

Responses of grassland arthropods to an invasion by nonnative grasses

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Abstract In grassland ecosystems, invasions by nonnative grasses typically decrease floristic diversity and structural heterogeneity in ways that alter the quantity and quality of habitat for animals. Grassland arthropods that rely directly on herbaceous plants for food, shelter, or as substrates for reproduction are especially vulnerable to these invasions because many have evolved specialized relationships with host plants that might be displaced. We evaluated how invasions by nonnative grasses affected abundance and richness of foliage-dwelling arthropods in semi-desert grasslands of Arizona, USA. On 90, 3.1-ha plots established along a gradient of invasion where dominance of nonnative grasses ranged from 0 to nearly 100% of grass cover, we captured > 90,000 arthropods from 11 orders during 270 surveys in 2014 and 2015. Although the invasion by nonnative grasses (primarily *Eragrostis lehmanniana* and secondarily *E. curvula*) increased the amount of herbaceous foliage available to arthropods, richness of arthropods decreased by an average of 2% and total abundance by an average of 7% for every 10% increase in

nonnative-grass dominance. Responses to the plant invasion, however, varied among taxa and functional groups. As dominance of nonnative grasses increased, abundances of most predators and specialist herbivores decreased, whereas abundances of most generalist herbivores were lowest at intermediate points of the invasion gradient. The changes we observed in the arthropod community have potential to alter broad-scale ecological processes, including energy flow and nutrient cycling, and to reduce food resources for insectivores, which can have adverse, cascading effects on imperiled grassland ecosystems.

Keywords *Eragrostis lehmanniana* · Exotic species · Insect · Invasive species · Invertebrate · Semidesert

Introduction

Nonnative grasses have been introduced to almost every grassland or savanna ecosystem in the world, which has had significant impacts on native species (D'Antonio and Vitousek 1992; Steidl et al. 2013). Typically, as nonnative grasses invade grasslands and increase in dominance, floristic diversity and structural heterogeneity decrease (D'Antonio and Vitousek 1992; Vilà et al. 2011), and vegetation cover and biomass increase (Brooks et al. 2004; Geiger 2006). These changes in composition and structure of

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grassland plant communities alter ecosystem processes, including primary production, decomposition, nutrient and carbon cycling, and hydrologic and disturbance regimes (Vitousek et al. 1996; Levine et al. 2003; Bradley et al. 2006). Consequently, invasions by nonnative grasses pose a serious threat to remaining grasslands, which are among the most biologically diverse and most threatened ecosystems in the world (Wilson et al. 2012; Murphy et al. 2016).

Collectively, changes in ecosystem structure, composition, and processes associated with plant invasions can affect the quantity and quality of habitat for animals that inhabit grasslands (Steidl et al. 2013). Arthropods may be especially vulnerable to changes in the plant community that result from invasions because many have limited mobility or have evolved specialized relationships with host plants that provide food or substrates for reproduction (Bernays and Graham 1988). For example, approximately 90% of all phytophagous insects feed on plants in only one or a few plant lineages, and these host plants may be displaced or reduced in abundance when novel plants invade a community (Strong et al. 1984; Bernays and Graham 1988; Tallamy 2004). Additionally, survival, reproduction, or distributions of all arthropods, including those not associated closely with specific plants, can change in response to invasions by nonnative plants if vegetation structure is altered in ways that affect microclimatic conditions, including light intensity, temperature, and soil moisture (Wolkovich 2010; Schirmel and Buchholz 2013). These changes in abundance and community composition of arthropods can affect broad-scale ecological processes, including decomposition, nutrient cycling, and pollination (Hladik et al. 2015; Nitschke et al. 2015), and are likely to have disproportionately strong effects on food webs because many taxa are key prey for insectivores. Grasshoppers (Orthoptera), for example, are the primary prey of many breeding grassland birds (George and McEwen 1992), a group that has declined more rapidly than any other group of birds in North America (Sauer and Link 2011).

Effects of plant invasions on arthropods may be strongest where invading plants have reduced vegetation heterogeneity markedly (Hovick et al. 2015), such as in semidesert grasslands of North America where two perennial C_4 grasses have come to dominate grasslands once characterized by a diverse flora of native grasses (Litt and Steidl 2011). *Eragrostis*

lehmanniana and *E. curvula* were introduced to southeast Arizona from southern Africa in the 1930s and 1940s in an attempt to revegetate degraded rangelands and mitigate soil erosion after prolonged drought (Anable et al. 1992). These two species have spread rapidly and are predicted to expand to an area $> 71,000 \text{ km}^2$ in southern Arizona and New Mexico alone (Anable et al. 1992; Schussman et al. 2006). Compared to most native grasses, these nonnative species grow more rapidly, produce more seeds and up to four times more aboveground biomass, and are less palatable to vertebrate herbivores (Cox et al. 1990; Geiger 2006). These attributes can increase fire intensity and frequency, a primary ecological process that governs spatial and temporal patterns of biodiversity in many grassland ecosystems (McPherson 1995; Brooks et al. 2004; Steidl et al. 2013).

