff (Lacey et al. 1989; Fraser and Carlyle 2011) and arthropod species can be affected by changes in temperature (Bokhorst et al. 2008). Vegetation was sampled 20–28 of June, 2017 at each of the 20 sites. 1 m × 1 m quadrats were placed 2 m away from each pitfall trap, totalling 80 quadrats. Within each quadrat, the number of spotted knapweed stems and the percent cover of all plants, bare ground, and litter were recorded. All plant species in each quadrat was identified and each species' percent cover within the quadrat was recorded. In addition, a 0.5 m × 0.1 m sample at the North side of each quadrat was clipped for live standing biomass. The plant biomass samples were separated as spotted knapweed as one component and all other live plants as the other component. The plant biomass samples were stored in brown paper bags and dried in a Yamato oven (Model No. DKN8132) at 65 °C for 48 h (as per Bassett and Fraser 2015) and weighed with an analytical balance to the nearest 0.00001 g (Fisher Scientific accuseries 225D). The biomass data were converted into g m^{-2}. The Shannon–Weiner Index and the Simpson diversity index of plant community diversity were calculated with the species cover data for each plot.

Arthropod specimens were stored in a – 20 °C freezer in 150-mL containers unique to each pitfall trap filled with 87% denatured ethanol. One container from each sampling site at each sampling date was taxonomically identified to functional group and sorted using sterile forceps and sorting dishes. Functional groups of specimens were determined based on the diet of adult life stages (using Marshall 2006). The functional groups included: herbivore, omnivore, detritivore, predator, or parasite. After being sorted into functional groups, specimens were dried in an oven at 65 °C for 48 h, and weighed with an analytical balance (as per Harrower 2016). Species richness was calculated, and functional Shannon–Weiner diversity and Simpson diversity were calculated using the number of individuals of each functional group.

Data analysis

All data were analyzed statistically using RStudio integrated under R 3.4.4 “Someone to Lean On” (The R Foundation for Statistical Computing). The data were checked for normality using boxplots and residual plots. Homogeneity of variance was assessed using the Fligner–Killeen test, and when non-normal, the data were transformed using a natural logarithm transformation or a log $(x+1)$ transformation for biomass and species richness data that contained zeroes. All data analyses were tested for a significance at the $[\alpha]$ 0.05 level.

Arthropod specimens from a total of 80 pitfall traps were counted, sorted, and weighed. The arthropod samples were collected monthly, thus a repeated measures design. However, there were several arthropod community variables that were not affected by the sampling date: Simpson diversity, herbivore biomass, detritivore biomass, and parasite biomass (Table 1, $P > 0.05$). Theses variables were, therefore, grouped for analysis. A one-way analysis of variance (ANOVA) and post hoc Tukey test were done to test the effects of the density of spotted knapweed (no, low, medium, and high density) on the biomass, species richness, and functional diversity of each arthropod guild captured.

Finally, principal components analyses (PCA) were conducted to examine the most influential functional group associated with arthropod community composition. Stepwise multiple regressions in both directions using AIC values were run using the principal components and the significant site variables to determine the best fitting model that each principal component represented. These regressions helped to explore interacting effects of site variables, spotted knapweed density, and functional groups.

Results

Plant community characteristics

Total plant biomass was significantly lower in plots with high spotted knapweed density (126.1 ± 20.9 g m^{-2})

Table 1 Analysis of variance results of the effects of spotted knapweed density and date sampled on arthropod community functional groups, $n = 80$, $df = 3$

