Grazing and an invasive grass confound spatial pattern of exotic and native grassland plant species richness

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Abstract

Previous work has shown exotic and native plant species richness are negatively correlated at fine spatial scales and positively correlated at broad spatial scales. Grazing and invasive plant species can influence plant species richness, but the effects of these disturbances across spatial scales remain untested. We collected species richness data for both native and exotic plants from five spatial scales (0.5–3000 m^2) in a nested, modified Whittaker plot design from severely grazed and ungrazed North American tallgrass prairie. We also recorded the abundance of an abundant invasive grass, tall fescue (*Schedonorus phoenix* (Scop.) Holub), at the 0.5-m^2 scale. We used linear mixed-effect regression to test relationships between plant species richness, tall fescue abundance, and grazing history at five spatial scales. At no scale was exotic and native species richness linearly related, but exotic species richness at all scales was greater in grazed tracts than ungrazed tracts. Native species richness declined with increasing tall fescue abundance at all five spatial scales, but exotic species richness increased with tall fescue abundance at all but the broadest spatial scales. Severe grazing did not reduce native species richness at any spatial scale. We posit that invasion of tall fescue in this working landscape of originally native grassland plants modifies species richness-spatial scale relationships observed in less disturbed systems. Tall fescue invasion constitutes a unique biotic effect on plant species richness at broad spatial scales.

Zusammenfassung

Bisherige Arbeiten haben gezeigt, dass die Pflanzenartenvielfalt von exotischen und einheimischen Arten auf kleinen räumlichen Skalen negativ und auf großen räumlichen Skalen positiv miteinander korreliert sind. Die Beweidung und invasive Pflanzen können den Pflanzenartenreichtum beeinflussen, aber die Auswirkungen dieser Störungen wurden bisher nicht über räumliche Skalen getestet. Wir sammelten Daten zum Artenreichtum der einheimischen und exotischen Pflanzen auf fünf räumlichen Skalen (0,5m^2 -3.000m^2) in einem geschachtelten, modifizierten Whittaker Flächendesign in einigen beweideten und nicht beweideten nordamerikanischen Langgrassteppen. Wir registrierten außerdem die Abundanz eines invasiven Grases, des Rohrschwingels (*Schedonorus phoenix* (Scop.) Holub), auf der 0,5m^2-Skala. Wir benutzten Regressionen mit gemischten Effekten um auf fünf räumlichen Skalen die Beziehung zwischen dem Pflanzenartenreichtum, der Rohrschwingelabundanz und der Beweidungsgeschichte zu testen. Der Artenreichtum der exotischen und einheimischen Arten stand auf keiner Skala in einer linearen Beziehung zueinander, aber der Artenreichtum der exotischen Arten war in beweideten Bereichen größer als in nicht

beweideten Bereichen. Der Artenreichtum der einheimischen Arten nahm mit einer Zunahme der Rohrschwingelabundanz auf allen fünf Skalen ab, aber der Artenreichtum der exotischen Arten nahm mit der Rohrschwingelabundanz auf allen Skalen zu, außer auf der größten Skala. Starke Beweidung reduzierte den Artenreichtum der einheimischen Arten auf keiner räumlichen Skala. Wir postulieren daher, dass die Invasion des Rohrschwingels in dieser funktionierenden Landschaft aus ursprünglich einheimischen Steppenpflanzen die Artenreichtums-Raumskala-Beziehungen modifiziert, die in weniger gestörten Systemen beobachtet werden. Die Invasion des Rohrschwingels hat einen einzigartigen biotischen Effekt auf den Pflanzenartenreichtum auf großen räumlichen Skalen.

Introduction

Ecologists have long studied the effects of herbivory and exotic species on native plant communities, with a recent emphasis on the relationship between spatial scale and plant species richness. Greater native species richness resists invasion in experimental plots (Lyons & Schwartz 2001; Kennedy, Naeem, Howe, Knops, & Tilman 2002), but communities with greater native species richness often contain greater numbers of exotic species in observational, regional studies (Stohlgren, Barnett, & Kartesz 2003; Harrison, Grace, Davies, Safford, & Viers 2006).

