Biol Invasions (2020) 22:3067–3081
https://doi.org/10.1007/s10530-020-02310-9

ORIGINAL PAPER

Effects of *Lespedeza cuneata* invasion on tallgrass prairie plant and arthropod communities

Sofia Varriano · Krishna Patel · Luke Lefler · Carolina Kirksey · Adam Turner · Matthew D. Moran

Received: 9 October 2019 / Accepted: 29 June 2020 / Published online: 4 July 2020

Abstract We examined effects of the invasive species *Lespedeza cuneata* on native plants and foliar arthropod communities in a tallgrass prairie. Through observational and manipulative experiments, we examined plant and arthropod responses to *L. cuneata* over one growing season. The observational study found little impact of the invasive plant on arthropods. By the end of the manipulative experiment, the combined biomass of native grasses and forbs was reduced by approximately 50% in *Lespedeza*-present plots, while total arthropod numbers were only about 15% lower. Seasonal differences were evident; *L. cuneata*-absent plots showed lower arthropod numbers in May, but higher abundances in June. Some feeding groups, notably carnivorous arthropods, appeared unaffected by *L. cuneata*. We tested three hypotheses (one bottom-up and two top-down processes) to explain the relatively weak response of the arthropod community to the invasive plant. Nitrogen content of native plants adjacent to *L. cuneata* areas was significantly higher compared to plants more distant. Ground arthropod predators were higher during mid-summer in *L. cuneata* areas, which may partially explain seasonal variation in foliar arthropods. Insectivorous birds were unaffected by *L. cuneata* abundance, suggesting that arthropod predation rates by birds are unchanged. We suggest that while *L. cuneata* has strong effects on native plants, its ability to increase neighboring plant quality compensates for the lower biomass of native plants in *L. cuneata* areas, moderating the arthropod response. While management of this invasive species remains a priority, tallgrass prairie food webs may be partly resistant to *L. cuneata* invasion.

Keywords Arthropods · *Lespedeza cuneata* · Sericea · Tallgrass prairie

Introduction

North American grasslands have been converted or modified by human activity, mostly due to intensive agriculture and other land-use changes (Sampson and Knopf 1994; Samson et al. 2004; Homer et al. 2015), and these threats continue to this day (Allred et al. 2015; Trainor et al. 2016; Moran et al. 2017; Wright et al. 2017; Wimberly et al. 2018; Hendrickson et al. 2019). Because of their large proportional loss, North American grasslands are of particular conservation

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-020-02310-9) contains supplementary material, which is available to authorized users.

S. Varriano · K. Patel · L. Lefler · C. Kirksey ·
A. Turner · M. D. Moran (✉)
Department of Biology, Hendrix College, 1600
Washington Ave., Conway, AR 72032, USA
e-mail: moran@hendrix.edu

interest and there have been numerous successful attempts to protect remaining grassland fragments from further degradation (Sampson and Knopf 1994; Comer et al. 2018). However, the remaining native grasslands of the North American plains have also suffered numerous plant invasions (Christian and Wilson 1999; Smith and Knapp 2001; Toledo et al. 2014). These invasions have caused declines in native plants (Christian and Wilson 1999; Toledo et al. 2014; Ashton et al. 2016), altered ecosystem function (Jordan et al. 2008; Toledo et al. 2014), and changed animal abundance and behavior (Sheley et al. 1998). Invasive species have therefore become an additional obstacle to conservation, further imperiling native species survival and requiring greater human and monetary resource expenditures (Pimental et al. 2002). For example, cheatgrass (*Bromus tectorum*) has invaded much of the sagebrush steppes of North America (Bradley et al. 2018), causing large losses to ranching interests, and costing taxpayers, businesses, farmers, ranchers, and conservation organizations billions each year in management costs (DiTomaso 2000).

Tallgrass prairies, now reduced more than 95% of their previous coverage, are the most endangered grassland systems in North America (Steinauer and Collins 1996). The last large and mostly contiguous region remaining is the Flint Hills of Kansas and Oklahoma, covering about 1.2 million hectares (Sampson and Knopf 1994). A major invasive species for this system is *Lespedeza cuneata*, commonly known as Chinese bush clover or sericea. It is a legume introduced from Asia and originally planted as erosion control in parts of the U.S. (Ohlenbush et al. 2001). *Lespedeza cuneata* often invades tallgrass prairies and, in that process, can dramatically alter the native plant community (Ohlenbush et al. 2001) through a combination of direct competition, allelopathy, and altered soil characteristics (Dudley and Fick 2003; Blocksome 2006; Allred et al. 2010; Yannarell et al. 2011; Coykendall and Houseman 2014). Brandon et al. (2004) found that *L. cuneata* can dramatically reduce native plant cover and richness. Currently, ranchers and conservation groups spend large amounts of resources and human capital on control of this species. For instance, the Tallgrass Prairie Preserve (Nature Conservancy) in Oklahoma spends about $100,000 annually on *L. cuneata* control using herbicides (B. Hamilton, personal communication). However, these control attempts achieve only moderate positive ecological results (Cummings et al. 2007), and repeated herbicide use has negative effects on native prairie plant richness (Koger et al. 2002).

While the effects of invasive plants on native plant communities are well-studied, impacts on consumers are less explored; especially rare are studies that simultaneously study plants and higher trophic levels (Vilà et al. 2011). Invasive plants have highly variable effects on consumers (Sunny et al. 2015), with over 40% of studies showing non-significant effects (for review, see Schirmel et al. 2016). *Lespedeza cuneata* is known to alter the behavior of pollinators (Woods et al. 2012), which could affect reproduction of other plants (Traveset and Richardson 2006). This invasive species also interacts with large mammal grazers by affecting grazing patterns (Cummings et al. 2007); grazing mammals will sometimes feed on it during the spring but avoid it as it becomes less palatable later in the growing season. This species can also cause adverse effects on grazing animals because, as it matures, it contains high levels of condensed tannins (Clarke et al. 1939; Ohlenbush et al. 2001).

The arthropod communities in North American tallgrass prairies are diverse and exhibit high consumer biomass; subsequently, they have important ecological effects throughout the food web (Warren et al. 1987; Gibson et al. 1990; Whiles and Charlton 2006; Moran 2014; Nickell et al. 2018). In a non-experimental study, Eddy and Moore (1998) observed lower arthropod richness in *L. cuneata* areas, but there is little additional information on how *L. cuneata* can cause effects that cascade through the variety of consumers in this system.

There are strong correlations between plant community structure and arthropod community structure. For instance, high plant diversity tends to support high arthropod diversity (Southwood 1961; Siemann et al. 1998; Knops et al. 1999). Since arthropod herbivores tend to specialize, the diversity of plants and their relative abundances can affect these animals greatly (Jaenike 1990). Therefore, the changes in tallgrass plant communities resulting from *L. cuneata* invasion presumably have a strong effect on the arthropod community. There is also strong experimental evidence that *L. cuneata* is not a preferred food source for native herbivorous insects, often having rates of herbivory many times lower compared to related species (Brandon et al. 2004; Han et al. 2008). While we could find no studies directly comparing arthropod numbers in areas with this invasive species, pure stands of *L. cuneata* have been shown to support low densities of arthropods (a maximum of 12 arthropods/m^2, Menhinick 1967), dramatically lower than typically found at the field site in this study (between 40 and 200 arthropods/m^2 depending on season and year of samples, Moran 2014; Nickell et al. 2018; Varriano et al. 2020). Considering that arthropods are important food sources for a variety of animals higher on the food chain (e.g., birds, Vickery et al. 2001), changes in this community could have profound implications for conservation of tallgrass habitats.

