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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

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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.

Keywords: Grazing history; Invasion ecology; *Schedonorus phoenix*; Plant–herbivore interactions; Species richness; Tall fescue; Tallgrass prairie; Working landscapes

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