ORIGINAL PAPER

The invasive *Lespedeza cuneata* attracts more insect pollinators than native congeners in tallgrass prairie with variable impacts

**Teresa M. Woods · Jayne L. Jonas ·
Carolyn J. Ferguson**

Abstract Invasive plant species can potentially exert competitive or facilitative effects on insect pollination services of native species. Factors that influence these effects include the degree of shared pollinator species, synchronous flowering phenology, similar flower morphology and color, relatedness of invasive and natives, and showiness and densities of flowers. We investigated such plant-pollinator dynamics by comparing the invasive *Lespedeza cuneata* and three native congeners, all sympatric with synchronous flowering, using in situ populations over 2 years during peak floral displays. Insect visitation rates of the invasive were significantly higher per plant in both years than on the native species. The invasive exerted a competitive effect on visitation of the two native species with fewer shared pollinators, and a facilitative effect on visitation of the native species with the highest degree of shared insect visitors. Positive correlations were found between floral density and visitation rate per plant in all the native species. Although no such correlation was found for the invasive, floral density in *L. cuneata* was at least twenty times higher than in the native species and likely saturated the response of the pollinator community. Analyses of insect visitor taxonomic data indicated the insect communities visiting each of the *Lespedeza* species were generally similar though with species-specific differences. The main exception was that the common honeybee, *Apis mellifera*, was a primary visitor to the invasive plant species, yet was never observed on the native *Lespedeza* species.

Keywords *Apis mellifera* · *Lespedeza* · Invasive · Pollination · Competition · Facilitation

T. M. Woods (✉) · C. J. Ferguson
Herbarium and Division of Biology, Kansas State University, Ackert Hall, Manhattan, KS 66506, USA
e-mail: twoods@ksu.edu

T. M. Woods
Curriculum and Instruction, College of Education, Kansas State University, Bluemont Hall, Manhattan, KS 66506, USA

J. L. Jonas
Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523, USA

Introduction

Invasive species provide unique opportunities to investigate both ecological and evolutionary dynamics (Lambrinos 2004). Comparisons of invasive plant species with natives indicate that interactions vary from direct competition for resources (Barrat-Segretain 2005; Thomson 2005) to facilitative interactions (Richardson et al. 2000; Callaway et al. 2004; Bruno et al. 2005), with the most severe impacts of invasive plant species due to high relative abundance (D'Antonio and Hobbie 2005; Traveset and Richardson 2006). The introduction history and breeding systems of

invasive species can also affect patterns of genetic structure in their adventive environments through dynamics of gene flow or isolation (Bossdorf et al. 2005; Dlugosch and Parker 2008), and rapid adaptation in some alien species has been documented (Lee 2002; Cox 2004; Prentis et al. 2008).

Understanding the reproductive systems of invasive species is fundamental to an improved understanding of their ecological and evolutionary dynamics. For instance, pollination can play a significant role in maintaining high propagule numbers, and high propagule pressure is often paramount to invasive plant success in establishment, maintenance of high relative abundance, and spread (Leung et al. 2004; Drake et al. 2005; Rejmánek et al. 2005). Lack of mutualist pollinators can limit the production of propagules in alien plants, as evidenced by several obligately outcross-pollinated *Ficus* species that only became invasive in Florida when their specialist pollinator wasp species were later introduced (McKey and Kaufmann 1988; Nadel et al. 1992). Rodger et al. (2010) additionally found that a plant invader, *Lilium formosanum*, that relies on a specialized pollinator can thrive in its adventive environment when that pollinator is naturally present. While lack of pollinators can constrain the spread of alien species by limiting seed set (Parker 1997; Larson et al. 2002), most invasive plant species are not pollinated through such specialist relationships, but rather receive pollination service through generalist vectors to maintain high propagule pressure (Barthell et al. 2001; Brown et al. 2002; Parker and Haubensak 2002; Stout et al. 2006). Plants that rely on generalist pollinators are hypothesized to be more successful invaders since highly specialized plant species would be unlikely to encounter their pollinator species in a new environment (Baker 1974; Richardson et al. 2000; Rejmánek et al. 2005). Rather, plants with generalist pollinators can rely on multiple pollinator species with varying ranges, on alternative pollinators that may serve similar functional groups (Dalsgaard et al. 2008), or on generalist pollinators that have also been introduced into the same adventive environment (Simberloff and VonHolle 1999; Simberloff 2006; Abe et al. 2011).

Insect pollination of native plant species can be impacted by co-flowering invasive species, with dynamics ranging from competitive to null to facilitative, depending on context (Bjerknes et al. 2007; Muñoz and Cavieres 2008; Sargent and Ackerly

2008). Some invasive plants successfully compete with native species for pollinator services through more attractive floral rewards or simply due to greater floral display (Morales and Traveset 2009). For instance, the presence of *Lythrum salicaria*, invasive in North America, has been shown to reduce insect visits, pollination and seed set in the native congener *L. alatum*, which has a much smaller floral display than the invasive (Brown and Mitchell 2001; Brown et al. 2002). The invasive *Impatiens glandulifera* had a similar effect on several native co-occuring plant species in Germany due to its relatively higher quality of nectar (Chittka and Schürkens 2001). In Japan, the native *Taraxacum japonicum* was negatively affected through reduced insect visits and seed set in the presence of the invasive congener, *T. officinale*, which produces higher quality nectar despite its reliance on apomixis (Kandori et al. 2009; Takakura et al. 2009). Another mechanism implicated in reduced seed set of natives in the presence of invasives is the asymmetric deposition of heterospecific pollen on stigmas of native flowers (Brown and Mitchell 2001; Kandori et al. 2009).

Despite these studies, little evidence demonstrates that native plants actually suffer strict pollinator limitation due to the presence of invasives (Totland et al. 2006; Nielsen et al. 2008), and in some cases, alien plant species may actually support populations and networks of insect pollinators that service native species (Bjerknes et al. 2007; Valdovinos et al. 2009). In Mediterranean communities, for example, invasive *Carpobrotus* species were found to exert both competitive and facilitative species-specific effects on different native species (Moragues and Traveset 2005; Bartomeus et al. 2008). Contextual factors that influence the effects of alien plant species on pollination services to native plants include: the degree of dependence on pollinators, the degree of shared pollinator species, synchronous flowering phenology, similar flower morphology and color, relatedness of invasive and native species, showiness and densities of flowers, amount of floral rewards, and population size and structure (Bjerknes et al. 2007; Muñoz and Cavieres 2008; Morales and Traveset 2009). These factors can work in concert, and can in fact be correlated; for instance, flower morphology is often similar in closely related plant species.

Shifts in pollinator visitation rates can affect the genetic diversity in native and invasive plant

populations (Barrett et al. 2008; Wilson et al. 2009). Native populations can suffer reduced gene flow if pollinator service is reduced (Traveset and Richardson 2006). Invasive species can undergo local adaptation in their adventive environments through dynamics of gene flow and isolation (Barrett 1992; Allard et al. 1993; Levin 2003; Parker et al. 2003). A plant's mating system directly influences such patterns, with outcross-pollination conferring greater genetic variation upon which selection can act, and uniparental reproduction (self-pollination or asexual reproduction) facilitating more rapid genetic differentiation among populations as well as reproductive assurance (Allard et al. 1972; Novak et al. 1991; Daehler 1998; Pappert et al. 2000; Lambrinos 2001; Levin 2003; Barrett et al. 2008). Additionally, seeds formed from outcrossing are often more viable than those formed from selfing (Chang and Rausher 1998; Barrett 2003; Carr and Dudash 2003). Thus, pollination services can be important to an invasive species even with a mixed mating system.

