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Invasive Saltcedar and Drought Impact Ant Communities and Isopods in South-Central Nebraska

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Abstract

The establishment and spread of non-native species often results in negative impacts on biodiversity and ecosystem function. Several species of saltcedar, *Tamarix* spp. L., have been recently naturalized in large portions of the United States where they have altered plant and animal communities. To test the prediction that saltcedar negatively affects invertebrates, we measured ant genera diversity and the activity density of the exotic isopod *Armadillidium vulgare* Latrielle (Isopoda: Oniscoidea) for 2 yr using pitfall traps located within 30 5-m^2 plots with or without saltcedar at a south-central Nebraska reservoir. From 2005 to 2006, we collected 10,837 ants representing 17 genera and 4,953 *A. vulgare*. Per plot, the average number of ant genera was not different between saltcedar ($\bar{x}$ = 3.9) and non-saltcedar areas ($\bar{x}$ = 3.9); however, saltcedar plots were compositionally different and more similar from plot to plot (i.e., they had lower beta diversity than control plots) in 2005, but not in 2006. Isopods were likewise temporally affected with higher activity density (+89%) in control plots in 2005, but higher activity density (+27%) in saltcedar plots in 2006. The observed temporal differences occurred as the drought that initially enabled the saltcedar invasion became less severe in 2006. Combined, our results suggest that invertebrate groups like ants, which are generally omnivorous, may be better equipped than more specialized taxa like detritivores to withstand habitat changes due to invasions by non-native species, especially during extreme weather events such as prolonged droughts.

Key words: arthropods, biodiversity, disturbance, drought, invasive species

In the United States, there are ~50,000 established non-native species that cost more than $137 billion annually in control and damages (Pimentel et al. 2000). While some of these species are listed as beneficial to humans (e.g., cattle), others have less documented effects. The introduction and naturalization of non-natives is also one of the leading causes of biodiversity loss (Wilcove et al. 1998, Bezemer et al. 2014). As many species provide important ecosystem services—including pollination, seed dispersal, soil perturbation, and pest control—the resulting loss in biodiversity can have adverse effects for whole ecosystems (Ehrlich and Mooney 1983, Losey and Vaughan 2006, Prather et al. 2013). Identifying and understanding how introduced species impact ecosystems is of particular interest from both a biological and economic perspective to ecologists, managers, and policy makers alike.

As many as 12 species of saltcedar trees, *Tamarix* spp. L (hereafter saltcedar), have been introduced into the United States from Europe and Asia, several of which are among the approximate 653 listed noxious weed species (USDA-NRCS 2007). While the degree of invasiveness varies across saltcedar species (Gaskin and Schaal 2002, Dudley and DeLoach 2004), their ecology is similar in that they are commonly found along rivers, streams, lakes, and reservoirs forming dense monotypic stands in areas with newly exposed soil from receding waters (Warren and Turner 1975, Di Tomaso 1998). Saltcedar species can survive in hostile abiotic environments [e.g., high soil salinity (Shafroth et al. 1995)] across a range of climatic conditions from deserts in Arizona to cold winters in Montana (Horton et al. 2001, Sexton et al. 2002, Pearce and Smith 2003). It should not be surprising that saltcedar's physiological traits have facilitated its increasing distribution and make it a potential threat as a disrupter of ecosystem function as it displaces native vegetation throughout its invaded range (Graf 1978, Di Tomaso 1998).