In 2017, we performed both observational and manipulative field studies investigating the effect of *L. cuneata* on the foliar arthropod community structure. Following the results of that field study, in 2018 and 2019, we developed and tested three hypotheses that would explain our 2017 results. These hypotheses included a bottom-up effect (changes in nitrogen levels), and two top down effects: insectivorous bird predation and interactions from larger carnivores within the arthropod community (ground predators). Therefore, our study attempted to address the effects of a major invasive plant on the ecologically important arthropod community and investigate possible mechanisms for our observational and experimental results.

Materials and methods

Field site

Our study was performed at the Tallgrass Prairie Preserve (TPP) located in Osage County, Oklahoma, USA (36.8461 N, 96.4229 W). The TPP is a 16,000-ha Nature Conservancy-owned protected area in the southern section of the Flint Hills ecoregion. Tallgrass prairies in this region are dominated by four species of grasses: big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and Indiangrass (*Sorghastrum nutans*) together with more than 300 species of forbs and a few woody species (Knapp et al. 1999, see Palmer 2007 for TPP checklist). The Preserve is managed using prescribed burning and grazing to simulate the pre-settlement disturbance regime. About 2/3 of the preserve is grazed all year by bison and almost 1/3 is grazed seasonally (growing season only) by cattle, while a small area is left ungrazed. The TPP is divided into numerous management units that are periodically subjected to prescribed fire, typically in a 2–7 year interval (Allen et al. 2009). All experiments described below were performed within bison-grazed units of the TPP.

Observational and experimental *L. cuneata* effects

In 2017, we sampled arthropods in areas with varying levels of *L. cuneata* infestation. Plots were 1 m × 1 m (N = 16 for each sample period) and arbitrarily selected amongst areas with the invasive plant and areas without it. The goal was to sample plots with *L. cuneata* cover rates from zero to as high as found in the area (typically maximized at about 90% cover). We did not perform a spatial analysis of *L. cuneata* dispersion, but qualitatively, *L. cuneata* distribution was "patchy" with some large areas (up to about 100 m^2) with dense coverage and smaller patches of plants scattered elsewhere. All plots were within a single "burn unit" that had last received a fire treatment about 14 months previous and all samples were taken within a two hectare area. To sample foliar arthropods, we sampled each entire 1 m^2 area plot by Dvac. Dvac sampling time was about 1 min for each plot. We assumed that Dvac sampling efficiency was unaffected by *L. cuneata* abundance. Arthropod samples were stored on ice in the field, later frozen, then returned to laboratory for sorting and analysis. In each sample, arthropods were first sorted to taxonomic order, then assigned a trophic position (herbivore, carnivore, or detritivore) based on each arthropod's predominant feeding strategy, and then counted in similar methods to previous experiments at this site (Moran 2014; Nickell et al. 2018). Our general method for assigning feeding strategy was to classify each arthropod to a small enough taxonomic level to determine its position in the food web. This process varies by arthropod order since some orders have predominantly similar feeding modes (e.g., all Araneae are predators), whereas others have greater variation (e.g., different Diptera species are herbivores, carnivores, or detritivores). One exception in our classification scheme was the ants (Formicidae), which because of the diversity of feeding strategies among species and difficulty for non-specialists to identify, were not assigned a feeding category. They were excluded from the analysis of feeding groups but were included in total arthropod numbers. We also photographed each plot and calculated percent cover of *L. cuneata*. Percent cover was estimated using hand drawn polygons on each sample image area (ImageJ software) that was delineated by a PVC quadrat sampler placed in the field. In order to study seasonal variation in the arthropod community, this sampling protocol (both plant cover and arthropods) was performed four times during the growing season: 11 May, 23 June, 7 August, and 30 September 2017.

During the same year, we also performed a manipulative experiment where we tested the effect of removing *L. cuneata* on both plants and arthropods. We established three experimental treatments: (1) plots with *L. cuneata* removed, (2) plots with *L. cuneata* left undisturbed, and (3) plots that naturally had *L. cuneata* absent. Plot from treatments 1 and 2 were in an area that had naturally moderate levels of *L. cuneata* invasion (about 30–50% cover at start of experiment). These plots were directly adjacent to each other in a 2 × 8 array and systematically interspersed. Plots in treatment 3 were in surrounding areas (within 20 m) that naturally did not have *L. cuneata* present. Since we could not control where *L. cuneata* was naturally absent, plots in treatment 3 were not randomly selected, limiting the spatial distribution of these plots. We initially had eight plots per treatment, but two absent plots (those naturally without *L. cuneata*) were invaded by *L. cuneata* and two of the unmanipulated plots (treatment 2) had *L. cuneata* disappear during the experiment. We therefore excluded these four plots from all analyses after the initial sampling. Plots were 2 m × 2 m square and open to the environment. In the *L. cuneata* removed plots, all *L. cuneata* were hand-pulled once every two weeks. We sham-manipulated the other treatment plots by physically disturbing them without removing any plants. Samples of foliar arthropods were taken four times during the course of the experiment: 12 May (pre-manipulation), 24 June, 8 August, and 31 September 2017, which is the same time (within one day) of the observational experiment. For each arthropod sample, a randomly selected point was selected and transect across the plot was sampled by Dvac. Sampling time by Dvac was about 30 s. All captured arthropods were frozen, sorted to order and trophic position (as described in the observational experiment), and then counted. At the end of the experiment, we also sampled the plant community by removing all above-ground vegetation from the center 1 m^2 of each plot. Plants were sorted to species, dried for 24 h at 50 °C, and weighed. Plants were only sampled once at the end of the experiment in order to minimize disturbance of the experimental plots.

Testing three hypotheses for observational and experimental *L. cuneata* results

After we tested the effect of *L. cuneata* presence on plant and arthropod community structure, we tested three hypotheses that could provide mechanisms for our results. These studies were designed to elucidate, in a preliminary way, possible processes that would explain the results in the observational and experimental studies. In each case, we were attempting to find an explanation for why plants were greatly reduced by *L. cuneata* presence, while the foliar arthropod response was attenuated and seasonally variable (see results).

Nitrogen and plant quality

Our first hypothesis was that *L. cuneata*, being a nitrogen fixer, enhances the nitrogen content of coexisting plants and causes a bottom-up process whereby nitrogen-limited arthropods respond to higher plant quality with increased abundance (Haddad et al. 2000, Throop and Lerdau 2004). On 17–18 July 2019, we sampled plant nitrogen content in three common plant species: *Asclepias sullivantii*, *Ambrosia artemisiifolia*, and *Andropogon gerardii*. We sampled plants from areas with at least 40% cover of *L. cuneata* and nearby areas that lacked the invasive plant. All samples of plants in “no *Lespedeza* areas” were at least 10 m from any *L. cuneata* plant. Samples were taken from a two-hectare area within a single management unit that had last been burned 15 months earlier. We used a plant press to extract at least 1/2 ml of plant sap from leaf and stem samples with a total of 20 samples (10 associated with *L. cuneata* and 10 distant from *L. cuneata*) for each species. Sap samples were analyzed for nitrate (ppm) using a Horiba Laquatwin® Model NO3-11 Compact Nitrate Ion Meter.

