

Plant community diversity and composition provide little resistance to *Juniperus* encroachment

Amy C. Ganguli, David M. Engle, Paul M. Mayer, and Eric C. Hellgren

Abstract: Widespread encroachment of the fire-intolerant species *Juniperus virginiana* L. into North American grasslands and savannahs where fire has largely been removed has prompted the need to identify mechanisms driving *J. virginiana* encroachment. We tested whether encroachment success of *J. virginiana* is related to plant species diversity and composition across three plant communities. We predicted *J. virginiana* encroachment success would (i) decrease with increasing diversity, and (ii) *J. virginiana* encroachment success would be unrelated to species composition. We simulated encroachment by planting *J. virginiana* seedlings in tallgrass prairie, old-field grassland, and upland oak forest. We used *J. virginiana* survival and growth as an index of encroachment success and evaluated success as a function of plant community traits (i.e., species richness, species diversity, and species composition). Our results indicated that *J. virginiana* encroachment success increased with increasing plant richness and diversity. Moreover, growth and survival of *J. virginiana* seedlings was associated with plant species composition only in the old-field grassland and upland oak forest. These results suggest that greater plant species richness and diversity provide little resistance to *J. virginiana* encroachment, and the results suggest resource availability and other biotic or abiotic factors are determinants of *J. virginiana* encroachment success.

Key words: eastern redcedar, *H'*, seedlings, species richness, woody plant expansion.

Résumé : Des poussées généralisées de l'espèce intolérante au feu, *Juniperus virginiana* L., dans les prairies de l'Amérique du Nord où on a généralement éliminé le feu, crée le besoin d'identifier le mécanisme favorisant l'invasion par le *J. virginiana*. Les auteurs ont vérifié si le succès de l'envahissement par le *J. virginiana* est relié à la diversité et la composition en espèces dans trois communautés végétales. Ils ont prédit que l'envahissement par le *J. virginiana* (i) diminuerait avec une augmentation de la diversité et (ii) ne serait pas lié à la composition en espèces. Ils ont simulé l'envahissement en introduisant des plantules du *J. virginiana* dans une prairie d'herbes hautes, une vieille prairie, et une forêt de chêne en hauteur. Ils ont utilisé la survie du *J. virginiana* et sa croissance comme index du succès d'envahissement et ont évalué le succès en fonction des caractères de la communauté végétale (p. ex., richesse en espèces, diversité des espèces, et composition en espèces). Les résultats indiquent que l'envahissement par le *J. virginiana* augmente avec une augmentation de la richesse et de la diversité des plantes. De plus, la croissance et la survie des plantules du *J. virginiana* coïncident avec la composition en espèces seulement dans la vieille prairie et la forêt de chêne en hauteur. Ces résultats suggèrent qu'une plus grande richesse et diversité en espèces végétales apporte peu de résistance à l'envahissement par le *J. virginiana*, et les résultats suggèrent que la disponibilité des ressources et autres facteurs biotiques et abiotiques serait déterminante pour assurer l'envahissement par le *J. virginiana*.

Mots-clés : genévrier de Virginie, *H'*, plantules, richesse en espèces, expansion d'espèces ligneuses.

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Introduction

Woody-plant encroachment is a global phenomenon in grassland and savanna ecosystems (Archer 1994; Binggeli 1996). Livestock grazing, fire suppression, and climate

change contribute to woody-plant encroachment by native species and invasion by nonindigenous species into grassland and savanna ecosystems (Archer 1994; Van Auken 2000; Sankaran et al. 2005). Although encroachment and in-

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A.C. Ganguli.^{1,2} Rangeland Ecology and Management, Department of Plant and Soil Sciences, Oklahoma State University, Stillwater, OK 74078, USA; US Forest Service, Rocky Mountain Research Station, Boise, ID 83702, USA.

D.M. Engle. Rangeland Ecology and Management, Department of Plant and Soil Sciences, Oklahoma State University, Stillwater, OK 74078, USA; US Forest Service, Rocky Mountain Research Station, Boise, ID 83702, USA; Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078, USA.

P.M. Mayer. US Environmental Protection Agency, Office of Research and Development, National Risk Management Research Lab, Ada, OK 74820, USA.

E.C. Hellgren. Cooperative Wildlife Research Laboratory, Southern Illinois University Carbondale, Carbondale, IL 62901, USA.

¹Corresponding author (e-mail: amyganguli@gmail.com).

²Present address: 322 East Front Street, Suite 401, Boise, Idaho 83702, USA..

vasion are functionally similar processes, most of the recent published literature has concerned species invasions and community invasibility. Ecologists have identified attributes of highly invasive species (Rejmánek and Richardson 1996; Williamson and Fitter 1996), as well as biotic attributes (e.g., plant community traits, soil microbes) and abiotic attributes (e.g., resource availability, disturbance) of invaded plant communities (Hobbs and Huenneke 1992; Tilman 1997; Davis et al. 2000; Callaway et al. 2004). However, consistent prediction of invasion success is complicated by complex species–environment relationships.

Plant species pool (Smith and Knapp 2001), community composition (Planty-Tabacchi et al. 1996; Larson et al. 2001; Dukes 2002; Stohlgren et al. 2002), and community diversity (Tilman 1997; Levine and D'Antonio 1999; Stohlgren et al. 1999; Kennedy et al. 2002) have been identified as drivers of nonindigenous species invasion. Such studies have focused on identifying communities (Planty-Tabacchi et al. 1996; Lonsdale 1999; Symstad 2000; Larson et al. 2001; Stohlgren et al. 2002) and successional stages (Planty-Tabacchi et al. 1996) susceptible to invasion by nonindigenous species. When species diversity increases, niche occupation also increases, providing potential for resistance to invasion (Elton 1958; Tilman 1997; Gurvich et al. 2005). Relationships between plant species diversity and invasibility vary among studies as a function of spatial scale at which studies were conducted (Tilman 1997; Lonsdale 1999; Kennedy et al. 2002; Stohlgren et al. 2002) and the lack of control of extrinsic factors (Robinson et al. 1995; Levine and D'Antonio 1999). However, a clearer understanding of plant community traits promoting invasion and woody plant encroachment is required to develop effective approaches for their management.

