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Native-species seed additions do not shift restored prairie plant communities from exotic to native states

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Abstract

Exotic- and native-dominated communities can exist as alternate states in landscapes, but whether exotic-dominated states are persistent in the face of propagule pressure from native species is not well known. Here, we asked whether adding native seeds to low diversity, exotic-dominated patches would shift them to a more diverse, native state by using a long-term experiment with tallgrass prairie species in Iowa, USA. Previous work established that community assembly history led to alternate exotic or native states of perennial species. We added native seeds to plots in the spring after removing aboveground biomass with fire. We found that an experimental seed addition did not cause a shift from exotic to native states. Plots seeded eight years earlier in spring and without a priority effect continued to have the highest abundance and diversity of native species and lowest proportion of exotics. Our results suggest that exotic-dominated states in restorations can persist in the face of native species propagule pressure. Thus, assembly history can play a strong role in generating and maintaining alternate states over long time frames that are relevant to restoration. New restoration projects in exotic-dominated landscapes should maximize effort toward establishing native species during initial stages of restoration.

Zusammenfassung

Von Exoten bzw. Einheimischen dominierte Gemeinschaften können als alternative Zustände in einer Landschaft existieren, aber darüber, ob von Exoten dominierte Gemeinschaften unter dem Diasporendruck der einheimischen Arten überdauern können, ist wenig bekannt. Hier fragten wir, ob die Zugabe von einheimischen Samen zu wenig diversen, exotenbeherrschten Arealen diese hin zu einem diverseren, einheimischen Zustand verändern würde. Hierzu nutzten wir ein langfristiges Experiment mit Arten der Tallgrass-Prairie in Iowa (USA). Frühere Arbeiten hatten ergeben, dass die Historie der Gemeinschaftsbildung zu wechselweise exotischen und einheimischen Gemeinschaften der perennierenden Arten führte. Wir säten einheimische Samen im Frühjahr auf Arealen aus, nachdem die oberirdische Biomasse abgebrannt worden war. Wir fanden, dass eine experimentelle Samenzugabe keinen Wandel vom exotischen zum einheimischen Zustand verursachte. Areale, auf denen acht Jahre

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zuvor im Frühjahr ohne Prioritätseffekt gesät worden war, behielten die höchste Abundanz und Diversität einheimischer Arten und den geringsten Anteil an Exoten. Unsere Ergebnisse legen nahe, dass von Exoten beherrschte Gemeinschaften bei Rekultivierungen unter dem Diasporendruck einheimischer Arten persistieren können. Somit kann die Historie einer Gemeinschaft über lange Zeiträume, die für die Rekultivierung relevant sind, eine wichtige Rolle bei Bildung und Erhalt von alternativen Zuständen spielen. Neue Rekultivierungsprojekte in von Exoten dominierten Landschaften sollten besondere Anstrengungen unternehmen, einheimische Arten während der frühen Phasen der Rekultivierung zu etablieren.

Keywords: Alternate states; Community assembly; Dispersal limitation; Exotic species; Invasive species; Novel ecosystem; Species diversity; Seed addition; Restoration

Introduction

The sequence and timing in which species join an ecological community is known as community assembly history (Fukami, Martijn, Mortimer, & van der Putten 2005). Community assembly history is of interest because the order in which species arrive, and when they arrive can lead to differences in community composition and relative dominance of different species, even under similar abiotic conditions (*e.g.*, Drake 1991; Ejrnæs, Brunn, & Graae 2006; Chase 2010; Fukami et al. 2010; Dickson, Hopwood, & Wilsey 2012; Martin & Wilsey 2012; Kardol, Souza, & Classen 2013).

Assembly history might underlie the formation of alternate states (also referred to as alternative attractors), in which two or more ecosystem states exist in the same environmental conditions on landscapes (Chase 2003; Scheffer & Carpenter 2003; Suding, Gross, & Houseman 2004). For example, novel, exotic-dominated ecosystems are common on landscapes across the globe, but ecosystems dominated by native species also occur within the same regions and under similar precipitation and temperature regimes (Hobbs et al. 2006; Kulmatiski 2006; Ellis 2011; Wilsey, Daneshgar, & Polley 2011; Martin, Polley, Daneshgar, Harris, & Wilsey 2014). Wilsey, Daneshgar, Hofmockel, & Polley (2014) found that exotic communities had equal stability (biomass variability) over a 5-year time period compared to native communities in the same environment, even with a much lower level of species richness. Although exotic and native states can occur side-by-side, we currently have little understanding of the long-term persistence of these states in the face of propagule pressure from native species (Seabloom 2010; Yelenik & D'Antonio 2013). Persistence of communities is an important aspect of community stability that occurs when species maintain their presence and abundances over time despite perturbations, such as invasion by other species (Pimm 1984; Rahel 1990; Huang, Martin, Isbell, & Wilsey 2013; Yelenik & D'Antonio 2013). It is unknown if exotic states are maintained primarily by factors such as soil legacy effects, competition, seed limitation of native species, or a combination of these factors (Yurkonis & Meiners 2004; Kulmatiski 2006; Kulmatiski, Beard, & Stark 2006). Here we focus on whether seed limitation of native species is an important factor contributing to the persistence of exotic states. If native species are rare in exotic-dominated systems solely due to seed limitation, then the addition of native species (or natural arrival of native species) should lead to the loss of the exotic state. However, if exotic states are stable and persistent, then they should be able to resist colonization by native propagules.

Different assembly history treatments (timing of arrival and order of arrival) have recently been found to generate alternate states of perennial exotic versus native species in the same abiotic conditions (Martin & Wilsey 2012). However, it is poorly understood whether the alternate states that form in these studies are persistent in the face of propagule pressure. Theory predicts that if the mechanisms that favor the states are strong, then species seeded later should not be able to colonize and establish (Law 1999; Fukami & Nakajima 2011). Thus, states that develop during community assembly should remain divergent. However, if the mechanisms are weak, then seeds should establish and cause a shift in the alternate states (Law 1999; Chase 2003; Fukami & Nakajima 2011).

Understanding whether or not adding seeds to exotic-dominated areas can cause shifts to native states is important to restoration ecology. Restoring ecosystems often requires purposefully attempting to shift a degraded ecosystem state, such as a low diversity, exotic-dominated system, to a diverse state dominated by native species (Scheffer & Carpenter 2003; Suding et al. 2004; Martin, Moloney, & Wilsey 2005; Foster et al. 2007). Repeated additions of seeds are predicted to increase establishment success of added species compared to single additions (*e.g.*, Von Holle & Simberloff 2005; but see Collinge & Ray 2009). However, more information is needed on whether adding native seeds can shift exotic-dominated states to native states in a restoration context (*e.g.*, Reinhardt Adams & Galatowitsch 2008; Seabloom 2010).

We tested whether seed additions can cause a low-diversity, exotic state to shift to a higher diversity, native state with an ongoing assembly history experiment (Martin & Wilsey 2012). Relatively diverse, native states comprised of C_4 grasses and C_3 forbs established when we added a 30-species prairie seed mix to bare ground in the spring and without priority effects (Martin & Wilsey 2012). In contrast, lower diversity states dominated primarily by C_3 exotic grasses arose when the same 30-species seed mix was planted on bare ground in late summer or after an early-arriving native