Bird community responses to L. cuneata

Our second hypothesis was that the insectivorous grassland bird habitat-use might decline in areas infested with large amounts of *L. cuneata*, which would reduce predation on arthropods in these areas leading to higher than expected arthropod abundance (a top-down process). Support for this hypothesis would be found if grassland insectivorous bird abundance was lower in areas with large amounts of *L. cuneata*. We therefore established 23 sites within the bison-grazing units of the TPP and performed point counts of all bird species present four times during the 2018 growing season: 21 May, 19 June, 7 July, and 1 September. All point counts were taken between 0600 and 1000 h, during clear conditions, and included all birds within a 100 m radius. In the center of each point count location, we established a 25 m transect and counted the number of *L. cuneata* stems that intersected the line. *Lespedeza cuneata* counts ranged from zero to > 450 per transect.

Ground predator abundance

Our third hypothesis was that ground arthropods were less abundant in areas of *L. cuneata* and would therefore exert less carnivory pressure on foliar arthropods (a top-down response). Most ground predators are cursorial spiders and predatory beetles (e.g., Carabidae). These species, because of their common location near the ground, are not captured by Dvac sampling at rates comparable to their abundance (personal observation). Although commonly called ground predators, they also ascend vegetation to prey upon foliar prey and have behavioral and population level effects on prey arthropods (Baldridge and Moran 2001; Schmitz and Suttle 2001; Boyer et al. 2003). To sample these arthropods, we established 40 pitfall traps: 20 in areas of dense *L. cuneata* (excess of 50% cover) and 20 in areas lacking the invasive species. Traps placed in *L. cuneata* absent areas were at least 10 m from any individual invasive plants. All samples were taken from a five hectare area. Traps were filled 1/3 of the way full with propylene glycol and left in place for 24 h. Captured arthropods were sorted and classified to a small enough taxon to determine their feeding strategy, and all carnivorous species were enumerated (see under *Observational and Experimental L. cuneata effects* for details on arthropod sorting). This experiment was performed three times during the growing season: 5 May, 8 July, and 2 September 2018.

Statistical analysis

The natural *L. cuneata* experiment which compared invasive plant percent cover to the arthropod community was analyzed by simple linear regression. We analyzed each date separately for each feeding group (herbivores, carnivores, and detritivores, plus total number of arthropods). We also analyzed each feeding group in a mixed model ANOVA with date as a random factor.

For the manipulative experiment where we manually changed *L. cuneata* abundance, the plant data, which was only measured once at the end of the experiment, was analyzed by MANOVA (forbs, grasses, and total as the three response variables), followed by ANOVA for individual contrasts. For the arthropods in the manipulative experiment, we first analyzed the feeding groups (described above) in the initial pre-manipulative sample (May) by one-way ANOVA to determine if there were pre-existing differences between treatment groups. The arthropod abundance for feeding groups in the manipulative experiment were then analyzed by repeated-measures MANOVA (each sample date is treated as a dependent variable), where a treatment × time interaction indicated a difference in the slopes of the trend lines while a between-subjects effect indicated relatively parallel trend lines, but consistent differences between treatments (Scheiner and Gurevitch 2001). This analysis follows our hypothesis that at the start of the experiment, the control plots would be different from the two plots with *L. cuneata* initially present. Over the course of the experiment, we predicted conditions in the removal treatment would diverge from the *L. cuneata* present plots so that by the end, the *L. cuneata* removal and absent plots would be similar, but statistically different from the plots where *L. cuneata* remained. To understand the conditions of the manipulative experiment at each time point, a Tukey post hoc analysis was performed on all sample dates. In all cases, plant biomass and arthropod abundance data were checked for homogeneity of variances before analysis and $\log_{10}$–transformed if significant differences were found.

Using the abundance of arthropods in each taxonomic order (and Formicidae for ants), we further analyzed the community data in the manipulative experiment by (nMDS) analysis (Bray–Curtis dissimilarity method). To test the null hypothesis that the community structure was the same between treatment groups at each date, we performed a permutational multivariate analysis (PERMANOVA). We included the four response variables on the nMDS figures that caused the greatest differences in community structure.

Data on plant nitrogen content were analyzed by two-way ANOVA, with plant species and *L. cuneata* presence as the two treatment variables, followed by pairwise comparisons of each species if invasive plant species presence was significant. Data on bird abundance versus *L. cuneata* abundance were analyzed by simple linear regression with % cover and total insectivorous bird abundance as the two continuous variables. For the ground arthropod predator samples, each date was analyzed by one-way ANOVA. While these data are presented as repeated samples, we were not able to use exactly the same sampling locations for pitfall traps (because of changing *L. cuneata* abundance), so repeated-measures analysis was not appropriate.

Results

Observationally, there was little evidence for a relationship between *L. cuneata* percent cover and abundance of arthropods from any major feeding group (or total arthropod abundance) during any time of the season (linear regression, Table 1, Supplemental Fig. S1). The only significant negative relationship was between detritivore abundance and plant density during the August sample. Our mixed model result was similar, with the random factor date significant for each feeding group plus total arthropod numbers, while percent cover was marginally significant in detritivores and non-significant for the other groups (Table 1). We wish to note however that, due to the high variability in arthropod numbers, power was low for most relationships (0.05–0.99, but only two were greater than 0.50). Therefore, this null result must be interpreted with caution.

In the manipulative experiment (May–September, 2018), for plots where *L. cuneata* was left unmanipulated, the mean amount of invasive plant at the end of the experiment was 70.13 g/m^2 (± 46.15 1SD) and mean proportion of total biomass per plot was 0.71 (± 0.28 1SD). In removal plots, *L. cuneata* biomass averaged 7.70 g/m^2 (± 5.99 1SD) per plot and had a mean proportion of total biomass of 0.22 (± 0.15 1SD) indicating that we were effective in reducing the non-native species (9 × higher in unmanipulated plots). Live plant biomass at the end of the experiment was significantly different between treatment groups (MANOVA, $F_{3,15} = 106.90$, $P < 0.001$, Fig. 1). Individual analyses of native forbs, native grasses, and total biomass were each significantly different (one-way ANOVA, Fig. 1). The plots where *L. cuneata* were manually removed tended to have native plant biomass amounts intermediate between the high native plant biomass in *L. cuneata* absent plots compared to low native plant biomass in *L. cuneata* present plots. These trends were similar for both native forbs and native grasses and supported by the Tukey test results, indicating that the removal treatment was converging upon the absent plots that naturally lacked *L. cuneata*. Plant species richness was not significantly different between any treatments (one-way ANOVA, $F_{1,17} = 1.47$, $P = 0.258$).

The major arthropod groups found in our experiment were Acari, Collembola, Hemiptera, Hymenoptera, and Thysanoptera, which together composed over 80% of all collected individuals. In the initial sample period (May), there was a significant treatment effect on arthropods (MANOVA, $F_{8,36} = 3.86$, $P = 0.002$, Fig. 2). For the individual groups (ANOVA), herbivores ($F_{2,21} = 15.32$, $P < 0.001$) and detritivores ($F_{2,21} = 9.99$, $P = 0.001$), as well as total number of arthropods ($F_{2,21} = 4.90$, $P = 0.018$) were significantly different with the control plots (*L. cuneata* naturally absent) having lower abundances compared to the other two treatment groups. Carnivorous arthropods were marginally significant ($F_{2,21} = 3.48$, $P = 0.05$) and showed the same trend.