Although invasions by these nonnative grasses have been shown to alter richness and abundance of many vertebrate taxa, effects on grassland arthropods are less well-understood (Steidl et al. 2013; Litt et al. 2014). We know, however, that richness and abundance of epigeic (i.e., surface-dwelling) insects decrease as dominance of *E. lehmanniana* increases, although responses vary among taxa (Litt and Steidl 2010). Here, we sought to understand the effects of these invasions on arthropods that use grasses or other herbaceous plants as their primary substrate (hereafter, foliage-dwelling arthropods). This group may be especially vulnerable to changes in grassland structure or floristics that accompany invasions because of their direct reliance on herbaceous plants for food, shelter, or reproduction (Gleditsch 2016). Specifically, we evaluated how abundance and richness of foliage-dwelling arthropods changed along a gradient of dominance by nonnative grasses in semidesert grasslands. This gradient represents a space-for-time substitution for the process by which nonnative-grass invasions transform grassland plant communities once composed of a diverse assemblage of native grass species into near-monocultures with few native species.

Methods

Study area

We surveyed arthropods and vegetation in southeastern Arizona, USA at three sites that span the range of variation in vegetation structure and management of semidesert grasslands in North America: Appleton-Whittell Research Ranch (31.6°N, 110.5°W), Fort Huachuca Military Reservation (31.6°N, 110.3°W), and Las Cienegas National Conservation Area (31.8°N, 110.6°W). Sites are located within a 40 × 55 km area where semidesert grasslands occur between 1350 and 1550 m elevation and annual precipitation averages 350 to 450 mm, most of which falls during a monsoon season between July and September that is preceded by 2–3 months that are hot and dry (McClaran 1995). Livestock have been excluded from Fort Huachuca Military Reservation since 1950 and Appleton-Whittell Research Ranch since 1968. Grasslands at Las Cienegas National Conservation Area are grazed by cattle, therefore we excluded areas that were scheduled to be grazed during the study.

Vegetation composition at all sites was dominated by a variety of C₄ perennial grasses. Common native grasses included *Aristida* spp., *Bothriochloa barbinodis*, *Bouteloua* spp., *Digitaria californica*, and *Eragrostis intermedia*. At each site, composition of perennial grasses ranged from 0 to nearly 100% nonnative species, with areas dominated by nonnative species occurring throughout each site. Of the nonnative grasses, *E. lehmanniana* was the most widespread and often dominated large areas, although *E. curvula* was abundant locally. Woody plants were composed almost entirely of native species (> 99% of woody cover), especially *Baccharis* spp., *Isocoma tenuisecta*, *Mimosa* spp., and *Prosopis velutina*, which has encroached many grasslands in this region transforming them to shrub savannas (Archer et al. 2017).

Arthropod sampling

We established 90, 100-m-radius circular plots (3.1-ha) at random throughout upland areas of the three sites. We excluded areas with obvious anthropogenic features (e.g., roads or buildings), those that were scheduled to be grazed, and those that had been burned or otherwise manipulated to reduce woody vegetation

during the previous 3 years. We surveyed 50 plots in 2014 and 40 different plots in 2015; 12 plots were located at Appleton-Whittell, 29 at Fort Huachuca, and 49 at Las Cienegas.

We surveyed arthropods on each plot three times between mid-June and mid-August. This period typically encompasses most monsoon precipitation, which coincides with the growing season for grasses and peak abundance of many arthropod taxa in semidesert grasslands (Whitford et al. 1995). To target foliage-dwelling arthropods, we used a 38-cm sweep net constructed of heavy sailcloth canvas to capture arthropods along three 60-m transects radiating from plot center at 120° intervals. Sweep sampling is well-suited for surveying these arthropods (Gardiner et al. 2005; Yi et al. 2012) and characterizes relative abundance and community composition accurately (Larson et al. 1999; Kati et al. 2004). To minimize variation among surveyors and variation induced by heterogeneity in vegetation density or height (Doxon et al. 2011), we standardized our sweeping procedure. Surveyors traversed each transect at a constant pace and made 30 fast sweeps (one 2-m sweep per pace) as close to the ground as permitted by vegetation (Neill et al. 2002). We emptied the contents of the net into a labeled 3.8 L freezer bag that we stored on ice soon after collection and transferred to a freezer within 3 days.

