Arthropod-Plant Interactions (2021) 15:657–668
https://doi.org/10.1007/s11829-021-09854-0

ORIGINAL PAPER

Your enemy may be my friend: invasive legume attracts exotic herbivore in a tallgrass prairie

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Received: 17 November 2020 / Accepted: 30 June 2021 / Published online: 12 July 2021
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Abstract

Effects of invasive exotic plants on plant communities are often profound, but interactions with higher trophic levels are less evident. Postulated effects of invasive plants on arthropods include increased abundances of herbivores through refuge and improved microclimate, facilitation of other exotic species, and altered arthropod diversity. We examined the impact on the arthropod community by *Lespedeza cuneata*, an exotic legume with dense, chemically defended foliage, by comparing arthropod numbers in unmanipulated 1-m^2 plots with *L. cuneata* shoots (= control) to arthropod numbers in plots from which shoots of *L. cuneata* were removed. *Lespedeza cuneata* removal produced no overall effect on arthropod abundance, but an invasive herbivore, *Popillia japonica* (Japanese Beetle), was twice as abundant in plots with *L. cuneata*. *Lespedeza cuneata* removal increased arthropod evenness in May then decreased it through the summer. In a second experiment we quantified chewing herbivory by placing individual potted plants from five native prairie species and *L. cuneata* within these same removal/no removal plots for 4 weeks. Removal of *L. cuneata* shoots from plots did not significantly affect herbivory of tagged leaves from the native species. However, entire *L. cuneata* leaves or plants disappeared more frequently regardless of plot treatment. Invasion by this exotic legume is likely due to direct effects on native plants, but indirect effects through facilitation of an exotic herbivore could contribute to its success in some areas.

Keywords *Lespedeza cuneata* · Herbivory · Invasion ecology · Tallgrass prairie

Introduction

Invasion by exotic plants poses a major ecological threat to native ecosystems (Mack et al. 2000; Vilá et al. 2011; Litt et al. 2014) and substantial burden to economies (Pimentel et al. 2005). As they become locally abundant, exotic plants may compete with native plant species for a variety of resources including light (Pattinson et al. 1998), nutrients (Liao et al. 2008), and safe sites for seeds (Lucero and Callaway 2018; Larson et al. 2013), and thereby depress abundances of plants that provide food (Bezemer et al. 2014), alter biotic interactions (Schweiger et al. 2010), and depress native animal diversity (Schirmel et al. 2016). When exotic plants possess novel volatile compounds, they may change the chemical complexity of the habitat, affecting communities both below (Yannarell et al. 2011) and aboveground (Callaway and Ridenour 2004; Bezemer et al. 2014).

Through bottom-up effects invasive exotic plants can significantly affect higher trophic levels (Vilá et al. 2011) but predicting effects on higher trophic levels remains a challenge (Litt et al. 2014; Varriano et al. 2020). Structural and functional diversity of plants are determinants of arthropod diversity (Lawton 1983) and arthropod species diversity is predicted to be greater where plant diversity is high (Siemann et al. 1998). Consequently, plant invasions that reduce plant diversity would be expected to reduce arthropod diversity. A review of arthropod responses found plant invasions depressed abundances and diversity of herbivores and predators in a preponderance of studies (Litt et al. 2014). In addition to dietary limitations, causes of reduced abundances or taxonomic diversity of arthropods include chemical deterrence, associational effects imposed by the exotic plant or increases in enemies (Bezemer et al. 2014; Litt et al. 2014).

While reduction in arthropod diversity is a more common response to plant invasions, increases in arthropod

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Handling Editor: Livy Williams.

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abundances and diversity occur when resources provided by invasive plants increase carrying capacity (Tepedino et al. 2008) or when traits of the invaders provide additional opportunities (Orrock et al. 2015). Herbivores may at least temporarily be released from enemies if exotic plants provide them with cover, a favorable microclimate, or suitable oviposition sites. This can result in apparent competition among plant species when herbivores of the invasive plant more strongly depress the fitness of native plants (Orrock et al. 2008; Dangremond et al. 2010; Bhattarai et al. 2017). As invasion progresses, depressed growth of other plants is predicted to reduce carrying capacities and niches for species in higher trophic levels, resulting in reduced abundances and species diversity with invasion. Spatial and temporal variation in the invasion may make these effects difficult to perceive until the invasion is well underway (Jarić et al. 2019).

Although exotic invasive plants may generally reduce numbers or species richness in higher trophic levels, they can facilitate the spread of other exotic species. Positive interactions among exotics potentially magnify the negative impact of invasion on the community, an effect termed invasional meltdown (Simberloff and Holle 1999; Simberloff 2006). Support for this hypothesis is broad, especially for non-reciprocal effects but evidence that communities or ecosystems are strongly affected remains scant (Braga et al. 2020).

Lespedeza cuneata (Dumont) G. Don. (Fabaceae) is an exotic perennial legume spreading aggressively along roadsides, disturbed areas, and through Eastern and Midwestern US grasslands, including prairies (Eddy and Moore 1998; Ohlenbusch et al. 2007; Foster et al. 2015). Rapidly growing shoots form dense stands that suppress competitors through shade (Brandon et al. 2004) and litter may have allelopathic effects (Dudley and Fick 2003; Kalburtji and Mosjidis 1992, 1993). Although at times used as forage (Harris and Drew 1943), its foliage contains higher concentrations of tannins than characteristic of native congeners (USDA 1950). Invasive genotypes exhibit greater induced resistance than native genotypes or genotypes first introduced to the USA and the invasive genotype also outcompetes these other genotypes (Beaton et al. 2011). Mixed with other plant material, condensed tannins in foliage offer promise as an antihelmintic (Mechineni et al. 2014) but in higher concentrations these bitter polyphenols deter feeding by inhibiting protein digestion in mammalian herbivores and are toxic to insects (Langdale and Giddens 1967; Kalburtji and Mosjidis 1993; War et al. 2012). Less preferred as food (Han et al. 2008), dense, unpalatable *L. cuneata* shoots may provide preferred habitat for consumers of competing plant species.