Moreover, saltcedar is suspected of reducing the diversity of animals, including insects, indirectly through habitat modification and by being unpalatable forage for many herbivores (Dudley et al. 2000, Ellis et al. 2000, Durst et al. 2008, Litt et al. 2014, Ralston et al. 2017). Currently, studies have focused on saltcedar invasions in the desert southwest where saltcedar has potentially altered hydrology and where the climate is characterized by long periods with little precipitation, high summer temperatures, and short winters that lack significant snowfall (Durst et al. 2008, Bateman and Ostoja 2012, Ralston et al. 2017). However, diverse geographic areas may be differentially impacted by saltcedar as this non-native plant has demonstrated different growth patterns, for example, in south-central Nebraska compared to southwestern U.S. habitats (Jurzenski and Hoback 2008). Thus, despite the documented effects of saltcedar on arthropods in Arizona, assessments of ground-dwelling invertebrate taxa are still needed to better quantify the ecological impacts of saltcedar as it moves into areas with different climatic conditions and hydrological systems.

Here, we focus on two invertebrate groups, ants (Hymenoptera: Formicidae) and isopods (Isopoda: Armadillidiidae), as biological indicators of ecosystem health after a saltcedar invasion that occurred because of a severe drought between 2003 and 2006 in south-central Nebraska (Jurzenski and Hoback 2008, Olds et al. 2011). Both taxa are regularly used in habitat assessments as they are easily monitored using standardized methods over multiple sampling events (e.g., pitfall traps) and are functionally important in ecosystems as predators, omnivores, and detritivores (Paoletti and Hassall 1999, Agosti et al. 2000, Andersen and Majer 2004, Lucky et al. 2013, Roeder et al. 2018). Using 2 yr of trapping data, our aim was to provide a first assessment of saltcedar's impact on invertebrate biodiversity in Nebraska, a state where little has been published on the distribution of saltcedar or its environmental impact. As biodiversity is often reduced in the wake of invasive species, we predicted that areas with non-native saltcedar would harbor lower ant richness and that those invaded assemblages would be compositionally distinct from uninvaded areas. We also hypothesized that isopods and litter-dwelling ants, which often require particular microclimate conditions to survive, would be negatively impacted by saltcedar presence.

Materials and Methods

Study Site

South-central Nebraska suffered a severe four-year drought between 2003 and 2006 (U.S. Bureau of Reclamation: HydroMet 2007), resulting in drying of the Republican River and lowering of water levels in associated reservoirs, including the Harlan County Reservoir. The severe drought reduced water levels by more than 50% volume (Olds et al. 2011) and exposed large areas of shoreline, facilitating the colonization of non-native saltcedar in this area. A number of other native plant species that also colonized the shoreline including eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.), sandbar willow (*Salix exigua* Nutt.), peachleaf willow (*Salix amygdaloides* Anderss.), black locust (*Robinia pseudoacacia* L.), Canadian horseweed (*Conyza Canadensis* (L.) Cronq.), common yarrow (*Achillea millefolium* L.), goldenrod (*Solidago* spp. L.), flagrant flatsedge (*Cyperus odoratus* L.), smartweed (*Polygonum* spp. L.), and witchgrass (*Panicum capillare* L.).

Invertebrate Sampling and Identification

We sampled invertebrates in 2005 and 2006 on the exposed shoreline of the Harlan County Reservoir (Supp Fig. 1 [online only], 40.07°N, 99.21°W). Thirty 5-m^2 research plots with saltcedar present (n = 13) or absent (n = 17) were established at least 20 m apart in this habitat. In each plot, we set four pitfall traps (opening diameter: 7.5 cm, depth: 10 cm), filled with a 50:50 nontoxic antifreeze: water solution, into the ground so that the lip was flush with the surface. Trap arrays were arranged in a y-shape with 0.5-m plastic lawn edging between each of the four cups, a method useful for funneling or guiding invertebrates to specific collection points (Winder et al. 2001). Sampling occurred in May, August, and October of 2005 and 2006 to capture seasonal changes in activity density of isopods and richness of ant genera. Traps were left open for 48 h during each sampling event.