Response variable	Knapweed density			Date		
	F	P	Effect	F	P	Effect
Overall species richness (n trap^{-1})	1.776	0.164	–	13.445	**< 0.001**	+
Overall biomass (g trap^{-1})	1.788	0.162	+	3.646	**0.033**	+
Shannon–Weiner diversity	1.402	0.249	+	3.625	**0.034**	–
Simpson diversity	1.643	0.192	+	0.950	0.394	–
Herbivore biomass (g trap^{-1})	2.849	**0.047**	–	0.266	0.767	+
Omnivore biomass (g trap^{-1})	2.529	*0.068*	–	5.952	**0.001**	–
Predator biomass (g trap^{-1})	1.006	0.389	+	7.982	**0.001**	–
Detritivore biomass (g trap^{-1})	1.536	0.660	–	1.281	0.287	+
Parasite biomass (g trap^{-1})	1.154	0.337	–	1.072	0.350	–
Daily ground temperature (°C)	7.450	**< 0.001**	+	15.854	**< 0.001**	+

Bold values indicate statistical significance at $P < 0.05$

Table 2 Analysis of variance results of the effects of spotted knapweed density on site variables, ± SE, $n = 20$, $df = 3$

Site variables	Knapweed density				F	P
	None	Low	Medium	High		
Plant biomass (g m^{-2})	404.6 ± 85.0^{a}	212.4 ± 67.8^{bc}	168.6 ± 25.3^{bc}	126.1 ± 20.9^{c}	3.37	**0.046**
Ground litter cover (%)	64.7 ± 9.8^{ab}	35.4 ± 8.1^{bc}	46.1 ± 3.0^{abc}	19.6 ± 2.1^{d}	8.20	**0.001**
Bare ground cover (%)	6.4 ± 3.2^{b}	15.9 ± 7.6^{ab}	16.8 ± 4.6^{ab}	23.0 ± 1.8^{a}	2.05	*0.099*
Daily ground temperature (°C)	18.8 ± 0.6^{b}	23.6 ± 1.2^{a}	21.7 ± 0.8^{ab}	22.2 ± 0.8^{a}	5.15	**0.003**
Native plant cover (%)	100 ± 6.4^{a}	53.1 ± 8.7^{b}	68.9 ± 6.8^{b}	48.0 ± 6.2^{b}	11.9	**< 0.001**
Invasive plant cover (%)	1.5 ± 0.5^{c}	20.3 ± 6.4^{b}	24.2 ± 1.6^{b}	41.4 ± 3.0^{a}	20.1	**< 0.001**
Shannon–Weiner diversity	3.9 ± 0.5^{b}	5.2 ± 0.2^{a}	4.8 ± 0.2^{ab}	4.4 ± 0.2^{ab}	3.01	*0.061*
Simpson diversity	5.6 ± 1.5^{b}	9.7 ± 1.3^{a}	8.0 ± 1.0^{ab}	6.0 ± 0.5^{ab}	2.62	*0.089*

Bold values indicate statistical significance at $P < 0.05$, italicized values indicate statistical significance at $P < 0.1$, superscripts denote the statistically significant differences in means compared to no spotted knapweed (404.6 ± 85.0 g m^{-2}, Table 2, $P=0.046$). High spotted knapweed density sites also resulted in the lowest plant ground litter cover ($19.6 \pm 2.1\%$, Table 2, $P=0.001$). Sites without spotted knapweed also had the lowest daily ground temperature throughout the summer compared to high knapweed sites (3.4 ± 0.7 °C colder, Table 2, $P=0.003$).

Sites with high spotted knapweed density had highest invasive plant cover ($41.4 \pm 3.0\%$, Table 2, $P<0.001$) and lowest native plant cover ($48.0 \pm 6.2\%$, Table 2, $P<0.001$). Sites with no spotted knapweed had highest native plant cover ($100 \pm 6.4\%$, Table 2) and lowest invasive plant cover ($1.5 \pm 0.5\%$, Table 2). Plant community diversity, measured using two diversity indices, was higher in sites with low densities of spotted knapweed compared to sites with no spotted knapweed present, however, not statistically significant (difference of 1.3 ± 0.5, $P=0.061$ and 4.1 ± 1.5, $P=0.089$, Table 2), while plant diversity at sites with medium and high densities of spotted knapweed did not differ between each other or between low/no densities of spotted knapweed (difference of 0.4 ± 0.2 and 2.0 ± 1.0, Table 2).