Several observational studies in the USA have demonstrated negative effects of *L. cuneata* on measures of animal diversity, including lower counts of macroinvertebrate and plant species in plots infested with *L. cuneata* in Kansas (Eddy and Moore 1998), and decreased diversity of a small mammal community with increasing *L. cuneata* in Oklahoma (Howard 2013). These studies suggest that at some point, high densities of the invader reduce heterogeneity in the plant community and in turn, the breadth of opportunities for *L. cuneata*'s enemies (Howard 2013). While manipulative experiments in southern Illinois (Brandon et al. 2004) and Oklahoma (Varriano et al. 2020) also demonstrated that *L. cuneata* reduces plant species diversity, Varriano et al. (2020) found little evidence that *L. cuneata*'s effects extended to higher trophic levels. Thus, the impact of *L. cuneata* on higher trophic levels may be overestimated by observational studies.

To better understand how an invasive plant affects the arthropod community we examined whether *L. cuneata* facilitates increased arthropod richness and abundance and whether abundance of *L. cuneata* affects herbivory of neighbors through two field experiments. In the first summer, we sampled arthropods four times at monthly intervals in *L. cuneata*-infested plots and in plots from which *L. cuneata* had been cut back repeatedly. We calculated arthropod evenness and taxonomic richness at the level of the order to see how current abundance of the invader vs. reduction of the invading plant's shoot density affect the arthropod community. If apparent competition aids the spread of *L. cuneata*, we predicted (a) higher abundance of arthropods in areas where *L. cuneata* is abundant, indicating that it provides more suitable shelter, (b) reduced herbivory on neighboring plants where *L. cuneata* has been removed, indicating a decreased abundance of herbivores, and (c) higher percent herbivory on the plants surrounding *L. cuneata* than on *L. cuneata* itself, indicating that herbivorous arthropods are not eating the invasive legume. During our study it was evident that *Popillia japonica* (Japanese Beetle), an exotic, invasive herbivore was a common species on this site. We evaluated this species' abundance separate from other species to determine whether it was more common where *L. cuneata* was most abundant, as predicted by the Invasional Meltdown hypothesis.

Materials and methods

Study species

Native to Russia, China, and Japan (Magness et al. 1971), *Lespedeza cuneata* was introduced to the USA to combat farmland erosion, cover mine spoils, and provide refuge for wildlife (Eddy and Moore 1998). *Lespedeza cuneata* is now established throughout the Southern and Central regions of the USA (USDA 2021), including remnant ecosystems (Guernsey 1970; Stevens 2002) and typically spreads rapidly in low-nutrient, high-light sites (Brandon et al. 2004; Eddy and Moore 1998; Stevens 2002). This exotic bush clover produces more seeds (Brandon 2000), vegetative buds, and chasmogamous flowers than native congeners (Woods et al. 2009). A long taproot provides resistance to drought (Hoveland and Donnelly 1985; Stevens 2002) and it is tolerant of a variety of soil conditions, including highly acidic soils and areas contaminated with aluminum (Henry et al. 1981; Hoveland and Donnelly 1985). *Lespedeza cuneata* can grow to 45 cm in its first season, reach full growth of 0.6–1.5 m in its second season, and branch 20 to 30 times from crown buds by its third and fourth season (USDA 1950) and thus, rapidly develop dense stands. Tannins present in *L. cuneata* foliage may depress germination and growth of other species and reduce its palatability to insects and mammalian herbivores (Langdale and Giddens 1967; Kalburtji and Mosjidis 1993; War et al. 2012). In Central Illinois, USA, *L. cuneata* is among the last species to flower and set seed, typically in September to October (Walder, unpubl. data).

The Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), is a highly invasive pest throughout the Midwestern, Southern, and Eastern United States, costing $450 million annually in damage to crops and ornamental plants (USDA 2000). This herbivore is subject to predation by small mammals and birds, but biological control has proved elusive (Potter and Held 2002). The Japanese beetle is one of the most polyphagous herbivorous insects, with adults feeding on shoots and larvae feeding on roots of more than 300 species of wild and cultivated plants (Fleming 1972, Ladd 1987, Ladd 1989). Anecdotal observation suggests its diet includes native prairie grasses and legumes (Helzer 2018). In native Japan, it does not reach densities commonly observed in invaded areas (CABI 2021). First found in the USA in the early 1900s it was recorded in Illinois by 1953 (Fleming 1976) and recorded in 59 counties in Illinois, including McLean Co., by 2002 (Cook 2003). The Japanese beetle is now a prominent invasive through the Midwest and its range in the USA (USDA APHIS 2018) overlaps broadly with that of *L. cuneata* (USDA 2021).

Field site and treatments

We conducted this study at the John English Prairie (coordinates: 40.621388, —89.014729, 1.9 ha), a tallgrass prairie reconstruction started in the 1970's within Comlara Park in Hudson, McLean Co., Illinois, USA. The prairie is bordered by a wooded creek, woods, an agricultural field, and a road. The prairie is generally burned annually in the spring, with a complete burn in 2017 and a patchy burn in 2018. *Lespedeza cuneata*'s presence was first recorded in the John English Prairie in 2006 and it has since spread throughout the prairie (Walder et al. 2019).