We conducted a controlled field experiment to investigate the role of plant community traits in encroachment success of a native woody plant, *Juniperus virginiana* L., a tree with a rapidly expanding distribution in the North American Great Plains (Coppedge et al. 2001a; Hoch et al. 2002). Although *J. virginiana* is indigenous to eastern North American, it was excluded by fire from large expanses of the Great Plains before settlement by Europeans (Arend 1950; Bragg and Hurlbert 1976). Grassland encroachment by *J. virginiana* changes plant and animal community composition (Gehring and Bragg 1992; Coppedge et al. 2001a; Hoch et al. 2002; Chapman et al. 2004a; Horncastle et al. 2005), reduces herbaceous productivity (Engle et al. 1987; Smith and Stubbendieck 1990; Hoch et al. 2002), and alters biogeochemistry (Norris et al. 2001; Smith and Johnson 2004).

Unlike those exotic plants that invade successfully because they have escaped disease and insects in their new environment (Blumenthal 2005), *J. virginiana* is a native woody plant already exposed to several disease and insect enemies (Lawson and Law 1983). Fire and grazing, two keystone ecosystem processes that originally limited the range of *J. virginiana*, have been altered, undoubtedly contributing to the expansion of *J. virginiana* in North American grasslands since European settlement. Yet, the encroachment of *J. virginiana* has recently accelerated (Coppedge et al. 2001a, 2001b), suggesting that other factors and more current changes to the landscape promote *J. virginiana* encroachment. Therefore, our overall objective

was to determine if plant community traits such as diversity and species composition offer resistance to encroachment by *J. virginiana*. Characterized by high reproductive output, neither seed dispersal (Lawson and Law 1983; Holthuijzen and Sharik 1985; Horncastle et al. 2004; Briggs et al. 2005) nor germination (Lawson and Law 1983; Holthuijzen et al. 1987) of *J. virginiana* limit spread of this species within the Great Plains grasslands and surrounding vegetation types of central North America. Hence, we ignored these steps in encroachment by studying the seedling stage.

We simulated *J. virginiana* encroachment success by transplanting *J. virginiana* seedlings into three distinct plant community types free of fire and livestock grazing. We evaluated the relationship of *J. virginiana* seedling survival and growth, indices of *J. virginiana* encroachment, as a function of plant community traits (i.e., species richness, species diversity, and species composition) in tallgrass prairie, old-field, and upland oak forest. We predicted that encroachment success would decrease with increasing plant species diversity and that encroachment would be unrelated to species composition.

Materials and methods

Site description

Our study was conducted from 2001 to 2003 in north-central Oklahoma, USA (36°03'N, 97°12'W). We selected study locations in each of three contiguous plant communities: tallgrass prairie, old-field, and upland oak forest. Domestic livestock lightly grazed the research sites before the study, but we excluded livestock during the study. Average annual precipitation is 831 mm, mostly falling from April through October, and the average frost-free growing period is 203 d (National Oceanic and Atmospheric Administration 1999).

The tallgrass prairie and old-field sites were composed of fine to fine-loamy soils (Renfrow–Coyle–Grainola Association) derived from weathered shale and sandstone under prairie vegetation (Henley et al. 1987). Understory vegetation on the tallgrass prairie site was characterized by *Schizachyrium scoparium* (Michx.) Nash (28.1%), *Andropogon gerardii* Vitman (18.0%), *Sorghastrum nutans* (L.) Nash (5.0%), *Ambrosia psilostachya* DC. (4.0%), and *Symphyotrichum ericoides* (L.) Nesom (1.8%) [nomenclature follows the PLANTS database (USDA, NRCS 2008)]. The tallgrass prairie site also contained isolated mottes of *Rhus* spp., *Symphoricarpos occidentalis* Hook., *Prunus angustifolia* Marsh., and *J. virginiana*. The old-field was abandoned farmland that was terraced and eroded during cultivation in the first half of the 20th Century. Vegetation reestablished naturally after cultivation ceased, and *J. virginiana* invaded southern and eastern portions of this site. The understory vegetation on the old-field was characterized by *Schizachyrium scoparium* (34.7%), *Aristida purpurascens* Poir. (9.9%), *Sorghastrum nutans* (9.0%), *Ambrosia psilostachya* (1.8%), and *Lespedeza virginica* (L.) Britt. (0.9%). Soils of the upland oak forest site are loamy to fine-loamy (Stephenville–Darnelli Association) derived from weathered sandstone under oak (Henley et al. 1987). Dominant overstory vegetation on this site was *Quercus stellata* Wangenh. and *Quercus marilandica* Münchh. The understory vegetation

Table 1. Mean (\bar{x}) and standard error (SE) of plant community traits sampled on 1 m \times 1 m plots in tallgrass prairie, old field, and upland oak forest.

Plant community	Species richness	Shannon's H'	DCA axis 1 Sample scores
Tallgrass prairie	16.0 \pm 0.1	1.7 \pm 0.01	2.0 \pm 0.01
Old-field	12.0 \pm 0.1	1.3 \pm 0.10	1.0 \pm 0.02
Upland oak forest	6.0 \pm 0.1	1.1 \pm 0.02	3.8 \pm 0.03

was characterized by *Symphoricarpos occidentalis* (9.2%), *Dichanthelium oligosanthes* (J.A. Schultes) Gould (4.2%), *Q. stellata* (4.2%), *Celtis occidentalis* L. (3.0%), *Schizachyrium scoparium* (2.3%), *Parthenocissus quinquefolia* (L.) Planch. (1.0%), and *Toxicodendron radicans* (L.) Kuntze (0.9%).

