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Nonnative plant shifts functional groups of arthropods following drought

Adam B. Mitchell · Andrea R. Litt

Abstract Nonnative plants alter the composition of native plant communities, with concomitant effects on arthropods. However, plant invasions may not be the only disturbance affecting native communities, and multiple disturbances can have compounding effects. We assessed the effects of invasion and drought on plant and arthropod communities by comparing grasslands dominated by nonnative Old World bluestem grasses (OWBs, *Dichanthium annulatum*) to grasslands dominated by native plants during a period of decreasing drought severity (2011–2013). Native plant communities had more species of plants and arthropods ($/m^2$) than areas dominated by OWBs during extreme drought, but richness was comparable as drought severity decreased. Abundance of arthropods was greater in native plant communities than in OWB communities during extreme drought, but OWB communities had more arthropods during moderate and non-drought conditions. We observed a shift in the arthropod community from one dominated by detritivores to one dominated by herbivores following plant invasion; the magnitude of this shift increased as drought severity decreased. Both plant communities were dominated by nonnative arthropods. A nonnative leafhopper (*Balclutha rubrostriata*) and native mites (Mochlozetidae) dominated OWB communities as drought severity decreased, and OWBs may serve as refugia for both taxa. Nonnative woodlice (*Armadillidium vulgare*) dominated native plant communities during extreme and non-drought conditions and abundance of this species may be associated with an increase in plant litter and available nutrients. Given the importance of arthropods for ecosystem services, incorporating arthropod data into conservation studies may demonstrate how changes in arthropod diversity alter ecosystem function where nonnative plants are dominant.

Keywords Detritivores · Grasslands · Herbivores · Old World bluestems · Plant invasion

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Introduction

Nonnative plants often reduce richness of native plant communities and change vegetation structure (Levine et al. 2003; Gaertner et al. 2009; Hejda et al. 2009; Vilà et al. 2011). These changes have concomitant effects on other organisms at different trophic levels, especially arthropods (Bezemer et al. 2014; Litt et al. 2014; van Hengstum et al. 2014). However, the response of

arthropods to changes in plant composition or structure resulting from nonnative plants may differ by taxa or functional group (Litt et al. 2014).

Plant-feeding arthropods are most likely to be affected directly by changes in plant composition (Bezemer et al. 2014; Litt et al. 2014). Many plant-feeding arthropods require specific plant species for food or reproduction sites (Bernays and Graham 1988; Tallamy 2004; Burghardt et al. 2010; Forister et al. 2015) and novel plants may not be recognized as habitat by native arthropod species. Herbivorous arthropods may not utilize nonnative plants due to physical and chemical defenses (Graves and Shapiro 2003; Burghardt et al. 2010). Plant-feeding arthropods generally are less abundant and diverse where nonnative plants are dominant (Litt et al. 2014; van Hengstum et al. 2014, but see Bezemer et al. 2014).

Although some arthropods do not feed on living vegetation, plant invasions still may have indirect effects on these species (Wolkovich 2010; Lenda et al. 2013). Changes in litter composition, soil moisture, mineralization, and soil pH following plant invasion can have adverse effects on the composition and abundance of litter-and-soil-dwelling arthropods (Kappes et al. 2007; Wolkovich et al. 2009; Alerding and Hunter 2013). Conversely, where nonnative plants are dominant, the abundance and availability of plant litter may increase, which may allow litter-associated arthropods to increase in abundance (Litt et al. 2014).