In May 2017 we established forty, 1-m^2 plots ≥ 2 m apart. All plots included *L. cuneata*. To reduce community heterogeneity plots were situated to also include *Coreopsis tripteris* L., a tall and abundant native dicot that produces large yellow composite inflorescences above all vegetation in August. We recorded maximum *C. tripteris* height and stem number in each plot, and total dry litter mass in a 20.3 cm^2 area from the center of each plot. These measurements were recorded as measures of initial similarity among plots. We paired plots that appeared to be similar in density of vegetation and location. One of each pair was randomly assigned a treatment (either control or removal of *L. cuneata* shoots) and the remaining plot received the alternative. Starting in May 2017 and continuing through September 2017, *L. cuneata* shoots were removed monthly from removal plots by snapping off at the base or using pruning shears to cut aboveground *L. cuneata* to about 2.5 cm. Below-ground *L. cuneata* was not removed to avoid damaging neighboring roots. We recorded cover of each plant species in the plots during July 2017 (Daubenmire 1959). A strip of about 0.5 m width around each plot was inevitably trampled while removing *L. cuneata* and sampling the plots, visibly separating each plot from surrounding vegetation.

Effect of *Lespedeza cuneata* removal on arthropod abundances and diversity

To understand how the presence of *L. cuneata* affects arthropods throughout the summer, and to determine if arthropod abundance is higher in plots with *L. cuneata* shoots (prediction a), we sampled each of the 40 plots with pitfall and pan traps at monthly intervals May through September during suitable weather conditions and time of day for arthropod presence. A pitfall trap, used to collect ground-dwelling arthropods, was centered in each plot at least 24 h before the first collection occurred. During the monthly collection period, the lids were removed before 9 am, and soapy water was placed in each cup, for a sampling time of 24 h. The following morning, samples were collected, and lids were replaced on the clear cups. Pan traps, used to collect flower-visiting arthropods, were white bowls attached to wire and placed in the center of the plots, at vegetation height. These were filled with soapy water each morning of collection and left out for 6 h beginning at 9 am local time (LeBuhn et al. 2003). We also conducted sweep net sampling and focal observations, but these methods returned few observations and were discontinued. Specimens were identified to order, and within order, specimens were grouped into operational taxonomic units based on morphology, using various online and book dichotomous keys and guides (Nentwig et al. 2017; Dodge 1953; Carleton College 2016; Goulet and Huber 1993, Borror et al. 1954).

Effect of *Lespedeza cuneata* removal on herbivory

To test predictions b and c, we quantified chewing damage using phytometers, which were individuals of six plant species grown singly under similar conditions and placed in the same 40, 1-m^2 plots from the previous season. Each plot received the same treatment as the previous year, with the first removal of *L. cuneata* shoots from treatment plots occurring from the end of May through the beginning of June, and a second removal occurring just before starting the herbivory experiment in August. The three common functional types in prairies are graminoids, legumes, and non-legume dicots (henceforth "forbs"). The test species were all species growing on the site, but not necessarily within every plot. These included native grasses *Elymus canadensis* L. (Canada wild rye—a native C_3 grass) and *Schizachyrium scoparium* Michx. Nash (Little bluestem—a native C_4 grass), legumes *L. cuneata* and *L. capitata* Michx. (Round-headed bush clover—a native congener of *L. cuneata*), and native forbs *Coreopsis tripteris* L. (Tall coreopsis) and *Oligoneuron rigidum* L. (Stiff goldenrod).

Elymus canadensis and *S. scoparium* seeds germinated upon sowing in trays with Pro-Mix® All-Purpose Professional Grower's Mix and individuals were transplanted into 1-L pots containing Pro-Mix®. *Lespedeza cuneata* seeds were scarified by grinding with sand for 1 min, sifting to remove larger chaff, and sown into 1-L pots. In advance, seeds of remaining species were stratified in a 1:1 mix of damp perlite:peat moss at 4 °C for 10 (*L. capitata*) or 60 days (*C. tripteris* and *O. rigidum*) and germinated in Pro-Mix® in trays until individuals were transplanted into 1-L pots containing Pro-Mix®. All plants germinated mid- to late-May 2018, were watered as needed, and received no fertilizer. After at least a week in a greenhouse under ambient light, each species was placed outside in a partially walled concrete enclosure to grow until they were transported into the John English Prairie on 2 August 2018.

Before pots were placed in the field, we selected, photographed, and tagged a leaf from each plant for estimating herbivory before and after the trial. We used the center leaflet of the third compound leaf from the top of the plant for *L. capitata* and *L. cuneata*, the least damaged center leaflet of the second compound leaf from the top for *C. tripteris*, the largest undamaged leaf for *O. rigidum*, and the second longest leaf in *E. canadensis* and *S. scoparium* for assessing herbivory. Six pots (one per species) were placed in each plot in two rows of three pots on 2 August 2018. Positions within each plot were randomly assigned. The potted plants were watered daily and retrieved after 4 weeks. The tagged leaves were again photographed, and leaf area lost due to chewing herbivory was determined using Image-J (Rueden et al. 2017) by outlining where the leaf would have grown in the absence of any herbivory. Percent herbivory = 100% − [(final area/total possible area) × 100%]. Because prior damage could affect subsequent herbivory, we re-visited initial photographs of *C. tripteris, O. rigidum,* and *L. capitata* and recorded whether each leaf had any holes, puncture marks, or discoloration before the trial. Because some initial images of the grass leaves were not captured in a way that allowed reliable evaluation of the leaf surface, we did not include *E. canadensis* and *S. scoparium* in this analysis.

Statistical analysis

Effect of *Lespedeza cuneata* removal on arthropod abundances and diversity

To confirm that the removal and control plots were similar prior to treatment, we analyzed dry litter mass, maximum *C. tripteris* height, and *C. tripteris* stem number as response variables in multivariate analysis of variance. We also tested the effects of *L. cuneata* removal on log-transformed sum of the graminoid cover, forb cover (including all legumes other than *L. cuneata*), and *L. cuneata* cover as response variables in MANOVA (PROC GLM, SAS 9.4).