Experimental design

We transplanted 2-year-old bare-root *J. virginiana* seedlings (Goldsby, Okla.) in a systematic grid design (180 m \times 180 m) within each plant community from 20 to 27 March 2001 following standard bare-root planting protocol. Tree planting bars (Jim-Gem[®]) 10 cm wide, 30 cm long, and 2.5 cm in thickness were used to plant the seedlings by hand to minimize disturbance effects, and the ground was locally compacted by foot to close the hole and eliminate air pockets. Following the transplant we did not use any cultural practices (e.g., water, fertilizer, or weeding) to influence seedling establishment rates. By systematically planting established seedlings, we intended to eliminate from the study the effects of germination and clumped distribution typical of *J. virginiana* seed dispersal by birds and mammals (Holthuijzen and Sharik 1985). In each grid, we transplanted 900 seedlings from 20–27 March 2001 so that each seedling was 6 m distant from each neighbor seedling. We established permanent 1 m \times 1 m plots centered on each seedling for vegetation measurements.

Field methods

We measured crown height and stem diameter of seedlings at the time of transplanting, and we measured crown height, stem diameter, and survival of seedlings at 6, 18, and 30 months following transplanting. Height of each seedling crown was measured by recording the standing height of the tallest leader, and stem diameter was measured with a digital caliper about 1 cm above the soil surface. Seedlings were considered dead if visibly lacking chlorophyll or if seedlings were removed (i.e., by herbivores or by animal excavation) from the location where they were transplanted. Average crown height and stem diameter of seedlings at the time of transplant were 255 mm and 5 mm, respectively. We combined seedling crown height and stem diameter into an index of seedling size (seedling size = seedling crown height \times seedling stem area) from which we calculated percent growth or the percent change in seedling size, [(final seedling size – initial seedling size) / initial seedling size] \times 100, so that we could assess seedling performance using a single response variable. The index of seedling size is equivalent to calculating stem volume of seedlings, a commonly used response variable in forestry investigations (Brandeis et al. 2002).

We estimated understory canopy cover by species as 0.25%, 0.5%, 1.0%, >1%–5%, >5%–10%, >10%–

25%, >25%–50%, >50%–75%, >75%–95%, or >95%–100%, within 1 m \times 1 m plots centered on each transplanted seedling. We sampled the tallgrass prairie and upland oak sites during the 2002 growing season and sampled the old-field site during the 2003 growing season. We calculated plant species richness (defined as the number of plant species present during the time of sampling; Magurran 2004) and species diversity (Shannon's H'); from cover data at the quadrat level (Ludwig and Reynolds 1988; Magurran 2004).

Statistical analysis

To determine whether species composition varied among and within plant communities, we performed detrended correspondence analysis (DCA) on square-root transformed species-cover data using CANOCO version 4.5 (Hill and Gauch 1980; ter Braak and Šmilauer 2002). The analysis down-weighted rare species, detrended by segments (using the default CANOCO option), and used nonlinear rescaling. We used axis 1 sample scores as an index of sample species composition in subsequent analyses within and across each plant community. Axis 1 sample scores of the DCA analysis are expressed as standard deviations of species turnover. Thus, plots that have sample scores that are closer together are indicative of plots with similar plant species composition. The three plant communities occupied distinct ordination space along axis 1 (Table 1).

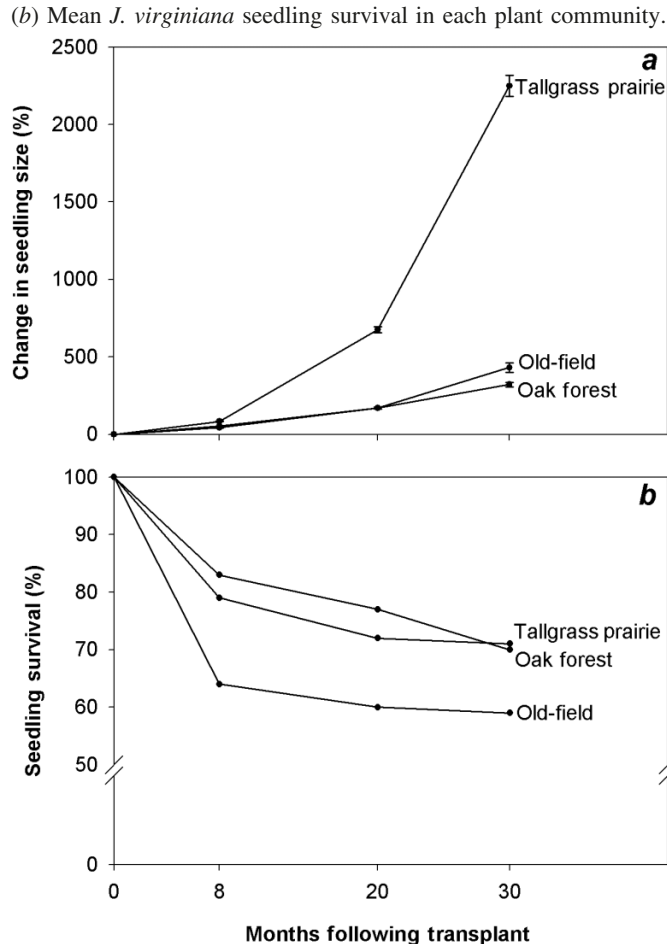
We used logistic regression to model 30 month probability of survival, a binomial variable (1 = alive, 0 = dead), of *J. virginiana* seedlings as a function of plant species richness, species diversity, and species composition (DCA axis 1 sample scores). We evaluated significance of logistic regression parameters using the Wald χ^2 statistic (Hosmer and Lemeshow 2000). We evaluated site (i.e., plant community) differences in *J. virginiana* seedling survival using χ^2 analysis (Sokal and Rohlf 1995).

We used regression analysis to model *J. virginiana* seedling growth as a function of plant community traits [plant species richness, species diversity, and species composition (DCA axis 1 sample scores) PROC REG; SAS Institute Inc. 2000]. Separate models were created for seedling growth at 30 months following seedling transplant with each of the three plant community traits.