Arthropod functional group biomass and diversity

Herbivore biomass was greater at no spotted knapweed density (18.6 ± 8.9 g, Table 3, $P=0.043$) compared to all other plots that contained spotted knapweed. Detritivore biomass was larger, however not statistically significant, in the absence of spotted knapweed (difference of 8.4 ± 4.6 g, Table 3, $P=0.066$).

Functional groups were affected differently by the density of spotted knapweed at different sampling periods throughout the summer (Table 4). May and July sampling yielded no significant differences of arthropod community composition at different spotted knapweed densities (Table 4). However, May sampling yielded much higher overall insect biomass than the other months. In June, herbivore biomass was 10–25 × higher in the absence of spotted knapweed than at sites with spotted knapweed (Table 4, $P=0.039$). Detritivore biomass decreased with increasing spotted knapweed density (Table 4, $P=0.026$). August sampling had highest predator biomass at low spotted knapweed densities (Table 4, $P=0.087$) and lowest predator biomass at no spotted knapweed.

Arthropod community trophic interactions

A PCA using the five functional groups' total summer biomass showed that components 1 and 2 accounted for 60.1% of the variation in functional group biomass and components 2 and 3 accounted for 42.3% of variation (Table 5). Component 1, controlled by spotted knapweed biomass (Table 6, $P=0.019$), negatively correlates with herbivore and parasite biomass ($r=-0.666$ and -0.683, respectively, Table 5). Component 2, controlled by litter cover and surface soil temperature (Table 6, $P=0.002$ and $P=0.001$, respectively), negatively correlates with omnivore and predator biomass ($r=-0.676$ and -0.685, Table 5). Finally, component 3, controlled by plant biomass and litter cover (Table 6, $P=0.025$ and $P=0074$, respectively), negatively correlates with detritivore biomass ($r=-0.929$, Table 5). The vectors reveal a negative relationship between herbivores/parasites versus predators/omnivores at all sites (Fig. 2).

Discussion

Increasing spotted knapweed density had divergent effects on the relative density and biomass of arthropod functional groups but had no effect on net arthropod diversity across functional groups. Divergent effects of increasing knapweed density may have been due to changes in foraging or reproduction opportunities (Bernays and Graham 1988), or

Table 3 Analysis of variance results of the effects of spotted knapweed density on arthropod community biomass, functional diversity and functional group biomass for May, June, July and August samples, ± SE, $n=80$, $df=3$

Overall summer	Knapweed density				F	P
	None	Low	Medium	High		
Overall biomass	192.7 ± 60.3	181.3 ± 66.6	161.3 ± 56.1	202.7 ± 74.5	1.788	0.162
Shannon–Weiner diversity	1.2 ± 0.2	1.3 ± 0.2	1.7 ± 0.1	1.6 ± 0.1	1.402	0.249
Simpson diversity	1.7 ± 0.2	1.8 ± 0.1	2.2 ± 0.1	2.1 ± 0.1	1.780	0.158
Herbivore biomass	18.6 ± 8.9^{a}	4.0 ± 1.6^{b}	3.8 ± 0.9^{b}	5.2 ± 2.5^{b}	2.857	**0.043**
Omnivore biomass	27.3 ± 8.0	23.6 ± 13.5	9.4 ± 3.4	19.0 ± 4.3	1.943	0.131
Predator biomass	85.4 ± 29.7	128.8 ± 56.4	123.9 ± 52.5	104.7 ± 26.4	1.006	0.389
Detritivore biomass	8.8 ± 4.8^{a}	3.9 ± 2.4^{ab}	0.1 ± 0.09^{b}	0.4 ± 0.2^{b}	2.739	*0.066*
Parasite biomass	3.3 ± 2.5	0.6 ± 0.3	0.1 ± 0.07	0.4 ± 0.2	1.832	0.148