The invasive *L. cuneata* (Dum. -Cours.) G. Don (Fabaceae) is an interesting case study where, via exclusion experiments, insect pollination has been shown to be important in seed set in a mixed mating system (Woods et al. 2009). *Lespedeza* species produce two types of flowers: showy chasmogamous flowers that can be pollinated by insects or by autonomous delayed-selfing (Woods 2006); and closed, inconspicuous, reduced cleistogamous flowers that are obligately self-pollinated. In a study comparing the invasive *L. cuneata* with three sympatric native congeners in tallgrass prairie, the invasive *L. cuneata* produced on average at least five times the number of seeds per plant than the native *Lespedeza* species (Woods et al. 2009). In the same study, the invasive *L. cuneata* also produced over twenty times the number of chasmogamous flowers (potentially insect-pollinated) than its sympatric native congeners, and was shown to benefit from insect pollination more than the co-flowering native *Lespedeza* species (Woods et al. 2009). While insect cross-pollination has been documented in most *Lespedeza* species (Stitt 1946; Donnelly 1955; Clewell 1964; Cope 1966), studies in the North American prairies have found evidence that native *Lespedeza* species may harbor less genetic variation among populations than the invasive *L. cuneata* (Cole and Biesboer 1992; Sundberg et al. 2002).

The general objective of this study was to assess plant-pollinator interactions of an invasive plant species in the context of its flexible breeding system. Our approach was to compare the plant-pollinator dynamics of the invasive *L. cuneata* with multiple congeneric native species in natural populations in the tallgrass prairie. Our general hypothesis was that the invasive *L. cuneata* would have more interactions with insect floral visitors than native congeners. Specific predictions were that, in natural populations: (1) the invasive *L. cuneata* would have a higher insect visitation rate than the native congeners; (2) size of floral display would correlate with insect visitation rate; and (3) the invasive *L. cuneata* would be more generalist-pollinated than the native species (that is, the taxonomic diversity of insects visiting would be greater than for the native congeners).

Materials and methods

Study species

Four species in the genus *Lespedeza* were studied: the non-native invasive *L. cuneata*; and three native species, *L. capitata* Michx., *L. violacea* (L.) Pers., and *L. virginica* (L.) Britton. All are perennial legumes that form natural populations in the North American tallgrass prairie of Kansas (Great Plains Flora Association 1986), and all occur sympatrically. *L. cuneata* is native to eastern Asia, and was introduced into eastern United States originally for erosion control. In tallgrass prairie, *L. cuneata* forms dense stands, rapidly displacing native grasses (Ohlenbusch et al. 2007). Voucher specimens of each species from each study site for this investigation have been deposited at the Kansas State University Herbarium (KSC).

All four species have seeds that require scarification for germination, with fire stimulating seedling emergence (Clewell 1966). They are also clonal, with vegetative buds on the stem base and woody rhizomes augmenting sexual reproduction. Each plant generally consists of multiple interconnected stems (hereafter referred to as *ramets*) that together comprise a separate and independent *Integrated Physiological Unit* (IPU) (Watson and Casper 1984), hereafter referred to simply as plant. Over time, some ramets become independent through senescence of the connecting rhizome. For the purposes of this study, ramets

emerging from a common base were considered to constitute one plant.

The species produce flowers for approximately 4 weeks from late July to mid-September, with all species overlapping in flowering phenology. Within this general timeframe, the four *Lespedeza* species studied demonstrate variable flowering patterns in varying environments (Woods et al. 2009). They produce single-seeded legumes that mature in 4–5 weeks, remaining potentially viable for over 50 years (Clewell 1966). The native species are known to hybridize among themselves, though hybridization of *L. cuneata* with the natives is precluded by differences in chromosome number: *L. cuneata* n = 19; North American *Lespedeza* species n = 10 (Clewell 1966).

The showy chasmagamous flowers typically open in the morning and last 1 day before wilting. These papilionaceous flowers are approximately 1 cm long with a standard, two wings and a keel, and the reproductive organs are contained within the keel. The greatly reduced, inconspicuous cleistogamous flowers are interspersed within the inflorescences and are obligately self-pollinating (Woods et al. 2009).

The corollas of *L. cuneata* and *L. capitata* are white to cream-colored, those of *L. violacea* and *L. virginica* are pink-purple, and flowers of all species have deep purple or magenta coloring at the base of the standard. The flowers of each species are borne on the stem in distinct patterns (Fig. 1). *Lespedeza cuneata* bears flowers in many axillary racemes along most of the length of the stem; *L. capitata* forms a dense terminal capitate inflorescence, often with thyrsoid inflorescences at nodes; *L. violacea* bears flowers in loose and well separated axillary racemes along its relatively thin stems; and *L. virginica* bears a few flowers in tight axillary racemes along the mid to upper parts of its stem, often culminating in a loose terminal thyrsoid inflorescence.

Each flower contains ten diadelphus stamens and a single carpel with a style that grows through the fused stamens. The style elongates and bends the stigma upward and often out of the keel prior to elongation of the filaments, with trichomes forming a slight barrier between the stigma and anthers (Clewell 1966; Cope 1966). Despite this physical barrier, a certain degree of autonomous self-pollination in chasmogamous flowers has also been found to occur (Woods et al. 2009). Nonetheless, through insect exclusion experiments, Woods et al. (2009) found that the chasmogamous flowers of these four species are primarily insect-pollinated. Although these *Lespedeza* species produce self-pollinated seeds through autonomy in chasmogamous and cleistogamous flowers, the seeds produced by chasmogamous flowers, and especially through outcrossing, are known to have significantly higher viability rates than those produced by cleistogamous flowers (Donnelly 1955; Schutzenhofer 2007).

Study sites

Six sites with wild populations of the *Lespedeza* species located in northeastern Kansas, USA, were utilized for this study. At least two sites per species of natural populations were utilized and replicated for 2 years (Table 1). Limitations to replication included

Fig. 1 Floral displays of the four study species, from *left* to *right*: *Lespedeza cuneata* (invasive); *L. capitata* (native); *L. violacea* (native); *L. virginica* (native)

Table 1 Field sites: location (county, latitude, and longitude) and brief description of field sites sampled indicating which *Lespedeza* species and years were studied at each site in Kansas (USA)

Site	Latitude/Longitude (County)	Description	L. cuneata	L. capitata	L. violacea	L. virginica
(FR) Fort Riley	39°10′N, 96°41′W (Riley)	Old agricultural fields	2004 2005	2005		
(K2A) Konza	39°06′N, 96°34′W (Riley)	Ungrazed site at KPBS*		2004 2005	2004 2005	
(WB) Konza	39°04′N, 96°34′W (Geary)	Ungrazed site at KPBS*		2004 2005	2004 2005	
(P2) Pottawatomie no. 2 State Lake	39°14′N, 96°31′W (Pottawatomie)	Prairie surrounded by mixed woodland	2004	2005	2004 2005	
(PL2) Private Land 2	39°21′N, 96°46′W (Riley)	Restored grassland surrounded by farm fields	2004 2005			2004 2005
(PL3A) Private Land 3A	39°16′N, 96°28′W (Pottawatomie)	Open field near riparian woodland			2005	2004 2005

* *KPBS* Konza Prairie Biological Station

lack of flowering in given sites and years (e.g., *L. capitata* at Fort Riley in 2004, *L. violacea* at PL3A in 2004), and eradication of the invasive species at Pottawatomie No. 2 State Lake in 2005. The region is characterized by a continental climate of warm, wet summers and dry, cold winters, and high levels of interannual variation in precipitation and temperature (Goodin et al. 2003). *Lespedeza* species were common but not dominant in terms of community composition. The *Lespedeza* species occurring sympatrically did so in estimated relative abundances that were similar, though it is worth noting that the greater number and size of ramets per plant of the invasive *L. cuneata* relative to its native congeners renders its spatial cover and vegetative density, including floral density, greater.

Field methods

To assess insect visitation, 20 min observations of the four *Lespedeza* species were made at regular intervals, with each observation period comprising one sample. One to five plants with open flowers occurring in 1-m radius circles were observed during the midpoint of seasonal peak flowering time, and between the hours of 11:00 and 17:00 (the time period found in a 2003 pilot study to include the majority of the insect visitation activity for the plant species). The 1 m radius circles were randomly chosen by marking a 25 m transect through the middle of the population, selecting 12 potential sampling points at 2 m intervals, and finding the nearest individual of the target plant species in a lateral direction. Transects were at least 30 m from prairie edge in all instances except the following: (1) Pottawatomie No. 2 State Lake, in which some samples were within 5 m of water's edge surrounded by prairie; and (2) Private Land 3A, in which some samples were within 5 m of riparian woodland surrounded by prairie. Each successive observation period was conducted on independent plants at least 10 m away, and individual plants were not resampled. When more than one species in the same site was observed, it was done when the invasive *L. cuneata* in the given site was flowering concurrently. Observation periods for different species growing in the same site were interspersed in time. Each site was monitored for 2 days. Weather conditions and limited flowering of native species limited sample size in some instances.