Results

Juniperus virginiana seedling survival did not differ between the tallgrass prairie and the upland oak forest, but seedling survival was lower in the old-field than in the other two communities ($\chi^2 = 42.9$, $df = 2$, $P < 0.001$). The tallgrass prairie site was more susceptible to encroachment by *J. virginiana* than the other two plant communities based on rapid seedling growth (Fig. 1a) and high seedling survival

Fig. 1. Growth (expressed as percent change in seedling size from $t = 0$ months through $t = 30$ months) and survival of *Juniperus virginiana* seedlings 8, 20, and 30 months following transplant within the tallgrass prairie, old-field, and upland oak forest. (a) Mean *J. virginiana* seedling growth \pm standard error of established seedlings in the tallgrass prairie (SD = 1691; CV = 75), old-field (SD = 689; CV = 160), and upland oak forest (SD = 370; CV = 115).



(Fig. 1b) in the tallgrass prairie site. In contrast, slower growth of *J. virginiana* seedlings in the upland oak forest and the old-field (Fig. 1a) combined with low seedling survival (Fig. 1b) in the old-field indicated that these two communities were less susceptible to encroachment by *J. virginiana*.

Seedling survival of *J. virginiana* increased with increasing species richness and species diversity only in the tallgrass prairie (Table 2; Figs. 2a–2h). In contrast, seedling growth (Figs. 3a–3d) of *J. virginiana* increased with increasing species richness across and within all of the plant communities and seedling growth increased with increasing species diversity across and within all of the plant communities except the tallgrass prairie (Figs. 3e–3h). Seedling growth varied widely across plant communities regardless of species richness or diversity (Figs. 3a–3h). However, high variance in seedling growth in the tallgrass prairie was reflected in high growth (>6000%) in a small group of seedlings, but high variance was spread equally across the gradient in species richness and species diversity in the tallgrass prairie (Figs. 3b and 3f).

Table 2. Logistic regression models of seedling survival (dependent variable) using species richness, species diversity (Shannon's H'), and DCA axis one sample scores as independent variables.

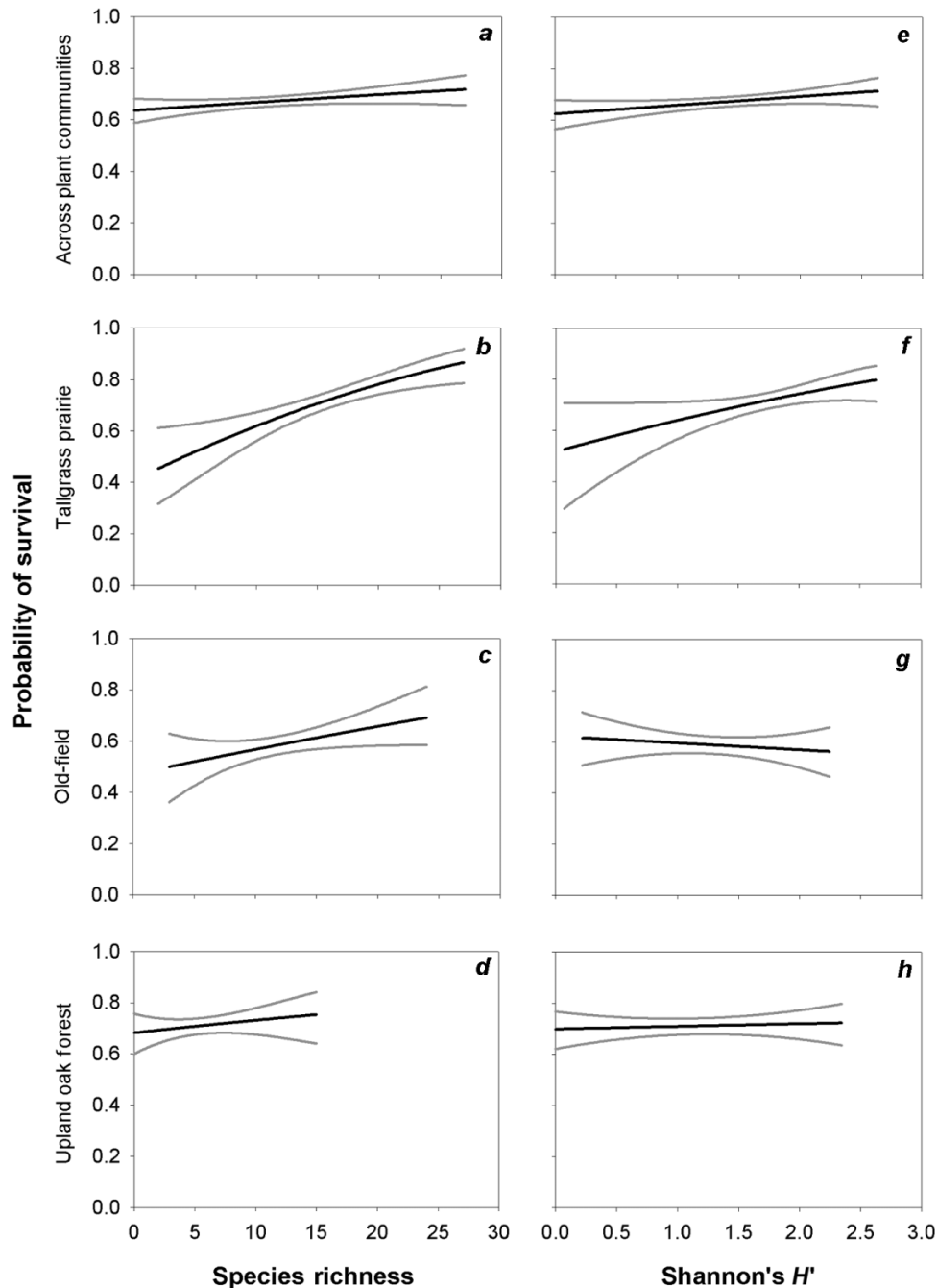
Site or variable	Parameter estimate	Standard error	Wald χ^2	P
Across plant communities				
Species richness	0.01	0.01	3.21	0.073
Shannon's H'	0.15	0.08	3.46	0.063
DCA axis 1	0.05	0.03	2.34	0.126
Tallgrass prairie				
Species richness	0.08	0.02	16.46	<0.001
Shannon's H'	0.49	0.21	5.22	0.022
DCA axis 1	-0.29	0.16	3.50	0.062
Old-field				
Species richness	0.04	0.02	2.85	0.091
Shannon's H'	-0.11	0.17	0.40	0.527
DCA axis 1	0.74	0.13	34.97	<0.001
Upland oak forest				
Species richness	0.02	0.03	0.76	0.383
Shannon's H'	0.05	0.14	0.13	0.724
DCA axis 1	-0.22	0.08	6.77	0.009