Plant invasion may be only one of many stressors influencing communities of native plants and arthropods; concurrent stressors can interact to have novel effects (Vitousek et al. 1996; Paine et al. 1998). For example, nonnative plants may better tolerate drought conditions, further reducing the ability of native plants to compete (Everard et al. 2010; Crous et al. 2012). Drought also may reduce abundance or richness of arthropod communities through changes in availability or quality of habitat or food (Kindvall 1995; Scheirs and De Bruyn 2005; McCluney and Sabo 2012; Buchholz et al. 2013). Litter-feeding arthropods may shift feeding preference to moist litter and predaceous arthropods may reduce hunting activity (i.e., searching for and attacking prey) that is energetically expensive when water resources are limited (Sabo et al. 2008; McCluney and Sabo 2009). Few studies have examined the combined effects of plant invasion and drought on arthropod communities, and understanding how native communities respond to

multiple environmental stressors may provide insights for conservation (Paine et al. 1998).

We developed a field-based study to compare plant and arthropod communities between landscapes dominated by nonnative grasses (Old World bluestem grasses or OWBs, *Bothriochloa* and *Dichanthium* spp.) and landscapes dominated by native plants. OWBs alter the composition of native plant and arthropod communities (Hickman et al. 2006; Woodin et al. 2010; Cord 2011) and we sought to build on previous work by focusing specifically on changes in the composition of arthropod communities at the level of functional group and species. Investigating changes in arthropods from a functional group perspective could demonstrate how ecological properties change following disturbance events such as plant invasion. We predicted that OWB-dominated landscapes would have fewer plant species, as well as lower species richness and abundance of herbivorous arthropods, but higher richness and abundance of detritivorous arthropods, than native plant-dominated landscapes.

In 2011, a severe drought occurred throughout the introduced distribution of OWBs (NDMC-UNL 2014). The drought persisted for several years in the southern portion of this range and provided us with the added opportunity to explore relationships between plant invasion and drought severity on plant and arthropod communities. OWBs are drought tolerant and more productive than native grasses under dry conditions (White and Dewald 1996; Bhat et al. 2011; Porensky et al. 2014), which may exacerbate effects of drought-induced stress on local plant and arthropod communities. We predicted that species richness for both plants and arthropods would decrease in the presence of drought for both plant communities, but the magnitude of the decrease would be greater in OWB-dominated areas than in areas dominated by native plants.

Methods

Study area

We conducted our research at the Welder Wildlife Refuge (N 28.12155, W 97.442808), a 3157-ha refuge located 12 km northeast of Sinton, Texas. We sampled within a plant community at the southernmost border of the refuge, which was classified historically as a

mesquite-buffalograss community (Box [1961]). However, this plant community now is dominated by Kleberg bluestem (*Dichanthium annulatum*), a representative species of OWBs; our work occurred in the southern portion of the introduced range of Kleberg bluestem. We also sampled within a plant community that was dominated by native grasses, but without OWBs, which was 1.3 km from the OWB monoculture. Prior to the study, the native plant community was relatively undisturbed, and the OWB-dominated plant community had been mowed annually to serve as a fire break (T. Blankenship, personal comm.).

We established 10, 6 × 9-m plots within the study area, five in the OWB-dominated community and five in the native plant community. We established plot size based on a concurrent study (Mitchell [2014]). We selected plots at random; plots in the OWB-dominated community were at least 1.5 m apart and plots in the native plant community were at least 32 m apart. We measured plant, soil, and arthropod characteristics on two, 1-m^2 quadrats per plot, every month from June–August during 2011 through 2013; this timing reflects peak arthropod activity during the growing season. We placed quadrats at random within each plot for each sampling period.

Precipitation

We obtained precipitation data from a nearby weather station on the refuge, approximately 386 m from the study area. We recorded monthly precipitation from October 2010 (from the start of the water year, Oct 1) until September 2013. We quantified precipitation 1 month prior to the start of each sampling period to better understand changes in the arthropod community and reflect typical lags between rain events and arthropod responses (Frampton et al. [2000]; Tanaka and Tanaka [1982]). We used the Palmer Drought Severity Index (NCDC-NOAA [2014]) as a measure of drought severity for each field season (June–August).