Arthropod abundances from all means of sampling in 2017 varied widely over time and among taxa, with many taxa absent in any given plot and sampling period. To avoid excessive zeros in the abundance data, we selected the arthropod orders that were common throughout the summer. We also included the Japanese beetle (*Popillia japonica* Newman) sums as a response variable separate from the other Coleoptera, because the Japanese beetle is a very common, generalist, invasive beetle (Potter 1998; Vittum et al. 1999). Within taxa we combined the pitfall and pan trap collections from each plot for each of the 5 months (May–September) and analyzed these sums with multivariate analysis of variance in SAS 9.4 (PROC GLM) to understand how the different arthropod taxa abundances responded to the removal treatment. The summed pitfall and pan trap abundances for each of the six orders and for Japanese beetle were the response variables, removal treatment was a fixed effect, and plot pair was the random effect.

To understand if diversity of arthropods was influenced by removal treatment, we conducted a multivariate repeated measures analysis of variance (PROC GLM, SAS 9.4). The number of arthropod orders (richness) was calculated by determining the total number of orders that were sampled in the combined pan-trap and pitfall trap counts within plots each month. Evenness was calculated as Shannon's H/Hmax for each plot, each month. Because they are not independent measures, richness and evenness from each of the 40 plots were the multiple response variables in this analysis and month was the within-subjects repeated factor. Pair and removal treatment were the between-subject factors. We also examined how total abundances changed for ground-dwelling arthropods and those up in the vegetation by conducting a similar multivariate repeated measures ANOVA on the monthly sums of all arthropods in pitfall and in pan traps.

Effect of *Lespedeza cuneata* removal on herbivory

To determine if *L. cuneata* presence increases herbivory (predictions b and c), we took two approaches. First, we analyzed how treatment affected the percentage of leaf missing from native species using repeated measures in SAS 9.4 (PROC GLIMMIX) with the variance matrix blocked by plot and species as the repeated measures. A negative binomial with log link function yielded the smallest AIC score. We conducted Fisher's exact test on the association between presence/absence of prior damage and subsequent damage for the three forbs to determine whether condition of the plants prior to placement in the field could have affected results. Some of the marked leaves or even entire plants disappeared during the 4-week period and so we next examined whether treatment significantly affected total herbivory (= either the whole leaf or entire plant missing) using a generalized linear mixed model on the binary response of eaten or not eaten. Each individual potted plant, including *L. cuneata*, was the response and *L. cuneata* removal treatment and species were fixed effects.

Results

A multivariate analysis of variance of *C. tripteris* height, *C. tripteris* stem number, and dry litter mass confirmed that the plots were similar before the onset of treatment (removal treatment: $F_{3,17} = 0.11$, $p = 0.953$; pair: $F_{57,51} = 1.53$, $p = 0.061$). Because only its shoots were removed, *L. cuneata* was not eliminated from removal plots. MANOVA ($F_{3,36} = 5.82$, $p = 0.0024$) indicated that removal changed percent cover recorded in plots in July and the response to removal was due to reduction in *L. cuneata* cover rather than a shift in other species (Online Resource 1). Summed together, pitfall and pan traps consistently sampled six arthropod taxa: Coleoptera, Diptera, Hemiptera, Hymenoptera, Orthoptera, and Araneae, and included ground dwellers and flyers (Fig. 1). Most of the 19 arthropod orders collected over the course of the season were only occasionally sampled.

Effect of *Lespedeza cuneata* removal on arthropod abundances and diversity

Lespedeza cuneata removal did not significantly affect arthropod abundances summed over the summer in the overall model, but a significant pair effect indicated that abundances varied spatially, with Japanese beetles (*Popillia japonica*) and other Coleoptera most strongly responding (standardized canonical coefficients, Table 1). While there was no significant effect across arthropod taxa, Japanese beetles showed the greatest response to removal treatment (Table 1) and in a univariate analysis, were significantly more abundant in the control plots (Fig. 2; $F_{1,19} = 5.85$, $p = 0.0258$). Japanese beetles were frequently observed in mating aggregations on *L. cuneata*. Orthoptera, the only well-sampled order consisting of just herbivores, showed no significant response to the removal treatment ($F_{1,19} = 0.77$, $p = 0.3901$) but varied in abundance across the site ($F_{19,19} = 4.41$, $p = 0.0011$).

Overall, at the level of order, *L. cuneata* affected the relationship between arthropod richness and evenness ($F_{2,36} = 4.19$, $p = 0.0232$) but spatial variation represented by the pair effect was not strong ($F_{2,36} = 2.85$, $p = 0.0710$). The relationship between richness and evenness changed over the season ($F_{8,30} = 3.38$, $p = 0.0070$) and this response to time differed between removal treatments ($F_{8,30} = 2.92$, $p = 0.0155$) but not among pairs ($F_{8,30} = 1.75$, $p = 0.1280$). Both richness and evenness increased after May (Fig. 3a). Relative to control plots, *L. cuneata* removal increased evenness in May ($p = 0.0209$), decreased it in June through August ($p < 0.05$ in each), and had no effect in September ($p > 0.05$; Fig. 3a). Richness was not significantly affected by treatment in any monthly pairwise comparison ($p > 0.05$ in each).

Pan traps and pitfall traps differed in how many arthropods were trapped ($F_{2,18} = 3217.3$, $p = 0.0001$) and when they were caught ($F_{8,12} = 77.4$, $p = 0.0001$). Pan traps collected many flies in May whereas pitfall traps caught abundant ants and Orthoptera in June (Figs. 1, 3b). Although *L. cuneata* removal was not a significant main effect ($F_{2,18} = 0.35$, $p = 0.7085$) this treatment marginally affected the pattern of collection by the two methods across the summer ($F_{8,12} = 2.73$, $p = 0.0567$). This effect was largely concentrated in May, with a tendency toward more arthropods (predominantly flies) in plots with unmanipulated *L. cuneata* ($p = 0.0685$). The pattern of collection by the two methods did not vary by location of the plots ($F_{38,38} = 1.3$, $p = 0.2127$).