There was a significant treatment × time interaction for herbivorous arthropods ($\log_{10}$-transformed data, repeated measures MANOVA, $F_{6,30} = 5.42$, $P = 0.001$, Fig. 2a). During the initial pre-manipulation May sample, herbivorous arthropod abundance in control plots was only about one-third of the abundance found in both plots with *L. cuneata*, while in June, abundance was about 25% higher in control plots (*L. cuneata* absent plots). Between-subjects results were non-significant ($F_{2,\ 17} = 0.77$, $P = 0.48$). By the last sample, herbivorous arthropod abundance

Table 1 Relationship between *L. cuneata* percent cover and three different feeding groups of arthropods and total arthropod numbers during four samples in the natural experiment

Individual analyses (simple linear regression)

Date	Trophic level	Coefficient	Coefficient standard error	F	*P*	R^2	Power
May	Herbivore	− 14.26	18.80	0.575	0.46	0.039	0.12
May	Carnivore	1.35	8.66	0.024	0.88	0.002	0.05
May	Detritivore	3.05	6.92	0.195	0.67	0.014	0.07
May	Total	− 8.74	29.61	0.091	0.77	0.006	0.06
June	Herbivore	12.05	44.71	0.073	0.79	0.005	0.06
June	Carnivore	− 5.56	10.51	0.279	0.61	0.020	0.08
June	Detritivore	− 14.12	26.89	0.276	0.61	0.019	0.08
June	Total	− 15.31	60.83	0.067	0.81	0.005	0.06
August	Herbivore	25.25	19.92	1.607	0.23	0.110	0.24
August	Carnivore	− 1.17	5.69	0.043	0.84	0.003	0.05
August	Detritivore	− 32.16	13.86	5.383	0.04*	0.293	0.66
August	Total	− 8.09	31.42	0.067	0.80	0.005	0.06
September	Herbivore	29.25	37.15	0.620	0.45	0.046	0.12
September	Carnivore	4.74	11.15	0.181	0.68	0.014	0.07
September	Detritivore	− 33.63	38.50	0.763	0.40	0.055	0.14
September	Total	− 1.23	72.04	0.000	0.99	0.000	0.05

Mixed model analyses

Variable	F	*P*	Power
Herbivores			
% cover	0.62	0.43	0.12
Date	6.89	< 0.001*	0.97
Carnivores			
% cover	0.92	0.92	0.05
Date	6.82	0.001*	0.97
Detritivores			
% cover	2.74	0.05	0.37
Date	6.75	0.001*	0.97
Total			
% cover	0.14	0.71	0.99
Date	11.17	< 0.001*	0.99

*Indicates significance $P < 0.05$

numbers were similar between all plots (Tukey test). Carnivore abundance did not show a significant treatment × time interaction ($\log_{10}$-transformed data, repeated measures MANOVA $F_{6,30} = 2.09$, $P = 0.085$), nor were the between-subjects results significant ($F_{2,17} = 2.42$, $P = 0.12$, Fig. 2b). Detritivore abundance showed a marginally significant treatment × time interaction ($\log_{10}$—transformed data, repeated measures MANOVA, $F_{6,30} = 2.41$, $P = 0.051$, Fig. 2c), and the between subjects results were nonsignificant ($F_{2,17} = 1.13$, $P = 0.35$). Tukey-test results showed differences in the June and August samples. For total arthropod abundance, there was a significant treatment × time interaction ($\log_{10}$-transformed data, repeated measures MANOVA, $F_{6,30} = 3.22$, $P = 0.015$) while between subjects

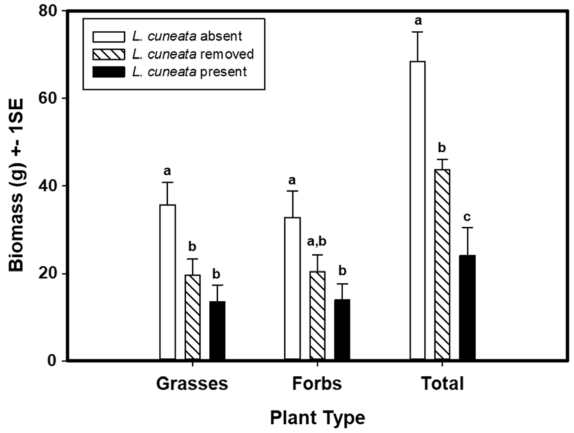

Fig. 1 Effect of *L. cuneata* removal experiment on biomass of native plant species at the end of the experiment. Letters indicate significant difference between treatment groups (Tukey post hoc analysis)

effects were non-significant ($F_{2,17} = 0.05$, $P = 0.096$). Tukey test results found differences only in the May and June samples with the trend being opposite in those two samples; *L. cuneata* absent plots had lower total abundance in May but higher total abundance in June.

The ordination analysis found significant differences in community structure (PERMANOVA) for the May ($F = 5.38$, $P < 0.001$, Stress = 0.13), June ($F = 3.50$, $P = 0.002$, Stress = 0.17), and August ($F = 2.70$, $P = 0.001$, Stress = 0.21) samples, while the September sample showed no significant differences ($F = 1.40$, $P = 0.21$, Stress = 0.14, Fig. 3). Bray–Curtis dissimilarity index values were moderately large between treatments, except during the September sample (Table 2). In all three significant samples, the absent plots (i.e., those naturally without *L. cuneata*) were statistically different from both the