Biomass is measure in mg trap^{-1}

Bold values indicate statistical significance at $P<0.05$, italicized values indicate statistical significance at $P<0.1$, superscripts denote the statistically significant differences in means

Table 4 Analysis of variance results of the effects of spotted knapweed density on arthropod community functional group biomass sampled each month, May, June, July and August, ± SE, $n = 20$, $df = 3$

	Knapweed density				*F*	*P*
	None	Low	Medium	High		
May						
Overall biomass	106.1	525.9	346.1	463.7	1.850	0.179
Shannon–Weiner diversity	1.2	1.8	1.7	1.6	0.481	0.700
Simpson diversity	1.7	2.3	2.2	2.2	0.680	0.577
Herbivore biomass	7.0	6.2	4.2	3.2	0.214	0.885
Omnivore biomass	11.5	23.8	6.8	19.7	1.393	0.281
Predator biomass	86.7	441.6	335.0	440.0	1.532	0.245
Detritivore biomass	0.3	1.9	0.04	0.6	0.394	0.759
Parasite biomass	1.3	1.2	0.01	0.03	0.831	0.496
June						
Overall biomass	324.6	76.6	157.4	240.3	1.546	0.241
Shannon–Weiner diversity	1.8	1.3	2.1	1.8	0.829	0.497
Simpson diversity	2.1	1.8	2.4	2.1	0.484	0.698
Herbivore biomass	38.6^{a}	1.5^{b}	3.8^{b}	2.6^{b}	3.513	**0.039**
Omnivore biomass	8.3^{a}	48.4^{b}	12.8^{ab}	31.4^{ab}	2.721	*0.079*
Predator biomass	163.2	54.6	140.1	204.7	1.294	0.311
Detritivore biomass	61.1^{a}	12.1^{b}	0.4^{b}	0.01^{b}	4.008	**0.026**
Parasite biomass	10.2	0.0	0.3	1.4	1.070	0.390
Daily ground temperature	16.5	20.5	18.9	18.9	2.277	0.119
July						
Overall biomass	81.2	101.3	136.0	82.2	0.714	0.558
Shannon–Weiner diversity	1.1	1.1	1.6	1.9	1.036	0.403
Simpson diversity	1.8	1.6	2.1	2.3	0.572	0.642
Herbivore biomass	4.1	3.6	2.9	0.8	0.823	0.500
Omnivore biomass	33.8	9.6	16.9	21.8	1.207	0.339
Predator biomass	30.7	4.7	20.0	32.9	2.220	0.125
Detritivore biomass	2.0	0.1	3.7	0.1	0.400	0.755
Parasite biomass	0.8	1.1	0.2	0.2	0.397	0.757
Daily ground temperature	20.2^{a}	25.9^{b}	23.9^{ab}	24.4^{ab}	2.644	*0.085*
August						
Overall biomass	6.3^{b}	21.6^{a}	5.4^{b}	24.7^{a}	2.732	*0.055*
Shannon–Weiner diversity	0.7	1.1	1.4	1.0	0.448	0.772
Simpson diversity	1.4	1.5	2.1	1.9	1.018	0.441
Herbivore biomass	8.9	4.1	3.9	5.2	0.760	0.533
Omnivore biomass	16.6	2.3	0.9	2.9	1.634	0.221
Predator biomass	0.9^{b}	31.5^{a}	0.6^{b}	7.1^{ab}	2.235	*0.087*
Detritivore biomass	3.9	1.0	0	0.6	0.424	0.739
Parasite biomass	0.8	0	0	0	1.000	0.418
Daily ground temperature	19.6^{a}	24.3^{b}	22.3^{ab}	23.3^{ab}	2.703	*0.082*

Biomass is measure in mg per pitfall trap. Bold values indicate statistical significance at $P < 0.05$, italicized values indicate statistical significance at $P < 0.1$, superscripts denote the statistically significant differences in means

through changes in native plant community through competition (Callaway and Ridenour 2004; Hansen and Ortega 2009), and changes in abiotic ecosystem factors such as amount of bare ground or litter cover and soil temperatures (Fraser and Carlyle 2011).