Vegetation sampling

We identified all plants to species and recorded density (plants/m^2), horizontal canopy cover (%), and maximum plant height (cm) in each quadrat for each sampling period. We considered grasses as separate individuals if the crowns from stolons occurred more than 10 cm from the original crown base. Biennial or perennial species that appeared dead were counted due to uncertain dormancy responses to drought. We grouped plant species into specific cover classes that included grasses, forbs (herbaceous broad-leafed plants), and woody plants. We also recorded bare ground and litter (dead vegetation not attached to soil) as cover classes. Finally, we measured the height of the tallest plant of each species for each quadrat, and averaged among species within each quadrat. We used species richness and canopy cover of plants as measures of community richness and composition, and plant density and height as measures of vegetation structure.

Soil sampling

Prior to each field season, we collected 1 L of soil from each quadrat up to a depth of 15 cm to determine soil chemistry. Soil samples were analyzed by Texas Plant and Soil Labs (Edinburg, TX) to quantify soil pH, organic matter (% O.M.), and available nutrients (NO_3 and P_2O_5). We used these soil characteristics to assess differences in soil chemistry between plant communities, which could influence the plant and arthropod communities (Brussaard [1997]; Levine et al. [2003]).

Arthropod sampling

In an attempt to sample the arthropod community completely, we used three techniques: pitfall traps, vacuum sampling, and Berlese–Tullgren funnels. Pitfall sampling is an effective technique to capture terrestrial arthropods, such as ground-dwelling beetles (Greenslade [1964]; Triplehorn and Johnson [2005]) and arachnids (Work et al. [2002]; Sabu et al. [2011]). Vacuum sampling is a useful method for sampling arthropods in vegetation or on the wing in grasslands (Standen [2000]; Brook et al. [2008]). Berlese–Tullgren funnels generally are considered an efficient method for sampling diversity of soil-dwelling arthropods (Sakchoowong et al. [2007]; Smith et al. [2008]; Triplehorn and Johnson [2005]) and are more efficient in dry environments when compared to other extraction methods (Sabu et al. [2011]). We started sampling arthropods 24 h after we completed vegetation sampling and waited at least 24 h between each technique to allow the arthropod community to recover.

We placed two pitfall traps (266-ml plastic cups) randomly within each quadrat, ensured that pitfall

traps were flush with the soil surface, and filled traps halfway with propylene glycol. We left the traps undisturbed for 24 h, after which we collected the contents of all traps. We used a vacuum sampler (Rincon-Vitova Insectaries, Ventura, CA) to sample each quadrat for 90 s and transferred specimens to a plastic bag. To prevent or reduce predation, we placed cotton balls soaked with ethyl acetate in the bag. Finally, we used Berlese-Tullgren funnels (BioQuip model 2845) and decreased the diameter of the mesh filter (0.32 × 0.32 cm) from the original model to keep soil particles from falling into the collecting cup. We collected 473 ml of soil from each quadrat and placed the sample within the upper part of the funnel. Soil and funnels were exposed to sunlight for 48 h to facilitate extraction.

We combined samples from all techniques within each quadrat to obtain more comprehensive estimates of the arthropod community. We identified all arthropods to family and morphospecies (Oliver and Beattie 1996) when possible, and assigned all arthropods to a functional group that represented the role of each taxon in an ecosystem. We focused on two functional groups—herbivores and decomposers—that would be most likely affected by changes in plant characteristics associated with invasion (Litt et al. 2014). We classified herbivores as arthropods that consume living vegetation as a majority of their diet. We classified decomposers as arthropods that either consume dead animal or plant matter as a majority of their diet, or consume microorganisms (i.e., bacteria and fungi) and concentrate available nutrients in excrements (Brussaard 1997). We classified arthropods that fed on fungi in living plant tissues as herbivores instead of decomposers, as this feeding guild did not depend directly on brown food webs. We did not characterize immature or larval specimens that represented different functional groups than their adult morphs due to a lack of taxonomic resolution; these specimens comprised <1 % of all individuals sampled (Mitchell 2014). We used species richness and abundance of all arthropods and each functional group as coarse measurements of community composition.