Ants were identified to genus using taxonomic keys (Creighton 1950, Hölldobler and Wilson 1990, Fisher and Cover 2007). Higher-level taxonomic identification (i.e., genus compared to species) allows for more rapid and cost-effective biomonitoring, often revealing similar patterns to species richness for invertebrate groups like ants, beetles, butterflies, and spiders (Gaston and Williams 1993, Pik et al. 1999, Timms et al. 2013). Furthermore, genus-level taxonomy for ants has been successfully used as a surrogate for species richness to test for differences in community structure and phylogenetic diversity across multiple continents (Andersen 1995, Groc et al. 2010, Smith 2015, Parr et al. 2016). For all analyses with ants, we used richness and not activity density as social taxa are often aggregated in space and thus bias abundance-based results (Gotelli et al. 2011). All isopods were counted and identified as *Armadillidium vulgare* Latrielle. Voucher specimens were deposited at the University of Nebraska at Kearney insect museum.

Statistical Analyses

Analyses were run in R, version 3.5.1. We used generalized linear models (GLMs) with Poisson distributions to compare our predictor variables of the presence or absence of saltcedar (hereafter saltcedar and control plots, respectively), seasons (n = 3) and years (n = 2) to our response variable of ant genera richness or isopod activity density. Pairwise contrasts between saltcedar and control plots were performed using the 'emmeans' package (Lenth et al. 2019). As our sampling protocol contained an uneven number of replicates, we created incidence-based rarefaction curves to test for differences in estimated ant genera richness by comparing 95% CIs in the 'iNEXT' package (Chao et al. 2016).

We next quantified differences in ant assemblage composition in three ways. First, we used a nonparametric multivariate analysis of variance (i.e., PERMANOVA) with 1,000 permutations to test if ant assemblages in saltcedar plots were compositionally different than assemblages in nonsaltcedar plots using an incidence based Jaccard's index of dissimilarity, which scales from 0 (completely similar) to 1 (completely dissimilar). PERMANOVA tests the null hypotheses of no difference among groups using random permutations of the data (Anderson 2001). We visualized differences in assemblage composition using nonmetric multidimensional scaling (NMDS) ordinations. Second, we tested for differences in beta diversity between control and saltcedar plots by calculating multivariate dispersion—the average distance of plots to the group centroid in multivariate space (Anderson et al. 2006). Significant differences in distance between groups were determined using ANOVA and the betadisper function in the 'vegan' package (Oksanen et al. 2019). Finally, we used indicator analyses (Dufrêne and Legendre 1997) to identify if specific ant genera were associated with the presence or absence of saltcedar. Statistical significance was determined using 999 permutations in the 'indispecies' package (De Caceres and Jansen 2016).

Results

We collected a total of 10,837 ants from 17 genera and 4,953 isopods, all of which were *Armadillidium vulgare*, from 30 plots across

2 yr of sampling. Because ants and isopods were analyzed differently, we discuss our results separately.

Saltcedar Reduced Ant Beta Diversity, But Not Overall Genera Richness

Genera richness of ants increased 1.6-fold on average per plot from 2005 to 2006 (GLM: χ^2 = 37.00; df = 1; P < 0.001); however, we did not detect any significant differences in richness between treatments (GLM: χ^2 = 0.01; df = 1; P = 0.907) or across seasons (GLM: χ^2 = 5.38; df = 2; P = 0.068). Incidence based rarefaction likewise indicated similar levels of estimated genera richness in control (2005 = 16.0; 2006 = 14.0) and saltcedar plots (2005 = 12.7; 2006 = 13.0) with overlapping 95% CIs across all treatments (Fig. 1) except control plots in 2005 (estimated richness range = 14.2–17.8) and saltcedar plots in 2006 (estimated richness range = 11.9–14.1). Because of the temporal increase, we analyzed differences in genera composition between treatments in 2005 and 2006 separately.