Plant community characteristics

Contrary to previous findings (Fraser and Carlyle 2011), spotted knapweed density was not correlated with plant community diversity, likely because the Fraser and Carlyle (2011) study was focused on primarily high-density

Table 5 Factor loadings of principal components analysis for all invertebrates collected in May, June, July and August, $n = 80$

Variable	Component 1	Component 2	Component 3
Herbivore	− 0.666	0.108	0.233
Omnivore	− 0.163	− 0.676	–
Predator	− 0.127	− 0.675	− 0.255
Detritivore	− 0.217	0.254	− 0.929
Parasite	− 0.683	0.101	0.124
Standard deviation	1.357	1.078	0.976
Variance (%)	36.8	23.3	19.0
Cumulative variance (%)	36.8	60.1	79.1

knapweed patches whereas our study selected a gradient. Higher spotted knapweed densities did negatively correlate with overall biomass of the plant community. Spotted knapweed is thought to secrete allelochemicals through its roots into surrounding soils that can shift microbial interactions, increase soil phosphorus and potassium availability (Thorpe et al. 2006), and reduce soil nitrogen availability for surrounding plants to uptake (Suding et al. 2004; Fraser and Carlyle 2011). Assuming that a similar pattern in soil chemistry with respect to knapweed density persisted in our experiment, which is reasonable considering that the Fraser and Carlyle (2011) study was conducted in the same grasslands as the current study, dense spotted knapweed stands could make the environment less hospitable for competing plants, reducing overall plant biomass. This was further validated by the observation of bare ground cover being highest and plant litter cover being lowest at high spotted knapweed densities. As found by Fraser and Carlyle (2011), the increase in bare ground likely lead to increased soil temperatures in the highest density spotted knapweed stands when compared to sites with no knapweed. It is important to note that this is inference based on past studies exploring spotted knapweed altering soil characteristics (Suding et al. 2004; Thorpe et al. 2006; Fraser and Carlyle 2011). Whether site characteristics determine spotted knapweed distribution or spotted knapweed influences site characteristics cannot be determined through our data at these sites. However, the sites were all located near one another to alleviate potential changes in temperature, precipitation, grazing pressures, and other ecologically significant differences that are inherent in field studies (Legendre 1993). Regardless, these ecosystem alterations can result in functional changes to the habitat for arthropods.

Arthropod functional group biomass and diversity

Arthropod functional diversity was not influenced by spotted knapweed density. Past studies have shown both increases (e.g., Kappes et al. 2007; Alerding and Hunter 2013) and decreases (e.g., Ernst and Cappuccino 2005; Bultman and DeWitt 2008; Burghardt et al. 2010) in arthropod community diversity with the introduction of invasive plants. It is possible that any negative effects of spotted knapweed on specific arthropod functional groups were counteracted by positive effects to other functional groups.

As predicted, the biomass of arthropod functional groups was uniquely negatively and positively affected by differing densities of spotted knapweed in the grassland ecosystems. This suggests that changes to arthropod habitat through the introduction of spotted knapweed may have been the driving force in the changes observed to functional group biomass. Any changes to arthropod functional groups could lead to changes in community dynamics that could have cascading effects throughout the ecosystem. Differences in arthropod community measures—except herbivore, detritivore, and parasite biomass—depended on the sampling period.

Herbivores

Herbivores, especially herbivore generalists, are commonly unable to use plant families as a food source when they do not share an evolutionary history with that plant (Tallamy 2004). Bernays and Graham (1988) found that 90% of all arthropod herbivores feed on plants in only a single family or a few genera. In a review paper by Litt et al. (2014), 42 out of 87 studies found that herbivorous arthropod abundance, species richness, or biomass decreased due to the presence of invasive plant species. Our study showed the same negative association between herbivore biomass and spotted knapweed biomass.

