

Does tallgrass prairie restoration enhance the invasion resistance of post-agricultural lands?

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Abstract There is building interest in the use of ecological restoration to enhance the biotic invasion resistance of disturbed lands. However, few studies have rigorously examined the effect of community restoration on biotic invasion resistance under conditions of controlled invader propagule pressure. Results are presented from a field experiment conducted in a post-agricultural grassland in eastern Kansas to explore the interplay of tallgrass prairie restoration and invader propagule pressure in modulating plant invasion. Seed additions of multiple native and non-native species were used to provide a general test of biotic invasion resistance under varied propagule availability. Restoration increased plant diversity, increased above ground productivity, reduced the

availability of light, soil moisture and bare soil microsites and strongly suppressed the invasion of all species sown into the experiment, including the highly invasive exotic legume, *Lespedeza cuneata*. In the absence of restoration, *L. cuneata* rapidly dominated plots where it had been sown, particularly at the highest propagule pressure. Results of multiple regression modelling suggested that restoration most likely increased community resistance to *L. cuneata* invasion through changes in functional guild composition rather than through changes in species diversity. Overall our study indicates that restoration of abandoned agricultural land to native tallgrass prairie can enhance invasion resistance in the face of substantial invader propagule pressures by altering community composition to dominance by native species that are efficient in utilizing resources.

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Introduction

There is building interest in the use of ecological restoration to mitigate losses of biodiversity and ecosystem services in lands degraded by human activity (Hobbs and Harris 2001; Funk et al. 2008; Oakley and Knox 2013). Restoration may enhance ecosystem services such as nutrient retention,

pollution mitigation, productivity, soil sustainability, hydrological services and pollination, just to name a few (Benayas et al. 2009). The capacity of ecological communities to resist exotic species is also an important ecosystem service and there is considerable interest in using restoration to enhance the biotic invasion resistance of degraded habitats (Bakker and Wilson 2004; Funk et al. 2008). Although the concept of using restoration to control invasions has a strong intuitive appeal and considerable theoretical justification, more empirical work is needed to evaluate the extent to which restoration may be effective in repelling invasions.

The mechanistic foundation for employing restoration as tool to manage invasions originates largely from basic research to understand the specific properties of communities that govern their resistance or susceptibility to invasion (Elton 1958; Farigione et al. 2003; Price and Weltzin 2003; Cleland et al. 2013). Processes that modulate the availability of resources to invaders have received a lot of attention in the plant invasion literature. (Davis et al. 2000; Tilman 2004). The theory of fluctuating resources (Davis et al. 2000) posits that plant communities will be most resistant to invasion when resource supply is closely matched by plant uptake. Communities may become more open to invasion when imbalances occur such as when resource pulses exceed plant uptake or when uptake is reduced by herbivory, disturbance or other sources of plant impairment. A complementary hypothesis, the diversity-invasibility hypothesis (Elton 1958; Fargione et al. 2003), posits that species diversity enhances invasion resistance by increasing the diversity of functional traits, by filling resource niche space and by enhancing resource-use complementarity among species. Alternatively, invasion resistance may be more closely tied to the traits and resource utilization of dominant species or to particular functional guilds rather than to diversity *per se* (mass ratio hypothesis; Grime 1998; Longo et al. 2013). These resource-based theories of invasion all have empirical support and thus provide a compelling basis for further research into the efficacy of restoration for invasive species management. Surprisingly, few rigorous and well-replicated experimental studies have explored the effectiveness of restoration in enhancing invasion resistance under conditions of controlled invader propagule inputs (see Blumenthal et al. 2005).

The availability of invader propagules to the recipient habitat (propagule pressure) may determine the extent to which the potential of a community to be invaded is realized (Davis et al. 2000; Foster and Dickson 2004; Von Holle and Simberloff 2005). From observational studies evaluating the regional distributions of introduced species it is difficult to separate the influence of invasion resistance and propagule pressure in determining observed patterns of variation in invader abundance among habitat types (Lonsdale 1999; Von Holle and Simberloff 2005). Lonsdale (1999) argued that biotic resistance has been overemphasized in the literature, with less attention focused on immigration and how it may interact with attributes of the recipient community to modulate invasion and govern the distribution of introduced species within the invaded region.

To what extent does invasion depend on propagule pressure relative to attributes of the community? Are there propagule pressures that overwhelm inherently resistant communities? Can we restore vulnerable habitats to communities capable of withstanding high invader propagule pressures of even the most capable invaders? Such questions are difficult to address with studies that do not directly manipulate propagule pressure. In this paper we utilize a field experiment to evaluate effects of tallgrass prairie restoration and propagule pressure on plant invasion in a successional post-agricultural grassland in eastern Kansas. Our approach involved the experimental sowing of twenty non-resident species into plots that had been previously restored to tallgrass prairie and into non-restored control plots that supported less diverse old-field vegetation. Seed of multiple native and non-native species were sown in mixture to provide a general test of invasion resistance and to evaluate the colonization/invasion success of native and non-native species. Throughout this paper experimentally-sown, non-native species are referred to as *invaders* while experimentally-sown native species are referred to as *native colonizers*. For simplicity we use the term *invasion* as a general reference to the colonization of plots by experimentally added species, regardless of whether the species are native or non-native.