Effect of *Lespedeza cuneata* removal on herbivory

Herbivory of the five native species varied considerably within species (Fig. 4) but removal of *L. cuneata* from plots did not affect the amount of chewing herbivory experienced by the individual sampled leaves ($F_{1,38} = 0.20$, $p = 0.656$). The five native species did not differ from each other significantly ($F_{4,152} = 1.38$, $p = 0.245$) and did not differ in response to the removal treatment ($F_{4,152} = 1.83$, $p = 0.127$). 53% of *O. rigidum* leaves exhibited some level of pre-trial damage,

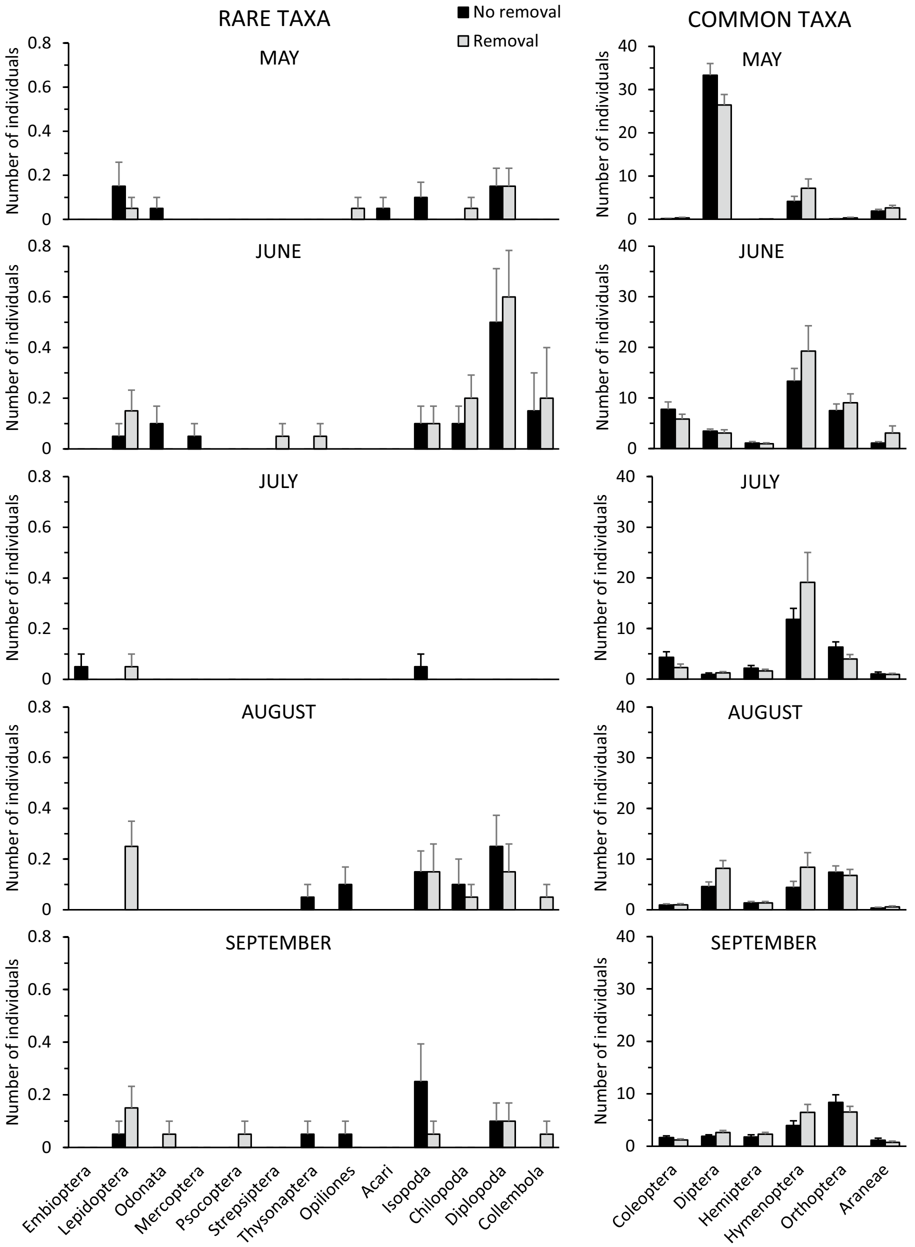

Fig. 1 Average (± se) number of individuals in all arthropod orders sampled in monthly collection by the pan-trap method and pitfall method in control plots and plots from which *Lespedeza cuneata* shoots were removed. Coleoptera includes Japanese beetles. Note the difference in scale for panels on the left (rare taxa) vs. right (common taxa)

Table 1 Results of the multivariate analysis of variance of the total abundances of individuals in various arthropod taxa in response to the independent variables *L. cuneata* removal treatment and plot pair assignment. Coleoptera data did not include *Popillia japonica* (Japanese beetles)

Effect	Pillai's trace			Standardized Canonical Coefficients						
	df	*f*	*P*	Araneae	Hymenoptera	Diptera	Hemiptera	Orthoptera	Coleoptera	*Popillia japonica*
Removal treatment	7,13	2.21	0.1029	0.858	0.765	−0.101	0.815	0.208	−0.650	−1.579
Pair	133,133	1.51	0.0087	−0.5259	0.0448	−0.861	−0.865	0.382	1.193	1.201

but prior condition was not associated with subsequent herbivory for this species ($p = 0.281$), nor for *C. tripteris* ($p = 0.668$) or *L. capitata* ($p = 0.446$). Removal treatment also did not affect the probability that the entire leaf or plant would disappear ($F_{1,38} < 0.01$, $p = 0.990$). The interaction of removal and species was not significant ($F_{5,183} = 0.41$,