Data analysis

We analyzed differences in vegetation, soil, and arthropod characteristics between plant communities using generalized linear mixed models. We included plant community (native and OWB) and year (as a proxy for drought) as independent factors in all models and explored evidence for a two-way interaction (plant community*year). We removed the interaction term from models when $P > 0.1$, but retained all simple effects in final models. When appropriate, we accounted for repeated measurements (repeated sampling of quadrats nested in plots) and considered three possible covariance structures: no within-group covariance, compound symmetric, or first-order autoregressive, selecting the most appropriate structure based on AIC values. When necessary, we transformed response variables to meet assumptions. We used the appropriate distribution and link function for each response variable; we used a Poisson distribution and log link to analyze differences in abundance. We completed all analyses using lme4 and nlme packages in R (Pinheiro et al. 2013; R Core Development Team 2013; Bates et al. 2014).

We analyzed bare ground and litter cover in 2011 only, as more than half of all values were zero in other years; we made informal comparisons in 2012 and 2013 based on means and 95 % confidence intervals. We did not examine differences in woody plant cover, as woody plants were <1 % of all individual plants sampled during the three-year study (Mitchell 2014).

Results

Precipitation

Total rainfall for the water year (Oct 1–Sep 30) measured 32.3 cm for 2011, 62.5 cm for 2012, and 69.1 cm for 2013, which was 36, 69, and 76 % of the long-term average, respectively (Mitchell 2014). Drought severity was extreme (<−4.00), moderate (−3.99 to −3.00), and none (−1.99 to 1.99) for 2011, 2012, and 2013, respectively.

Vegetation

Nearly all of the characteristics of vegetation composition and structure we measured differed between plant communities and the magnitude of some differences changed over time as drought severity decreased (Table 1). Native plant communities had 2.6 more plant species/m^2 (95 % CI 1.3–3.8) than communities dominated by OWBs (Fig. 1a). Plant density was similar in both plant communities during extreme

Table 1 Variables affecting vegetation characteristics with plant invasion (community) and drought (year), southern Texas, summers 2011–2013

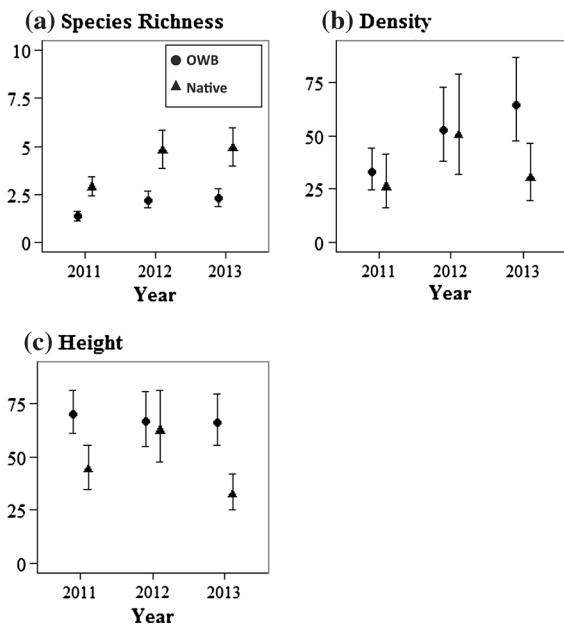| Vegetation	Community		Year		Community*Year	
	$F_{1,8}$	P	$F_{2,68}$	P	$F_{2,66}$	P
Characteristic						
Richness	94.76	<0.001	16.09	<0.001		
Plant density	6.72	0.032	12.59	<0.001	6.85	0.002
Plant height	74.63	<0.001	16.29	<0.001	15.59	<0.001
Canopy cover						
Bare ground[a]	15.27	0.005				
Litter[a]	0.76	0.410				
Grass	21.46	0.002	9.86	<0.001	12.79	<0.001
Forb	300.16	<0.001	14.29	<0.001		