In this study we pay particular attention to the experimentally sown legume, *Lespedeza cuneata* (Dum. Cours.) G. Don which is a problematic exotic and noxious weed in Kansas and across the south-eastern and mid-western US (USDA-NRCS 2001). *L.*

cuneata is native to Asia, originally introduced to the US from Japan (Guernsey 1970) for use as forage, mine-reclamation, erosion control and vegetation in rights-of-way, among other uses (Silliman and Maccarone 2005). This species commonly invades disturbed habitats such as roadsides, old-fields and pastures (Eddy and Moore 1998) and is viewed as a threat to tallgrass prairie in Kansas (Silliman and Maccarone 2005). Our own studies in the agricultural landscapes of northeastern Kansas have shown that *L. cuneata* is more common in over-grazed pastures and post-agricultural fields than in intact tallgrass prairie (Jog et al. 2006; Houseman et al. 2014). Although the observed landscape distributions of *L. cuneata* may give the appearance that tallgrass prairie is more invasion resistant than abandoned agricultural land, the extent to which these distributions may reflect spatial variations in invader propagule pressure versus variation in the inherent invasion resistance of the vegetation is not known. The experimental addition of *L. cuneata* seeds to intact native prairie could clarify the issue but would be unethical to carry out. As an alternative, we evaluate the invasion resistance of prairie vegetation through the use of controlled experimental restoration plantings and ask if the invasion resistance of restored communities varies with propagule input. We also explore whether variation in biotic resistance to *L. cuneata* invasion in our experiment is better explained by shifts in resident plant diversity, in accordance with the diversity-invasibility hypotheses (Elton 1958), or through changes in functional guild composition or productivity.

Methods

Study site

This study was conducted in an abandoned cool-season hay-field at the University of Kansas Field Station (KUFS) in northeastern Kansas (Jefferson County; 39°N, 94°W). Soils at the site are clay and silty loams over glacial till. Mean annual precipitation is 900 mm with mean annual temperature of 13 °C. The site has a history of tillage and row crop production but was converted to cool-season hay production several decades before the initiation of the current study. When research at the site began in 1999 it was dominated by introduced C₃ perennial grasses

that had been planted for hay: *Bromus inermis* Leyss. and *Schedonorus arundinaceus* (Schreb.) Dumort., nom. cons. Other common species present at the time were *Poa pratensis* L. (introduced C₃ perennial grass), *Andropogon virginicus* L. (native C₄ grass), *Solidago canadensis* L. (native forb), *Kummerowia stipulacea* (Maxim., introduced legume), *Solanum carolinense* L. (native forb).

Experimental procedure

For this study we re-purposed plots from a previous experiment established in 1999. Below we describe only the details of the original experimental design pertinent to the present study. Full details of the original experiment can be found in Foster and Dickson (2004) and in Online Resource 1.

Fall 1999, sixty-four 1 m² plots were established in an 8 × 8 grid with 2 m buffers between plots. Half of the plots were assigned to receive seeds of 32 plant species with the other half left as controls. Seeds added to plots in 2000 and 2001 included those of 25 native prairie species (Foster and Dickson 2004). Prior to the addition of the manipulations discussed below, plant cover surveys were conducted in 2003 (Foster and Dickson 2004 and 2007). Relevant to the present study, the original sowing treatment shifted the community to native prairie species dominance relative to the non-sown controls (see results below). Hereafter we refer to this treatment as the restored treatment.

Fall 2007 we initiated a new experiment in a subset of the original 64 plots to investigate effects of restoration and propagule pressure on invasion. The new design constitutes a factorial experiment with two factors: Restoration (REST) and invader/colonizer Propagule Pressure (PP). *REST* (two levels: non-restored; restored): In 2007, prior to the addition of invader/colonizer species, abundant species in restored plots included: *Andropogon gerardii* Vitman (Big bluestem); *Panicum virgatum* L. (Switchgrass), *Schizachyrum scoparium* (Michx.) Nash (Little bluestem); *Sorghastrum nutans* (L.) Nash (Indian grass) and *Lespedeza capitata* Michx. (Roundhead lespedeza). *PP* (three levels): In December 2007 seeds of the invasive legume, *L. cuneata*, and 19 other species (Table 1) were hand sown into plots at rates of 0, 40, and 400 viable seeds per species. Plots sown at each level of propagule pressure were replicated 8 times yielding a total of 48 plots included in the

Table 1 Characteristics of sown species and their abundances (% cover in 2008 and 2010) in the not-restored and restored plots to which they were added