Control and saltcedar assemblages differed in taxonomic composition in 2005 (PERMANOVA: pseudo-F = 2.37; df = 1, 28; P = 0.020; Fig. 2a), but not in 2006 (PERMANOVA: pseudo-F = 1.31; df = 1, 28; P = 0.299; Fig. 2b). Our metric of beta diversity, multivariate dispersion, also suggested control plots were further from the group centroid than saltcedar plots in 2005 (ANOVA: F = 7.47; df = 1, 28; P = 0.011; Fig. 2a) but not in 2006 (ANOVA: F = 0.05; df = 1, 28; P = 0.819; Fig. 2b). In other words, control plots harbored not only different genera when compared to saltcedar plots, but those control plots were also more compositionally dissimilar from plot to plot. In both years, the most frequently encountered ants for both control and saltcedar plots were *Crematogaster*, *Lasius*, and *Pheidole* (Table 1). The genera *Aphaenogaster*, *Camponotus*, *Solenopsis*, *Tapinoma*, and *Temnothorax* were collected more commonly in control plots in 2005, yet indicator analyses revealed that only *Tapinoma* was indicative of nonsaltcedar areas (Indicator value = 0.471; P = 0.020) in part because uncommon taxa occurred in only a small number of plots (Table 1).

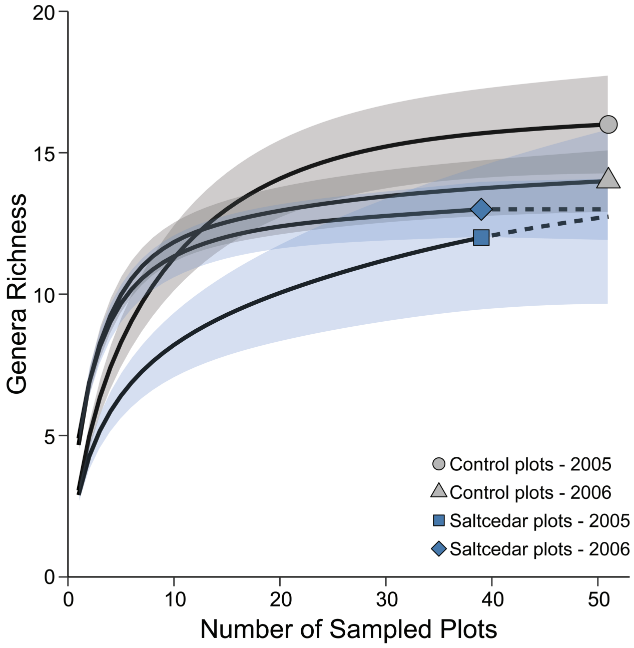

Fig. 1. Incidence based rarefaction for ant genera across habitat type and year. Data were compiled from each of the 17 control (gray) and 13 saltcedar plots (blue) per month (n = 3) resulting in 51 and 39 sampled plots, respectively, for 2005 and 2006. Shaded areas represent 95% CIs for each line. Extrapolated data (dashed lines) for saltcedar plots were calculated to reach the number of sampled control plots (n = 51).

Saltcedar Decreased Isopod Activity Density

Isopods varied in activity density by up to three orders of magnitude across plot type, season, and year (Fig. 3). When all data were pooled, control plots maintained more individuals than saltcedar (GLM: χ^2 = 7.50; df = 1; P = 0.006); however, there were significant temporal effects (Fig. 3a and b). Isopods were 1.6-fold more abundant in 2006 compared to 2005 (GLM: χ^2 = 263.35; df = 1; P < 0.001) with control plots harboring on average 89% more isopods in 2005 (GLM: χ^2 = 171.95; df = 1; P < 0.001) and saltcedar stands containing 27% more isopods on average in 2006 (GLM: χ^2 = 44.17; df = 1; P < 0.001). Seasonally, isopods peaked in activity density during August, averaging 34.78 individuals per plot (GLM: χ^2 = 187.25; df = 2; P < 0.001), with control stands containing almost 59% more individuals during this month. In contrast, saltcedar stands contained more isopods on average in May (+17%) and October (+24%).