[a] 2011 data only

Fig. 1 Vegetation characteristics (means and 95 % CIs) of communities dominated by Old World bluestems (OWB) and native plants (Native) with decreasing drought severity over time, including **a** species richness (species/m^2), **b** density (plants/m^2), and **c** maximum height (cm), southern Texas, summers 2011–2013

Fig. 2 Canopy cover by cover class (%, means and 95 % CIs) in communities dominated by Old World bluestem (OWB) and native plants (Native) with decreasing drought severity over time, southern Texas, summers 2011–2013

(2011) and moderate drought (2012), but was 34.1 plants/m^2 lower (27.9–40.2) in native plant communities than OWBs when drought subsided (2013, Fig. 1b). Plants in native plant communities were shorter than OWB-dominated communities during extreme drought (26.2 cm, 25.6–26.4) and when drought subsided (33.8, 30.2–37.5), but height did not differ between communities during moderate drought (Fig. 1c).
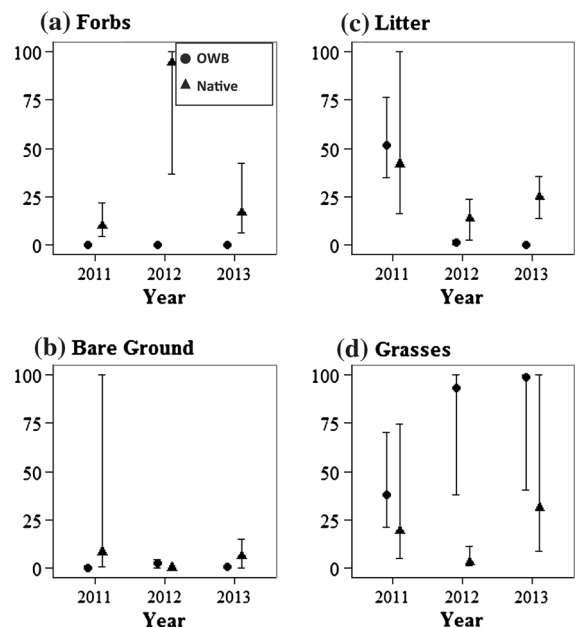
Native plant communities had more forb cover during extreme (9.2 % more, 4.1–21.9), moderate (94.3, 36.7–99.6) and non-drought conditions (16.3, 6.4–42.0), relative to OWB-dominated communities (Fig. 2a). Prevalence of bare ground and litter cover were similar between communities during extreme drought (2011), but litter cover generally was higher in native plant communities, relative to OWBs, as drought severity decreased (Fig. 2b, c). OWB-dominated communities had more grass cover (74.1 %, 37.1–89.2) relative to native plant communities during

moderate drought (2012, Fig. 2d); all grass cover in OWB-dominated communities was comprised of OWBs (Mitchell 2014).

Soils

All of the soil characteristics we measured differed between plant communities and the magnitude of some differences changed over time as drought severity decreased (Table 2). Soils in native plant communities were more acidic (1.9 units pH, 95 % CI 1.7–2.2) and had 1.6 % more organic matter (0.1–3.9) than communities dominated by OWBs. Soils in the native plant community also had more available nitrogen and phosphorous relative to OWBs, but the differences between communities decreased as drought severity decreased. Native plant communities had 87.5 kg/ha more nitrogen (31.7–236.4) during extreme (2011) and moderate drought (2012), relative to OWB-dominated communities, but only 16.3 kg/ha more nitrogen (5.9–43.6) when drought subsided (2013). Native plant communities also had 66.4 kg/ha more phosphorous (28.3–151.5) during extreme drought (2011) and 18.5 kg/ha more (6.2–53.4) during moderate drought (2012), but phosphorous differed little between communities when drought subsided.