Species name	Mean % cover 2008		Mean % cover 2010	
	Invaded not-restored plots	Invaded restored plots	Invaded not-restored plots	Invaded restored plots
Native species				
<i>Astragalus Canadensis</i> (L)	0.02	0.01	0	0.33
<i>Bouteloua curtipendula</i> (C4G)	0	0	0.49	0.22
<i>Bouteloua gracilis</i> (C4G)	0	0	0	0
<i>Chamaecrista fasciculata</i> (L)	13.25	10.98	0.09	0.04
<i>Coreopsis lanceolata</i> (F)	0.63	0.34	0.04	0
<i>Coreopsis tinctoria</i> (F)	0.44	0.30	0	0
<i>Dracopis amplexicaulis</i> (F)	2.87	2.7	0	0
<i>Heliopsis helianthoides</i> (F)	1.17	0.70	1.1	0.58
<i>Helianthus maximiliani</i> (F)	1.10	0.47	6.67	0.79
<i>Koeleria macrantha</i> (C3G)	0	0	0	0
<i>Oenothera macrocarpa</i> (F)	0.39	0.18	0	0
<i>Oligoneuron rigidum</i> (F)	0.04	0.01	0.09	0
<i>Pascopyrum smithii</i> (C3G)	0	0	0	0
<i>Penstemon digitalis</i> (F)	0.66	0.2	1.22	0.5
<i>Symphyotrichum novae-angliae</i> (F)	0.03	0.01	0.4	0.01
<i>Verbena stricta</i> (F)	0.02	0.01	0.15	0
Non-native species				
<i>Dactylis glomerata</i> (C3G)	0	0	0	0.05
<i>Hesperis matronalis</i> (F)	0	0	0	0
<i>Lespedeza cuneata</i> (L)	1.35	0.75	69.08	7.71
<i>Phleum pratensis</i> (F)	0	0.01	0.01	0.0

Taxonomy follows USDA plants (<http://plants.usda.gov>). C3G C₃ grass, C4G C₄ grass, F forb, L legume

current study. The other 19 sown species included 17 native prairie species and two non-native species all common in nearby habitats but absent from the experimental plots in 2007. Seeds of *L. cuneata* were collected from nearby populations during fall 2006. Seeds of other species were purchased from a regional supplier. Prior to the addition of invader/colonizer seed all plots were burned in March 2006. After the experimental addition of invader/colonizer species the plots were burned again in March 2010, early in the last year of the study.

Data collection and analysis

A percent cover survey was conducted August 2007 to evaluate pre-invasion community states in terms of: overall species composition; total plant cover; cover of

prairie species in aggregate; cover of non-prairie species in aggregate; species richness; community evenness; species diversity (exponent of Shannon entropy: $e^{H'}$), and functional guild diversity ($e^{H'}$ based on aggregate covers of C₃ graminoids; C₄ graminoids; forbs, legumes). Percent cover was estimated independently for each species such that the sum of cover for a plot could exceed 100 %. To assess microsite conditions and resources at the time of sowing (2008) we measured % bare ground cover, leaf area index (LAI), light availability and % soil moisture. LAI and Photosynthetically Active Radiation at soil surface (percentage of PAR penetration) were measured August 2008 using a 0.8-m PAR ceptometer (Decagon Devices, Pullman, Washington, USA). Soil moisture (% volumetric) within the top 11 cm of soil was measured in July 2008 using Time Domain

Reflectometry (TDR: TRIME-FM, Mesa Systems Co., Medfield, Mass. USA.), 5 days following rainfall. All community characteristics measured just prior to invasion (2007) and within the first year of invasion (2008) are presented to illustrate major differences between non-restored and restored plots at the time that this current invasion study began and to investigate how initial community states may have influenced invasion success as measured in the last year of the study (2010). Henceforth we refer to these measurements jointly as *initial community characteristics*.

Annual post-invasion cover surveys were conducted August 2008–2010. To evaluate invader/colonizer seedling emergence in the first year post-invasion (2008) we counted seedlings of all added invader/colonizer species at the time of the cover survey within a 20 × 20 cm frame placed at the center of each plot. During the 2009 and 2010 cover surveys we also recorded incidence of *L. cuneata* reproduction by noting when at least one individual in a plot was found in flower or with flower buds. August 2010, we harvested plant biomass by clipping a 0.1 × 1 m strip from each plot. Biomass was sorted to live and litter fractions. The live fraction was further sorted to species. Biomass fractions were dried to constant mass at 70 °C in a forced air oven and weighed.

Univariate ANOVAs were used to evaluate effects of restoration on initial community characteristics and post-invasion responses. Post-invasion response variables included the following invasion metrics: invader/colonizer species richness; aggregate abundance of native colonizer species (seedling emergence, cover and biomass); and abundance of the dominant non-native invader, *L. cuneata* (seedling emergence, cover and biomass).

Because the objective was to examine the impact of REST and PP on the invasion success of added species, analysis of each invasion metric excluded plots with PP = 0. Two-factor repeated measures ANOVA (RM-ANOVA) was used to evaluate effects on metrics measured in multiple years (invader/colonizer richness and cover). Two-factor ANOVA was used for metrics measured in only a single year (seedling emergence in 2008; biomass in 2010). For all ANOVAs normality was evaluated by examining the frequency histogram of residuals, skewness, kurtosis and normal probability plots of residuals. Homoscedasticity was examined using Levene's test.