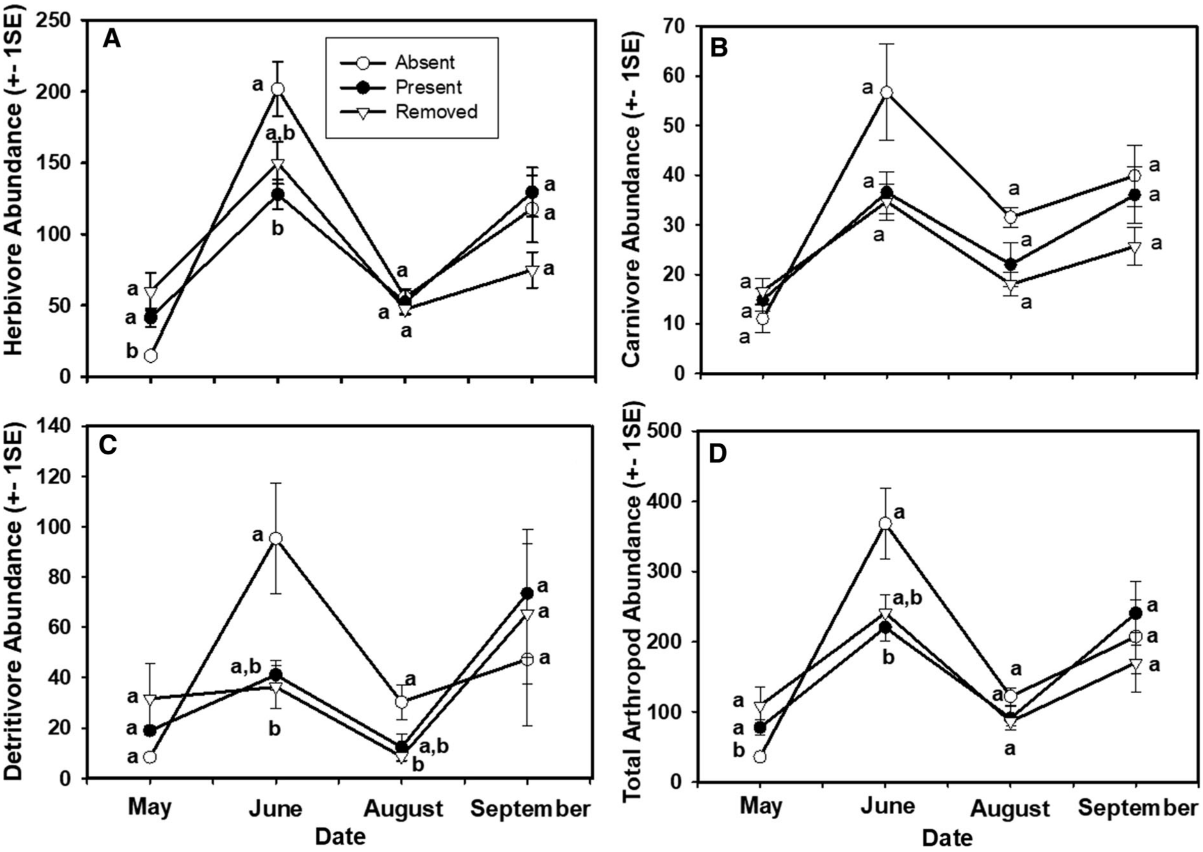

Fig. 2 Effect on *L. cuneata* presence or removal on arthropod feeding groups during one growing season in the *L. cuneata* manipulation experiment for **a** herbivorous arthropods, **b** carnivorous arthropods, **c** detritivorous arthropods, and **d** total number of arthropods. Letters indicate significant difference between treatment groups (Tukey post hoc analysis)

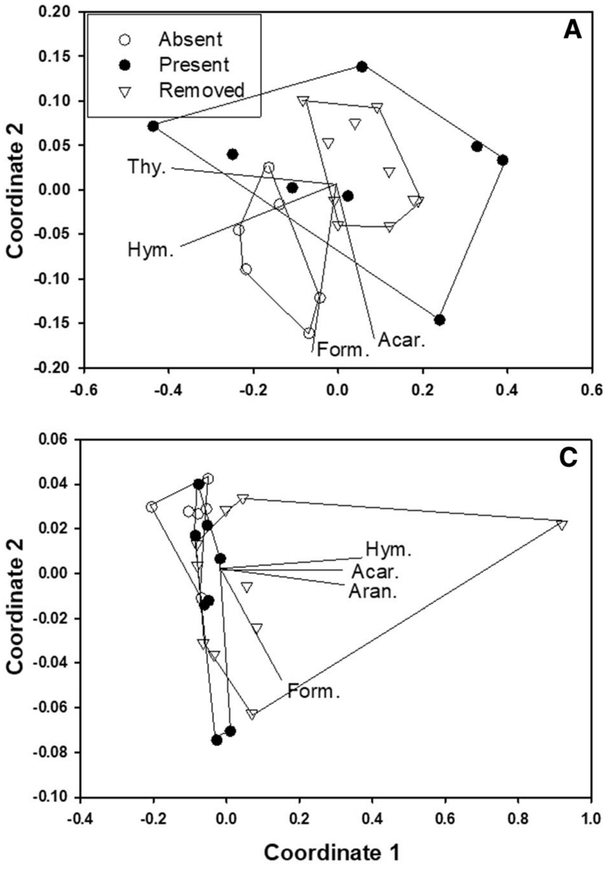

Fig. 3 Results of ordination analysis of arthropod community structure during four times sampled in the *L. cuneata* manipulation experiment. Absent = *L. cuneata* naturally absent, Removed = *L. cuneata* removed, Present = *L. cuneata* unmanipulated. Acar. = Acari, Form. = Formicidae, Coll. = Collembola, Hym. = Hymenoptera (Formicidae excluded), Col. = Coleoptera, Aran. = Araneae, Dip. = Diptera, Hemi. = Hemiptera, Orth. = Orthoptera. **a** May, **b** June, **c** August, **d** September

Table 2 Bray–Curtis dissimilarity index between three treatment groups in the *L. cuneata* manipulative experiment

Sample date	C–R dissimilarity	C–P dissimilarity	R–P dissimilarity
5/17	58.59	52.84	41.92
6/17	34.53	33.29	27.93
8/17	41.60	50.17	44.63
9/17	28.99	24.49	27.53

experimentally removed (Removed) and natural present (Present) plots. Graphical representation of these relationships showed that, while statistically different, there remained some overlap in community structure during all samples (Fig. 3).

Nitrogen content in plant tissues was significantly higher in areas with *L. cuneata* (two-way ANOVA, $F_{1,53} = 19.20$, $P < 0.001$) and significantly different between species ($F_{2,53} = 92.54$, $P < 0.001$), while the interaction term was non-significant ($F_{2,53} = 0.72$, $P = 0.490$). In all three species, the trend was for higher N content in areas with *L. cuneata* presence, while among the pairwise comparisons, only *Ambrosia artemisiifolia* and *Andropogon gerardii* showed a significant response to the invasive species.

Five species of birds—dickcissel (*Spiza americana*), red-winged blackbird (*Agelaius phoeniceus*), grasshopper sparrow (*Ammodramus savannarum*), northern bobwhite (*Colinus virginianus*), and American cliff swallow (*Petrochelidon pyrrhonota*)—made up 94% of all birds recorded. Each of these species is either an arthropod specialist or consumes large quantities of arthropods (Rodewald 2015), especially during breeding season. There was no relationship between *L. cuneata* density and grassland bird abundance during any time of the season (Table 3). The same trend was present when the total number of birds recorded for the entire season were summed and compared to mean density of *L. cuneata* plants.

The ground predators, which mostly consisted of cursorial spiders and ground beetles, were captured in equal numbers during May (one-way ANOVA, $F_{1,38} = 0.02$, $P = 0.89$) and September (one-way ANOVA, $F_{1,38} = 0.90$, $P = 0.81$). In July, ground predators were more than twice as abundant in *L. cuneata* plots compared to *L. cuneata*-absent plots (one-way ANOVA, $F_{1,38} = 10.60$, $P = 0.002$, Fig. 4).

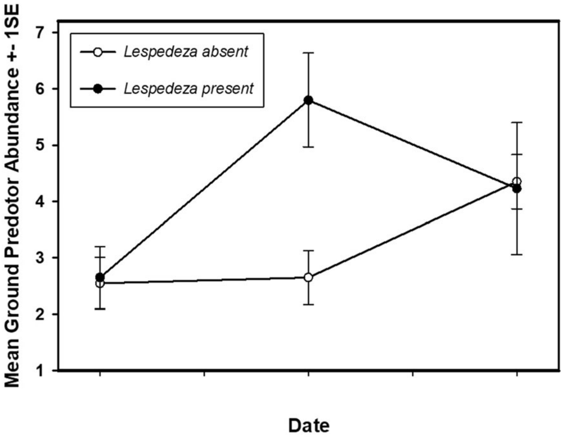

Fig. 4 Number of carnivorous arthropod ground predators captured in pitfall traps in *L. cuneata* areas versus areas without the invasive plant

Discussion

The native plant community responded rapidly to the removal of the invasive plant *Lespedeza cuneata*. By the end of the experiment, the biomass of native grasses and forbs appeared to be approaching values seen in plots where *L. cuneata* was absent. Since we did not see an effect on plant species richness, we assumed existing species were simply increasing in biomass. However, we suspect that an additional growing season would have been necessary for a return to pre-invasion conditions. Although the effect on the plant community was pronounced, there was a surprisingly weak effect of *L. cuneata* on the arthropod community. The response of arthropods was also seasonally variable, with abundance of herbivores, carnivores, and detritivores, as well as total arthropod numbers, generally higher in *L. cuneata* plots in the spring, lower during the summer, and nearly identical to other treatments near the end of the growing season. According to the nMDS analysis, community structure was also seasonally variable with significant differences and identity of taxonomic groups differing according to which month the samples were obtained (Fig. 5).