Arthropods

We captured a total of 14,181 arthropods ($n = 6975$ in OWB plots, $n = 7206$ in native plots), representing 30 orders, 157 families, and 271 morphospecies (Mitchell 2014). Nearly all of the arthropod characteristics we measured differed between plant communities and the magnitude of some differences changed as drought severity decreased (Table 3). Native plant communities had more species of arthropods than communities dominated by OWBs, but the differences were most pronounced during extreme drought (8.0 species/m^2,

95 % CI 5.3–11.6, Fig. 3a). During extreme drought (2011), native plant communities also had 131.1 more arthropods/m^2 (88.0–205.9), but this pattern shifted as drought severity decreased (Fig. 3b). Native plant communities had 36.3 fewer arthropods (33.6–50.0) during moderate drought (2012) and 46.4 fewer arthropods (44.1–48.5) when drought subsided (2013), relative to OWB-dominated communities (Fig. 3b).

Herbivores

Native plant communities had 0.8 more species/m^2 of herbivores (0.5–4.3), but as drought severity decreased, herbivores were much more abundant in OWBs (Fig. 3c, d). Herbivore abundance did not differ between plant communities during extreme drought (2011), but OWBs had 38.8 more herbivores/m^2 (28.6–52.33) during moderate drought (2012), and 145.4 more arthropods (105.7–200.0) as drought subsided (2013, Fig. 3). Herbivores comprised 61 % (4234) of arthropods sampled in OWBs, in comparison to 12 % (872) in native plant communities. Mochlozetid mites and a species of leafhopper (*Balclutha rubrostriata*) were the main contributors to differences in herbivore abundance between communities. Mochlozetid mites represented 53 % (2238) of all herbivorous arthropods in OWBs, compared to 13 % (111) of herbivorous arthropods in native plant communities. *B. rubrostriata* represented 43 % (1830) of all herbivorous arthropods in OWBs; we did not collect this species in native plant communities.

Decomposers

We did not detect differences in species richness of decomposer arthropods between plant communities, but abundance differed (Table 3; Fig. 3e, f). Native plant communities had more decomposers than OWB-dominated communities during extreme drought

Table 2 Variables affecting soil characteristics with plant invasion (community) and drought (year), southern Texas, 2011–2013

Soil	Community		Year		Community*Year	
	$F_{1,7}$	P	$F_{2,9}$	P	$F_{2,7}$	P
Characteristic						
pH	361.75	<0.001	11.25	0.004		
% Organic matter	37.16	<0.001	1.82	0.216		
NO$_3$	57.89	<0.001	12.39	0.005	20.97	0.001
P$_2$O$_5$	36.05	<0.001	40.12	<0.001	3.82	0.076

Table 3 Variables affecting arthropod characteristics with plant invasion (community) and drought (year), southern Texas, summers 2011–2013

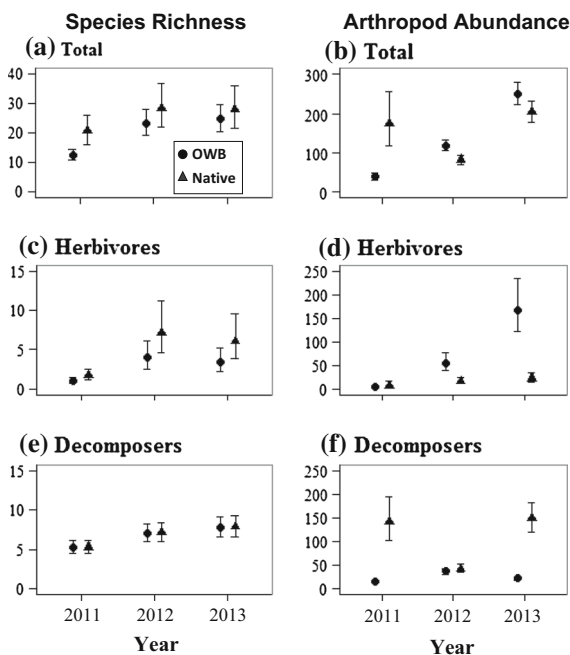| Arthropod	Community		Year		Community*Year	
	$F_{1,8}$	P	$F_{2,66}$	P	$F_{2,68}$	P
Characteristic						
Richness						
Total	23.05	0.001	33.90	<0.001	4.30	0.018
Herbivores	7.43	0.026	18.13	<0.001		
Decomposers	0.06	0.817	11.45	<0.001		
Abundance						
Total	0.39	0.645	788.06	<0.001	348.60	<0.001
Herbivores	51.63	<0.001	646.84	<0.001	94.51	<0.001
Decomposers	106.43	<0.001	169.45	<0.001	332.72	<0.001