Survival of *J. virginiana* seedlings was not related to plant species composition across plant communities (Table 2; Fig. 4a); however, seedling growth (Fig. 5a) was related to plant species composition across plant communities, albeit poorly. Survival (Figs. 4b–4d) and growth (Figs. 5b–5d) of *J. virginiana* seedlings varied with plant species composition within each plant community. Survival was more sensitive to change in species composition than to change in species richness or diversity, especially in the old-field, where probability of survival varied from 25% to 75% over a relatively short compositional gradient (Fig. 4c), and to a lesser extent in the upland oak forest (Fig. 4d). Lowest survival occurred among plants typically associated with disturbance on fine-textured soil, including *Bothriochloa laguroides* (DC.) Herter (DCA axis 1 species score = -0.12) and *Amphiachyris dracunculoides* (DC.) Nutt. (DCA axis 1 species score = 0.40; Table 2; Fig. 4c). Highest seedling survival in the upland oak forest (Table 2; Fig. 4d) was associated with species normally found in glades in this region including *Sorghastrum nutans*, *Schizachyrium scoparium*, and *Andropogon gerardii* (Table 3). However, seedling survival across the three plant communities (Fig. 4a) was not obviously associated with change in species composition across communities (Table 2). Seedling growth, although highly variable, varied relatively little with changes in plant species composition (Figs. 5a–5d). Despite differences in seedling survival and growth, and plant composition among the three plant communities we investigated (Fig. 1; Table 1) there was no relationship between species composition and seedling survival (Fig. 4a) and a weak relationship with seedling growth (Fig. 5a) across plant communities.

Discussion

We found that more species rich and diverse plant communities are not less susceptible to *J. virginiana* encroachment, and that *J. virginiana* encroachment was related to

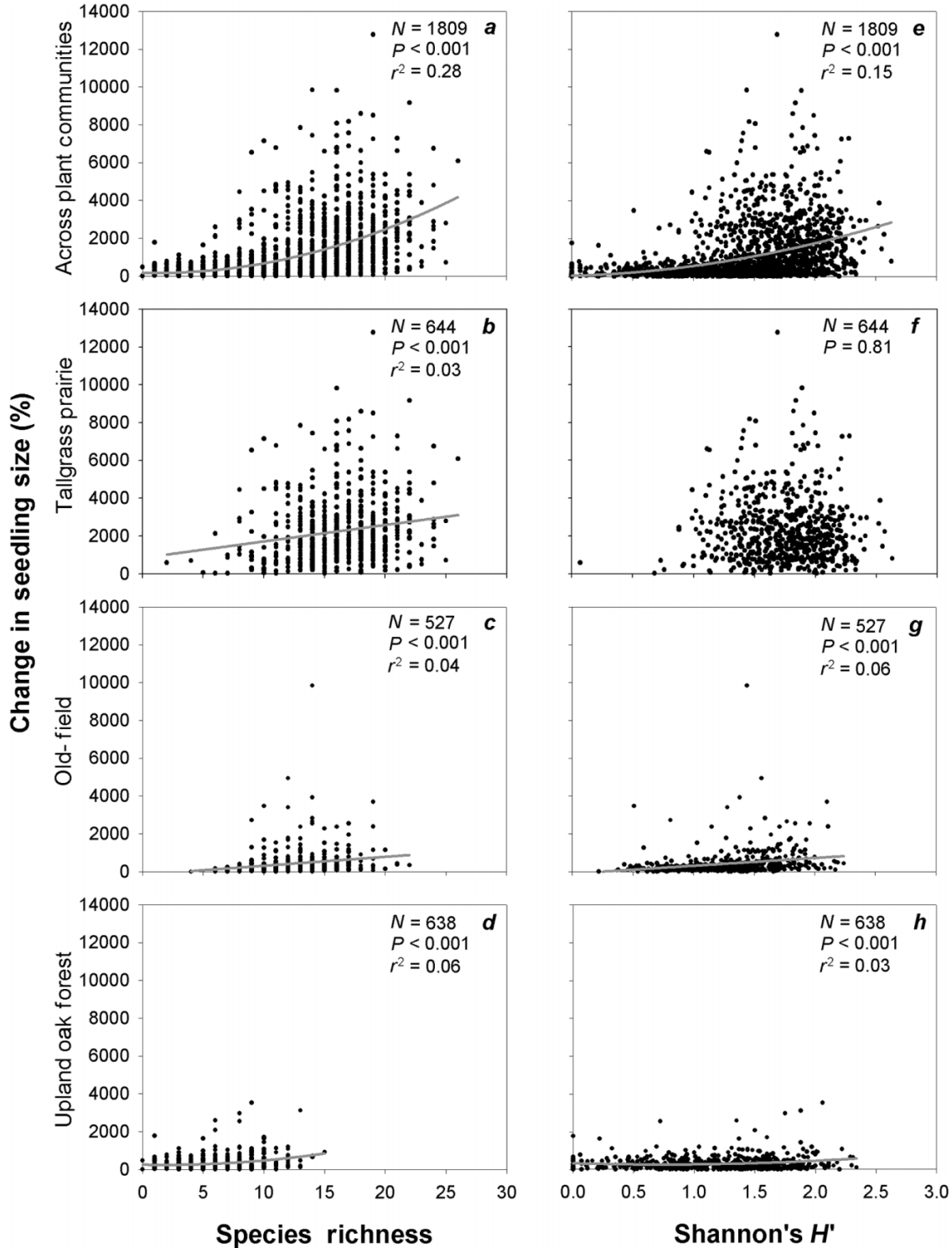
Fig. 2. Results of logistic regressions of *Juniperus virginiana* seedling survival as a function of the following plant community diversity traits (with 95% confidence intervals for predicted values). (a) Plant species richness across all three plant communities. (b) Plant species richness in the tallgrass prairie. (c) Plant species richness in the old-field. (d) Plant species richness in the upland oak forest. (e) Shannon's H' across all three plant communities. (f) Shannon's H' in the tallgrass prairie. (g) Shannon's H' in the old-field. (h) Shannon's H' in the upland oak forest.