An insect visit was recorded if an insect contacted the reproductive organs or the keel of an individual flower. A new insect visit was counted each time an insect visited a new flower. Vouchers of insect visitors were collected and were identified by Department of Entomology personnel at Kansas State University, generally to the genus level. Specimens are housed in the Kansas State University Herbarium (KSC).

The number of flowers per ramet was sampled by species and site each day. The number of aboveground ramets per plant (IPU) was also recorded to estimate plant size. More than one plant was frequently observed within the same time period (see Potts 2005). Thus, to account for overall floral density, the number of open conspecific flowers within a 5 m radius of each species under observation was also recorded for each observation period.

Analysis

Insect visitation rates were compared among species for the separate years 2004 and 2005. Visitation rate (VR) was calculated in two ways: (1) the rate per flower [VR_{flr} = (no. insect visits)/(flower × min)]; and (2) the rate per plant [VR_{plnt} = (no. insect visits/ (flower × min)) × (mean no. flowers/plant)]. The VR_{flr} was calculated directly from observed insect observation periods. VR_{plnt} was calculated using the VR_{flr} and the calculated daily number of flowers per plant from the same plant species, sites and years (Woods et al. 2009). The VR_{plnt} was calculated due to its greater relevance for community questions (Potts 2005) and to enable consideration of population level issues associated with invasion. Visitation rates (VR_{flr} and VR_{plnt}) were compared by conducting tests for differences among species using a mixed model restricted maximum likelihood (REML) analysis, allowing for unequal variances within species, and conducting pairwise comparisons using differences in least-squares means (SAS Institute Inc. 2002–2003).

The Wilcoxon rank-sum exact test (SAS Institute Inc. 2002–2003) was used to examine the impact of the presence of the invasive *L. cuneata* on visitation rates for the natives *L. capitata* (2005 only), *L. violacea* (2004), and *L. virginica* (2004 and 2005) by comparing VR_{flr} and VR_{plnt} at sites where the native species occurred with *L. cuneata* versus without *L. cuneata*. In 2004, flowering plants of *L. capitata* and *L. cuneata* did not co-occur at any sites sampled.

In 2005 *L. violacea* failed to flower. Due to small sample sizes, skewed distributions and wide ranges of observations in the datasets for the native species, the non-parametric test was deemed the most appropriate approach to assessing the effect of the invasive species on pollinator visitation rates of the natives.

To test for a relationship between insect visitation rate and floral density, VR_{plnt} was plotted against the number of conspecific flowers within a 5 m radius of the flowers under observation (floral density) using a simple linear regression. Data were pooled for 2004 and 2005 within plant species and transformed to achieve normality, with the inverse of VR_{plnt} (VR_{plnt}^{-1}) plotted against log (floral density). For ease of interpretation, values were back-transformed to the original scale for presentation and discussion of relationships.

To compare diversity of insect visitors, rarefaction curves were developed using EstimateS software (Colwell 2005). Rarefaction curves allow comparison of different communities, in this case insect visitors to different plant species, given different sample sizes. A sample was considered a single observation period. Mau's tao calculations were used, with 100 randomized runs with replacement. The similarity of insect taxa visiting each plant species was compared. For purposes of analysis, insect visitors on each plant species were considered one insect community, and insect taxonomic groups identified at the finest level (either species or genus as described above) were considered a single species for purposes of analysis. For each year, the following were calculated: the number of insect taxa observed on each plant species, the number of shared insect taxa observed, and the Morisita-Horn community similarity index (Colwell 2005).

Insect visitor community composition was assessed for each plant species in each year by determining the percentage of visits attributed to each insect order. Because the majority of insect visitors were hymenopterans, the percentages of visits within this order were further determined to the family level.

Results

A total of 98 insect visitation observation periods (samples) were conducted over 2 years: 38 in 2004; and 60 in 2005. Insect visitation rates among the plant

species differed significantly when calculated on the basis of both flower (VR$_{flr}$) and plant (VR$_{plnt}$) in 2004 ($F_{3,34} = 3.55$, $P = 0.245$; and $F_{3,22.8} = 8.16$, $P = 0.0007$; respectively), but only in VR$_{plnt}$ in 2005 ($F_{2,5.73} = 6.68$, $P = 0.0318$) (Fig. 2). In both years the native *L. capitata* had the highest VR$_{flr}$, and the invasive *L. cuneata* had the highest VR$_{plnt}$. In 2004, the mean VR$_{plnt}$ for *L. cuneata* was nearly ten times that of any other native *Lespedeza* studied, and in 2005 the mean VR$_{plnt}$ for *L. cuneata* was over eight times those of the native congeners. The differences between VR$_{flr}$ and VR$_{plnt}$ are related to the prolific number of flowers per stem and stems per plant in *L. cuneata* relative to the other species (Woods et al. 2009).

Sampling was somewhat uneven due to the uneven chasmogamous flowering between seasons and sites among the species. For instance, *L. violacea* had low flowering in 2004, and failed to flower in 2005 (for more details, see Woods et al. 2009). Sites continued to be monitored even when flowering did not occur.