In the lab, we counted and classified individuals to morphospecies based on recognizable visual characteristics, an efficient approach that produces estimates of richness similar to those obtained by specialists who identify specimens to species (Oliver and Beattie 1993, 1996). Additionally, we classified most (99.3%) individuals to order and individuals from the three most abundant orders to suborder (Hemiptera) or family (Coleoptera and Orthoptera). We classified taxa thought to be functionally homogeneous into functional groups for analysis (Table 1). Specifically, we classified taxa as generalist herbivores, specialist herbivores, and predators based on information provided in Triplehorn and Johnson (2005) and Litt et al. (2014).

Vegetation sampling

Although our primary objective was to evaluate responses of arthropods to variation in dominance of nonnative grasses, arthropod populations also reflect

Table 1 Number of individuals or taxa captured (No.), non-focal vegetation and temporal covariates included in final model, and linear effect of dominance of nonnative grasses on abundance and richness of arthropod taxa and functional groups ($n = 90$ plots). Estimates reported on the log scale and back transformed as the percentage change in abundance for

every 10% increase in dominance of nonnative grasses (10% increase). Letters in parenthesis indicate functional groups (G = generalist herbivores, P = predators, S = specialist herbivores). Estimates for non-focal covariates provided in “Appendix 1 of Electronic Supplementary Material”

Response	Taxa or functional group	No.	Covariates	Estimate	SE	Z	P	10% increase
Abundance	Araneae (P)	4690	Year, day ² , time ² , forb	- 0.03	0.05	- 0.47	0.64	- 0.8
	Coleoptera	4765	Year, day ²	- 0.30	0.07	- 4.47	< 0.001	- 9.4
	Chrysomelidae (G)	2128	Day ² , forb, grass	- 0.20	0.09	- 2.19	0.03	- 6.2
	Cleridae (P) ^a	482	Day, wood, grass	- 0.35	0.13	- 2.57	0.01	- 10.7
	Curculionidae (S)	703	Year, day ² , wood	- 0.26	0.11	- 2.48	0.01	- 8.3
	Meloidae	116	Day ² , wood	0.02	0.22	0.08	0.94	0.6
	Melyridae (P)	1279	Year, day	- 0.53	0.18	- 2.89	0.004	- 16.1
	Diptera	861	Year, day ² , time ²	- 0.28	0.09	- 3.05	0.002	- 8.7
	Hemiptera (S)	69,698	Year, forb, grass	- 0.30	0.09	- 3.16	0.002	- 9.3
	Auchenorrhyncha (S)	56,945	Year, day, time, forb, grass	- 0.30	0.11	- 2.70	0.007	- 9.4
	Heteroptera (S)	12,753	Year, day ² , grass	- 0.24	0.09	- 2.83	0.005	- 7.7
	Hymenoptera	1911	Year, day ² , time ² , forb	0.15	0.09	1.69	0.09	5.0
	Lepidoptera (S)	1532	Year, day ² , grass	0.10	0.08	1.19	0.23	3.4
	Mantodea (P)	42	Day, time, wood	0.43	0.21	1.99	0.05	15.1
	Neuroptera (P)	55	Day, wood	0.39	0.18	- 2.89	0.03	13.6
	Orthoptera (G) ^a	8702	Year, day, forb	- 0.03	0.09	- 0.35	0.73	- 1.0
	Acrididae (G) ^a	5869	Year, day ² , time, wood, forb, grass	- 0.05	0.09	- 0.56	0.58	- 1.7
	Gryllidae (G)	121	Day ² , time, forb, grass	- 0.04	0.22	- 0.18	0.86	- 1.3
	Tettigoniidae ^a	2712	Year, day ² , forb	0.04	0.15	- 0.27	0.79	- 1.3
	Parasitiformes	29	Year, day ² , wood, grass	0.85	0.32	2.67	0.007	32.2
	Phasmatodea (G) ^a	512	Year, time, wood, grass	- 0.05	0.11	- 0.50	0.62	- 1.8
	All taxa combined	93,418	Year, day, forb, grass	- 0.21	0.07	- 3.07	0.002	- 6.8
	Generalist herbivores ^a	11,342	Year, day, forb	- 0.05	0.07	- 0.64	0.52	- 1.5
	Specialist herbivores	71,933	Year, day ² , forb, grass	- 0.27	0.09	- 2.98	0.003	- 8.5
	Predators	6548	Year, day ² , time ²	- 0.13	0.06	- 2.27	0.02	- 4.2
Richness	Orders	11	Year, day, time	0.01	0.03	0.54	0.59	0.5
	All taxa	131	Year, day, time ² , forb, grass	- 0.21	0.07	- 3.07	0.002	- 1.9
	Coleoptera	32	Year, day ² , time ² , grass	- 0.14	0.04	- 4.08	< 0.001	- 4.6
	Hemiptera	31	Year, day ² , forb, grass	- 0.04	0.03	- 1.36	0.18	- 1.4
	Orthoptera	38	Year, day, forb	- 0.12	0.04	- 2.69	0.007	- 3.8