Grazing also can either increase or decrease plant species richness (Olff & Ritchie 1998) depending on ecosystem productivity and evolutionary history of grazing (Milchunas, Sala, & Lauenroth 1988; Milchunas & Lauenroth 1993). Grazing generally increases species richness in mesic grassland and generally reduces species richness in more arid grassland (Bakker, Blair, & Knapp 2003; Altesor, Pineiro, Lezama, Jackson, & Sarasola 2006; Dorrough, Ash, Bruce, & McIntyre 2007; Burns, Collins, & Smith 2009). Grazing severity, a function of primary productivity and grazing intensity, also influences the effect of grazing on plant species richness (Hickman, Hartnett, Cochran, & Owensby 2004).

Many ecological processes that influence plant species richness are scale-dependent (Huston 1999; Dorrough et al. 2007). Theory suggests that plant-level competition controls richness at the fine spatial scales at which individuals interact, but at broad spatial scales, environmental heterogeneity determines species richness maxima for both native and exotic species (Shea & Chesson 2002). Grazing effects on richness are also scale-dependent: individual plant responses to herbivory and herbivore selective grazing shape competitive interactions at fine spatial scales, whereas environmental heterogeneity dominates the influence of grazing on species richness at broad spatial scales (Chaneton, Perelman, Omacini, & Leon 2002). The influence of grazing on richness of exotic compared to richness of native plant species, especially at broad scales, cannot be generalized because individual plant and plant community responses to grazing are often ecosystem-specific (e.g., Kimball & Schiffman 2003; Dorrough et al. 2007).

We test the effect of two factors of grassland degradation on exotic and native species richness across spatial scales in North American tallgrass prairie: a history of severe grazing by cattle (*Bos taurus*) and invasion by a specific exotic plant species, tall fescue (*Schedonorus phoenix* (Scop.) Holub). Tall fescue can reduce native plant species richness and alter disturbance regimes (Rudgers, Mattingly, & Koslow 2005; McGranahan, Engle, Fuhlendorf, Miller, & Debinski 2012). Tall fescue has a relatively long stand duration compared to other pasture grasses (e.g., Beck, Gunter, Lusby, West, & Watkins 2008), which suggests resistance to grazing. Little is known about the spatial ecology of tall fescue invasion on either native or exotic species richness, although other invasive grasses reduce species richness at broad spatial scales (Heidinga & Wilson 2002). As the spatial resource heterogeneity hypothesis predicts broad-scale patterns of richness to be determined by environmental variability and not plant interactions, invasive species that reduce either native or exotic plant species richness at broad spatial scales constitute a unique biotic effect.

Aware of the range in definitions and distinctions applied to the terms exotic and invasive species, we use "exotic" in reference to plant species listed as non-native to the study region in the United States Department of Agriculture PLANTS database (USDA-NRCS 2012), and in this paper reserve the term "invasive" specifically for tall fescue. Tall fescue is a Eurasian grass that occupies more than 14 million ha in eastern North America (Fribourg, Hoveland, & Gwinn 1991). Tall fescue is also the most frequently occurring and most abundant plant species in our study system, occurring in 80% of sampled plots with a mean canopy cover of 38% (McGranahan 2008). As a working landscape managed for economic and conservation objectives, this ecosystem presents an opportunity to test the universality of basic ecological theory relating to native/exotic richness, grazing, and spatial scale in an applied context (Sagarin & Pauchard 2010).

Our hypotheses include: (1) we predict a negative correlation between exotic plant species richness and native plant species richness at fine scales, and an increasingly positive correlation as spatial scale increases from fine to broad (Davies, Chesson, Harrison, Inouye, & Melbourne 2005; Kumar, Stohlgren, & Chong 2006; Pauchard & Shea 2006). (2) We expect grazing to increase both native and

exotic species richness at all spatial scales in this mesic grassland (Bakker et al. 2003; Altesor et al. 2006). (3) We expect a negative relationship between tall fescue abundance and both native and exotic species richness (Christian & Wilson 1999; Heidinga & Wilson 2002). We tested these hypotheses with data from tallgrass prairie in Iowa and Missouri, USA, collected at five spatial scales (0.5–3000 m^2).

Materials and methods

Study area

This research was conducted in nine tallgrass prairie tracts in the Grand River Grasslands (GRG) of Ringgold County, Iowa, and Harrison County, Missouri (Debinski, Moranz, Delaney, Miller, & Engle 2011). Tract area varied between 15 and 31 ha with 91 cm mean annual precipitation (McGranahan, Engle, Fuhlendorf, Winter, & Miller 2012). Soils in the GRG belong to the Gara–Armstrong–Pershing association and study tracts are dominated by Gara loam and Armstrong loam (USDA-NRCS 2010). Approximately 70% of plants in the study tracts are native tallgrass prairie species, and exotic species include several forage grasses and legumes (McGranahan 2008).