Modest deviations from normality and homogeneity for cover and biomass variables were successfully improved through ln-transformation. Transformation of *L. cuneata* cover could not overcome among-year heteroscedasticity due to low variance in 2008. As a result, RM-ANOVA conducted on this invasion metric excluded 2008 data.

Finally, to further explore potential predictors of invasion resistance across all plots that were experimentally invaded we employed a Generalized Linear Model evaluating the dependence *L. cuneata* biomass as measured in 2010 (ln-transformed) on select community attributes and resource measures. A central objective of this analysis was to examine whether variation in *L. cuneata* invasion (or resistance to *L. cuneata* invasion) can be better explained by plant species diversity of the recipient community prior to invasion after controlling for other factors, and thus supporting the diversity-invasibility hypothesis of community invasion resistance, or by the independent influence of changes in dominant functional guild composition and/or plant productivity. Because of limited sample size the number of predictor variables used was restricted to those that showed bi-variate associations with *L. cuneata* biomass at the $P < 0.10$ level (Pearson correlation). Predictor variables entered into the model included: exponent of Shannon entropy (e^H) in 2007; functional guild composition in 2007; total plant cover in 2007 (a surrogate for total above ground productivity); % PAR penetration in 2008; and soil moisture in 2008. We also included propagule pressure in the model as a categorical factor, allowing us to isolate the contributions of the predictor variables of interest apart from the known effects of varied seed input. Total plant cover was used as a surrogate for overall above ground productivity rather than LAI because the latter was found to be co-linear with PAR penetration. The predictor variable representing variation in functional guild composition was derived via data reduction using Principle Component Analysis (PCA). The first PCA axis produced by an analysis of the relative covers of forbs, legumes, C₃ grasses and C₄ grasses, comprised 83 % of the variation in the data. All subsequent axes produced Eigen values less than one and so were not used. An interpretation of this PCA axis from its loading coefficients is discussed in the results and discussion sections. All predictor variables were standardized (z-transformation) prior to analysis. In the Generalized Linear Model the dependent

variable was modeled as a linear scale response with model parameters estimated using maximum likelihood. All statistical analyses conducted for this study were performed using SPSS (v. 20).

Results

Initial community characteristics

As measured in the year prior to invasion (2007) and the initial year of invasion (2008) restoration led to changes in a whole suite of plant community characteristics (Tables 1, 2) Relative to non-restored plots, restored plots exhibited greater native prairie species cover (6338 % increase), species richness (31 % increase), community evenness (57 % increase), species diversity (112 % increase), functional guild diversity (58 % increase), LAI (84 % increase) and total plant cover (62 % increase). Restored plots exhibited reduced non-prairie species cover (69 % decrease), PAR penetration (54 % decrease), bare ground (74 % decrease) and soil moisture (17 % decrease).

Invader/colonizer responses

Overall, 16 of the 20 added species emerged over the course of the study (Table 1), 14 of which were recorded in the first year survey in 2008. The other two

appeared in later surveys. All but one of the added species recorded in the initial survey exhibited lower mean cover in restored versus non-restored plots (2008), significantly more than would be expected by chance (binomial test: $P < 0.01$). In 2008, the native annual legume *Chamaecrista fasciculata* (Michx.) Greene was the most abundant added species, followed by perennial forbs *Dracopis amplexicaulis* (Vahl) Cass (native perennial forb) and *L. cuneata* (Table 1). At termination of the experiment in 2010 *L. cuneata* was by far the most abundant of the added species, with cover values over 10 times greater than the next most abundant added species, *Helianthus maximiliani* Schrad, in both the non-restored and restored plots.

Invader/colonizer seedling emergence, measured as seedling density in 2008, was increased significantly by propagule pressure but was unaffected by restoration (Fig. 1a, b). This was true when evaluating the seedling emergence of all native colonizers in aggregate (Fig. 1a) and when evaluating the seedling emergence of *L. cuneata* alone (Fig. 1b).

For the invasion metrics derived from cover survey data (invader/colonizer species richness, native colonizer cover, *L. cuneata* cover), RM-ANOVAs revealed significant variation associated with the main effects of year, restoration and propagule pressure (Fig. 2). Invader/colonizer species richness declined over time, was reduced by restoration, but was

Table 2 Initial characteristics of the plant community (Mean \pm 1 SE) in not-restored and restored plots