Comparisons of visitation rates for native *Lespedeza* species with and without *L. cuneata* as a sympatric species yielded variable results. The presence of *L. cuneata* had a marginally negative impact on VR$_{flr}$ of *L. capitata* in 2005 ($S = 25.0$, $P = 0.0781$) as well as on *L. violacea* in 2004 ($S = 6.0$, $P = 0.0571$), and it had no effect on
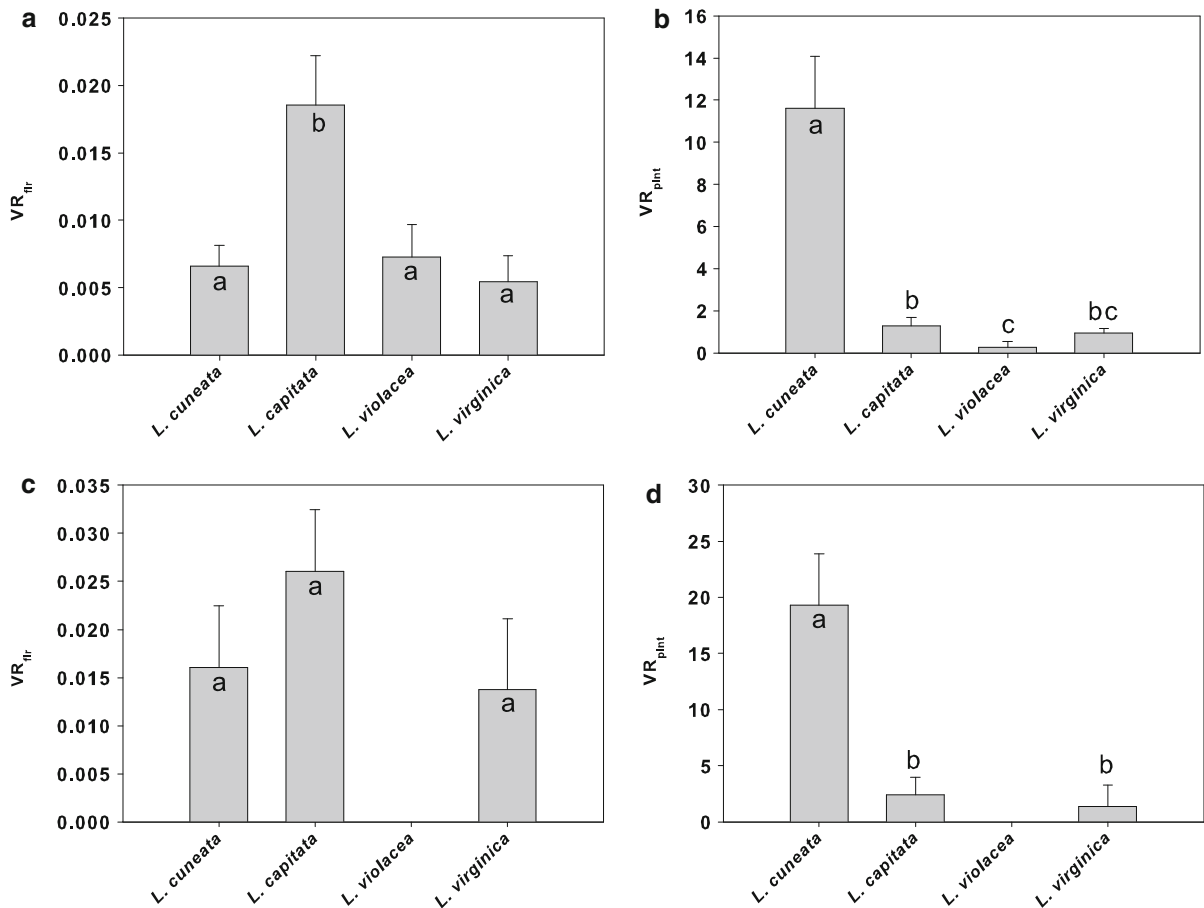
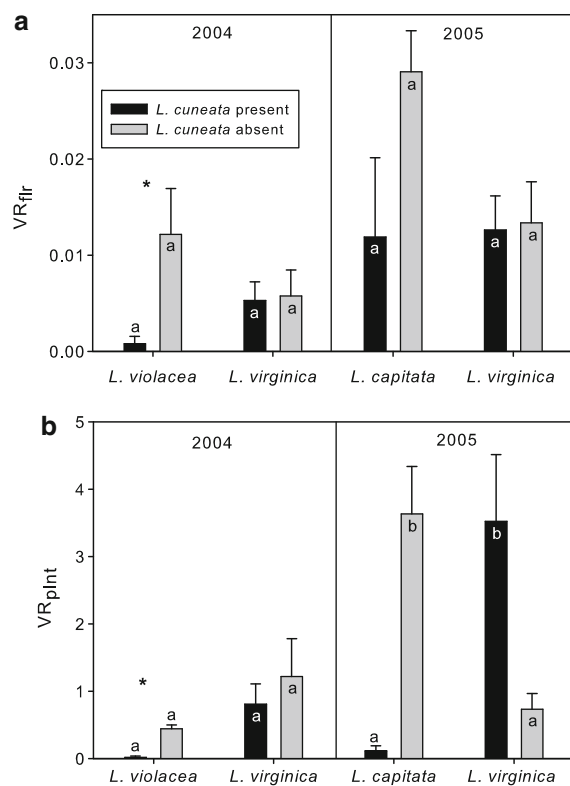**Fig. 2** Insect visitation rates among *Lespedeza* species: **a** visitation rates per flower (VR$_{flr}$) in 2004, **b** visitation rates per plant (VR$_{plnt}$) in 2004, **c** visitation rates per flower (VR$_{flr}$) in 2005; and **d** visitation rates per plant (VR$_{plnt}$) in 2005. Each sample represents one observation period monitoring numerous ramets on up to five plants. In 2004, n = 17 for *L. cuneata*, n = 3 for *L. capitata*, n = 7 for *L. violacea*, and n = 11 for *L. virginica*. In 2005, n = 18 for *L. cuneata*, n = 22 for *L. capitata*, and n = 19 for *L. virginica*. Note the lack of data due to no flowering in *L. violacea* in 2005. *Different letters* indicate significant differences between species (*P* value < 0.05)

L. virginica in either 2004 ($S = 25.0$, $P = 0.8848$) or 2005 ($S = 64.5$, $P = 0.7170$) (Fig. 3a). However, analysis of the more ecologically relevant VR_{plnt} showed that in the presence of *L. cuneata*, insect visitation rates were significantly lower for *L. capitata* in 2005 ($S = 14.0$, $P = 0.0031$), marginally lower for *L. violacea* in 2004 ($S = 6.0$, $P = 0.0571$), unaffected for *L. virginica* in 2004 ($S = 27.0$, $P = 0.6182$), but significantly greater for *L. virginica* in 2005 ($S = 85.5$, $P = 0.0227$) (Fig. 3b).

In assessing the relationship between visitation rates and floral density among the plant species, a significant correlation was found between VR_{plnt}^{-1} and

log (floral density) in all native species, where no significant correlation was found in the invasive *L. cuneata* (Fig. 4). In terms of back-transformed relationships, greater floral density was associated with greater insect visitation rates for all native species. The linear equations, r^2-values, and P values for these species are reported in Fig. 4.

The rarefaction curve analysis demonstrated that while there was a higher species richness of insect visitors to *L. cuneata* than to the native species in both years, the difference was not significant (using a 95% confidence interval), except relative to *L. violacea* in 2004 (Fig. 5). Sampling was greater in 2005, though the trends remained the same with *L. capitata* and *L. virginica* showing less insect visitor species richness, respectively, than the invasive *L. cuneata* (*L. violacea* was not sampled in 2005 due to lack of flowering that year). Pairwise comparisons for each year of the visiting insect communities to each plant species resulted in Morisita-Horn similarity indices between 0.670 and 0.863 (Tables 2, 3), indicating that a majority of the visiting insect taxa visited more than one of these plant species. The Morisita-Horn comparisons indicated that *L. cuneata* was visited by more insect taxa than the native species except in relation to *L. capitata* in 2005 (Table 3). The discrepancy between these comparisons and those shown by the rarefaction curves is due to the latter analysis accounting for uneven sampling sizes.

The taxonomic breakdown of insects visiting each plant species (Fig. 6) shows that hymenopterans were the primary visitors in all cases except to *L. capitata* in 2004, in which case coleopterans were the most frequent visitors. Analysis of Hymenoptera visitors revealed that the primary visitor to all the native plants was the genus *Megachile*. In 2004, the primary insect visitors to *L. cuneata* were nearly evenly split between *Megachile* spp. and *Apis mellifera*, the common honeybee, while in 2005, the primary visitor to *L. cuneata* was *A. mellifera*.

Fig. 3 Insect visitation rates for the native species *Lespedeza capitata, L. violacea* and *L. virginica* as influenced by the presence or absence of the invasive *L. cuneata*: **a** visitation rates per flower (VR_{flr}), **b** visitation rates per plant (VR_{plnt}). Data were analyzed separately for each species × year; data to make these comparisons were only available for *L. capitata* from 2005 (n = 4 with and n = 18 without *L. cuneata*), for *L. violacea* from 2004 (n = 3 with and n = 4 without *L. cuneata*), and *L. virginica* from 2004 (n = 7 with and n = 4 without *L. cuneata*) and 2005 (n = 6 with and n = 13 without *L. cuneata*). *Different letters* indicate significant differences (*P* value < 0.05), * indicates marginally significant differences (0.05 < *P* value < 0.06)