Decreases in herbivorous arthropods can adversely affect higher trophic levels, especially grassland birds, which feed on large herbivores such as *Lepidoptera* (butterflies and moths) and *Orthoptera* (Wiens and Rotenberry 1979). Decreased herbivore biomass could also have been influenced by predaceous arthropod functional groups through top-down control. When predator biomass was high, herbivore biomass was low. The ratio of predator: herbivore biomass increased with increasing spotted knapweed density (none = 4.59; low = 32.2; medium = 32.6; high = 20.1, suggesting that the habitat created by spotted knapweed could have facilitated better hunting conditions for predators or adverse refuge for herbivores.

Omnivores

Omnivore biomass did not show trends based on spotted knapweed density, and also differed greatly between months. Omnivores are a difficult group to predict and analyze because they play many ecosystem roles and have varying diets and environmental needs (Triplehorn and Johnson

Table 6 Three multiple regression analyses for significant site variables predicting principal component 1, 2, and 3, $n = 80$, $df = 56$

Variable	Component 1 F-stat = 2.39, $P = 0.078$, $R^2 = 0.130$				Component 2 F-stat = 7.56, $P = 0.001$, $R^2 = 0.222$				Component 3 F-stat = 2.59, $P = 0.062$, $R^2 = 0.132$			
	Estimate	SE	T	P	Estimate	SE	T	P	Estimate	SE	T	P
Intercept	− 1.872	1.172	− 1.597	0.116	− 3.668	1.005	− 3.648	**0.001**	− 2.550	2.136	− 1.194	0.238
Spotted knapweed biomass (g m^{-2})	0.201	1.109	2.400	**0.019**								
Plant biomass (g m^{-2})									0.890	0.386	2.300	**0.025**
Litter cover (%)					1.868	0.573	3.257	**0.002**	− 1.800	0.988	− 1.823	*0.074*
Bare ground cover (%)	− 1.729	1.373	− 1.259	0.213								
Daily ground temperature (°C)	0.076	0.030	1.259	0.213	0.118	0.034	3.411	**0.001**	− 0.039	0.043	− 0.912	0.366

Bold values indicate statistical significance at $P < 0.05$, italicized values indicate statistical significance at $P < 0.1$