These weak effects were also seen in our observational study, in which *L. cuneata* density was generally not correlated with arthropod abundance, even though we were able to measure a range of *L. cuneata* from zero to over 90% cover. Considering that native plant biomass was considerably lower in plots with

Table 3 Relationship between *L. cuneata* abundance and grassland bird abundance during four sampling dates and for all four dates combined

Sample	Coefficient	Coefficient standard error	F	*P*	R^2
May	0.003	0.005	0.49	0.62	0.01
June	0.003	0.004	0.45	0.51	0.02
August	− 0.003	0.005	0.48	0.50	0.02
September	0.007	0.006	1.36	0.26	0.06
Combined	0.001	0.003	0.22	0.64	0.01

Simple linear regression

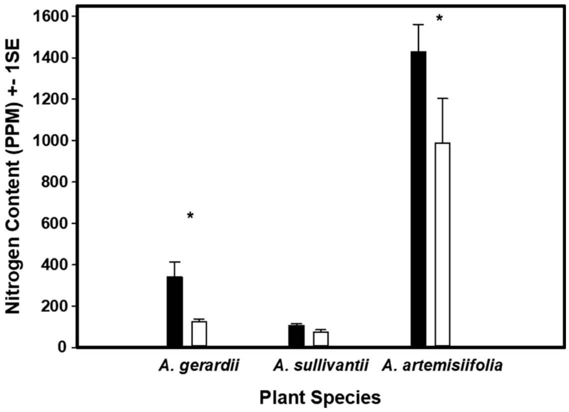

Fig. 5 Comparison of nitrogen content (NO^{-3} PPM) in three different species of plants growing in the presence and absence of *L. cuneata*. Closed bars = *L. cuneata* present, open bars = *L. cuneata* absent

L. cuneata, and that *L. cuneata* is not a preferred food source for most native arthropods (Menhinick 1967; Brandon et al. 2004; Han et al. 2008), we speculated that *L. cuneata* may be causing changes in the system that ameliorates the strongly negative effects on the plant community.

We tested three hypotheses that might explain the muted effect of *L. cuneata* on the arthropod community. Our first hypothesis was a bottom-up effect of a modified nitrogen cycle from the presence of the invasive plant. Nitrogen content of native plants was significantly higher in *L. cuneata* plots compared to plots in which the invasive was absent. We argue the nitrogen enhancement of surviving native plants represents higher plant quality. Many herbivorous arthropods are nitrogen limited (Mattson 1980; Ritchie 2000), so although *L. cuneata* displaces a large proportion of native plant biomass, that biomass which remains is a better food source. As has been shown in many studies, plant quality can be a much stronger influence on food web characteristics compared to plant quantity (Hunter 2016). Therefore, the nitrogen fixing ability of *L. cuneata* could be compensatory, increasing plant quality, and subsequently limiting cascading effects through the food web. One potential long-term negative feedback could be increases in native plant quality could enhance arthropod herbivory levels on these species, further increasing the competitive advantage of *L. cuneata*, which generally lacks arthropod herbivores in this system.

One might also argue that *L. cuneata* was simply colonizing areas with pre-existing higher soil N levels, a potentially confounding effect in our experimental design. However, it has been shown that this invasive species more readily invades areas of low nitrogen (Houseman et al. 2014) and is partly inhibited in high nitrogen areas. Therefore, we believe the nitrogen response we detected is a real effect of *L. cuneata* invasion and not an experimental artifact.

If habitat use by insectivorous birds in *L. cuneata* infested plots was reduced, lower predation rates on arthropods would be predicted. However, bird abundance was not significantly correlated with *L. cuneata* abundance. Therefore, variation in bird predation is unlikely to explain our results. Ground arthropod predator abundance may partially explain some of our foliar arthropod results, however. These predators were more abundant in *L. cuneata* areas in the summer, corresponding to a time when foliar arthropod abundance was generally lower in *L. cuneata* plots compared to control plots. However, it should be noted that we predicted lower foliar arthropod numbers regardless of ground predator abundance, so it is unclear if these responses are related. Additionally, ground predator abundance would not explain the early season foliar arthropod patterns, where foliar arthropod numbers were generally higher in *L. cuneata* plots and ground predator numbers were unchanged. In terms of a mechanism for our ground predator results, we suggest that *L. cuneata* areas are preferentially utilized by ground predators in summer for thermoregulation. *Lespedeza cuneata* grows tall and branching by mid-summer, shading the ground (Allred et al. 2010), a stark contrast to the surrounding prairie which tends to have areas of sunlight penetrating to the surface, especially in grazed areas. Since this region is characterized by high temperatures in the mid-summer (over 35 °C many days), it would be logical to assume that large ectothermic ground predators may choose the shaded areas that *L. cuneata* provides during these times.

Our manipulative study was conducted for one growing season and the plant community only partially recovered in our *L. cuneata* removal plots, so more time might be necessary for the arthropods to respond fully. However, our natural experiment, where *L. cuneata* had been presumably established for multiple years, also found little effect on arthropods These results, combined with our small and seasonally variable effects in the manipulative experiment, indicate a relatively weak response (although seasonally variable) of the arthropod community to this invasive plant. Furthermore, dissimilarity measures in our ordination analyses between treatments plots before *L. cuneata* removal were similar to those after removal, which also supports a notion of a relatively small effect. It should be noted though that particular groups of arthropods, notably Formicidae, Acari, and Hymenoptera (minus ants) were found to be strong contributors to differences in community during multiple sample dates. In our removal experiment, plots were in close proximity to each other, so we assumed that arthropods could move freely and occupy sites where *L. cuneata* was removed.

Our study shows that the effect of this invasive plant appears to attenuate through the food web, severely affecting plant community structure (Brandon et al. 2004; Ohlenbush et al. 2001), but having limited effects on arthropods and apparently causing no effects on at least one higher level of the food web (e.g., birds). Numerous studies have investigated the effect of invasive plants on native plant communities, but far fewer investigate cascading food web effects (for review, see Schirmel et al. 2016). At least in this case, it does not appear the plant effects are commensurate with the consumer effects, a pattern seen in reviews of plant invasions (Vilà et al. 2011; Pyšek et al. 2012), including analyses that have shown weak effects in grassland systems (McCary et al. 2016, although individual studies have shown strong bottom-up effects of invasive species, Simao et al. 2010). Reviews of invasive plant effects on birds have also found weak effects on this important consumer group (Nelson et al. 2017). We suggest that the changes in soil chemistry and subsequent changes in plant quality shown here with *L. cuneata* presence (Yannarell et al. 2011; Coykendall and Houseman 2014) act as a moderating effect on ecosystem function. This change in function is therefore making this consumer community at least partially resistant to invasion of this species. While there may still be changes to overall community structure, as seen in our ordination analyses, there do not appear to be drastic changes in overall arthropod abundance.