Community characteristics At the time of invasion	Not restored (Mean \pm 1 SE)	Restored (Mean \pm 1 SE)
Prairie species cover (%)	1.90 \pm 1.10	122.34 \pm 3.40***
Non-prairie species cover (%)	91.91 \pm 2.42	27.99 \pm 2.31***
Species richness	8.28 \pm 0.43	10.87 \pm 0.42***
Evenness	0.49 \pm 0.02	0.77 \pm 0.01***
Species diversity ($e^{H'}$)	2.98 \pm 0.18	6.32 \pm 0.24***
Functional guild diversity ($e^{H'}$)	1.73 \pm 0.10	2.73 \pm 0.06***
Total plant cover (%)	93.07 \pm 2.45	150.81 \pm 3.42***
LAI	2.71 \pm 0.0.15	5.00 \pm 0.30***
PAR penetration (%)	26.50 \pm 2.25	12.12 \pm 1.76***
Bare-ground cover (%)	3.54 \pm 1.02	0.91 \pm 0.44***
Soil moisture (%)	23.42 \pm 1.03	19.54 \pm 0.80**

One way ANOVA ($df = 1, 31$): * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The effect of restoration on prairie species cover was evaluated using a non-parametric test (Mann–Whitney U test). All response variables except soil moisture remained significant after adjustment for multiple comparisons (for 11 tests; * $P < 0.0045$)

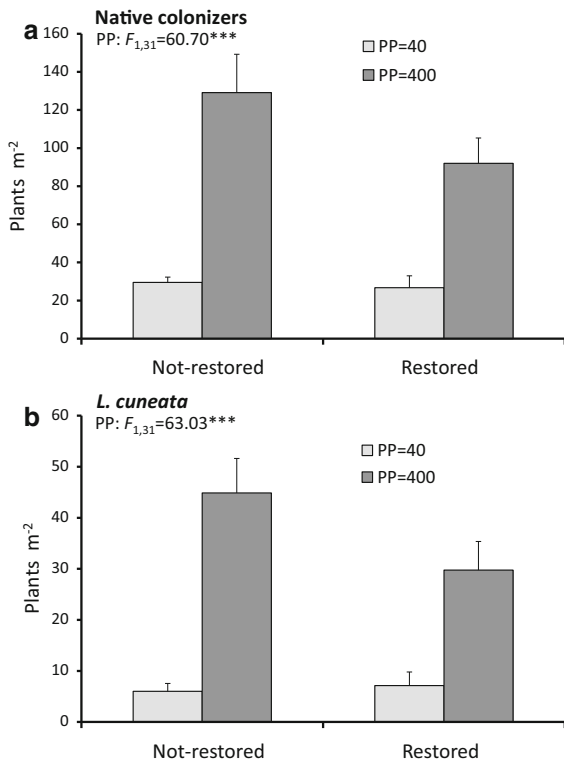


Fig. 1 Seedling emergence measured in 2008 as seedling density (mean + 1 SE) of native colonizers in aggregate (a) and *L. cuneata* (b) in response to experimental treatments. Sources of variation in ANOVA: PP = propagule pressure; REST = restoration. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Note difference in scaling of the y-axis between a and b

increased by propagule pressure (Fig. 2a). Native colonizer cover was reduced by restoration to the greatest extent in 2009 when it peaked in non-restored plots (YEAR × REST; Fig. 2b). Native colonizer cover was increased by propagule pressure. *L. cuneata* cover was reduced by restoration, an effect that became more pronounced overtime (YEAR × REST; Fig. 2c). *L. cuneata* cover increased in response to enhanced propagule pressure and increased dramatically over time in non-restored plots, particularly at high propagule pressure where it approached 100 % cover by 2010. In contrast, in restored plots *L. cuneata* cover was strongly suppressed to less than 4 % cover.

Measured in the final growing season (2010), native-colonizer biomass and *L. cuneata* biomass were both significantly reduced by restoration and increased by propagule pressure (Fig. 3a, b). A significant interaction term for native colonizers

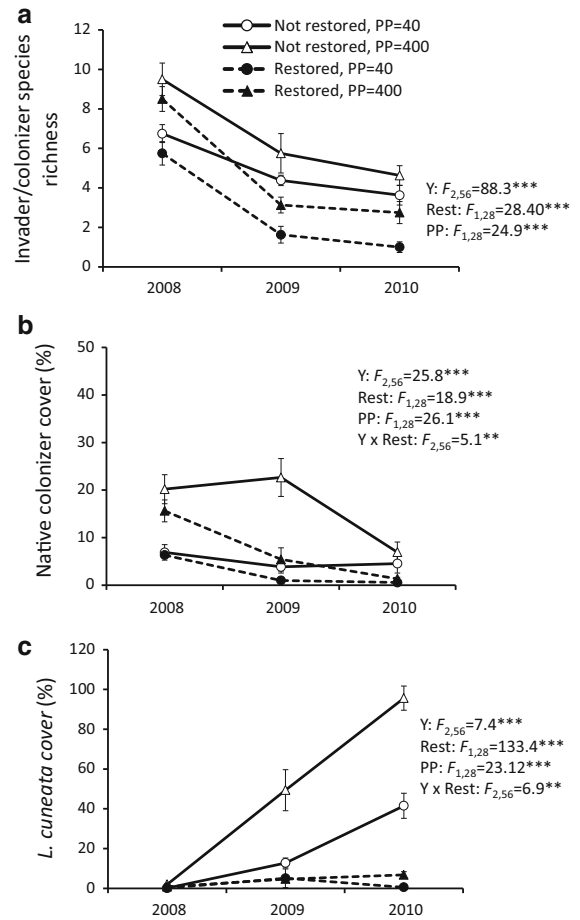


Fig. 2 Treatment responses (mean ± 1 SE) over time for the three invasion metrics: Invader/colonizer species richness (a) Native colonizer cover (b) and *L. cuneata* cover (c). Sources of variation in RM-ANOVA: PP = propagule pressure; REST = restoration. RM-ANOVA: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Note differences in scaling of the y-axis among a, b and c