The GRG is a working landscape in which grazing and row-crop agriculture occurs alongside conservation management areas (Miller, Morton, Engle, Debinski, & Harr 2012). Grazing history for each of the nine tracts was determined by interviewing current and previous landowners and managers. Four tracts were labeled "severely grazed" – up to 15 animal unit months/ha within at least five years prior to our study – and five tracts not reported in any interview to have been previously grazed at any point were labeled "ungrazed."

Sampling

Six, 25-m × 20-m (500-m^2) modified Whittaker plots (total of 3000 m^2) (Stohlgren, Bull, & Otsuki 1998) were located in each of the nine tracts, controlling for catena and soil type (McGranahan 2008; Debinski et al. 2011). Modified Whittaker plots use a nested design to quantify exotic and native species richness at multiple spatial scales (Stohlgren, Binkley, Chong, Kalkhan, & Schell 1999). We sampled at the following spatial scales: 0.5 m^2, 2.5 m^2, 250 m^2 and 500 m^2, in addition to the 3000 m^2 of sampled area per tract, across the six, 500-m^2 modified Whittaker plots. Sub-plot dimensions were proportional to the 25-m × 20-m modified Whittaker plot. From fine to broad, these spatial scales are consistent with those used elsewhere in tallgrass prairie: our finest scale, 0.5 m^2, is consistent with the "plant neighborhood" in tallgrass prairie (Naeem, Knops, Tilman, Howe, & Kennedy 2000; Collins, Glenn, & Briggs 2002).

Within each Whittaker plot, we recorded species richness at five spatial scales as follows: we recorded the presence of all species within 10 0.5-m^2 sub-plots and 2 2.5-m^2 sub-plots, and the presence of additional species at the broader 250-m^2 and 500-m^2 spatial scales. We averaged species richness for the ten 0.5-m^2 and two 2.5-m^2 sub-plots. Tall fescue canopy cover (hereafter, abundance) was sampled within the 10, 0.5-m^2 quadrats using the Daubenmire (1959) scale of cover classes. We averaged tall fescue abundance across the 10 quadrats to calculate abundance at 0.5–500-m^2 spatial scales and averaged across all six plots to calculate abundance at the 3000-m^2 spatial scale. Observations were made in the spring and late summer of 2006, to account for seasonal changes in community composition and tall fescue abundance. We combined data from both periods into a single species list for each plot, and used the maximum seasonal value of tall fescue abundance.

Data analysis

We used linear mixed-effect (LME) regression models to account for random site effects (6 modified Whittaker plots within each of nine tracts) as we tested for linear relationships within fixed effects (i.e., exotic species richness vs. native species richness, grazing history; and total, native, and exotic species richness vs. tall fescue abundance and grazing history). We fit the LME models by maximizing log-likelihood and allowing the slope and intercept in the random effects term to vary, using the lme function in the nlme package in the R statistical environment (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team 2011).

Each test consisted of a comparison of three LME models: a single model with a single independent variable; a multiple model that included grazing history ("grazed" or "ungrazed") + the independent variable; and a third model that included an interaction term between grazing history and the independent variable. We compared the models within each three-model set with analysis of variance using the anova function in R. LME model selection was informed by information-theoretic criteria (Burnham & Anderson 2002). Specifically, we selected models from each three-model set with the least Akaike's An Information Criterion (AIC) value and greatest weight (AIC$_w$) as calculated with the AIC function in R. These procedures were used for the following tests (at each of the sampled scales: 0.5 m^2, 2.5 m^2, 250 m^2, 500 m^2, and 3000 m^2): exotic vs. native species richness; and total, exotic, and native species richness vs. tall fescue abundance. Complete LME model results, including results of AIC model selection, are provided in Appendix A: Results of Linear Mixed-Effect Models.