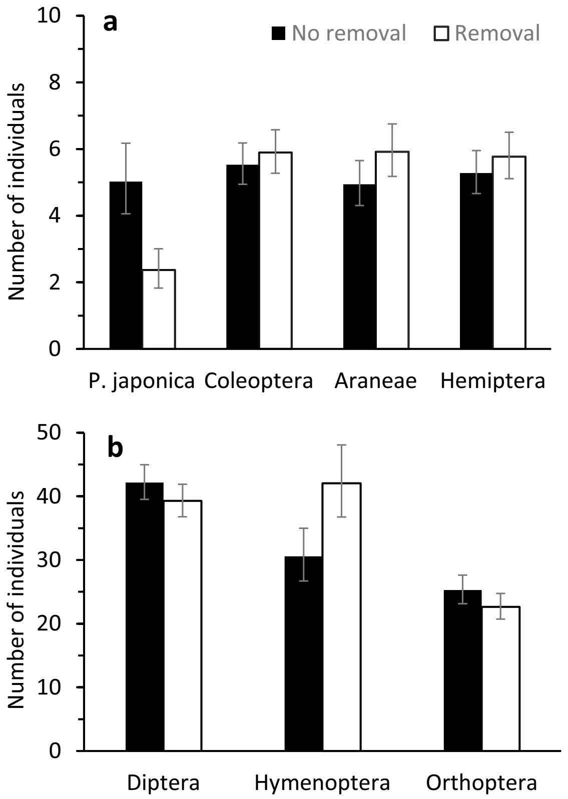

Fig. 2 Average (± se) abundances of *Popillia japonica* (Japanese beetles) and major taxa in plots from which *Lespedeza cuneata* shoots remained intact (control) or were repeatedly removed. Plots were sampled monthly with pan and pitfall traps and values were summed over the five sampling periods and methods. Coleoptera abundances do not include *P. japonica*

$p = 0.840$), but the species nonetheless differed from each other (species: $F_{5,183} = 4.66$, $p = 0.0005$), with *L. cuneata* marked leaf or entire plant most likely to be missing (Fig. 5).

Discussion

Despite its rapid advance over more than a decade (Walder et al. 2019) and overwhelming presence on this site late in the season (Fowler and Borowicz, pers. obs.), reduction of *Lespedeza cuneata* in plots in a reconstructed prairie yielded surprisingly little effect on insect abundance or herbivory. Only the Japanese beetle, which is an exotic invasive species (Potter and Held 2002), decreased in abundance in plots in which *L. cuneata* was reduced. Reduced abundance of an herbivore is predicted under apparent competition if removal of the exotic invasive plant eliminates some benefit such as refuge from enemies or inhospitable microclimate (Orrock et al. 2008; Dangremond et al. 2010; Bhattarai et al. 2017). The Japanese beetle is a diurnally active scarab that climbs to the tops of plants, where it is exposed to visual predators including predatory insects and birds (Fleming 1972) and consequently *L. cuneata* is unlikely to provide greater protection. Although Varriano et al. (2020) found no effect of *L. cuneata* removal on birds, ground predators such as spiders and ground beetles were more abundant in mid-summer where *L. cuneata* was present, further suggesting that this invader does not provide herbivores with greater protection from enemies. The bulky Japanese beetle adults typically congregate at the tops of plants where they bask in the sun and form mating masses. Perhaps the benefit provided by

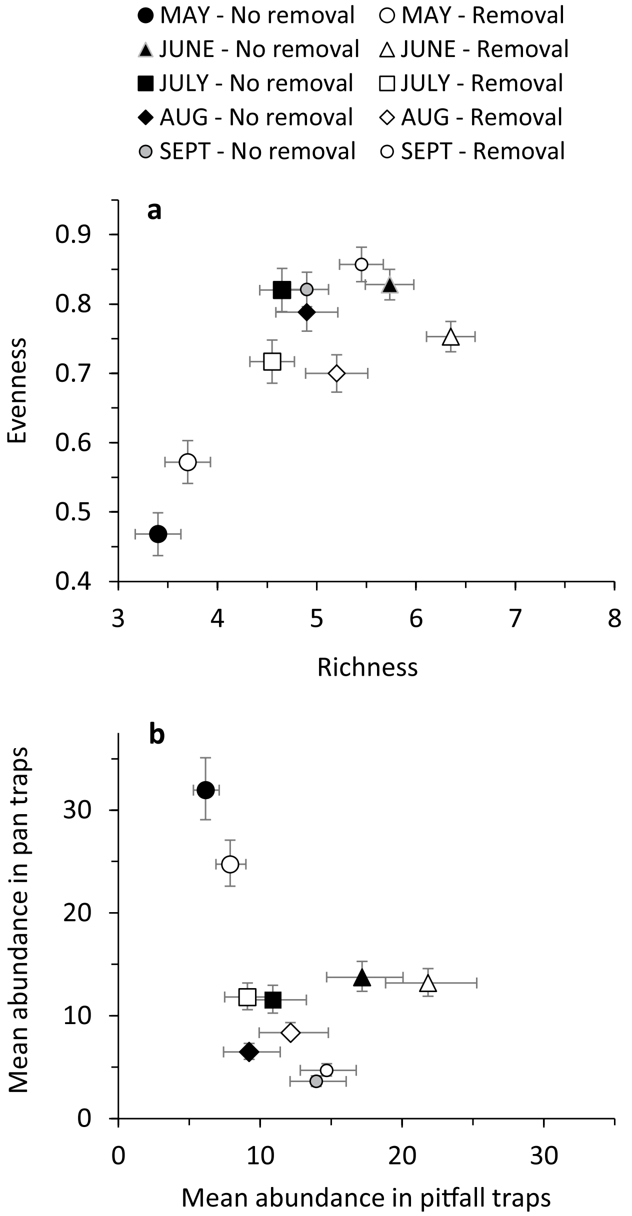

Fig. 3 Monthly averages (± se) for **a** evenness and number of orders (richness) from combined pan and pitfall traps, and **b** numbers of arthropods collected in pan and pitfall traps in plots from which *L. cuneata* was present (filled symbols) or removed (open symbols)