In light of our findings, we suggest that tallgrass prairie management practices can be refocused on moderate control of *L. cuneata*, rather than eradication. Moderate control over the spread of this invasive legume can save human and monetary resources, while still having positive effects on native plant species. Even in our plots where we attempted to remove the invasive species, it still was present in small amounts. Yet, native plant species had already begun to recover toward biomass levels seen in areas where *L. cuneata* was absent. The intensive method of eliminating *L. cuneata*, typically involving repeated herbicide treatments, can harm surrounding native species and does not lead to long-term eradication. While some invasive plants need intense vigilance in management, *L. cuneata* control that limits effects on this ecosystem may be achieved with more modest efforts. For instance, other studies have shown that using fire and grazing regimes that are historically found in the Flint Hills is more effective than chemical techniques (Fuhlendorf and Engle 2004; Cummings et al. 2007). A patch-burn fire regime in conjunction with native (bison) or exotic (cattle) grazers appears to be effective in limiting the abundance of *L. cuneata* (Cummings et al. 2007). We therefore argue that reestablishing the historical ecological interactions (i.e., fire and grazing regimes) of this endangered ecosystem may be the most effective way to mitigate the negative effects of this invasive species.

Acknowledgements Thanks to the staff of the Tallgrass Prairie Preserve (The Nature Conservancy) for their logistically help and support for this project. A. Monroe assisted in field collections. This work was supported by the Hendrix College Odyssey Program.

References

Allen MS, Hamilton RG, Melcher UK, Palmer MW (2009) Lessons from the prairie: research at The Nature Conservancy's tallgrass prairie preserve. Oklahoma Academy of Science, Stillwater

Allred BW, Fuhlendorf SD, Monaco TA, Will RE (2010) Morphological and physiological traits in the success of the invasive plant *Lespedeza cuneata*. Biol Invasions 12:739–749. https://doi.org/10.1007/s10530-009-9476-6

Allred BW, Smith WK, Twidwell D, Haggerty JH, Running SW, Naugle DE, Fuhlendorf SD (2015) Ecosystem services lost to oil and gas in North America. Science 348:401–402. https://doi.org/10.1126/science.aaa4785

Ashton IW, Symstad AJ, Davis CJ, Swanson DJ (2016) Preserving prairies: understanding temporal and spatial patterns of invasive annual bromes in the Northern Great Plains. Ecosphere 7:e01438. https://doi.org/10.1002/ecs2.1438

Baldridge CD, Moran MD (2001) Bahavioral means of coexisting in old fields by heterospecific arthropod predadaors (Araneae: Lycosidae, Salticidae; Insecta:; Coleoptera, Carabidae. P Entomol Soc Wash 103:81–88

Blocksome CE (2006) Sericea lespedeza (*Lespedeza cuneata*): seed dispersal, monitoring, and effect on species richness. Doctoral dissertation, Kansas State University

Boyer AG, Swearingen RE, Blaha MA, Fortson CT, Gremillion SK, Osborn KA, Moran MD (2003) Seasonal variation in top-down and bottom-up processes in a grassland arthropod community. Oecologia 136:309–316. https://doi.org/10.1007/s00442-003-1272-x

Bradley BA, Curtis CA, Fusco EJ, Abatzoglou JT, Balch JK, Dadashi S, Tuanmu MN (2018) Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. Biol Invasions 20:1493–1506. https://doi.org/10.1007/s10530-017-1641-8

Brandon AL, Gibson DJ, Middleton BA (2004) Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. Biol Invasions 6:483–493. https://doi.org/10.1023/B:BINV.0000041561.71407.f5

Christian JM, Wilson SD (1999) Long-term ecosystem impacts of an introduced grass in the northern Great Plains. Ecology 80:2397–2407. https://doi.org/10.1890/0012-9658(1999)080%5b2397:LTEIOA%5d2.0.CO;2

Clarke ID, Frey RW, Hyland HL (1939) Seasonal variation in tannin content of *Lespedeza sericea*. J Agric Res 58:131–139

Comer PJ, Hak JC, Kindscher K, Muldavin E, Singhurst J (2018) Continent-scale landscape conservation design for temperate grasslands of the Great Plains and Chihuahuan Desert. Nat Area J 38:196–212. https://doi.org/10.3375/043.038.0209

Coykendall KE, Houseman GR (2014) *Lespedeza cuneata* invasion alters soils facilitating its own growth. Biol Invasions 16:1735–1742. https://doi.org/10.1007/s10530-013-0623-8

Cummings DC, Fuhlendorf SD, Engle DM (2007) Is altering grazing selectivity of invasive forage species with patch burning more effective than herbicide treatments? Rangeland Ecol Manag 60:253–260. https://doi.org/10.2111/1551-5028(2007)60%5b253:IAGSOI%5d2.0.CO;2

DiTomaso JM (2000) Invasive weeds in rangelands: species, impacts, and management. Weed Sci 48:255–265. https://doi.org/10.1614/0043-1745(2000)048%5b0255:IWIRSI%5d2.0.CO;2

Dudley DM, Fick WH (2003) Effects of sericea lespedeza residues on selected tallgrass prairie grasses. Trans Kans Acad Sci 106:166–171. https://doi.org/10.1660/0022-8443(2003)106%5b0166:EOSLRO%5d2.0.CO;2

Eddy TA, Moore CM (1998) Effects of sericea lespedeza (*Lespedeza cuneata* (Dumont) G. Don) invasion on oak savannas in Kansas. Trans Wis Acad Sci Arts Lett 86:57–62

Fuhlendorf SD, Engle DM (2004) Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. J Appl Ecol 41:604–614. https://doi.org/10.1111/j.0021-8901.2004.00937.x

Gibson DJ, Freeman CC, Hulbert LC (1990) Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. Oecologia 84:169–175. https://doi.org/10.1007/BF00318268

Haddad NM, Haarstad J, Tilman D (2000) The effects of long-term nitrogen loading on grassland insect communities. Oecologia 124:73–84. https://doi.org/10.1007/s004420050026

Han X, Dendy SP, Garrett KA, Fang L, Smith MD (2008) Comparison of damage to native and exotic tallgrass prairie plants by natural enemies. Plant Ecol 198:197–210. https://doi.org/10.1007/s11258-008-9395-0

Hendrickson JR, Sedivec KK, Toledo D, Printz J (2019) Challenges Facing Grasslands in the Northern Great Plains and North Central Region. Rangelands 41:23–29. https://doi.org/10.1016/j.rala.2018.11.002

Homer C, Dewitz J, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold N, Wickham J, Megown K (2015) Completion of the 2011 National Land Cover Database for the conterminous United States–representing a decade of land cover change information. Photogramm Eng Rem S 81:345–354

Houseman GR, Foster BL, Brassil CE (2014) Propagule pressure-invasibility relationships: testing the influence of soil fertility and disturbance with *Lespedeza cuneata*. Oecologia 174:511–520. https://doi.org/10.1007/s00442-013-2781-x

Hunter M (2016) The phytochemical landscape: linking trophic interactions and nutrient dynamics. Princeton University Press, Princeton

Jaenike J (1990) Host specialization in phytophagous insects. Annu Rev Ecol Syst 21:243–273. https://doi.org/10.1146/annurev.es.21.110190.001331

Jordan NR, Larson DL, Huerd SC (2008) Soil modification by invasive plants: effects on native and invasive species of mixed-grass prairies. Biol Invasions 10:177–190. https://doi.org/10.1007/s10530-007-9121-1

Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG (1999) The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. Bioscience 49:39–50. https://doi.org/10.1525/bisi.1999.49.1.39

Knops JM, Tilman D, Haddad DN, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol Lett 2:286–293. https://doi.org/10.1046/j.1461-0248.1999.00083.x

Koger CH, Stritzke JF, Cummings DC (2002) Control of sericea lespedeza with triclopyr, fluroxypyr, and metsulfuron. Weed Technol 16:893–900. https://doi.org/10.1614/0890-037X(2002)016%5b0893:COSLLC%5d2.0.CO;2