Results

Exotic plant species richness and native species richness were not related at any of the sampled spatial scales (Fig. 1 and Table 1). However, at each spatial scale, severe grazing
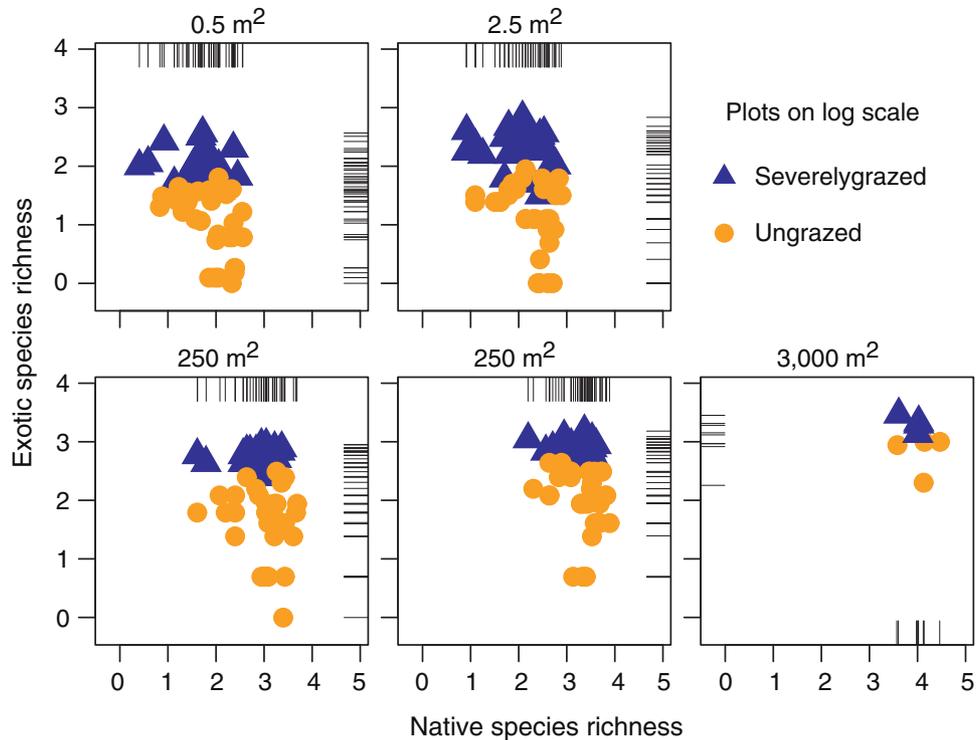
Fig. 1. Exotic plant species richness at five spatial scales as a function of native plant species richness and grazing history (severely grazed, $n = 5$ tracts; ungrazed, $n = 4$ tracts) in tallgrass prairie. Each axis is plotted on a logarithmic scale. Tickmarks within axes align with individual observations in the plot; thick or closely spaced tickmarks indicate overlapping data points. Severely grazed tracts appear as blue triangles and ungrazed tracts as orange circles (dark and light in greyscale, respectively) to denote grazing history was a significant term in the selected linear mixed-effect regression model ($p < 0.05$); see Methods for model selection details and Appendix A for complete results of all models. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 1. Results of linear mixed-effect (LME) regression models used to test the relationships between exotic plant species richness, native plant species richness, and grazing history at five spatial scales in tallgrass prairie (Hypothesis 1). Exotic species richness was the dependent variable in each model. The Fixed effect column presents the terms included in the model selected from the following three-model sets for each spatial scale: a single variable model with native species richness as the independent variable ("E~N"); a multiple variable model with native species richness and grazing history as independent variables ("E~N + H"); and a multiple variable model with native species richness, grazing history, and their interaction term as independent variables ("E~N + H"). Models were compared with Akaike's AIC and selected by lowest Akaike weight (AIC_w), which indicates the relative likelihood of the selected LME model from among the three competing models at each spatial scale. See Appendix A for complete results of all models.