neighboring species composition. Greater plant species richness and diversity in three distinct plant communities of central North America did not reduce encroachment by *J. virginiana*. Indeed, species richness and diversity was either unrelated or positively associated with *J. virginiana* survival and growth. In fact, species richness and diversity were only related to seedling survival in the tallgrass prairie, despite considerable differences in species richness and diversity across plant communities (Table 1). Our results con-

trast with invasion studies in which more species rich or diverse plant assemblages resisted invasion (Tilman 1997; Dukes 2002; Kennedy et al. 2002). Most of the relationships we observed between encroachment and species richness and diversity were not strong, a result consistent with studies using similar plot size (i.e., 1 m²) in naturally occurring populations of invasive species (Stohlgren et al. 2003). Our findings support a growing body of literature demonstrating a positive relationship between diversity and invasion

Fig. 3. Regression analysis of *Juniperus virginiana* seedling growth (expressed as percent change in seedling size from $t = 0$ months through $t = 30$ months) as a function of either plant species richness or Shannon's H' . (a) Plant species richness for each of three plant communities ($y = 166.0 - 13.8x + 6.5x^2$). (b) Plant species richness in the tallgrass prairie ($y = 844.0 + 87.1x$). (c) Plant species richness in the old-field ($y = -162.2 + 47.2x$). (d) Plant species richness in the upland oak forest ($y = 250.6 - 12.7x + 3.5x^2$). (e) Shannon's H' for each of three plant communities ($y = 37.0 + 183.9x + 338.3x^2$). (f) Shannon's H' in tallgrass prairie. (g) Shannon's H' in the old-field ($y = -103.3 + 412.7x$). (h) Shannon's H' in the upland oak forest ($y = 332.6 - 180.7x + 122.9x^2$).



(Levine and D'Antonio 1999; Lonsdale 1999; Stohlgren et al. 1999; Thompson et al. 2001; Huston 2004). Diversity often covaries with factors that facilitate greater species co-

existence and therefore, elevated diversity might indicate increased susceptibility of a community to invasion (Levine and D'Antonio 1999; Thompson et al. 2001; Huston 2004).

Fig. 4. Results of logistic regression of *Juniperus virginiana* seedling survival as a function of plant species composition (DCA axis 1 sample scores) (with 95% confidence intervals for predicted values) in (a) the threeplant communities, (b) the tallgrass prairie, (c) the old-field, and (d) the upland oak forest.

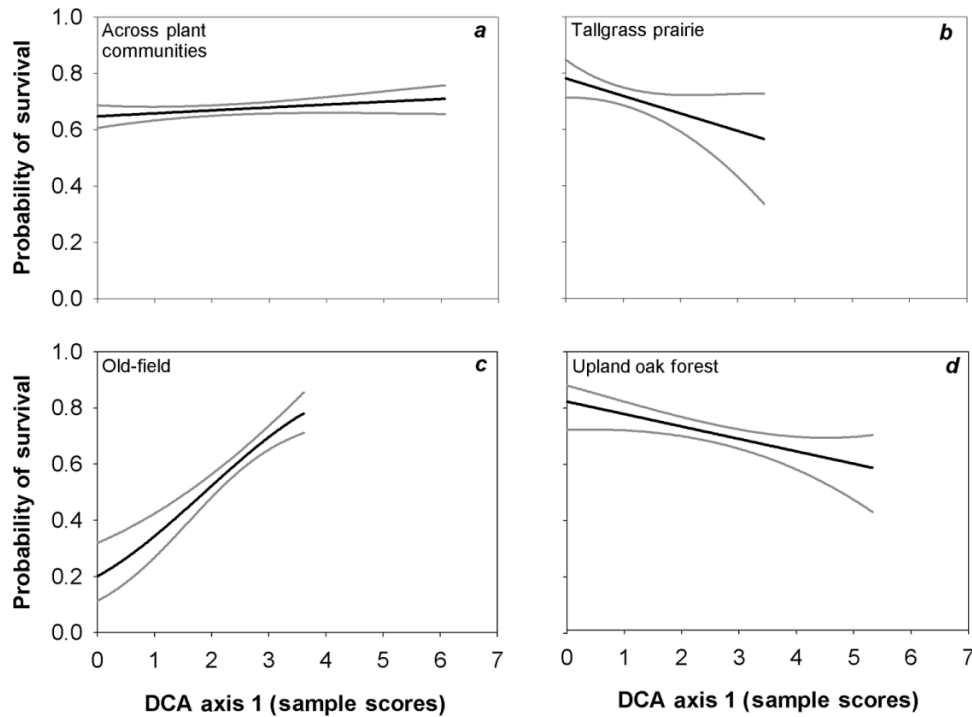


Fig. 5. Regression analysis results of *Juniperus virginiana* seedling growth (expressed as percent change in seedling size from $t = 0$ months) as a function of plant species composition (DCA Axis 1 sample scores) in (a) the 3 plant communities ($y = -124.7 + 1389x - 288.5x^2$), (b) the tallgrass prairie ($y = 1087.8 + 1911.9x - 658.0x^2$), (c) the old-field ($y = 1016.0 - 239.83x$), and (d) the upland oak forest ($y = 717.7 - 247.3x + 31.0x^2$).