Discussion

Our study examined the plant-pollinator interactions in natural populations of an important invasive plant species, *L. cuneata*, in relation to three native congeners, all of which utilize multiple reproductive modes and a mixed mating system. The invasive *Lespedeza*
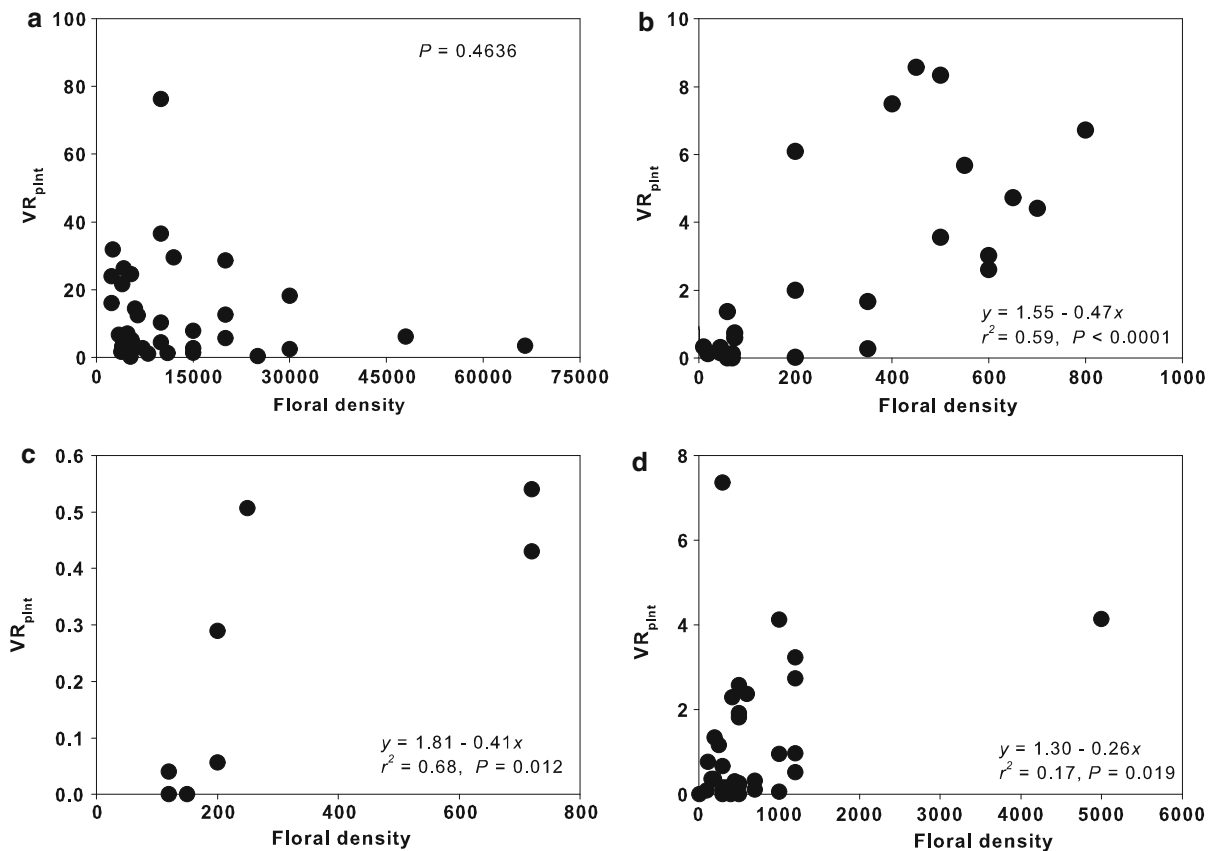
Fig. 4 Correlation of insect visitation rates per plant (VR_{plnt}) to floral density: **a** *L. cuneata* (invasive), **b** *L. capitata* (native), **c** *L. violacea* (native); and **d** *L. virginica* (native). Linear equations and regression coefficients (r^2) are provided for significant least squares regressions where $y = VR_{plnt}^{-1}$ and $x = \log$ (floral density $+ 1$). Plotted values were back-transformed to the original scale for ease of interpretation

species demonstrated a far greater insect visitation rate per plant than its native congeners, and impacted the visitation rates of native species in competitive, null and facilitative ways that varied by species and year. Insect visitation rates correlated with floral density in the native species, while the extreme floral density of the invasive likely saturated the response of the pollinator community. The insect communities visiting each of the *Lespedeza* species were generally similar, with the exception that *A. mellifera* was a primary visitor to the invasive species, but was never observed on the native *Lespedeza* species.

Previous studies show that factors affecting the impacts of invasive plant species on the pollination dynamics of native plant species include: showiness and densities of flowers, degree of dependence on pollinators, degree of shared pollinators, synchronous flowering phenology, similar flower morphology and color and relatedness of invasive and native species (Bjerknes et al. 2007; Muñoz and Cavieres 2008; Mitchell et al. 2009; Morales and Traveset 2009).

The four *Lespedeza* congeners studied here share similar flower morphology, size and deep purple coloring at the base of the standard. All four species overlap in peak flowering phenologies and grow sympatrically in tallgrass prairie. Woods et al. (2009) established through insect exclusion experiments that insect pollination was important in chasmogamous seed production to all species. Furthermore, chasmogamously produced seeds have been shown to have higher viability rates than those produced by cleistogamous flowers (Donnelly 1955; Schutzenhofer 2007).

Lespedeza cuneata had an insect visitation rate eight to ten times greater per plant than the native *Lespedeza* species. On a per flower basis, though, the
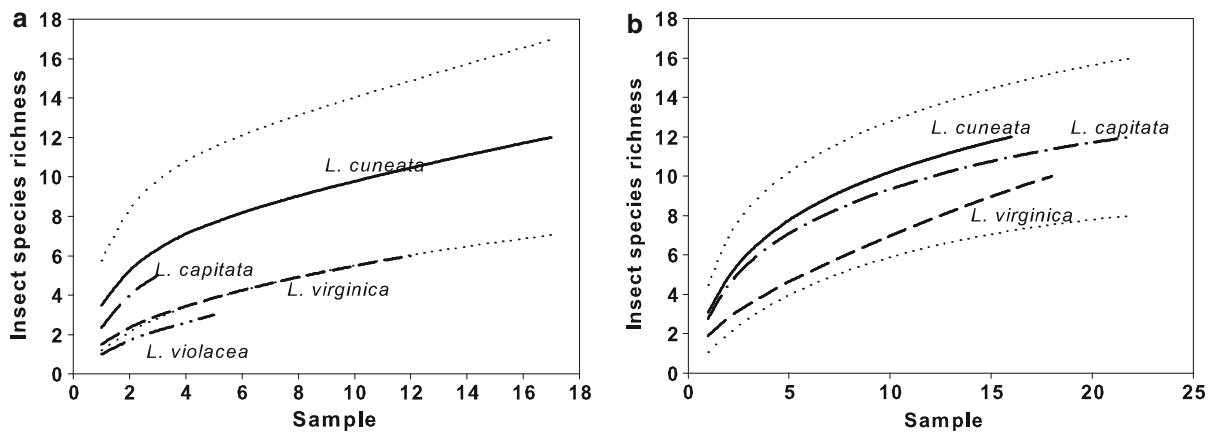
Fig. 5 Insect visitor diversity for different plant species during (**a**) 2004, and (**b**) 2005. Insect diversity was based on insect visitors to each plant species, and one sample was considered one observation period. Different sample sizes were due to variable flowering in years and sites among species (there were no samples for *L. violacea* in 2005 as it failed to flower in all sites). *Dotted lines* indicate 95% confidence interval (CI) of the species with the widest CI (*L. cuneata* in 2004 and *L. capitata* in 2005). The *solid line* represents *L. cuneata* (invasive); *dashed* and *single dotted line* represents *L. capitata*; dashed line represents *L. virginica*; dashed line and *double dotted line* represents *L. violacea*. Analysis based on EstimateS (Colwell 2005)

Table 2 Morisita-Horn community similarity index of insect visitors among *Lespedeza* species in 2004, listed from lowest to highest index value

Plant species 1	Plant species 2	S_{obs1}	S_{obs2}	Shared $S_{obs1–2}$	Morisita-Horn
L. cuneata	**L. capitata**	**14**	**6**	**2**	**0.670**
L. capitata	L. virginica	6	8	1	0.696
L. capitata	L. violacea	6	4	1	0.707
L. cuneata	**L. violacea**	**14**	**4**	**3**	**0.725**
L. cuneata	**L. virginica**	**14**	**8**	**6***	**0.743***
L. violacea	L. virginica	4	8	3	0.863

S = The number of insect taxa observed visiting each plant species, Shared S = Shared insect taxa observed visiting both plant species. Comparisons of interest between the invasive and native *Lespedeza* species are in bold, with the highest values of these denoted by asterisks

Table 3 Morisita-Horn community similarity index of insect visitors among *Lespedeza* species 2005, listed from lowest to highest index value

Plant species 1	Plant species 2	S_{obs1}	S_{obs2}	Shared $S_{obs1–2}$	Morisita-Horn
L. cuneata	**L. capitata**	**13**	**17**	**8**	**0.780**
L. cuneata	**L. virginica**	**13**	**12**	**10***	**0.797***
L. capitata	L. virginica	17	12	8	0.852