Discussion

Invasive plant species routinely reduce biodiversity and homogenize communities. Yet along the shore of a Nebraska reservoir, we found that saltcedar trees—a nonnative from central Europe and Asia—did not decrease the genera richness of ants. Instead the presence of saltcedar, when combined with the effects of drought in 2005, constrained the composition of ant species within sampled plots and reduced isopod activity density. However, when drought conditions lessened in 2006, the previously observed constraints on species composition became relaxed and isopod activity density increased.

Patterns of Ant Diversity

From 2005 to 2006, over 65% of the known Nebraska ant genera were collected (Lamsal 2006, Jurzenski et al. 2012) indicating that even recently disturbed areas may contain diverse assemblages. Surprisingly though, and in contrast to our first hypothesis, we observed little difference in the number of supported genera when saltcedar was present. In New Mexico, ants were likewise minimally affected by saltcedar as both richness and abundance were similar to that in cottonwood stands (Ellis et al. 2000). Our results may be an indication that saltcedar does not adversely affect all invertebrate groups equally in an ecosystem. Yet despite the observed similarities in the number of supported genera, areas with saltcedar contained compositionally different groups of ants during 2005. For example, *Aphaenogaster* and *Camponotus*, both of which are commonly found in more forested habitats (Lessard et al. 2007, Stuble et al. 2013, Roeder and Roeder 2016, Mahon et al. 2017), were primarily collected in areas that were dominated by cottonwood trees that lacked saltcedar. Similar results have been observed by Ralston et al. (2017) who found that *Camponotus* occurred more often in upper riparian zones that contained less saltcedar along a 25-km stretch of the Colorado River. In contrast, only one genus—*Tetramorium*—was found solely in saltcedar plots, where it was collected in a single plot.

Our working hypothesis for why differences between saltcedar and control plots disappeared in 2006 is that drought became less severe in the second year of sampling (U.S. Bureau of Reclamation: HydroMet 2007). Increases in precipitation likely created microhabitats in saltcedar areas that supported ant genera like *Hypoponera*, which feed