Mattson WJ (1980) Herbivory in relation to plant nitrogen content. Annu Rev Ecol Syst 11:119–161. https://doi.org/10.1146/annurev.es.11.110180.001003

McCary MA, Mores R, Farfan MA, Wise DH (2016) Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: a meta-analysis. Ecol Lett 19:328–335. https://doi.org/10.1111/ele.12562

Menhinick EF (1967) Structure, stability, and energy flow in plants and arthropods in a Sericea lespedeza stand. Ecol Monogr 37:255–272. https://doi.org/10.2307/1948440

Moran MD (2014) Bison grazing increases arthropod abundance and diversity in a tallgrass prairie. Environ Entomol 43:1174–1184. https://doi.org/10.1603/EN14013

Moran MD, Taylor NT, Mullins TF, Sardar SS, McClung MR (2017) Land-use and ecosystem services costs of unconventional US oil and gas development. Front Ecol Environ 15:237–242. https://doi.org/10.1002/fee.1492

Nelson SB, Coon JJ, Duchardt CJ, Fischer JD, Halsey SJ, Kranz AJ, Parker CM, Schneider SC, Swartz TM, Miller JR (2017) Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review. Biol Invasions 19:1547–1563. https://doi.org/10.1007/s10530-017-1377-5

Nickell Z, Varriano S, Plemmons E, Moran MD (2018) Ecosystem engineering by bison (Bison bison) wallowing increases arthropod community heterogeneity in space and time. Ecosphere 9:e02436. https://doi.org/10.1002/ecs2.2436

Ohlenbush PD, Bidwell T, Fick WH, Kilgore G, Scott W, Davidson J, Clubine S, Mayo J, Coffin M (2001) Sericea lespedeza: history, characteristics and identification. Publication MF-2408. Kansas State University Agricultural Experiment. Station and Cooperative Extension Service, Manhattan, KS, USA

Palmer MW (2007) The vascular flora of the tallgrass prairie preserve, Osage County, Oklahoma. Castanea 72:235–247. https://doi.org/10.2179/06-29.1

Pimental D, Lach DL, Zuniga R, Morrison D (2002) Environmental and economic costs associated with non-indigenous species in the United States. In: Pimental D (ed) Biological invasions: economic and environmental costs of alien plant, animal, and microbe species. CRC Press, New York, pp 285–303. https://doi.org/10.1641/0006-3568(2000)050%5b0053:EAECON%5d2.3.CO;2

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Glob Change Biol 18:1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

Ritchie ME (2000) Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. Ecology 81:1601–1612. https://doi.org/10.1890/0012-9658(2000)081%5b1601:NLATVA%5d2.0.CO;2

Rodewald P (2015) The birds of North America. Cornell Laboratory of Ornithology, Ithaca

Sampson F, Knopf F (1994) Prairie conservation in North America. Other Publ Wildl Manag 41:418–441. https://doi.org/10.2307/1312365

Samson FB, Knopf FL, Ostlie WR (2004) Great Plains ecosystems: past, present, and future. Wildlife Soc B 32:6–15. https://doi.org/10.2193/0091-7648(2004)32%5b6:GPEPPA%5d2.0.CO;2

Scheiner SM, Gurevitch J (2001) Design and analysis of ecological experiments. Oxford University Press, Oxford

Schirmel J, Bundschuh M, Entling MH, Kowarik I, Buchholz S (2016) Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: a global assessment. Glob Change Biol 22:594–603. https://doi.org/10.1111/gcb.13093

Schmitz OJ, Suttle KB (2001) Effects of top predator species on direct and indirect interactions in a food web. Ecology 82:2072–2081. https://doi.org/10.1890/0012-9658(2001)082%5b2072:EOTPSO%5d2.0.CO;2

Sheley RL, Jacobs JS, Carpinelli MF (1998) Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). Weed Technol 12:353–362. https://doi.org/10.1017/S0890037X00043931

Siemann ED, Tilman J, Haarstad Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. Am Nat 152:738–750. https://doi.org/10.1086/286204

Simao MCM, Flory SL, Rudgers JA (2010) Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels. Oikos 119:1553–1562. https://doi.org/10.1111/j.1600-0706.2010.18382.x

Smith MD, Knapp AK (2001) Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. Int J Plant Sci 162:785–792. https://doi.org/10.1086/320774

Southwood TRE (1961) The number of species of insect associated with various trees. J Anim Ecol 30:1–8. https://doi.org/10.2307/2109

Steinauer EM, Collins SL (1996) Prairie ecology—the tallgrass prairie. In: Samson FB, Knopf FL (eds) Prairie conservation. Island Press, Washington, D.C., pp 39–52

Sunny A, Diwakar S, Sharma GP (2015) Native insects and invasive plants encounters. Arthropod-Plant Inte 9:323–331

Throop HL, Lerdau MT (2004) Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. Ecosystems 7:109–133. https://doi.org/10.1007/s10021-003-0225-x

Toledo D, Sanderson M, Spaeth K, Hendrickson J, Printz J (2014) Extent of Kentucky bluegrass and its effect on native plant species diversity and ecosystem services in the Northern Great Plains of the United States. Invas Plant Sci Mana 7:543–552. https://doi.org/10.1614/IPSM-D-14-00029.1

Trainor AM, McDonald RI, Fargione J (2016) Energy sprawl is the largest driver of land use change in United States. PLoS ONE 11:e0162269. https://doi.org/10.1371/journal.pone.0162269

Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. Trends Ecol Evo 21:208–216. https://doi.org/10.1016/j.tree.2006.01.006

Varriano S, Lefler LH, Patel K, Kirksey C, Turner A, Moran MD (2020) The complementary relationship of bison grazing and arthropod herbivory in structuring a tallgrass prairie community. Rangeland Ecol Manag. https://doi.org/10.1016/j.rama.2020.02.008

Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. JAppl Ecol 38:647–664. https://doi.org/10.1046/j.1365-2664.2001.00626.x

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14:702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Warren SD, Scifres CJ, Teel PD (1987) Response of grassland arthropods to burning: a review. Agr Ecosyst Environ 19:105–130. https://doi.org/10.1016/0167-8809(87)90012-0

Whiles MR, Charlton RE (2006) The ecological significance of tallgrass prairie arthropods. Annu Rev Entomol 51:387–412. https://doi.org/10.1146/annurev.ento.51.110104.151136

Wimberly MC, Narem DM, Bauman PJ, Carlson BT, Ahlering MA (2018) Grassland connectivity in fragmented agricultural landscapes of the north-central United States. Biol Conserv 217:121–130. https://doi.org/10.1016/j.biocon.2017.10.031

Woods TM, Jonas JL, Ferguson CJ (2012) The invasive *Lespedeza cuneata* attracts more insect pollinators than native congeners in tallgrass prairie with variable impacts. Biol Invasions 14:1045–1059. https://doi.org/10.1007/s10530-011-0138-0

Wright CK, Larson B, Lark TJ, Gibbs HK (2017) Recent grassland losses are concentrated around US ethanol refineries. Environ Res Lett 12:044001. https://doi.org/10.1088/1748-9326/aa6446

Yannarell AC, Busby RR, Denight ML, Gebhart DL, Taylor SJ (2011) Soil bacteria and fungi respond on different spatial scales to invasion by the legume *Lespedeza cuneata*. Front Micro 2:127. https://doi.org/10.3389/fmicb.2011.00127