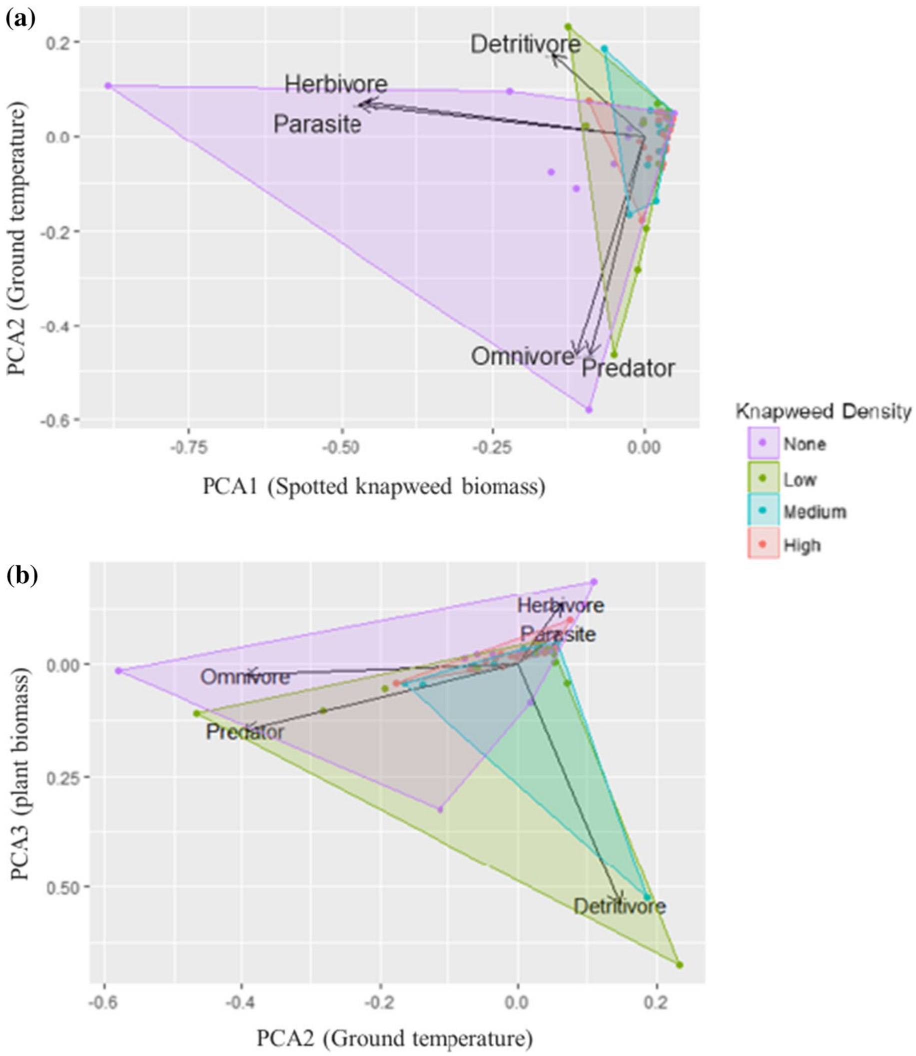

Fig. 2 Principal components analyses using data from May, June, July and August to examine the influence of each functional group on total arthropod community composition graphed using (**a**) components 1 and 2, and (**b**) components 2 and 3, $n = 80$

2005; Trigos-peral et al. 2018). This could make the group more resilient to the introduction of invasive species and subsequent changing of the habitat (Wolkovich et al. 2009).

Over 90% of the omnivore samples collected were from the family *Formicidae* (ants), which are eusocial animals. Some eusocial animals, such as ants, follow scent trails (Andersson 1984), which could skew results of functional group biomass with numerous individuals following one another into the trap. It is important to understand how changing ecosystems affect Formicidae because this diverse functional group can play many environmental roles, including acting as seed disperses and prey items (Schmidt et al. 2012).

Predators

Some past studies have shown predators being adversely affected by invasive plants indirectly through changes in prey items (Gratton and Denno 2005; Bultman and DeWitt 2008). However, the predator biomass in this study followed a non-significant unimodal distribution of more biomass at intermediate spotted knapweed densities, and lowest biomass at no-knapweed sites and at highly dense sites. Site characteristics including higher ground temperatures, less litter cover, and more bare ground at intermediate spotted knapweed densities could all contribute to improved mobility and preferred hunting habitat for predaceous *Lycosidae* (wolf spiders) and *Carabidae* (ground beetles) that were frequently found in traps. *Carabidae* have been observed to hunt more actively and effectively in warmer temperatures (Frank and Bramböck 2016) and several *Araneae* (spiders) and other predators have had increased hunting mobility and web-creating availability in the presence of invasive plants (Pearson 2009). These site characteristics persist at high spotted knapweed densities. Most studies exploring changes in predaceous arthropod biomass associated with invasive plants are observation-based studies, not controlled experiments that lead to cause and effect relationships (Litt et al. 2014).

Parasites

Parasite biomass did not differ with spotted knapweed density. These non-significant results were due to the large standard error associated with the samples. Parasite host animals such as birds (Hickman et al. 2006), small mammals (Bateman and Ostoja 2012), and larger arthropods (Bultman and DeWitt 2008) have been shown to prefer native-dominated grassland areas compared with areas invaded by non-native plants, though our study found no evidence for this.