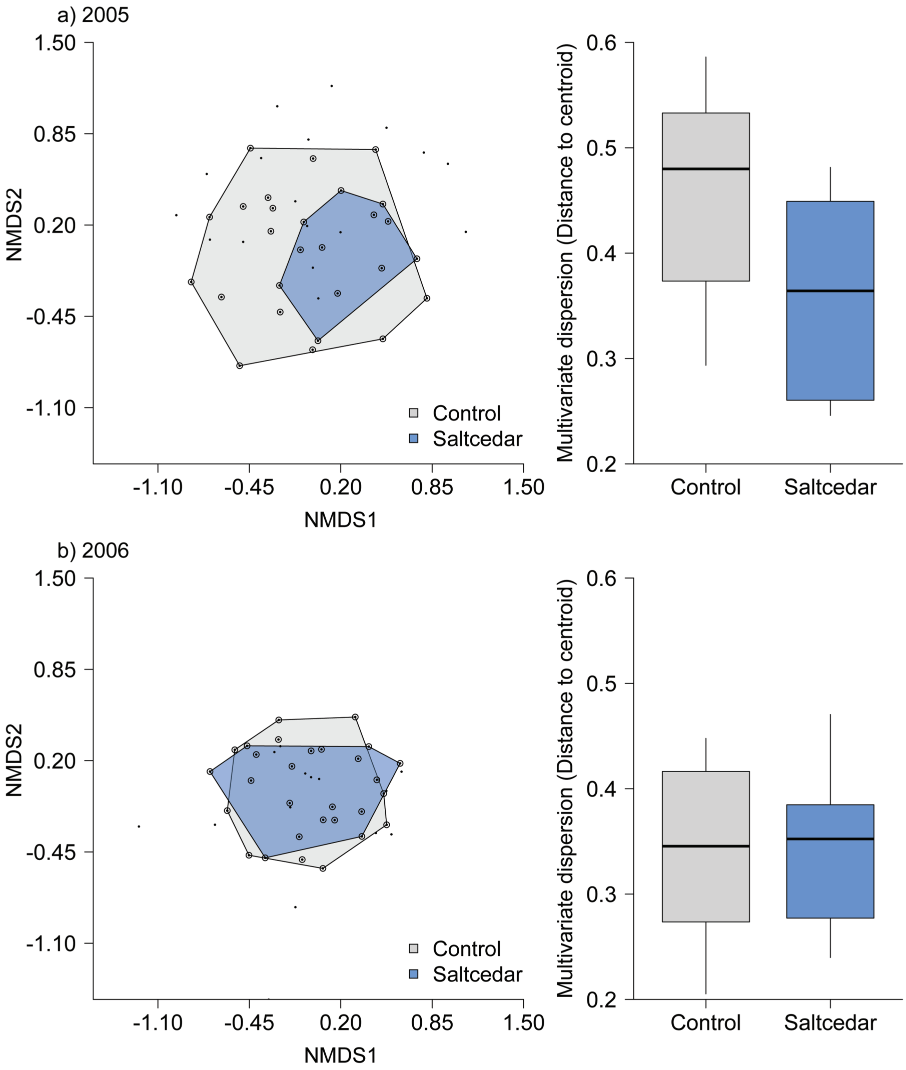

Fig. 2. NMDS ordination of ant communities in control and saltcedar plots. Panel (a) shows data from 2005, while panel (b) shows data from 2006. For each, lighter shading denotes control plots and darker denotes saltcedar plots. Communities are indicated by circles and species by small black dots. Each NMDS is accompanied by a boxplot of the multivariate dispersion (i.e., beta diversity) which is the average distance of plots to the group centroid in multivariate space.

on invertebrate taxa (e.g., Collembola) that are patchy and reliant on moisture (Metz and Dindal 1975, Heiniger et al. 2015, Deyrup 2016). Perhaps, this is also why ants like *Tapinoma*—a mobile taxa that seeks out leaf litter pockets with enough moisture and humidity to promote the development of their eggs, larvae, and pupae (Buczkowski and Bennett 2008, Toennisson et al. 2011)—were statistically indicative of nonsaltcedar areas in 2005 but not in 2006. We base this working hypothesis on the assumption that saltcedar habitats in the drought were asymmetrically impacted as saltcedar uses more water than many competing plants, consuming as much as 760 liter of water per day (Di Tomaso 1998) and desiccating springs and perennial streams when infestation levels are high (Johnson 1987). Such water consumption can dramatically decrease soil moisture (Hughes 1970, Di Tomaso 1998) and thus relief from drought conditions may result in a larger response in saltcedar plots, compared to control plots, by invertebrate taxa that can opportunistically take advantage of newly created pockets of moisture. This is also likely why we observed a greater difference in beta diversity across nonsaltcedar plots in 2005 as those plots were able to support a larger diversity of, but potentially not a greater number of, genera from the regional pool.

Isopod Response

In contrast to the ants collected in this study, the terrestrial isopod *A. vulgare* was introduced into the contiguous United States through soil ballast and agriculture. It has spread across a variety of terrestrial habitats including grasslands and forests (Paris 1963, Miller and Cameron 1987). The ability to persist in these habitats is likely because of *A. vulgare*'s wide diet breadth consisting of detritus from both native plants like cottonwood, *Populus deltoides* Bartr. ex Marsh, and exotic plants like Russian olive, *Elaeagnus angustifolia* L. (Rushton and Hassall 1983, Abelho and Molles 2009). Yet previous research has revealed *A. vulgare* responds differently in both preference and development to native and nonnative plant detritus, its primary food source (Paris 1963, Rushton and Hassall 1983, Abelho and Molles 2009). Consequently, isopods have been found to be more abundant in areas with nutrient rich cottonwood detritus compared to saltcedar dominated areas (Ellis et al. 2000, Smith et al. 2006). If saltcedar presence alters the detritus of an area and is less palatable to *A. vulgare*, then this may be one reason why isopods would have lower activity in saltcedar areas. However, our results were variable across years and seasons with higher activity density