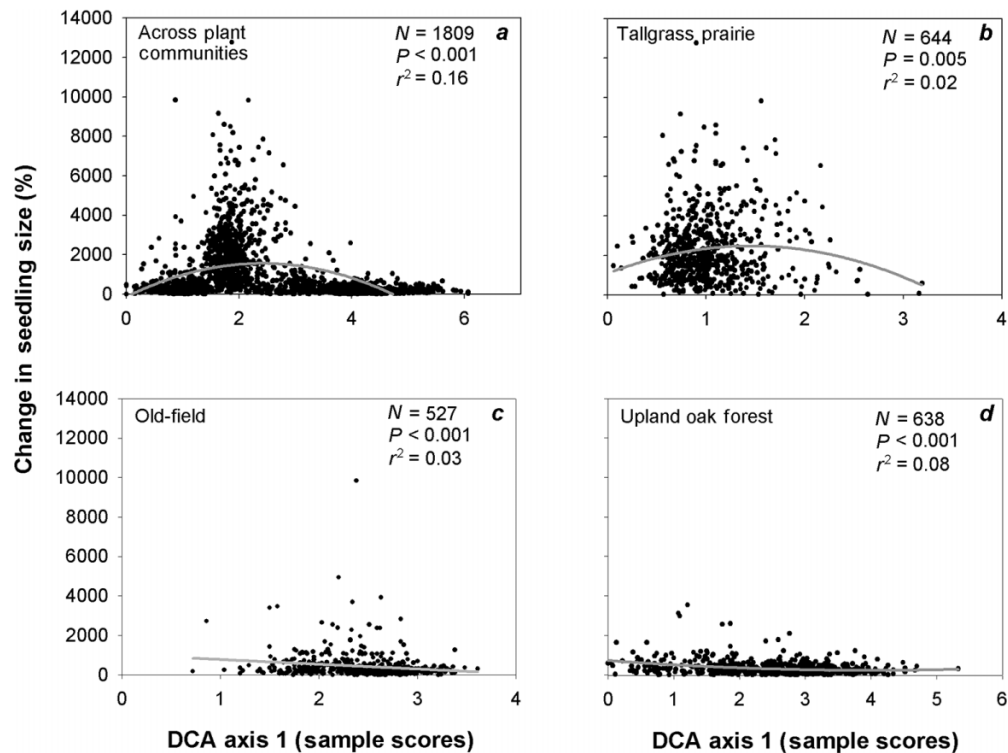


Table 3. Detrended correspondence analysis axis-1 species scores for an inclusive list of the 10 most abundant plant species within the tallgrass prairie, old-field, and upland oak forest.

Species	Separate DCA of each plant community			Combined DCA (all three sites)
	Tallgrass prairie	Old-field	Upland oak forest	
	DCA axis 1 sample scores			
<i>Ambrosia psilostachya</i>	0.16 [†]	0.65 [†]	0.95	1.65 [†]
<i>Andropogon gerardii</i>	1.73 [†]	3.24	0.17 [†]	2.43 [†]
<i>Aristida purpurascens</i>	-2.10	3.95 [†]	—*	-0.56
<i>Bromus japonicus</i>	2.14 [†]	-1.35	0.95	2.41
<i>Carex</i> spp.	1.26 [†]	2.84 [†]	1.50 [†]	2.45 [†]
<i>Celtis occidentalis</i>	3.20	2.73	3.30 [†]	4.79
<i>Coelorachis cylindrica</i>	-0.16 [†]	3.05	0.16	1.72
<i>Dichanthelium oligosanthes</i>	1.66 [†]	1.37 [†]	1.57 [†]	3.18 [†]
<i>Dichanthelium scoparium</i>	0.26	4.17 [†]	1.38	0.49
<i>Digitaria cognatum</i>	0.91	2.38 [†]	0.45	0.88 [†]
<i>Lespedeza virginica</i>	0.49	2.80 [†]	0.37	0.12
<i>Parthenocissus quinquefolia</i>	4.44	2.64	3.54 [†]	4.93
<i>Quercus stellata</i>	3.68	4.18	4.26 [†]	6.07
<i>Schizachyrium scoparium</i>	0.61 [†]	2.20 [†]	-0.29	1.00 [†]
<i>Smilax bona-nox</i>	3.70	—*	3.08 [†]	4.47
<i>Sorghastrum nutans</i>	0.62 [†]	2.39 [†]	-0.60	0.82 [†]
<i>Sporobolus compositus</i>	0.43 [†]	-0.34	0.90	2.33 [†]
<i>Symphoricarpos occidentalis</i>	3.18	0.77	2.62 [†]	3.72 [†]
<i>Symphotrichum ericoides</i>	1.24 [†]	1.01 [†]	0.16	1.48 [†]
<i>Tridens flavus</i>	2.57	2.57	1.22 [†]	3.43
<i>Ulmus americana</i>	4.26	-0.38	2.40 [†]	4.33

*Not present in this plant community.

[†]Most common species within a plant community.

Our results support those of other studies that found positive relationships between species diversity and invasion success, including studies conducted at large spatial scales (Lonsdale 1999; Stohlgren et al. 1999, 2002, 2003) and natural settings (Robinson et al. 1995; Planty-Tabacchi et al. 1996; Wisser et al. 1998; Levine and D'Antonio 1999). Other studies that have found inconsistent or negative correlations between species diversity and invasibility may reflect choice of an experimental design (Zavaleta and Hulvey 2004). Choice of spatial scale, control of factors influencing invasion, and selection of response variables differ markedly among studies and might influence outcomes. For example, diversity and invasion were negatively correlated in controlled studies conducted at small spatial scales (Tilman 1997; Dukes 2002; Kennedy et al. 2002) and poorly correlated in studies conducted in a natural setting at small spatial scales (Stohlgren et al. 2003). Choice of the response variable (e.g., germination, survival, growth, reproduction) potentially influences outcomes in invasion studies because factors such as establishment and impact of invasion vary independently over environmental gradients (Huston 2004; Levine et al. 2004).