Fig. 3 Arthropod species richness (species/m^2) and abundance (individuals/m^2, means and 95 % CIs) in communities dominated by Old World bluestem (OWB) and native plants (Native) with decreasing drought severity over time, southern Texas, summers 2011–2013

(126.7, 90.8–176.7) and when drought conditions subsided (127.4, 103.5–156.9), but abundance of decomposers was similar between plant communities during moderate drought (Fig. 3). Decomposers comprised 61 % (4384 arthropods) of all arthropods in the native plant community, in comparison to 16 % (1093) in the OWB-dominated community. Nonnative woodlice (*Armadillidium vulgare*) were the main contributor to differences between communities, representing 71 % (3420) of decomposer arthropods in native plant communities, compared to 10 % (110) in OWBs.

Discussion

Arthropods are important indicators of biodiversity that provide many ecological functions, including pollination, decomposition, and herbivory (Wilson 1987; Folgarait 1998; Potts et al. 2010). Arthropods also are sensitive to changes in the environment, and any change in conditions as a result of plant invasion could alter the habitat quality for arthropods (Bezemer et al. 2014; Litt et al. 2014; van Hengstum et al. 2014). We present evidence that plant invasion and drought interact to alter composition of vegetation and arthropod communities. We found that differences in certain vegetation characteristics between native plant- and OWB-dominated communities, notably plant species richness and density, were more pronounced as drought conditions subsided, suggesting that effects of drought may supersede effects of plant invasion. However, differences in arthropod communities between grasslands dominated by native and nonnative plants depended mainly on a few arthropod taxa.

Plant-feeding arthropods generally decrease in diversity and abundance with increased dominance of nonnative plants (Litt et al. 2014; van Hengstum et al. 2014) because native arthropods have not evolved with these novel hosts (Bernays and Graham 1988; Niemela and Mattson 1996). Like Cord (2011), we found that communities of herbivorous arthropods were less diverse in communities dominated by

OWBs, but we also observed that herbivores were more abundant in monocultures of OWBs during moderate and non-drought conditions. Woodin et al. (2010) reported plant-feeding arthropods were abundant in OWBs, specifically leafhoppers (Cicadellidae). Similarly, we found that a single species of leafhopper (*Balclutha rubrostriata*) dominated the arthropod community in OWB monocultures.

Balclutha rubrostriata is a nonnative species whose native range overlaps with OWB grasses and has been associated with OWBs in the insect's introduced range (Zahniser et al. 2010; Morgan et al. 2013; Andreason et al. 2015). We collected nearly all *B. rubrostriata* (∼99 %) when Kleberg bluestem plants were flowering, and this species may use flowering OWBs as refugia in its introduced range. We are not aware of studies on the habitat characteristics of *B. rubrostriata* in its native range, and further research is needed to determine the combined effect of OWBs and *B. rubrostriata* where both have been introduced. Given that *B. rubrostriata* is a vector for disease in sugarcane (Haboonsong et al. 2006) and OWBs grow well in disturbed areas (Coyne and Bradford 1985), OWBs may facilitate crop loss without effective management tools.