^aTaxa for which there was evidence for a nonlinear response to nonnative dominance ($P < 0.05$); see “Appendix 1 of Electronic Supplementary Material”

other vegetation features. Therefore, we characterized species composition and structure of the entire plant community on each plot using a design that

complemented the approach we used to sample arthropods. We surveyed vegetation by establishing eight 10-m diameter subplots systematically on each

plot, two along each cardinal axis with one 25 m and another 75 m from plot-center. On each subplot, we estimated canopy cover and composition (as percent of total cover) of grasses, canopy cover of woody plants and forbs (i.e., herbaceous dicots), and surface cover of ground litter and bare ground by combining visual estimates from four quadrants. Additionally, we measured grass height at eight points spaced systematically on the periphery of each subplot. We surveyed vegetation in September, when presence of grass inflorescences aided identification. Although we surveyed vegetation later in the season than arthropods, composition of C_4 perennial grasses remains stable during summer months (Geiger 2006), therefore dominance of nonnative grasses likely changed little between surveys. To reduce observer-induced variation, only two observers measured vegetation each year and each measured half of the subplots on every plot. For analysis, we averaged estimates of vegetation cover, composition, and grass height across the eight subplots on each plot.

Data analysis

For all analyses, we quantified dominance of nonnative grasses as the proportion of perennial grass cover comprised by nonnative species. We used simple linear regression to evaluate how vegetation features on plots varied with dominance of nonnative grasses; we used Shannon's Index to characterize diversity of grasses. To reduce the number of non-focal vegetation variables in models, we considered only cover of woody plants, forbs, and grasses as covariates because grass cover was correlated with cover of bare ground ($r = -0.90$), litter ($r = -0.53$), and grass height ($r = 0.61$).

Our overarching approach to analysis was to evaluate the effect of dominance of nonnative grasses on each arthropod response after accounting for other sources of variation among plots. As responses, we considered richness of orders, richness of morpho-species for all taxa combined and the three orders with highest abundances, and abundance of all orders combined (hereafter 'total abundance'), each taxa individually, and each functional group. For each response, we began with a generalized linear mixed model that included all vegetation covariates except for nonnative grasses, plus site, plot, and three covariates to describe timing of surveys: year, Julian

day, and time-of-day; we considered both linear and quadratic effects for Julian day and time-of-day. We treated all terms as fixed effects except for plot, which we treated as a random effect. We then used backwards elimination to eliminate vegetation and temporal covariates with little explanatory power ($P > 0.10$ based on Wald Z-tests). Lastly, we added terms for dominance of nonnative grasses (both linear and quadratic forms) to a model that included all remaining covariates, which provided a direct test of the influence of nonnative grasses on each response variable after accounting for other important features (Ramsey and Schafer 2002). We standardized all covariates to Z-scores (mean = 0, standard deviation = 1) to improve numerical convergence of models.

To model abundance, we specified a log link function and a negative binomial error distribution because counts of arthropods were overdispersed. To model richness, we specified a log link function and a Poisson error distribution. We fit models with the R package lme4 (Bates et al. 2015). To aid interpretation, we report the percentage change in each response for every 10% increase in dominance of nonnative grasses (Ramsey and Schafer 2002).

Results

Vegetation

Sites were dominated by perennial grasses and our plots spanned the gradient of invasion by nonnative grasses on each site (Table 2, Fig. 1). Across all sites and plots, composition of perennial grasses averaged 48% native species and 49% nonnative species (3% were unidentified), and ranged from 0 to 99% nonnative species (Table 2). Native grasses were represented by 27 species, none of which comprised > 10% of perennial grass cover, which illustrates the high degree of diversity in this category. Nonnative grasses were represented by three species that were locally abundant (Table 2). *Eragrostis lehmanniana* was by far the most common, comprising 95% of nonnative grass cover and 47% of perennial grass cover across all plots (Table 2). As dominance of nonnative grasses increased, grass diversity decreased markedly, simplifying the plant community (Fig. 1c). In addition to altering species

Table 2 Mean, standard error, minimum and maximum cover of vegetation and composition of perennial grasses, including the three most common nonnative species across sites, plots, and years ($n = 90$ plots)