Spatial scale (m^2)	Fixed effect	AIC_w	Model terms	DF	t-Value	p-Value
0.5	E~N + H	0.71	Intercept	44	3.51	0.00
			Native	44	−1.04	0.31
			History	7	5.69	0.00
2.5	E~N + H	0.65	Intercept	44	3.39	0.00
			Native	44	−0.96	0.34
			History	7	7.01	0.00
250	E~N + H	0.56	Intercept	44	2.85	0.00
			Native	44	1.24	0.22
			History	7	7.74	0.00
500	E~N + H	0.60	Intercept	44	3.96	0.00
			Native	44	0.45	0.65
			History	7	6.68	0.00
3000	E~N + H	0.54	Intercept	6	2.82	0.03
			Native	6	−0.50	0.63
			History	6	2.41	0.05
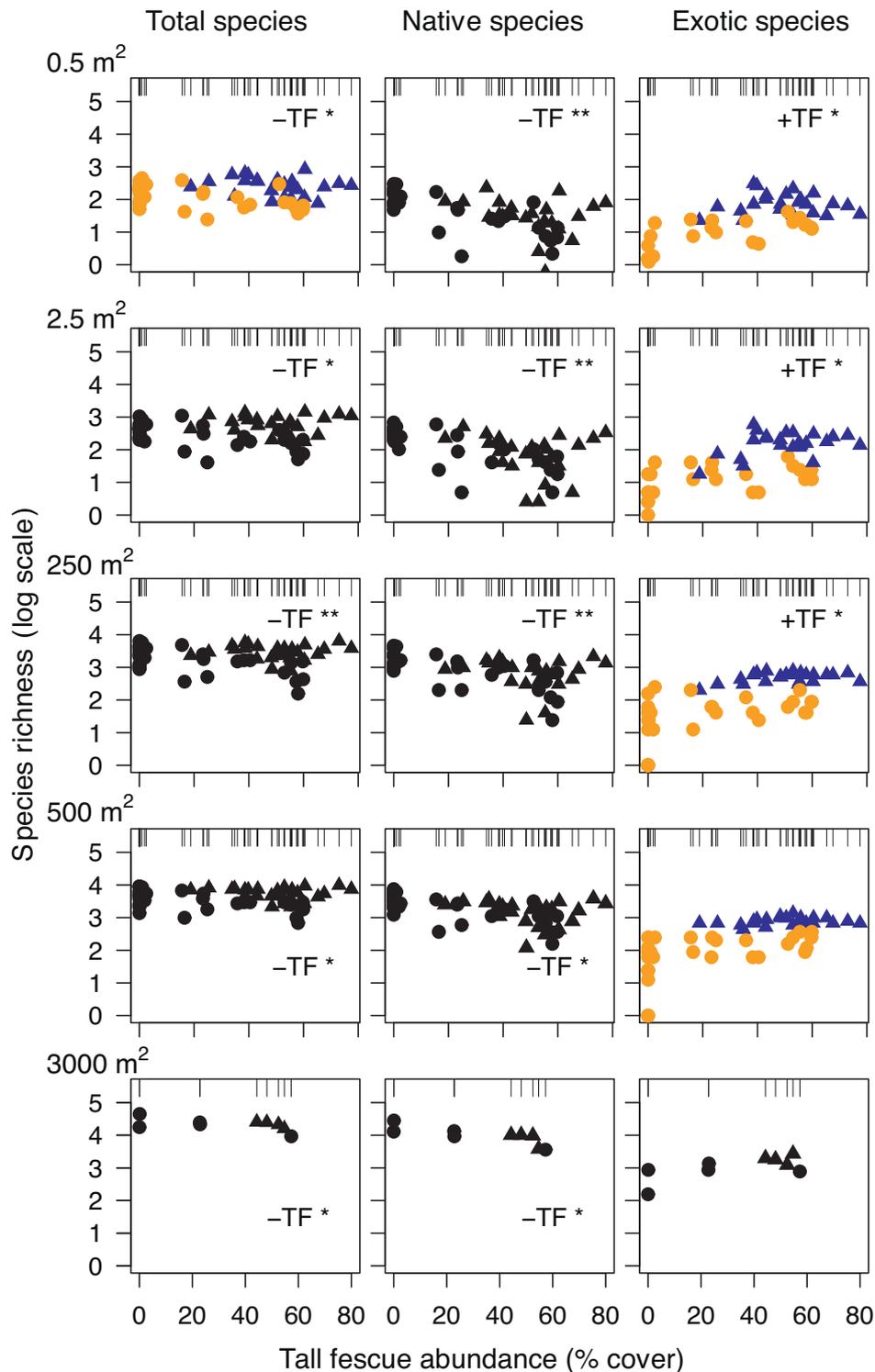
Fig. 2. Total (all plants) species richness, native species richness, and exotic species richness at five spatial scales as a function of tall fescue abundance and grazing history (severely grazed, $n = 5$ tracts; ungrazed, $n = 4$ tracts) in tallgrass prairie. Tickmarks within axes align with individual observations in the plot; thick or closely spaced tickmarks indicate overlapping data points. Severely grazed tracts appear as blue triangles and ungrazed tracts as orange circles (dark and light in greyscale, respectively) when grazing history is a significant term in the selected linear mixed-effect regression (LME) model ($p < 0.05$); when grazing history is not significant, all symbols are plotted in black. Initials "TF" indicate that tall fescue abundance was a significant term in the selected LME model (*$p < 0.05$, **$p < 0.01$); positive or negative sign indicates sign of t statistic in the selected LME model. See Methods for model selection details and Appendix A for complete results of all models. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 2. Results of linear mixed-effect (LME) regression models used to test the relationships between plant species richness (total, native, and exotic, respectively), grazing history, and tall fescue abundance for A. total species, B. native species, and C. exotic species at five spatial scales in tallgrass prairie (Hypotheses 2 and 3). Plant species richness was the dependent variable in each model. The Fixed effect column presents the terms included in the model selected from the following three-model sets for each spatial scale: a single variable model with tall fescue abundance as the independent variable ("R~TF"); a multiple variable model with tall fescue abundance and grazing history as independent variables ("R~TF + H"); and a multiple variable model with species richness, grazing history, and their interaction term as independent variables ("R~TF × H"). Models were compared with Akaike's AIC and selected by lowest Akaike weight (AIC$_w$), which indicates the relative likelihood of the selected LME model from among the three competing models at each spatial scale. See Appendix A for complete results of all models.