Mochlozetid mites also were substantially more abundant in OWB-dominated areas relative to native plant communities. Although this arthropod group typically is associated with grasses, these species are assumed to feed on fungal spores and hyphae (Norton 1983). Mites may not be associated with specific hosts, but higher densities of Mochlozetid mites found with OWBs may suggest that the monocultures are more susceptible to infection than diverse plant communities. A variety of fungal pathogens can affect OWBs (Bhat et al. 2011), but no studies have investigated the impact of these pathogens on arthropod food webs.

Detritus- and fungal-feeding arthropods may benefit from increases in plant litter and decomposition from microbes associated with plant invasion (Gratton and Denno 2006; Levin et al. 2006; Kappes et al. 2007; Wolkovich 2010). In addition, litter from nonnative plants may have different chemical properties that may alter soil conditions to benefit certain arthropod taxa (Standish 2004; Alerding and Hunter 2013). Although we found abundant litter in both plant communities during extreme drought, we did not observe similar decomposer communities.

We found that the differences in abundance of decomposers between plant communities were driven by woodlice (*Armadillidium vulgare*). *A. vulgare* is a detritivore introduced from Europe that can replace native detritivores (Ellis et al. 2000; Frouz et al. 2008; Singer et al. 2012). Although we found higher densities of *A. vulgare* in acidic soils found in the native plant community, this woodlouse is sensitive to changes in soil pH and prefers near-neutral soils (van Straalen and Verhoef 1997; Zimmer et al. 2002). *A. vulgare* was nearly three times more abundant in communities of native plants relative to OWBs, despite the same litter cover. Plant tissues of OWBs have higher C:N ratios than native grasses (Reed et al. 2005) and litter may be less palatable for detritivores, which suggests that although *A. vulgare* uses both plant communities, the quantity and composition of litter has a greater influence on habitat quality than the soil properties. Furthermore, *A. vulgare* can accelerate rates of decomposition and mineralization in soil communities (Frouz et al. 2008); increased abundance of *A. vulgare* may explain the increase in available N, P, and % O.M. observed in native plant-dominated sites. More abundant woodlice in native plant communities also may increase habitat quality for native arthropods and other wildlife that forage for *A. vulgare* in the litter layer (Paris 1963; Fisher and Cover 2007; Rezáč and Pekár 2007). Therefore, changes in litter composition and abundance following plant invasion and drought may affect other trophic levels.

We expected diverse communities of both plants and arthropods in areas dominated by native plants. However, we observed fewer species of arthropods than expected, which suggest that the effects of multiple disturbances (i.e., nonnative arthropods, nonnative plants, and drought) severely reduced the diversity of native communities. The plants we observed are drought-tolerant species that persisted throughout the study (Mitchell 2014); other plant species may not compete well in such poor conditions. Landscapes that are not affected by other disturbances prior to invasion may reveal larger decreases in richness of native plant and arthropod communities. However, our results demonstrate shifts in the composition of arthropod communities that could have profound effects on ecosystem services (Gratton and Denno 2006; Levin et al. 2006).

Changes in the composition of arthropods in grassland ecosystems associated with plant invasion can alter habitat quality for many fauna (Wiens and

Rotenberry 1979; Wilson 1987; Hickman et al. 2006; Woodin et al. 2010). Plant invasion may reduce the availability of arthropods that are essential to the reproduction and development of insectivorous animals, such as breeding grassland birds (Flanders et al. 2006). As the frequency and intensity of anthropogenic disturbances increase the likelihood of plant invasions (Bradley et al. 2009; Hobbs et al. 2009), successful conservation efforts will require managing habitat for native arthropod communities in addition to organisms that depend on arthropods as a food source. Therefore, we recommend incorporating arthropod data into studies that seek to conserve habitat for wildlife to improve our understanding of how nonnative plants alter ecosystem function where they are dominant.

Compliance with ethical standards

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

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