Measure	Category	Mean	SE	Min	Max
Cover (%)	Bare	18.4	1.2	2.5	51.7
	Forbs	9.8	1.0	0.3	52.5
	Litter	4.3	0.3	0.3	12.9
	Woody plants	7.8	0.8	0.0	33.5
	Annual grasses	6.6	1.1	0.0	44.2
	Perennial grasses	64.7	1.8	29.6	95.4
Composition (%) ^a	Native grasses	48.3	3.1	1.3	100.0
	Nonnative grasses	49.1	3.2	0.0	98.8
	<i>Eragrostis lehmanniana</i>	46.7	3.2	0.0	98.8
	<i>Eragrostis curvula</i>	1.9	0.9	0.0	66.3
	<i>Bothriochloa ischaemum</i>	0.5	0.2	0.0	14.3

^a2.6% of perennial grasses could not be classified as native or nonnative

composition, nonnative grasses also altered vegetation structure and reduced vegetation heterogeneity. For every 10% increase in dominance of nonnative grasses, mean grass height increased by 1.5 cm (SE = 0.34, $t_{88} = 4.59$, $P < 0.0001$) and total grass cover increased by 1.4% (SE = 0.58, $t_{88} = 2.47$, $P = 0.015$; Fig. 1a, b). Cover of bare ground averaged 18% (Table 2) and decreased by an average of 0.8% (SE = 0.40, $t_{88} = 1.98$, $P = 0.051$) for every 10% increase in dominance of nonnative grasses. Cover of forbs averaged 10% and woody plants 8% across plots (Table 2), neither of which varied systematically with dominance of nonnative grasses ($t_{88} < 0.95$, $P > 0.35$).

Arthropods

We captured 93,418 arthropods from 11 orders during 270 surveys on 90 plots (Table 1). Four orders comprised 94% of individuals captured: 75% were Hemiptera (true bugs), 9% Orthoptera (grasshoppers, crickets and katydids), 5% Coleoptera (beetles), and 5% Araneae (spiders).

Total abundance of arthropods decreased by an average of 7% for every 10% increase in dominance of nonnative grasses (Table 1). Excluding the two most abundant Hemipteran morphospecies, which represented 43% of all individuals captured, did not change the direction of this effect but did reduce its magnitude to 5% (SE = 1.51, $X^2 = 8.92$, $P = 0.003$) for every 10% increase in dominance of nonnative grasses.

Although total abundance of arthropods decreased as dominance of nonnative grasses increased, effects varied widely among orders. Abundance of 3 of 11 (27%) orders decreased as dominance of nonnative grasses increased (Table 1). Abundance decreased by an average of 9% in Coleoptera, Hemiptera, and Diptera for every 10% increase in dominance of nonnative grasses (Table 1). For Coleoptera, the decrease was driven by decreases in four of the five most common families (Table 1). Abundance decreased by an average of 16% in Melyridae (flower beetles), 11% in Cleridae (checkered beetles), 8% in Curculionidae (weevils), and 6% in Chrysomelidae (leaf beetles) for every 10% increase in dominance of nonnative grasses (Table 1, Fig. 2). Among suborders within Hemiptera, abundance decreased by an average of 9% for Auchenorrhyncha (cicadas, hoppers, spittlebugs) and 8% for Heteroptera (true bugs) for every 10% increase in dominance of nonnative grasses (Table 1, Fig. 2).

Abundance of 4 of 11 (36%) orders increased as dominance of nonnative grasses increased (Table 1). Abundance increased by an average of 32% in Parasitiformes (ticks), 15% in Mantodea (mantises), 14% in Neuroptera (net-winged insects), and 5% in Hymenoptera (bees and ants) for every 10% increase in dominance of nonnative grasses (Table 1).

Abundances did not vary linearly with dominance of nonnative grasses for 3 of 11 (36%) orders: Araneae, Phasmatodea (stick insects), Lepidoptera (butterflies and moths; 86% of which were larvae), and