Species richness	Spatial scale (m^2)	Fixed effect	AIC$_w$	Model terms	DF	t-Value	p-Value
A. Total	0.5	R~TF + H	0.68	Intercept	44	11.18	0.00
				Tall fescue	44	−2.35	0.02
				History	7	3.72	0.01
	2.5	R~TF × H	0.69	Intercept	43	11.24	0.00
				Tall fescue	43	−2.57	0.01
				History	7	0.51	0.62
				TF × H	43	1.90	0.06
	250	R~TF × H	0.72	Intercept	43	12.30	0.00
				Tall fescue	43	−2.77	0.00
				History	7	−0.01	0.99
				TF × H	43	2.01	0.05
	500	R~TF × H	0.48	Intercept	43	13.54	0.00
				Tall fescue	43	−2.44	0.02
				History	7	0.43	0.68
				TF × H	43	1.48	0.15
	3000	R~TF + H	0.53	Intercept	6	13.19	0.00
				Tall fescue	6	−2.68	0.04
				History	6	1.76	0.13
B. Native	0.5	R~TF × H	0.53	Intercept	43	11.45	0.00
				Tall fescue	43	−4.65	0.00
				History	7	−1.35	0.22
				TF × H	43	2.11	0.04
	2.5	R~TF × H	0.42	Intercept	43	11.11	0.00
				Tall fescue	43	−3.98	0.00
				History	7	−1.24	0.25
				TF × H	43	1.90	0.06
	250	R~TF × H	0.57	Intercept	43	13.25	0.00
				Tall fescue	43	−4.08	0.00
				History	7	−1.53	0.17
				TF × H	43	2.20	0.03
	500	R~TF	0.44	Intercept	44	12.01	0.00
				Tall fescue	44	−2.51	0.02
	3000	R~TF + H	0.41	Intercept	6	12.74	0.00
				Tall fescue	6	−3.56	0.01
				History	6	1.30	0.24
C. Exotic	0.5	R~TF × H	0.68	Intercept	43	2.37	0.02
				Tall fescue	43	2.50	0.02
				History	7	4.49	0.00
				TF × H	43	−1.86	0.07
	2.5	R~TF + H	0.69	Intercept	44	2.83	0.00
				Tall fescue	44	2.24	0.03
				History	7	5.71	0.00
	250	R~TF + H	0.71	Intercept	44	5.38	0.00
				Tall fescue	44	2.07	0.04
				History	7	7.67	0.00
	500	R~TF + H	0.67	Intercept	44	7.10	0.00
				Tall fescue	44	1.57	0.12
				History	7	6.63	0.00

Table 2 (*Continued*)

Species richness	Spatial scale (m²)	Fixed effect	AIC$_w$	Model terms	DF	*t*-Value	*p*-Value
	3000	R∼TF+H	0.50	Intercept	6	5.43	0.00
				Tall fescue	6	0.83	0.44
				History	6	1.52	0.18

was associated with an increase in exotic compared to native species richness (Fig. 1 and Table 1). Table 1 presents the LME regression models selected by AIC model selection; see Appendix A: Results of Linear Mixed-Effect Models for full sets of all compared models.