indicated a stronger suppression of biomass by restoration at high propagule pressure (87 % decrease) than at low propagule pressure (51 % decrease) and a stronger enhancement of biomass by increased propagule pressure in non-restored plots (1673 % increase) than restored plots (354 % increase). The effects of restoration and propagule pressure on *L. cuneata* biomass were additive (no interaction). Restoration reduced *L. cuneata* biomass by 97 %. Enhanced propagule increased *L. cuneata* biomass by 135 %.

In the 2009 and 2010 surveys, *L. cuneata* was found to be in flower in significantly more non-restored plots

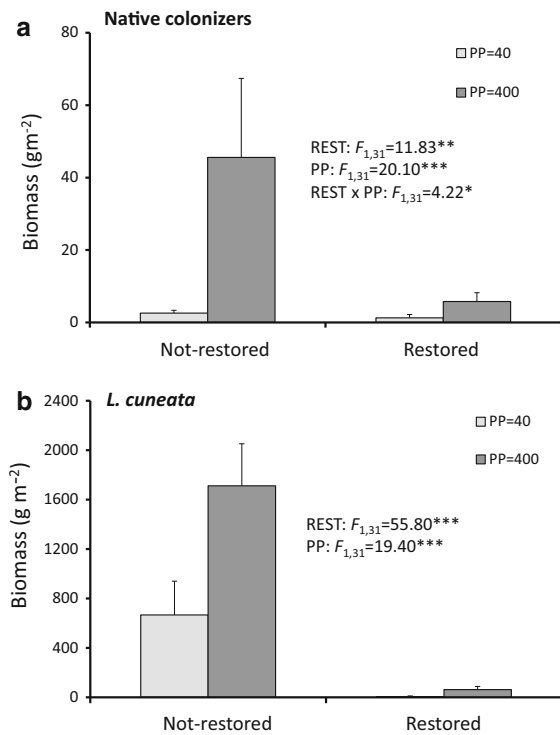


Fig. 3 Biomass (mean + 1 SE) of native colonizers in aggregate (a) and *L. cuneata* (b) in response to experimental treatments as measured in 2010. Sources of variation in ANOVA: PP = propagule pressure; REST = restoration. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Note difference in scaling of the y-axis between a and b

than restored plots (binomial tests: $P < 0.01$). In 2009, *L. cuneata* was found in flower in all but one of the non-restored plots (15 out of 16) to which it had been sown, but found in flower in none of the restored plots. In the 2010 survey *L. cuneata* was found in flower in all 16 of the non-restored plots to which it was sown but found in flower in none of the restored plots.

A Generalized Linear Model evaluating the dependence of *L. cuneata* biomass on community attributes and resource measures across all experimental plots identified functional guild composition as the only predictor (other than propagule pressure) that remained significant after accounting for all other predictor variables (Table 3). Loading coefficients on the functional guild PCA axis reflect a contrast between C_3 grasses at the negative end (loading = -0.92) and C_4 grasses and legumes at the positive end (C_4 grass loading = 0.90 ; legume loading = 0.88). The negative coefficient for functional

guild composition in the model indicates reduced *L. cuneata* invasion in plots that were relatively more abundant in C_4 grasses and legumes compared to C_3 grasses.

Discussion

In this study we found that restoration of an abandoned hay field to diverse native prairie vegetation strongly increased biotic resistance to invasion in the face of substantial propagule pressures from a suite of native colonizers and an aggressive exotic legume of significant economic concern in Kansas: *Lespedeza cuneata*. Although altered propagule pressure and restoration both influenced invasion rates significantly, an order-of-magnitude increase in seed input did not overwhelm the invasion resistance of restored vegetation. Overall our study confirms the inherent invasion resistance of intact native tallgrass prairie vegetation at our study site and supports the use of restoration as a tool to enhance invasion resistance of successional plant communities on abandoned agricultural land.

Invasion rates may vary depending on a community's inherent susceptibility to invasion, invader identity and invader propagule pressure (Eschtruth and Battles 2009; Van Kleunen et al. 2010). Our study was established to evaluate the potential interplay of all three of these factors. We added a seed mixture of species that included native colonizers and non-native invader species to provide a general assessment of how restoration might influence invasion processes at multiple rates of propagule pressure. The exotic legume, *L. cuneata*, was by the far the most successful sown species, both in non-restored and restored plots. However, the full expression of its invasive potential was revealed in non-restored plots where it rose to dominance over all other species after three growing seasons. Native colonizers in aggregate attained modest abundance in 2009 within the non-restored plots that received high propagule pressure, largely reflecting the contribution of two perennial forbs: *Helianthus maximiliani* Schrad. (Maximilian sunflower) and *Heliopsis helianthoides* (L.) Sweet (Oxeye daisy). However, aggregate native colonizer cover in this treatment declined markedly by the third year likely due to competitive suppression by *L. cuneata* that was sown with them in the species mixture.