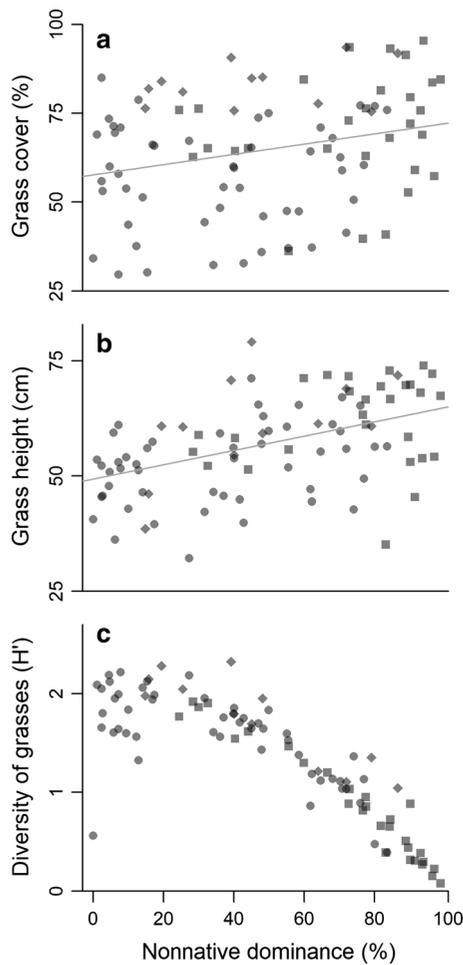


Fig. 1 Grass cover (a), grass height (b), and diversity (Shannon’s Index) of perennial grasses (c) versus dominance of nonnative grasses. Point shapes represent the three different sites we surveyed and demonstrate the range of nonnative grass dominance at each site

Orthoptera (Table 1). Phasmatodea and Orthoptera, however, varied nonlinearly along the invasion gradient, with abundances being similar at the gradient extremes and lowest at intermediate levels of nonnative grass dominance (Fig. 2, “Appendix 1 of Electronic Supplementary Material”). For Orthoptera, this pattern was driven by nonlinear responses in two of three families: Acrididae (grasshoppers) and Tettigoniidae (bush crickets; Fig. 2, “Appendix 1 of Electronic Supplementary Material”).

Among functional groups, abundance decreased by an average of 9% for specialist herbivores and 4% for predators for every 10% increase in dominance of nonnative grasses (Table 1, Fig. 3). Abundance of

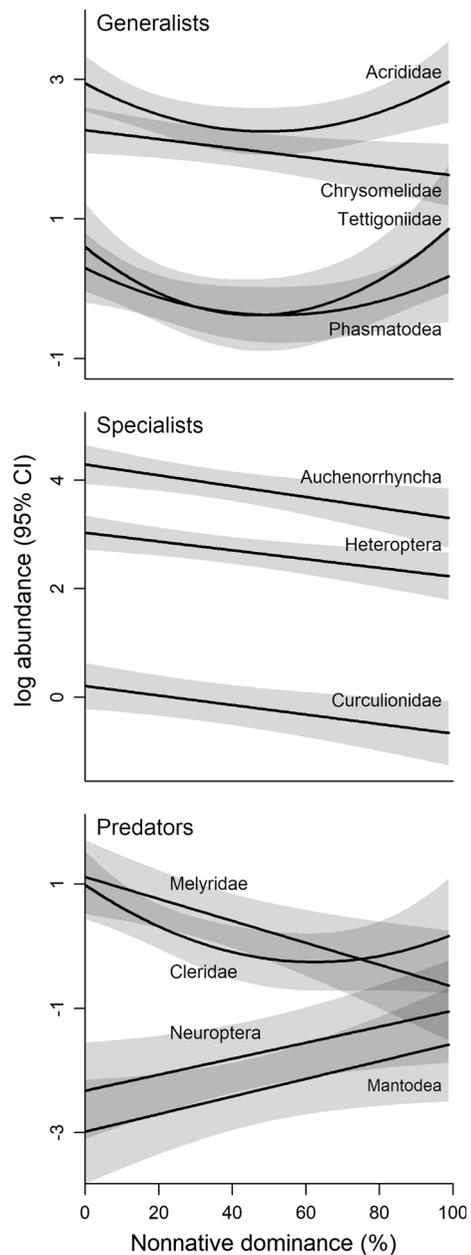


Fig. 2 Log abundance (95% CI) of arthropod taxa versus dominance of nonnative grasses for generalist herbivores (top panel), specialist herbivores (middle panel) and predators (bottom panel). Only those taxa where abundance varied appreciably are shown (Table 1)

generalist herbivores changed nonlinearly along the invasion gradient, with abundances similar at the gradient extremes and lowest where composition of nonnative grasses was approximately 50% (Fig. 3, “Appendix 1 of Electronic Supplementary Material”).

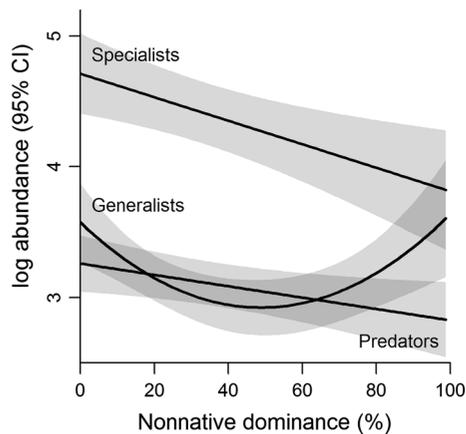


Fig. 3 Log abundance (95% CI) of arthropod functional groups versus dominance of nonnative grasses. Taxa comprising each group are shown in Table 1

Richness decreased as dominance of nonnative grasses increased for three of the five taxonomic groups we considered (Table 1). Specifically, richness of morphospecies decreased by an average of 2% for all taxa combined, 5% within Coleoptera, and 4% within Orthoptera for every 10% increase in dominance of nonnative grasses (Table 1). Richness of orders and richness within Hemiptera did not vary along the invasion gradient (Table 1).