Seedling success of *J. virginiana* was associated with plant species composition, especially in the disturbed old-field. Therefore, *J. virginiana* seedling survival, which we found to be greatest in association with plants typically found on disturbed sites, was at least partially a function of soil resource availability (Davis et al. 2000; Huston 2004; McKinley and Van Auken 2005). Soil resources and vegetation in old-fields are typically heterogeneous as a result of

historical cultivation (Sietman et al. 1994; Tunnell 2002). Thus, soil resource availability is not likely to be as heterogeneous in the uncultivated tallgrass prairie and upland oak forest sites, even though species composition within the oak forest is more diverse than in the old-field. Light, a factor that clearly limits *Juniperus* seedling survival and seedling growth (Lassoie et al. 1983; McKinley and Van Auken 2005; Van Auken and McKinley 2008), might exert less influence in the upland oak forest than soil resources exert in the old-field. Seedling survival was not associated with and seedling growth was poorly related to species composition across plant communities. The scale of this investigation with small but numerous experimental units may have potentially masked relationships between species composition, seedling survival, and seedling growth when species composition data from the three plant communities was integrated.

We suspect that intracommunity differences in species composition driven by abiotic factors (i.e., soil resource availability in the old-field and light availability in the oak forest), might regulate *J. virginiana* encroachment. Plant community composition has long been viewed as an influence on community invasibility (Elton 1958). Research in tallgrass prairie has recently demonstrated that dominance, measured as the relative proportion of C₄ perennial grasses, was strongly related to invasion by an exotic legume, and that invasion was more strongly related to dominance than species richness (Smith et al. 2004). Dominant species may sequester resources to an extent that resource scarcity constrains invasion. Because acquisition of resources is species-specific, interspecific competition also might dictate

invasion success (Grime 1977). Indeed, Levine et al. (2004) concluded from a meta-analysis that competition from resident plants is an important contributor to biotic resistance. Resource availability can alter competition intensity within the resident plant community, such that intensity decreases as unused resources increase (Davis et al. 1998, 2000). Thus, opportunistic woody species such as *J. virginiana* might encroach more successfully if resource availability reduces the competition intensity of resident vegetation (Davis et al. 2000). Resource availability can change within a plant community as a result of disturbance that alters the use of resources by resident vegetation and biogeochemical processes that increase resource availability (Tilman 1985; Davis et al. 2000). Controlled experiments would elucidate the relationship between resource availability and *J. virginiana* encroachment.

Our results also demonstrate that only a few rapidly growing *J. virginiana* individuals might greatly alter ecosystems regardless of plant species diversity and species composition. This is especially the case in our tallgrass prairie site where a few *J. virginiana* seedlings grew much more rapidly than the average. These rapidly growing individuals were equally spread across the diversity gradient. This result is ecologically significant because these few individuals represent potential, effective ecosystem transformers (Engle and Kulbeth 1992) that rapidly grow and subsequently influence plant and animal community structure (Gehring and Bragg 1992; Coppedge et al. 2001b; Chapman et al. 2004b) and ecosystem function (Norris et al. 2001; Hoch et al. 2002). Moreover, because of their height and area of influence, seedlings that rapidly reach large size are most likely to survive the natural control process of fire (Buehring et al. 1971) and further reduce their exposure to fire by reducing surface layer fuel loading (Engle et al. 1987; Smith and Stubbendieck 1990).

In the absence of fire, a few rapidly growing *J. virginiana* individuals within a plant community might serve as the catalyst for accelerated encroachment and eventual irreversible plant community shift to *J. virginiana* woodland (Hoch et al. 2002). Accelerated encroachment might occur through a series of positive feedback mechanisms when *J. virginiana* trees in grassland attract frugivorous birds that favor vertical structure (Holthuijzen et al. 1987; Coppedge et al. 2001a). Frugivorous birds feeding on *J. virginiana* seed also disperse *J. virginiana* seed into favorable microsites, which often surround trees (Joy and Young 2002) and other perch points (Livingston 1972) utilized by avian dispersers. Mammals may increase the intensity of *J. virginiana* dispersal on local scales as communities become increasingly homogenized to *J. virginiana* (Horncastle et al. 2004, 2005). The strength of positive feedback likely differs among the three plant communities we studied because growth and survival of *J. virginiana* differ among communities. Thus, the rates of conversion to *J. virginiana* woodlands would also vary among the three plant communities we studied.

All habitats studied here were susceptible to encroachment, differing only in the probable rates of conversion to *J. virginiana* woodland. These data suggest that management to preempt *J. virginiana* encroachment or to remove established individuals initially should target tallgrass prairie areas given the rapid growth of *J. virginiana* in tallgrass

prairie. Eliminating isolated, fruit-bearing *J. virginiana* trees in tallgrass prairie and old-fields may reduce seed dispersal and circumvent establishment of *J. virginiana* clusters within grasslands. Encroachment in upland oak forest by *J. virginiana* may be slower than in tallgrass prairie, perhaps allowing more time for management intervention. Slower growth but high seedling survival in upland oak forest suggests that encroachment and conversion in this habitat type may be slow but certain. *Juniperus virginiana* that eventually reach crown height in oak forest might outcompete deciduous trees, shade new recruits, and increase the risk of fire damage to oak forest. Exhaustive efforts to remove encroaching *J. virginiana* appear justified especially in tallgrass prairie but also in old-growth oak forest (*Quercus stellata* and *Q. marilandica*) stands because conservation of these rare ecosystems is a priority (Clark et al. 2005).

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