Table 3 Generalized linear model evaluating the dependence of *L. cuneata* invasion (biomass 2010) on propagule pressure, community attributes and resource measures at the onset of invasion

Parameter	Beta	SE	Lower 95 % CI	Upper 95 % CI	Wald X^2	df	P
(Intercept)	2.12	0.74	0.67	3.58	8.21	1	0.004
Propagule pressure	0.78	0.18	1.13	0.44	19.44	1	<0.001
Species diversity ($e^{H'}$)	0.02	0.22	-0.40	0.45	0.01	1	0.910
Functional guild composition (PCA1)	-0.53	0.21	-0.94	-0.12	6.53	1	0.011
Total plant cover (%)	-0.30	0.23	-0.75	0.14	1.76	1	0.184
Soil moisture (%)	-0.03	0.03	-0.09	0.03	0.86	1	0.355
PAR penetration (%)	-0.02	0.16	-0.34	0.30	0.01	1	0.919

Omnibus test: Likelihood ratio $X^2 = 41.05$, $df = 6$, $P < 0.001$

Dominance of *L. cuneata* over the other 19 added species precludes a detailed comparative analysis of how the added species differed in their capacity to invade or a nuanced analysis of traits associated with invasion success across all species. This is a significant limitation of the experimental design. However, our findings do highlight the clear competitive superiority of *L. cuneata* over the other added species in non-restored plots. We note that in the initial year of invasion (2008), *L. cuneata* seedling density and cover was much lower than the aggregate density and cover of native colonizers in aggregate. Despite this initial disadvantage in numbers, *L. cuneata* was able to increase rapidly in abundance over time and eventually dominate the native colonizers and all other resident species in the non-restored plots. Clearly this species possesses novel features that suit it well for the invasion of abandoned lands in this region. These features may include early emergence, rapid growth rate, prolific seed production and seedbank, nitrogen-fixation, drought-resistance, resistance to natural enemies, exudation of allelopathic compounds and alterations of the soil microbial community (Donnelly 1954; Kalburtji et al. 2001; Schutzenhofer and Knight 2007; Allred et al. 2009; Coykendall and Houseman 2013; Lingzi et al. 2014).

Despite its tremendous capacity to invade and dominate non-restored plots that were initially occupied by introduced C_3 grasses and other old-field species, experimental restoration reduced *L. cuneata* biomass by over 97 % as measured in the final year of the experiment. We also found that restoration almost completely suppressed the flowering and seed production of this species. Enhanced propagule pressure increased *L. cuneata* invasion, an effect that was additive to the effect of restoration. This additivity

indicates that increased propagule pressure elevated *L. cuneata* biomass to the same relative extent in restored plots as non-restored plots. However, the absolute increase of *L. cuneata* biomass in restored plots was dwarfed by the increase observed in non-restored plots, indicating very strong biotic resistance to invasion in spite of an order-of-magnitude increase in seed input. These results support the contention that the low incidence of *L. cuneata* observed in tallgrass prairie remnants in northeastern Kansas (Jog et al. 2006; Hall and Foster in preparation) is probably not explained entirely by low rates of propagule pressure, but also likely reflects the contribution of biotic invasion resistance.

Although the effects of restoration on invasion in the study were impressive, we caution that our results report invasion dynamics through only three growing seasons. *L. cuneata* was still present in restored plots, albeit at low abundance, when the study was terminated. We can't know if *L. cuneata* would have eventually disappeared under competitive suppression by native plants or if it would have slowly increased to dominance over a longer time frame. For ethical reasons we terminated the experiment after 2010. Another limitation is that invader propagules were added only once and constrained to either 40 or 400 seeds per plot. Under even greater propagule pressure or a more realistic scenario of multi-year seed input, the results may have come out differently. We do not wish to imply that native and restored prairies are immune to invasion by *L. cuneata*. In fact, instances of infestation of tallgrass prairie and rangeland by this species have been documented, (Eddy and Moore 1998; Silliman and Maccarone 2005), although it is unclear the extent to which these incidences may have been facilitated by disturbance. However, our findings

suggest that restoration can at least greatly slow establishment and reproduction of *L. cuneata* in early stages of invasion, extending a window of opportunity to intervene with other more targeted control strategies before populations reach critical size or before individuals become reproductive. This is an important point because once reproductive populations and seed banks of invasive species are established, control is likely to be much more difficult and costly (Carter and Ungar 2002). This may be especially true for *L. cuneata* due to its prolific seed production, high seed viability and propensity to form persistent seed banks (Carter and Ungar 2002; Wong et al. 2012).