Detritivores

Detritivore biomass was near zero in medium and high spotted knapweed densities and, although not statistically significant, was lower than no-knapweed site biomass ($P < 0.1$). This finding was surprising as other studies reviewed by Litt et al. (2014) found that detritivores are most likely to benefit from a plant invasion, as was observed in 58 out of 87 studies reviewed, and no studies documenting decreases. Detritivores are likely to benefit from the introduction of invasive plants because invasive plants are generally more productive, which increases ground litter and decaying vegetation (Siemann et al. 2006; Bartomeus et al. 2008). This should provide more food and preferred habitat conditions for detritivores (Longcore 2003) such as *Collembola* (springtails) and *Microcoryphia* (jumping bristletails), which were frequently sampled. An explanation for our unexpected results is the peculiar site characteristics associated with spotted knapweed invaded sites in this study. High-density spotted knapweed sites had significantly less litter cover and higher bare ground cover, as was also observed in this region by Fraser and Carlyle (2011). This is the opposite of what is expected at high-density invasive plant patches (Alerding and Hunter 2013). However, if we consider that spotted knapweed is a fast-growing plant that, therefore, has the potential to have highly palatable and fast decomposing litter (Cornelissen 1996), it is possible that sites with high knapweed density supported an overall higher detritivore productivity but absolute numbers are suppressed by carnivores (Fraser and Grime 1997). In addition, the high-density spotted knapweed sites in our study may have been affected by the commonly high winds of the upper grasslands of LDB, where the dominant grass species is rough fescue (*Festuca scabrella*). Rough fescue is a densely tufted grass, which grows in large clumps and has persistent old sheaths and leaf bases that form large dead vegetation litter mats (Parish et al. 1996). Spotted knapweed outcompeting rough fescue in this specific habitat may lead to decreased litter cover, exposing the habitat to winds and poor conditions for detritivorous arthropods in this specific study site. The detritivores could also have not preferred to consume the invasive plant (Litt et al. 2014). Duplicating this experiment at other semi-arid grassland locations in Western North America could provide a better understanding of the effects of spotted knapweed on detritivores.

Arthropod community trophic interactions

Our study suggests that there are numerous site characteristics and interacting trophic relationships that contribute to differing biomass of arthropod functional groups in this grassland ecosystem. All three components used in the PCA are associated with different site characteristics that have differing influences on functional groups. The result that more spotted knapweed biomass led to less herbivore and parasite biomass was likely due to the interacting effects of spotted knapweed outcompeting native plants and providing less food sources for herbivores (Triplehorn and Johnson 2005; Litt and Steidl 2010), as well as less host organisms for parasites using invaded sites (Bultman and DeWitt 2008; Bateman and Ostoja 2012). Herbivores and parasites were almost exclusively grouped into the no-knapweed sites. More litter cover could lead to more difficult hunting for predators (Frank and Bramböck 2016), possibly explaining the negative relationship with predator biomass.

The negative relationship between herbivores/parasites and predators/omnivores at all sites could suggest top-down control, with more predators leading to less herbivores, at sites with more spotted knapweed and less litter cover. The introduction of spotted knapweed seems to facilitate ideal hunting habitat with less litter cover for predators to control the biomass of herbivores (Frank and Bramböck 2016). In addition, higher parasite abundance at sites without spotted knapweed could control host predator and omnivore species (Gratton and Denno 2005; Bultman and DeWitt 2008).

Conclusion

The results from this study suggest that the density of spotted knapweed patches in semi-arid grasslands have varying effects on arthropod functional groups. High density of spotted knapweed was associated with decreases in plant biomass, with less foraging availability, there were subsequent decreases in herbivorous arthropod biomass. This had no significant effect on omnivore or parasite biomass. The presumed allelopathic chemicals released into the soil from spotted knapweed may have suppressed germination of native plants, which may have resulted in more bare ground, higher ground temperatures, and less litter cover in sites with spotted knapweed, thus providing a better hunting habitat for predators at intermediate spotted knapweed densities. Detritivore biomass was highest at no-knapweed grassland sites and significantly lower at spotted knapweed invaded sites presumably due to the lack of food availability with limited ground litter cover. Any changes to arthropod functional groups due to the introduction of invasive species could lead to changes in overall community dynamics felt throughout the ecosystem.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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