Table 1. Incidence of ant genera across plot type and year

Genus	Control		Saltcedar	
	2005	2006	2005	2006
Aphaenogaster	0.12	0.18	—	—
Brachymyrmex	0.06	—	0.08	—
Camponotus	0.24	0.06	—	0.08
Crematogaster	0.59	1.00	0.77	0.92
Dorymyrmex	0.12	0.29	0.38	0.38
Forelius	0.29	0.53	0.15	0.38
Formica	0.18	0.53	0.08	0.69
Hypoponera	0.35	0.18	0.54	0.46
Lasius	0.76	0.94	0.92	1.00
Monomorium	0.18	0.59	0.15	0.23
Myrmica	0.59	0.71	0.31	0.46
Pheidole	0.94	1.00	1.00	1.00
Pogonomyrmex	0.18	0.53	0.31	0.62
Solenopsis	0.24	0.47	—	0.31
Tapinoma	0.47	0.41	—	0.46
Temnothorax	0.12	—	—	—
Tetramorium	—	—	0.08	—

Values represent the proportion of plots (control = 17, saltcedar =13) containing a particular genus. Horizontal — lines indicate that no individuals were collected.

in control plots during 2005 and higher activity density in saltcedar plots in 2006.

Microhabitat differences likely play a key role in the spatial distribution of litter taxa like isopods (Paris 1963, Miller and Cameron 1987, Zimmer 2004, Reid and Hochuli 2007). While anecdotal, our saltcedar plots contained more bare ground and less leaf litter in which these invertebrates are commonly found (J. J., personal observation). Thus, a testable hypothesis that more available habitat (e.g., leaf litter) would support more individuals could be examined in future studies by quantifying litter depth in saltcedar and non-saltcedar areas.

Impacts of Drought on Invertebrate Communities

As climates change, droughts are predicted to increase in frequency and intensity (IPCC 2014). Increased drought frequency poses a direct challenge for many invertebrate taxa, especially isopods that are terrestrial crustaceans with limited morphology to mitigate water loss (Barnett and Facey 2016), reducing survival of their offspring through desiccation (Johnson et al. 2010, Gantz and Lee 2015). Experimental manipulations have further revealed that drought can homogenize and reduce the diversity of aquatic and terrestrial invertebrate communities (Chase 2007, Johnson et al. 2011, Lenhart et al. 2015). Such changes in community composition will directly affect the services provided by insects and overall ecosystem function.

Drought can also impact invertebrate communities indirectly by changing the abundance and richness of primary producers and seasonal detritus (Johnson et al. 2011, Griffin-Nolan et al. 2019). For example, Carnicer et al. (2011) have documented the impacts of drought-induced defoliation on insect food webs in European forests while studies in Arizona have documented similar 8- to 10-fold decreases in arthropod abundance and richness associated with drought stress to plants (Trotter et al. 2008, Stone et al. 2010). The observed negative effects of saltcedar on insects in the dry, southwestern United States may increase when drought conditions occur and could potentially explain why the negative effects of saltcedar on invertebrates are more prevalent in habitats where moisture is commonly limited (Di Tomaso 1998, Durst et al. 2008).