S = The number of insect taxa observed visiting each plant species, Shared S = Shared insect taxa observed visiting both plant species. Comparisons of interest between the invasive and native *Lespedeza* species are in bold, with the highest values of these denoted by asterisks

invasive had a similar or lower mean insect visitation rate relative to the native species. This indicates that the higher visitation rate per plant of the invasive is due to its relatively high floral display and density in relation to the native *Lespedeza* species. While the relative abundance per plant of each of the four *Lespedeza* species was similar in these natural populations, the invasive *L. cuneata* has a significantly

Fig. 6 Insect visitor taxonomic composition. For each plant species in each year, insect visitor taxa are represented on the vertical bar in the proportion they contributed to total visitation. **a** *Differentiated bars* represent different insect orders. Hymenopterans comprised the majority of visits in each instance, except for *L. capitata* in 2004. **b** Each bar represents total Hymenopteran visits, with differentiations representing different taxa. When major family visitors consisted of a single genus or species, it is indicated in the legend. The non-native bee, *A. mellifera*, was a primary visitor to the invasive *L. cuneata*, yet was never observed on the native *Lespedeza* species
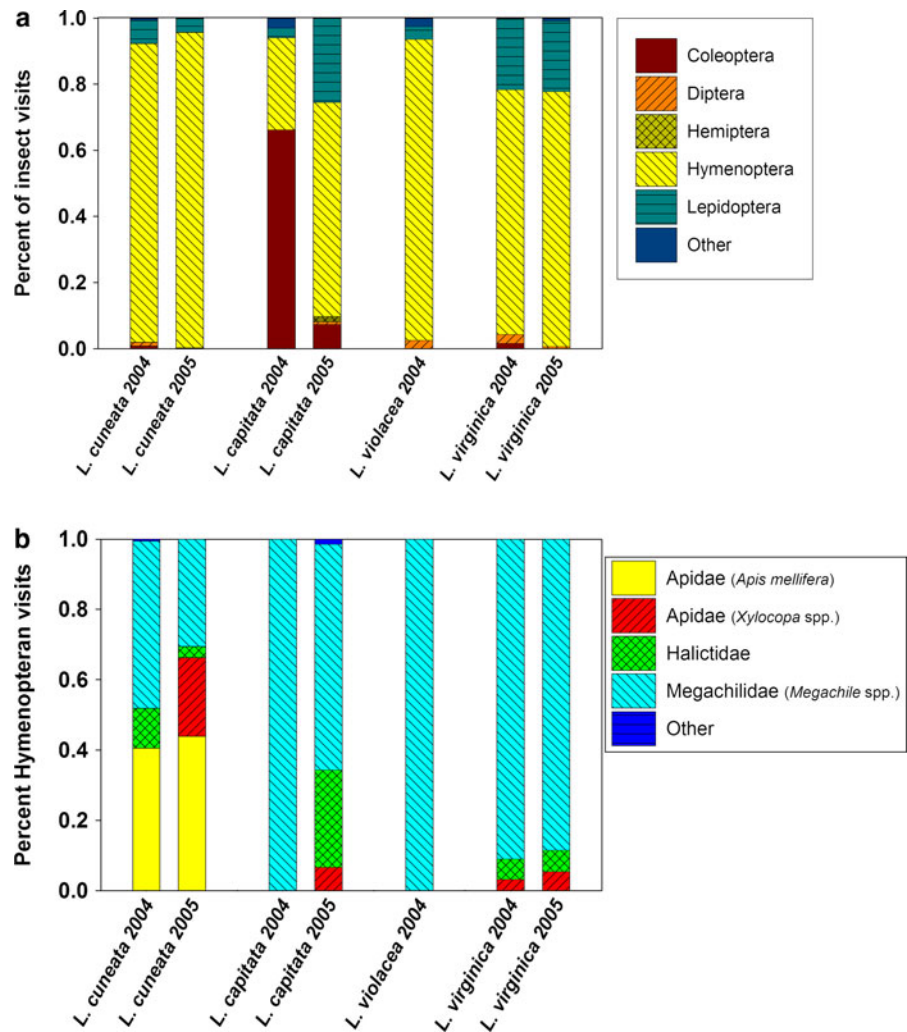
greater number of ramets per plant and greater numbers of flowers per ramet, resulting in a floral display that averages at least twenty times those of the three native *Lespedeza* species (Woods et al. 2009).

Muñoz and Cavieres (2008) report that competitive effects for pollinators among native and invasive plant species primarily occur at high densities of the invasive relative to the natives. The positive correlation found in this study between floral density and insect visitation in the native *Lespedeza* species with no such correlation in the invasive *L. cuneata* suggests that the native plants would likely garner more insect visitors with greater floral density, but that the invasive *L. cuneata* exceeded the floral density required to attract more insects. Although the floral display of *L. cuneata* was more than 95% greater than

those of the native species, competition for pollinators was only indicated for *L. capitata* and *L. violacea*, while *L. cuneata* seemed to facilitate pollinator visitation in *L. virginica*. Based on these in situ findings, controlled experimental tests on the native plants with and without the presence of the invasive are warranted to further elucidate the competitive and facilitative effects that *L. cuneata* exerts on insect pollination in co-occurring native *Lespedeza* species.

Lespedeza cuneata and the native species were shown to generally, though not completely, share a similar insect pollinator community in these tallgrass prairie sites. While *L. cuneata* was visited by a greater number of insect taxa, the difference was not significant. Interestingly, the largest number of shared insect taxa (63%) existed between the invasive *L. cuneata*

and the native *L. virginica*. *L. virginica* is also the native species registering a facilitative effect from insect visitors to the invasive. The overall plant architecture of these two species is similar, even though their flowers are different colors (cream colored, and pink, respectively). Conversely, in 2005 the native *L. capitata* shared only 21% of visitor taxa with *L. cuneata* and also had lower VR_{plnt} when growing sympatrically with *L. cuneata*. These results suggest that the presence of the invasive *L. cuneata* may exert a facilitative effect on visitation rates of native species when they share similar pollinator communities.

The most prominent insect visitor overall was the genus *Megachile*, and the bodies of these bees are particularly well-suited to pollination of these *Lespedeza* flowers. As the bees land on the keel and forage at the nectaries, they tend to work the keel open with their legs, exposing the anthers which deposit pollen directly onto the abdomen of the bees. On more than one occasion, *Megachile* were directly observed moving between the *L. capitata* and *L. violacea*. These two native plant species often hybridize to form *Lespedeza × manniana* Mack. & Bush (pro sp.), and hybrid individuals were documented at those sites (Woods 2006).

The prominence of the insect *A. mellifera* as a visitor to the invasive *L. cuneata*, when it was never recorded on any of the native *Lespedeza* species, is an important finding in this study. *Apis mellifera* is native to Eurasia and Africa, and has been introduced to most of the rest of the world, including North America. The honeybee has facilitated the invasion of numerous alien plant species through its pollination service (Barthell et al. 2001; Parker and Haubensak 2002; Stout et al. 2002). While it is unlikely that *L. cuneata* is as dependent on *A. mellifera* pollination as some other invasive plants, these findings suggest it may be affecting pollinator networks, such as shifts in native bee foraging. Schaffer et al. (1979, 1983) found changes in patterns of niche-partitioning among bee communities in the presence of *A. mellifera*, with native bees shifting to less productive foraging sites and flower species, while the introduced honeybees preferentially foraged at the most productive floral resources. The results of this study are consistent with this phenomenon: the invasive *L. cuneata*, the most productive and dominant of the congeners in terms of floral resources, was the only *Lespedeza* species on

which *A. mellifera* was observed visiting. Gross (2001) also found a negative correlation between native bee presence and introduced honeybee presence on an endemic shrub in Australia, with the honeybee ranking as the primary pollinator. Studies examining pollinator networks with and without the presence of *L. cuneata* could elucidate the influence that both the invasive plant, and its facilitation of *A. mellifera* populations, have on native species.