Total and native species richness declined as tall fescue abundance increased at the five spatial scales sampled in this study (Fig. 2 and Table 2A,B). Conversely, exotic species richness increased as tall fescue abundance increased at the scales of 0.5 m², 2.5 m², and 250 m², although there was no relationship at spatial scales greater than 250 m² (Fig. 2 and Table 2C). Table 2 presents the LME models selected by AIC model selection; see Appendix A: Results of Linear Mixed-Effect Models for full sets of all compared models.

Total species richness at the finest (0.5 m²) spatial scale was greater in severely grazed tracts, but there was no relationship between grazing history and total species richness at spatial scales greater than 0.5 m² (Fig. 2 and Table 2A). Native species richness did not vary with grazing history at any spatial scale (Fig. 2 and Table 2B). However, exotic species richness was greater in severely grazed tracts at all but the 3000 m² spatial scale (Fig. 2 and Table 2C).

Discussion

The relationship of native species richness to severe grazing and tall fescue abundance differed from the relationship of exotic species richness. Exotic species richness is often greater at all spatial scales in grasslands with a history of severe grazing (Chaneton et al. 2002; Altesor et al. 2006). Native species richness did not vary between severely grazed and ungrazed tracts in our study. Our data support the pattern that native species richness in mesic grassland might be more resistant to, or even maintained by, grazing (Burns et al. 2009), including severe grazing as in our study.

These data indicate that native species richness declined with increasing abundance of tall fescue, but exotic species increased with increasing abundance of tall fescue. Differences in the evolutionary history of tall fescue, other exotic species, and native plants might account for this trend. Exotic and native species may have different ecological traits because species in each group share a different evolutionary history (Wilsey & Polley 2006; Long, Trussell, & Elliman 2009; Wilsey, Teaschner, Daneshgar, Isbell, & Polley 2009). In this manner, tall fescue and most of the Eurasian exotic species in our study have a shared evolutionary history that

might contribute to co-existence as a suite of naturalized exotic species in North America.

Divergent responses of native and exotic species to tall fescue invasion might be informed by the "driver/passenger" model, which distinguishes between native species that respond subordinately to exotic dominants (drivers) and the community of exotic species (passengers) that thrive free of the constraints that limit native species (MacDougall & Turkington 2005). While the idea that a single species – e.g., tall fescue – can "drive" ecological change has been debated (Gurevitch & Padilla 2004; Didham, Tylianakis, Hutchison, Ewers, & Gemmell 2005; MacDougall & Turkington 2005), individual exotic species have been associated with altered native plant diversity (Christian & Wilson 1999; Heidinga & Wilson 2002). While our data neither indicate what mechanisms might have created a favorable environment for exotic species, nor whether tall fescue contributed to these conditions, increasing exotic species richness with increasing abundance of tall fescue is consistent with a "passenger" pattern of invasion.

An invading species that reduces native species richness at broader spatial scales is an unexpected biotic effect on species richness because the influence of plant interactions should wane as spatial scale increases; i.e., the spatial resource heterogeneity hypothesis predicts that environmental heterogeneity controls species richness at broader spatial scales (Shea & Chesson 2002). In our study, the decrease in native species richness with increasing tall fescue abundance at the broader special scales contrasts with other research that supports the spatial resource heterogeneity hypothesis (Davies et al. 2005; Kumar et al. 2006). A single, dominant invasive species exerting biotic competitive pressure might override the effect of spatial resource heterogeneity and alter the relationship between native and exotic species richness in this ecosystem. This merits further research.

Establishment of exotic populations is often controlled by different processes than those that regulate the native community (Alpert 2006). As a widespread and productive forage species (Fribourg et al. 1991), tall fescue responds to agronomic management practices (e.g., nitrogen amendments), which might have contributed to abundant tall fescue on previously grazed native prairie tracts. Thus, it follows that the observed pattern of tall fescue invasion is the result of anthropogenic introduction and promotion rather than random introduction, naturalization, and invasion processes (Brooks, Antonio, Richardson, Grace, & Keeley 2004). That the spatial pattern of native and exotic diversity reported here does not follow the pattern observed in less disturbed systems might

have resulted from agronomic management practices. This underscores the importance of considering land use history when applying basic ecological theory to complex, working landscapes, and suggests additional research is needed to differentiate direct effects of exotic invasion on species richness from the indirect effects of land-use history.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2012.09.011.

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