Discussion

In the grasslands we studied, height and cover of grasses increased as nonnative grasses increased in dominance, a pattern similar to that observed in many other invaded grasslands (Brooks et al. 2004). Although these changes increased the quantity of substrate available to foliage-dwelling arthropods, total abundance and richness decreased as dominance of nonnative grasses increased. This suggests that any benefits from increased foliage to this community of arthropods were outweighed by costs associated with changes in vegetation composition or structure, such as reduced structural heterogeneity or grass diversity (Fig. 1).

Changes in abundance of foliage-dwelling arthropods along the invasion gradient varied considerably among taxa, as some orders decreased in abundance as the invasion intensified (Coleoptera, Diptera, Hemiptera), whereas others increased (Hymenoptera,

Mantodea, Neuroptera, Parasitiformes) or were unaffected (Araneae, Lepidoptera, Orthoptera, Phasmatodea). A spectrum of responses has been reported for studies that considered the effects of plant invasions on multiple arthropod taxa, which may be attributable to how different functional groups respond to changes in plant composition and structure (Litt et al. 2014).

Relative to other groups, herbivorous insects are especially vulnerable to floristic changes from plant invasions because 90% feed only on plants from one or a few lineages and may not use novel plants as food, at least for species whose diets are known (Strong et al. 1984; Bernays and Graham 1988; Tallamy 2004). In the grasslands we studied, as dominance of nonnative grasses increased, abundance of specialist herbivores decreased more steeply than the other functional groups (Fig. 3). Among taxa in this group, which are characterized largely by monophagous or oligophagous herbivores, we found that abundance of Curculionidae and both suborders of Hemiptera decreased markedly as dominance of nonnative grasses increased, a pattern consistent with other studies (reviewed in Litt et al. 2014). Similarly, many Lepidoptera require specific plants for feeding or reproduction, therefore their abundances typically decrease when nonnative plants invade a community (Tallamy and Shropshire 2009; Burghardt et al. 2010). In Arizona grasslands, however, we and others observed no systematic variation in abundance of lepidopterans with dominance of nonnative grasses (Litt and Steidl 2010). This finding was not an artifact of a bias towards adults, which are vagile and more likely than larvae to be captured on plants that they do not use for food or reproduction, because 86% of lepidopterans that we captured were caterpillars. We acknowledge, however, that larvae of many species, including those that bore into stems or feed within leaf sheaths, were likely underrepresented in our sample and might respond to invasions differently than other groups. The lack of an effect for Lepidoptera may be attributable to the way that grass invasions affect forbs, which are the focus of many lepidopteran-plant specializations (Futuyma 1976). Typically, forbs decrease in abundance and diversity as dominance of nonnative plants increase (Geiger 2006), but we found no systematic changes in forb cover along the invasion gradient. The absence of a decrease in forbs along the invasion gradient might also explain why abundance

of Hymenoptera, an important pollinator taxa, did not decrease in our study. Like specialist herbivores, pollinators typically are less common in invaded areas because the flowering plants they rely on for food generally are less abundant (Montero-Castaño and Vilà 2012; Litt et al. 2014).

Generalist herbivores may be more likely to feed on novel plant species than forage-specialized arthropods (Strong et al. 1984; Tallamy 2004). Consequently, taxa dominated by polyphagous species might be less vulnerable to invasions that displace their native food sources, especially if nonnative grasses lack effective defenses against evolutionarily novel herbivores (Parker et al. 2006; Avanesyan and Culley 2015). They might even increase in abundance if nonnative plants produce more biomass than native species. In our study, abundances of generalist herbivores were similar (Orthoptera, Phasmatodea) or lower (Chrysomelidae) in areas dominated by nonnative grasses relative to areas dominated by native grasses. Interestingly, though, we found that abundances of Phasmatodea and Orthoptera (including two of three families, Acrididae and Tettigoniidae) were nonlinear, with lower abundances at intermediate levels of nonnative dominance than at the gradient extremes (Fig. 2).