The high insect visitation rate per plant found for the invasive *L. cuneata* (eight to ten times that of any of the three native *Lespedeza* species) may be most important in terms of the maintenance of genetic variation within populations relative to the native species. Other studies on *Lespedeza* species in North American prairies indicate interesting patterns of genetic diversity. Cole and Biesboer (1992) found low levels of heterozygosity in the widespread native *L. capitata*, yet strong genetic differentiation among populations. This is consistent with high levels of self-pollination. Cole and Biesboer (1992) contrasted populations of *L. capitata* with populations of the native *L. leptostachya* Engelm., which is threatenened and endangered, finding that the former maintained far greater genetic variation and gene flow than existed in the latter, suggesting that even a low level of outcrossing is important in maintaining viable populations. In contrast, Sundberg et al. (2002) found considerable genetic variability in invasive *L. cuneata* plants selected from different populations. This may be due to relatively greater outcrossing levels that maintain greater genetic diversity within and among populations, or due to a history of multiple introductions of *L. cuneata*, or both. Cope (1966) found outcrossing levels in *L. cuneata* between 16 and 43% of seed set by chasmogamy.

Lespedeza species have complex reproductive systems, enabling them to produce local propagules vegetatively as well as sexually. More specifically, they reproduce through rhizomatous buds, and through seeds produced through both selfing and outcrossing. This suite of reproductive modes can be advantageous in various and varying conditions, contributing not only to high propagule production but also to reproductive fitness homeostasis in the invasive (Barrett et al. 2008; Woods et al. 2009). Propagules produced asexually or through self-pollination can be advantageous in establishing new populations where mates or pollinators may be absent,

while clonal reproduction can ensure persistence and increasing density over time by enlarging existing clones (Brock et al. 1995; Pyšek et al. 2001). The density created by vegetative budding is a dominant strategy of *L. cuneata* in shading neighboring plants (Brandon et al. 2004), and is also implicated in formation of its relatively dense and showy floral display (Woods et al. 2009). In contrast, plants that reproduce only through outcross pollination confer greater standing genetic diversity, providing an advantage in the potential for adaptive evolution (Lambrinos 2001; Dlugosch and Parker 2008). Most models of the reproductive biology of invasive or colonizing plant species predict selective advantages for mixed mating systems that balance reproductive assurance through self-pollination or asexual reproduction, with the benefits of genetic variation through outcross-pollination (Lloyd 1992; Pannell and Barrett 1998; Barrett et al. 2008).

Such selective advantages of the mixed mating system of native North American *Lespedeza* species have been highlighted by Clewell (1964, 1966). Additionally, the findings of higher genetic diversity among invasive *L. cuneata* populations in relation to native *Lespedeza* populations (Cole and Biesboer 1992; Sundberg et al. 2002) are consistent with our finding that the invasive *L. cuneata* maintains an insect visitation rate eight to ten times that of the native *Lespedeza* species. This higher insect visitation rate suggests a higher degree of gene flow through pollination than its native congeners. Future studies comparing the genetic diversity among the invasive and native *Lespedeza* species would be fruitful, and exploration of whether *L. cuneata* demonstrates evidence of clinal or local adaptation could shed light on the role of its flexible reproductive system and mixed mating system in its successful spread.

References

Abe T, Wada K, Kato Y, Makino S, Okochi I (2011) Alien pollinator promotes invasive mutualism in an insular pollination system. Biol Invasions 13:957–967

Allard RW, Babbel GR, Clegg MT, Kahler AL (1972) Evidence for coadaptation in *Avena barbata*. Proc Natl Acad Sci 69:3043–3048

Allard RW, García P, Sáenz-de-Miera LE, MPdl Vega (1993) Evolution of multilocus genetic structure in *Avena hirtula* and *Avena barbata*. Genetics 135:1125–1139

Baker HG (1974) The evolution of weeds. Annu Rev Ecol Syst 5:1–24

Barrat-Segretain MH (2005) Competition between invasive and indigenous species: impact of spatial pattern and developmental stage. Plant Ecol 180:153–160

Barrett SCH (1992) Genetics of weed invasions. In: Jain SK, Botsford LW (eds) Applied population biology. Kluwer Academic Publishers, The Netherlands, pp 91–119

Barrett SCH (2003) Mating strategies in flowering plants: the outcrossing-selfing paradigm and beyond. Phil Trans R Soc Lond B 358:991–1004

Barrett SCH, Colautti RI, Eckert CG (2008) Plant reproductive systems and evolution during biological invasion. Mol Ecol 17:373–383

Barthell JF, Randall JM, Thorp RW, Wenner AM (2001) Promotion of seed set in yellow star-thistle by honey bees: evidence of an invasive mutualism. Ecol Appl 11:1870–1883

Bartomeus I, Vilà M, Santamaría L (2008) Contrasting effects of invasive plants in plant-pollinator networks. Oecologia 155:761–770

Bjerknes A, Totland Ø, Hegland SJ, Nielsen A (2007) Do alien plant invasions really affect pollination success in native plant species? Biol Conserv 138:1–12

Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D (2005) Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia 144:1–11

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

Brock JH, Child LE, deWaal LC, Wade M (1995) The invasive nature of *Fallopia japonica* is enhanced by vegetative regeneration from stem tissues. In: Pyšek P, Prach K, Rejmánek M, Wade M (eds) Plant invasions, general aspects and special problems. SPB Academic Publishing, Amsterdam, pp 131–139

Brown BB, Mitchell RJ (2001) Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. Oecologia 129:43–49

Brown BB, Mitchell RJ, Graham SA (2002) Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology 83:2328–2336

Bruno JF, Fridley JD, Bromberg KD, Bertness MD (2005) Insights into biotic interactions from studies of species invasions. In: Sax DF, Stachowicz JJ, Gaines SD (eds) Species invasions: insights into ecology, evolution and biogeography. Sinauer Associates, Inc., Sunderland, pp 13–40

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427:731–733

Carr DE, Dudash MR (2003) Recent approaches into the genetic basis of inbreeding depression in plants. Phil Trans R Soc Lond B 358:1071–1084

Chang SM, Rausher MD (1998) Frequency-dependent pollen discounting contributes to maintenance of a mixed mating system in the common morning glory Ipomoea purpurea. Am Nat 152:671–683

Chittka L, Schürkens S (2001) Successful invasion of a floral market. Nature 411:653

Clewell AF (1964) The biology of the common native lespedezas in southern Indiana. Brittonia 16:208–219

Clewell AF (1966) Natural history, cytology and isolating mechanisms of the native American Lespedezas. Bull Tall Timbers Res Stn 6:10–12

Cole CT, Biesboer DD (1992) Monomorphism, reduced gene flow, and cleistogamy in rare and common species of Lespedeza (Fabaceae). Am J Bot 79:567–575

Colwell RK (2005) Estimates: statistical estimation of species richness and shared species from samples. Version 7.5

Cope WA (1966) Cross-pollination in Sericea Lespedeza. Crop Sci 6:469–470

Cox GW (2004) Alien species and evolution. Island Press, Washington

Daehler CC (1998) Variation in self-fertility and the reproductive advantage of self-fertility for an invading plant (Spartina alterniflora). Evol Ecol 12:553–568

Dalsgaard B, Gonzalez AMM, Olesen JM, Timmermann A, Andersen LH, Ollerton J (2008) Pollination networks and functional specialization: a test using Lesser Antillean plant-hummingbird assemblages. Oikos 117:789–793

D'Antonio CM, Hobbie SE (2005) Plant species effects on ecosystem processes. In: Sax DF, Stachowicz JJ, Gaines SD (eds) Species invasions. Sinauer Associates, Inc., Sunderland, pp 65–84

Dlugosch KM, Parker IM (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. Mol Ecol 17:431–449

Donnelly ED (1955) The effects of outcrossing on forage and seed yields in sericea lespedeza, L. cuneata. Agron J 47:466–467

Drake JM, Baggenstos P, Lodge DM (2005) Propagule pressure and persistence in experimental populations. Biol Lett UK 1:480–483