It is also important to note that although restoration greatly reduced *L. cuneata* biomass and cover as measured in year three, the initial emergence of *L. cuneata* seedlings as measured in 2008 was unaffected by restoration. Large numbers of seedlings readily emerged in non-restored and restored plots and propagule pressure increased *L. cuneata* emergence in both treatments. This suggests that the intensity of invasion resistance of a community may vary with life stage of the invader. In this case it appears that the resistance of restored plots to invasion resulted more from the suppression of seedling survivorship and/or subsequent seedling growth than from suppression of germination and initial seedling emergence. Although we did not measure the size of *L. cuneata* individuals in this study it was clear from casual inspection that *L. cuneata* plants in the restored plots were dwarfed by those in the non-restored plots in 2010 (personal observation, B. Foster), indicating suppression of growth.

Although not confirmatory, our general findings are consistent with resource-based theories of invasion resistance (Davis et al. 2000; Tilman 2004; Fargione and Tilman 2005). The more invasion resistant restored plots exhibited greater attenuation of PAR by the canopy, lower soil moisture and fewer bare ground microsites available for seedling establishment than non-restored plots. Restored communities also had much greater aboveground productivity as indicated by greater total plant cover and greater leaf area, consistent with more complete utilization of limiting resources by the community. Our findings are also broadly consistent with the diversity-invasibility hypothesis (Elton 1958; Levine and D'Antonio 1999; Tilman 2004), showing greater species and functional guild diversity in restored plots, coincident

with reduced invasion. Despite the congruence of our results with the predictions of the diversity-invasibility hypothesis and other resource-based theories of invasion resistance, our findings are largely correlative. Our experiment was designed to evaluate the effects of prairie restoration on invasion resistance but not to fully distinguish between alternative mechanisms of invasion resistance or to fully gauge the relative contributions of the numerous and potentially confounded community attributes altered by restoration. With this limitation in mind, the results of a Generalized Linear Model do suggest that enhanced invasion resistance in this experiment was more closely associated with the abundance of the C₄ grass and legume functional guilds than through changes in species diversity or through changes in aboveground productivity. Although we interpret this model with caution, this result is more consistent with the mass-ratio hypothesis of invasion resistance (Grime et al. 1998; Longo et al. 2013) which posits that changes in community invasion resistance result more from shifts in dominant species or functional guild composition than through changes in species diversity *per se*.

Although C₄ grass and legume species were present in both restored and non-restored plots they were more abundant in restored plots and likely played a key role in mediating invasion resistance. C₄ tall grasses have been found to be more complete in their reduction of available soil nitrogen (*N*) than C₃ grasses (Lower R* for N; Tilman and Wedin 1991). Efficient resource reduction by C₄ prairie grasses has been linked to their low *N* requirement and extensive root systems (Tilman and Wedin 1991), but also to reduced soil *N* mineralization associated with low quality litter (low C:N) inputs (Wedin and Tilman 1990). We did not measure root biomass or available soil *N* in this study but it is almost certain that restoration increased root biomass in our restored plots. In a separate study conducted nearby in the same field it was found that prairie restoration led to more than a three-fold increase in root biomass, almost entirely attributable to C₄ prairie grasses (Foster et al. 2007). It is possible that reduced soil moisture measured in our restored plots was the result of greater root biomass and it is reasonable to surmise that soil *N* availability may have been negatively affected as well. However, it is also possible that any such reduction of *N* availability could be countered by N-fixation associated with the dominant prairie legume, *Lespedeza capitata*. Given

that C₄ grasses were the most consistently abundant and the tallest species in restored plots it is also probable that this functional guild contributed to the reduction in light availability observed in those plots as well. The abundance of the native legume, *Lespedeza capitata*, in restored plots raises the intriguing possibility that *L. cuneata* invasion was limited in restored plots by its phylogenetic and functional similarity to the abundant congener already present in the community, consistent with the niche-based principle of limiting similarity (Funk et al. 2008). Although this is an intriguing possibility it is beyond the scope of this study to confirm or reject the contribution of this mechanism. More controlled experimentation such as that employed by Turnbull et al. (2005) would be needed to address this question. In that study it was found that invading legume species were less able to invade grassland plots dominated by resident legumes than plots dominated by other functional groups.

Conclusion

Despite the recent emphasis on restoration as a tool to enhance the biotic resistance of degraded communities, relatively few well-replicated experiments have been conducted in the field to test the concept in the context of tallgrass prairie under conditions where invader propagule input has been accounted for (but see Blumenthal et al. 2005). Our study indicates that the restoration of abandoned post-agricultural land to diverse native prairie vegetation can enhance biotic invasion resistance in the face of substantial invader propagule pressures. In our study experimental restoration likely enhanced biotic resistance to invasion through shifts in community composition to dominance by native species that are efficient in utilizing resources rather than through effects of increased diversity *per se*. This study clarifies the importance of biotic invasion resistance as an important ecosystem service provided by native tallgrass prairie vegetation.

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Compliance with ethical standards

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

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