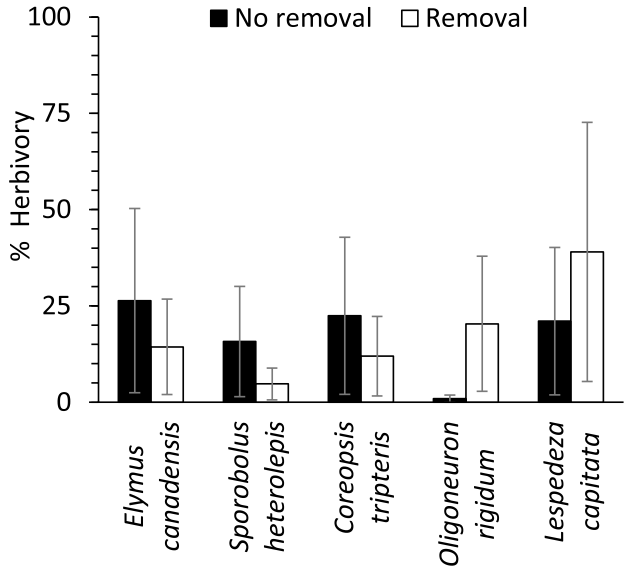

Fig. 4 Average (± se) herbivory experienced by marked leaves on native plants placed in control and *L. cuneata*-removal plots for 4 weeks

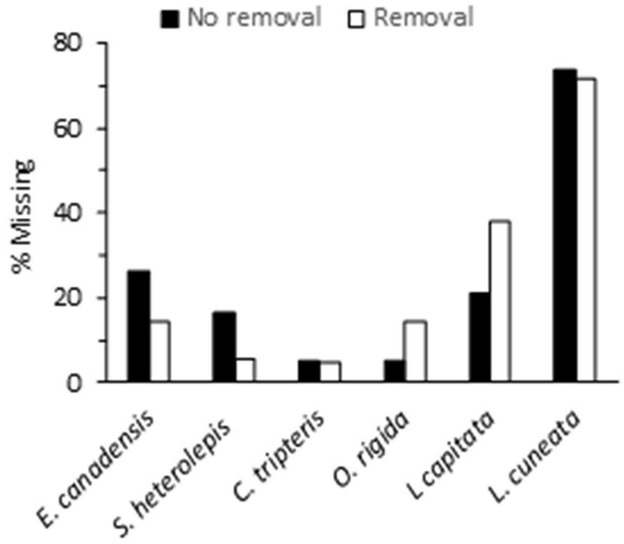

Fig. 5 Percentage of pots from which the marked leaf or entire plant was missing after 4 weeks in control or *Lespedeza cuneata*-removal plots

L. cuneata is its height or rigid structure, enabling a greater number of beetles to join the mating masses.

For apparent competition to be at work, increased abundance of the invasive plant should result in greater herbivory of neighbors (Orrock et al. 2008). We found no evidence that this was the case in our assessment of aboveground herbivory. While the Japanese beetle was less abundant in removal plots, reduced numbers did not translate to reduced herbivory of phytometers serving as *L. cuneata*'s neighbors. The timing of the herbivory experiment (August) precluded much opportunity for feeding by Japanese beetle adults, which were abundant the previous year in the mid-June and mid-July sampling with pan traps. Nonetheless, predominantly herbivorous insect orders, e.g., Orthoptera, were abundant throughout the summer yet we observed no increase in herbivory on native species. Contrary to the hypothesis, entire *L. cuneata* phytometers were most likely to disappear. Several studies have shown that tannins in *L. cuneata* make it unpalatable to mammal and insect herbivores (Langdale and Giddens 1967; Kalburtji and Mosjidis 1993; War et al. 2012) and *L. cuneata* experienced less herbivory than a native congener in a field study (Schutzenhofer et al. 2009) and so we expected the least damage to *L. cuneata* phytometers. Following the trial, whole stems were missing or severed and laying on the soil in the pot, suggesting that *L. cuneata* individuals were damaged by mammals rather than consumed by arthropod herbivores. Regardless, our observations of herbivory did not accord with the apparent competition hypothesis.

Greater abundance of Japanese beetle adults in areas of dense *L. cuneata* is consistent with the Invasional Meltdown hypothesis (Simberloff and Holle 1999) where non-native species positively interact to facilitate each other's invasion by supporting increased establishment. Massing for reproduction indicates the legume benefits the insect at mating. *Lespedeza cuneata* may also affect oviposition site suitability by altering factors such as light (Dalthorp 1999) and soil moisture (Régnière et al. 1979; Allsopp et al. 1992). However, we do not know whether the interaction between the species is reciprocal (Braga et al. 2018). As an herbivore both above and belowground, the Japanese beetle could reduce growth of competing plant neighbors through aboveground herbivory earlier than when we assessed herbivory, and belowground as larvae feeding on neighbors' roots (Potter and Held 2002; Blossey and Hunt-Joshi 2003). The association between the advance of *L. cuneata* and abundance of the Japanese beetle in natural communities warrants more attention as both species continue to spread through the Midwest.