Goodin DG, Fay PA, McHugh MJ (2003) Climate variability in tallgrass prairie at multiple timescales: Konza Prairie Biological Station. In: Greenland D, Goodin DG, Smith RC (eds) Climate variability and ecosystem response at long-term ecological research sites. Oxford University Press, NY, pp 411–424

Great Plains Flora Association (1986) Flora of the great plains. University Press of Kansas, Lawrence

Gross CL (2001) The effect of introduced honeybees on native bee visitation and fruit-set in Dillwynia juniperina (Fabaceae) in a fragmented ecosystem. Biol Conserv 102:89–95

Kandori K, Hirao T, Matsunaga S, Kurosaki T (2009) An invasive dandelion unilaterally reduces the reproduction of a native congener through competition for pollination. Oecologia 159:559–569

Lambrinos JG (2001) The expansion history of a sexual and asexual species of Cortaderia in California, USA. J Ecol 89:88–98

Lambrinos JG (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. Ecology 85:2061–2070

Larson KC, Fowler SP, Walker JC (2002) Lack of pollinators limits fruit set in the exotic Lonicera japonica. Am Midl Nat 148:54–60

Lee CE (2002) Evolutionary genetics of invasive species. Trends Ecol Evol 17:386–391

Leung B, Drake JM, Lodge DM (2004) Predicting invasions: propagule pressure and the gravity of allee effects. Ecology 85:1651–1660

Levin DA (2003) Ecological speciation: lessons from invasive species. Syst Bot 28:643–650

Lloyd DG (1992) Self- and cross-fertilization in plants: the selection of self-fertilization. Int J Plant Sci 153:370–380

McKey DB, Kaufmann SC (1988) Naturalization of exotic Ficus species (Moraceae) in south Florida. Paper presented at proceedings of the symposium on exotic pest plants 1988. University of Miami, Florida

Mitchell RJ, Flanagan RJ, Brown BJ, Waser NM, Karron JD (2009) New frontiers in competition for pollination. Ann Bot 103:1403–1413

Moragues E, Traveset A (2005) Effect of Carpobrotus spp. on the pollination success of native plant species of the Balearic Islands. Biol Conserv 122:611–619

Morales CL, Traveset A (2009) A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. Ecol Lett 12:716–728

Muñoz AA, Cavieres LA (2008) The presense of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. J Ecol 96:459–467

Nadel H, Frank JH, Knight RJ (1992) Escapees and accomplices: the naturalization of exotic Ficus and their associated faunas in Florida. Fla Entomol 75:29–38

Nielsen C, Heimes C, Kollmann J (2008) Little evidence for negative effects of an invasive alien plant on pollinator services. Biol Invasions 10:1353–1363

Novak SJ, Mack RN, Soltis DE (1991) Genetic variation in Bromus tectorum (Poaceae): population differentiation in its North American range. Am J Bot 78:1150–1161

Ohlenbusch PD, Bidwell T, Fick WH, Scott W, Clubine S, Coffin M (2007) Sericea lespedeza: history, characteristics and identification. Kansas State University Agricultural Experiment Station and Cooperative Extension Service, Manhattan

Pannell JR, Barrett SCH (1998) Baker's Law revisited: reproductive assurance in a metapopulation. Evolution 52:657–668

Pappert RA, Hamrick JL, Donovan LA (2000) Genetic variation in Pueraria lobata (Fabaceae), an introduced, clonal, invasive plant of the southeastern United States. Am J Bot 87:1240–1245

Parker IM (1997) Pollinator limitation of *Cytisus scoparius* (scotch broom), an invasive exotic shrub. Ecology 78:1457–1470

Parker IM, Haubensak KA (2002) Comparative pollinator limitation of two non-native shrubs: do mutualisms influence invasions? Oecologia 130:250–258

Parker IM, Rodriguez J, Loik ME (2003) An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. Conserv Biol 17:59–72

Potts SG (2005) Recording pollinator behaviour on flowers. In: Dafni A, Kevan PG, Husband BC (eds) Practical pollination biology. Enviroquest, Ltd., Cambridge, pp 330–339

Prentis PJ, Wilson JRU, Dormontt EE, Richardson DM, Lowe AJ (2008) Adaptive evolution in invasive species. Trends Plant Sci 13:288–294

Pyšek P, Mandák B, Francírková T, Prach K (2001) Persistence of stout clonal herbs as invaders in the landscape: a field test of historical records. In: Brundu G, Brock J, Camarda I, Child L, Wade M (eds) Plant invasions: species ecology and ecosystem management. Backhuys Publishers, Leiden, pp 235–244

Rejmánek M, Richardson DM, Higgins SI, Pitcairn MJ, Grotkopp E (2005) Ecology of invasive plants: state of the art. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (eds) Invasive alien species: a new synthesis. Vol 63: SCOPE. Island Press, Washington, pp 104–161

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions—the role of mutualisms. Biol Rev 75:65–93

Rodger JG, vanKleunen M, Johnson SD (2010) Does specialized pollination impede plant invasions? Int J Plant Sci 171:382–391

Sargent RD, Ackerly DD (2008) Plant-pollinator interactions and the assembly of plant communities. Trends Ecol Evol 23:123–130

SAS Institute Inc. (2002–2003) SAS 9.1 TS level 1M3, Cary, NC

Schaffer WM, Jensen DB, Hobbs DE, Gurevitch J, Todd JR, Schaffer MV (1979) Competition, foraging energetics and the cost of sociality in three species of bees. Ecology 60:976–987

Schaffer WM, Zeh DW, Buchmann SL, Kleinhans S, Schaffer MV, Antrim J (1983) Competition for nectar between introduced honey bees and native North American bees and ants. Ecology 64:564–577

Schutzenhofer MR (2007) The effect of herbivory on the mating system of congeneric native and exotic *Lespedeza* species. Int J Plant Sci 168:1021–1026

Simberloff D (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecol Lett 9:912–919

Simberloff D, VonHolle B (1999) Positive interactions of non-indigenous species: invasional meltdown. Biol Invasions 1:21–32

Stitt RE (1946) Natural crossing and segregation in sericea lespedeza, *Lespedeza cuneata* (Dumont) G. Don. J Am Soc Agron 38:1–5

Stout JC, Kells AR, Goulson D (2002) Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. Biol Conserv 106:425–434

Stout JC, Parnell JAN, Arroyo J, Crowe TP (2006) Pollination ecology and seed production of *Rhododendron ponticum* in native and exotic habitats. Biodivers Conserv 15:755–777

Sundberg MI, Slaughter DM, Crupper SS (2002) Application of randomly amplified polymorphic DNA (RAPD) fingerprinting to detect genetic variation in sericea lespedeza (*Lespedeza cuneata*). T Kans Acad Sci 105:91–95

Takakura K-I, Nishida T, Matsumoto T, Nishida S (2009) Alien dandelion reduces the seed-set of a native congener through frequency-dependent and one-sided effects. Biol Invasions 11:973–981

Thomson D (2005) Measuring the effects of invasive species on the demography of a rare endemic plant. Biol Invasions 7:615–624

Totland Ø, Nielsen A, Bjerknes A, Ohlson M (2006) Effects of an exotic plant and habitat disturbance on pollinator visitation and reproduction in a boreal forest herb. Am J Bot 93:868–873

Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. Trends Ecol Evol 21:208–216

Valdovinos FS, Ramos-Jiliberto R, Flores JD, Espinoza C, Lopez G (2009) Structure and dynamics of pollination networks: the role of alien plants. Oikos 118:1190–1200

Watson MA, Casper BB (1984) Morphogenetic constraints on patterns of carbon distribution in plants. Annu Rev Ecol Syst 15:233–258

Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. Trends Ecol Evol 24:136–144

Woods TM (2006) A comparison of the reproductive systems of the invasive *Lespedeza cuneata* (Dum.-Cours.) G. Don (Fabaceae) with three native congeners in the Flint Hills region of the tallgrass prairie. M.S. Thesis, Kansas State University

Woods TM, Hartnett DC, Ferguson CJ (2009) High propagule production and reproductive fitness homeostasis contribute to the invasiveness of *Lespedeza cuneata* (Fabaceae). Biol Invasions 11:1913–1927