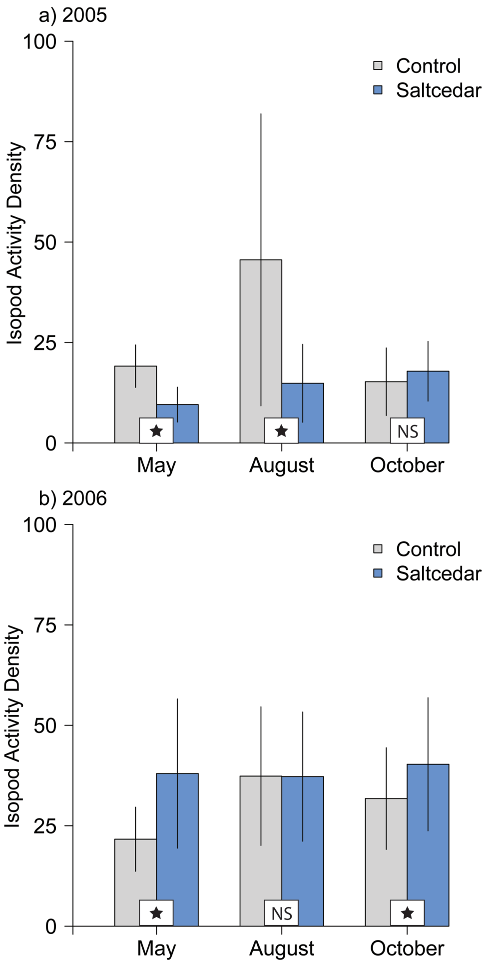

Fig. 3. Temporal changes in isopod activity density (i.e., average number of isopods per plot) across years, seasons, and plot type. Panel (a) shows data from 2005, while panel (b) shows data from 2006. For each, lighter bars denote the average isopod activity density in control plots and the darker bars denote activity density in saltcedar plots, each with standard error bars. Significant differences ($P < 0.05$) between control and saltcedar plots at each sampling point are denoted by a star or are marked as nonsignificant (NS).

In our study, drought facilitated the spread of non-native saltcedar on the shore of the Harlan County Reservoir in Nebraska. In 2005, during the drought, abiotic conditions were more hostile for invertebrates. However, these effects were reduced when increased precipitation occurred in 2006, the second year of our sampling. As we observed year effects in both of our statistical analyses of ants and isopods (Figs. 2 and 3), we posit that drought may not only be enabling the spread of saltcedar but also intensifying its effect on invertebrate communities.

Caveats and Conclusions

Non-native vascular plants make up 13.6% of all vascular plants in the Great Plains of the United States (Vitousek et al. 1996). Saltcedar, one such non-native, has been known to degrade habitat and consequently change species composition of plants and animals (Everitt 1980, Bailey et al. 2001, Shafroth et al. 2005); yet, results are still inconclusive for insects (Hopkins and Carruth 1954, Ellis et al. 2000, Durst et al. 2008). In this study, we compared isopod activity and ant genera richness response to saltcedar and found mixed results across years as drought lessened. Our results suggest differential responses to invasion by these groups; however, our analyses do not directly evaluate this and the metrics used differed by taxa (richness and activity density) and are thus not directly comparable. While ants are regularly used as bioindicators of ecosystem health (Andersen 1997, King et al. 1998, Roeder et al. 2018), our comparisons using ant genera were mixed. One likely source of variance is that ants were identified to genus while more accurate documentation of changes in richness and composition would be possible at the species level. However, higher-level taxonomic identification allows for more rapid and cost-effective biomonitoring, often revealing similar patterns to species richness for invertebrate groups like ants, beetles, butterflies, and spiders (Gaston and Williams 1993, Pik et al. 1999, Timms et al. 2013).

Before the results of this study could be fully analyzed and communicated, above average precipitation in 2007 returned the reservoir to full capacity, which inundated the saltcedar stands. Thus, it is impossible to determine whether saltcedar had a lingering effect on ants and isopods at this location in Nebraska. Yet, the absence of negative impacts on ant richness between areas with saltcedar and areas without saltcedar suggest trophically diverse assemblages may be buffered against invasion by non-native plants like saltcedar. Additionally, drought may intensify the impact that non-native species have on arthropods as we observed yearly differences in isopod activity density during drought and when moisture was increasing. Future research is needed to test if saltcedar will negatively impact other invertebrate taxa in the Great Plains and if the effect of saltcedar on ecosystems may be exacerbated by extended droughts.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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