No clear pattern of *L. cuneata*'s effects on higher trophic levels have emerged. In Kansas oak savannas, *L. cuneata* abundance was high where native plant diversity and numbers of macroinvertebrate families were low (Eddy and Moore 1998) and in Oklahoma, richness in some taxa peaked at intermediate levels of *L. cuneata* cover (Kaplan 2019). Despite significantly depressing *L. cuneata* abundance in removal plots, Varriano et al. (2020) found little effect on the arthropod community. Similarly, we found our removal treatment had little impact on the number of orders but did affect arthropod evenness, primarily through effects on Diptera in May. Proximity to a stream and lake may explain the large influx of flies at that time, but the attraction to *L. cuneata* is not clear. Flies are an abundant pollinator in tallgrass prairies (Robson 2008) but *L. cuneata* does not flower until September and flies are not common visitors to their flowers (Woods et al. 2012). When in flower late in the summer, *L. cuneata* removal did not have significant effects on community metrics in our study. However, species-specific effects of *L. cuneata* on pollinators and potential saturation of pollinators have been recorded in Kansas grasslands (Woods et al. 2012), suggesting *L. cuneata* may have less apparent effects on functional groups.

Site history may explain variation among studies in effects of *L. cuneata* on higher trophic levels. We manipulated aboveground abundance of *L. cuneata* in areas already heavily infested which could leave a legacy effect in the soil that attenuated arthropod responses compared to observational studies that placed plots where *L. cuneata* was still absent (control) vs. in invaded sites (Eddy and Moore 1998), or where existing stands of *L. cuneata* met criteria for density (Kaplan 2019). When they did detect an impact on arthropods, Varriano et al. (2020) found the difference was between unmanipulated plots where *L. cuneata* was naturally absent and experimental plots both with and from which *L. cuneata* was removed, and postulated that nitrogen fixation by this legume increases the quality of other plants as food for herbivores, compensating for its poorer quality. As it increases, density-dependent effects expressed through shade, litter, and effects on the soil community suppress other plant species (Brandon et al. 2004) and we would expect secondary effects on higher trophic levels to become more evident. More than a decade after it was first recorded on our site, the impact of *L. cuneata* invasion on abundance and diversity of arthropods may have already occurred over a broad area.

In addition to a legacy effect in the soil, other factors could obscure or negate arthropod responses to *L. cuneata* removal. Although the shoots were repeatedly removed and aboveground vegetation from other plants rose above resprouts, some arthropods, especially ground-dwelling taxa, may continue to be affected by this background level of *L. cuneata* or accumulated litter. Fire is usually applied annually to our site and we have observed that *L. cuneata* litter does not burn well such that a layer was present in many plots. Our pre-manipulation assessment of plots showed no pre-existing differences in litter between removal and non-removal plots. An existing litter layer may explain the general lack of effect of *L. cuneata* shoot removal on pitfall trap collection although Hymenoptera, primarily ants, tended toward greater abundance in removal plots. Because ants are ecosystem engineers that respond to plant diversity in prairies (Wodika et al. 2014), the impact of *L. cuneata* on this group of arthropods deserves a closer look. The scale of our manipulation was small relative to the extent of some *L. cuneata* patches or the distance some arthropods routinely travel, and separation of plots by as little as 2 m could have allowed spillover of arthropods between plots and diminished the ability to detect effects of *L. cuneata* removal. Because of the potential spatial effect, which was significant as a block effect in some analyses, we kept distances between paired plots assigned different treatments low to ensure common vegetation before manipulation. Despite these shortcomings, the Japanese beetle, a mobile species responded to treatments, and over the course of the summer, evenness at the level of the order also differed between treatments, demonstrating that this invasive plant species affects the arthropod community.

Understanding how this noxious plant alters communities to promote invasion can aid in preventing it from going over the threshold beyond which control is not possible (Suding and Hobbs 2009). The interplay observed aboveground between this invasive legume and the exotic Japanese beetle is especially intriguing and better knowledge could help avoid invasional meltdown. We observed no feeding on *L. cuneata* shoots and have found no information regarding interactions between roots of this legume and Japanese beetle larvae. A preference for short grass and sunlight for oviposition sites (Shanovich et al. 2019) suggests the interior of *L. cuneata* patches would not be suitable but higher nitrogen in vegetation adjacent to this nitrogen-fixing legume may attract females. This raises the possibility of apparent competition via root herbivory if larvae concentrate feeding on native species adjacent to *L. cuneata*. Japanese beetles are an increasing concern in maize and soybean production (Shanovich et al. 2019). If polyphagy extends to native grasses and legumes, prairies isolated in a matrix of agricultural fields may be especially vulnerable to the impact of this exotic herbivore spilling over from adjacent crops. Examination of plant–herbivore interactions belowground in prairies, an endangered habitat, will be especially important if this threat from an exotic herbivore extends belowground through apparent competition between *L. cuneata* and the native flora.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11829-021-09854-0.

Acknowledgements We thank D. Byers and S. Juliano for advice and comments on an earlier draft, S. Juliano for statistical support, and A. Scheidel, T. Martin, E. Berry, H. Smith, S. Savici, R. Stramaglia, K. Corcoran, R. DiPietro, and A. Kew for assistance with data collection. McLean County Parks and Recreation granted access to the field site. This research was funded by grants to J.R.F. from the Beta Lambda Chapter of the Phi Sigma Biological Honors Society and the Illinois Native Plant Society.

Author contributions JRF and VAB designed the experiment, JRF collected and analyzed the data and wrote the first draft of the manuscript.

Funding This research was funded by grants to J.R.F. from the Beta Lambda Chapter of the Phi Sigma Biological Honors Society and the Illinois Native Plant Society.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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