Nonlinear variation in abundance along the invasion gradient likely reflects species-level variation in responses of generalist herbivores. The decrease in abundance associated with early stages of invasion suggests that some species were unable to use nonnative grasses, which generally are considered less palatable to herbivores than native species because of lower tissue nitrogen and higher lignin content (Haddad et al. 2001; Geiger 2006). As nonnative grasses continued to increase in dominance, however, abundance of generalist herbivores increased, suggesting that other species may have been preadapted to use nonnative grasses, the most common of which are congeners of a locally common native species (*Eragrostis intermedia*). These species may have benefitted from the increased quantity of foliage in invaded areas or from structural changes that accompanied invasion by nonnative grasses. For example, some orthopterans are associated closely with habitat features common to areas dominated by nonnative grasses, such as increased litter depth or vegetation biomass, which increase humidity and moderate temperature extremes (Samways 1990;

Szinwelski et al. 2012). Conversely, other species are associated with habitat features common to areas dominated by native grasses, such as high structural heterogeneity, patches of bare ground, or areas open to direct sunlight (Whitford et al. 1995; Chambers and Samways 1998). Collectively, these species-specific responses could explain the nonlinear changes in abundance that we observed.

Because their diets are less specialized than herbivores, predaceous arthropods are thought to respond more to changes in vegetation structure than to floristics (Pearson 2009; Litt et al. 2014). Consequently, their abundance and richness often increase with height and complexity of vegetation (Tscharntke 1995; Haddad et al. 2009). In our study, however, predator abundance decreased as dominance of nonnative grasses increased, despite increases in grass height and density (Fig. 1a, b). When taxa were considered individually, abundances of the four most common predator-dominated taxa remained consistent (Araneae, Meloidae, which have predatory larvae) or decreased (Melyridae, Cleridae) along the invasion gradient, likely reflecting decreased abundance of herbivore prey. This suggests that decreases in abundance of herbivorous arthropods are unlikely the result of top-down pressure from predators exploiting increased habitat along the invasion gradient.

Arthropods in semidesert grasslands of Arizona have been sampled with sweep nets (this study) and pitfall traps (Litt and Steidl 2010), with each method chosen to target a subset of arthropods that use different primary substrates. Taxonomic composition differed between these two subsets, but among those taxa well represented in both studies, the direction of responses of foliage- and surface-dwelling (i.e., epigeic) arthropods to invasions by nonnative grasses were generally similar (Litt and Steidl 2010). For both groups abundances of Coleoptera and all taxa combined decreased similarly as dominance of nonnative grasses increased, whereas abundances of foliage-dwelling Hemiptera and Diptera decreased more sharply than their surface-dwelling counterparts. Responses to the plant invasion differed directionally across studies for only two well-represented taxa. Abundance of surface-dwelling Orthoptera decreased markedly as dominance of nonnative grasses increased (Litt and Steidl 2010) whereas abundance of foliage-dwelling Orthoptera was similar at the extremes of the invasion gradient and lowest at intermediate levels of

nonnative grass dominance. The decrease in abundance of surface-dwelling Orthoptera may be attributable to the importance of open ground or microclimatic conditions for many species, features that likely change when larger, denser-growing grasses invade grasslands (Fig. 1a, b). Conversely, abundance of foliage-dwelling Hymenoptera increased as dominance of nonnative grasses increased whereas abundance of ground-dwelling Hymenoptera did not change (Litt and Steidl 2010). The response of ground-dwelling Hymenoptera was driven strongly by Formicidae (ants), however, which comprised 63% of total individuals captured by pitfall trap (Litt and Steidl 2010) but that we captured only rarely on foliage.

In summary, total abundance and richness of foliage-dwelling arthropods decreased as dominance of nonnative grasses increased, although abundances of some groups increased or largely were unaffected by invasions of nonnative grasses. As nonnative grasses continue to expand into grassland and savanna systems as predicted (Schussman et al. 2006), the abundance and distribution of many arthropods is likely to continue to change. Changes in arthropod communities in response to changes in the plant community could have far-reaching consequences for imperiled grassland ecosystems and the native organisms they support. For example, changes in populations of pollinators or herbivores could influence composition and structure of grassland plant communities (Bezemer et al. 2014). Additionally, decreases in abundance of foliage-dwelling arthropods have the potential to disrupt food webs because these arthropods are the primary prey for many insectivorous species, including groups of high-conservation concern, such as breeding grassland birds (George and McEwen 1992; Rzanny and Voigt 2012). Further, given their key role in ecological processes, including energy flow and nutrient cycling, changes to arthropod communities would be expected to alter how grassland ecosystems function (Whiles and Charlton 2006). Consequently, understanding how arthropod communities change in response to invasions by nonnative grasses will become increasingly important for guiding conservation and restoration strategies for grasslands and the organisms and ecological processes they support.

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