

Is community persistence related to diversity? A test with prairie species in a long-term experiment

Y. Huang^{a,b}, L.M. Martin^a, F.I. Isbell^c, B.J. Wilsey^{a,*}

^aDepartment of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011, USA

^bInstitute of Grassland Science, Northeast Normal University, Changchun 130024, PR China

^cDepartment of Ecology, Evolution, and Behavior, University of Minnesota, St Paul, MN 55108, USA

Received 24 August 2012; accepted 23 January 2013

Available online 16 February 2013

Abstract

Community persistence, or the ability of a community to maintain species composition and diversity through time, is a component of stability that is important to restoration. We ran a biodiversity–ecosystem functioning experiment for three years, and then stopped weeding it for 5–6 years, which allowed us to test whether increased plant species diversity and dissimilarity in height would lead to increased community persistence in the face of high invasion pressure by non-native species. Our approach was unique in that the experiment varied richness (one or four species) and evenness (three levels plus monocultures of the dominant species) using two separate dissimilarity types (having all tall species or having tall and short species combined) in six spatiotemporal blocks. Persistence was quantified as to how well positive productivity–diversity relationships, proportion of planted native species, and species richness remained unchanged over time. Thus, high persistence values indicate low levels of invasion and local extinction. We found that the positive relationship between diversity measures and productivity persisted after cessation of weeding. The proportion of planted species was 32% higher in mixture than in monoculture plots, indicating that monocultures were more heavily invaded by non-native species. Reduced evenness did not affect persistence measures in plots with dissimilar heights, but measures declined linearly with decreased evenness in plots with all tall species. Our results suggest that (1) persistence–diversity relationships are likely to vary with the traits of species becoming rare and going extinct, and (2) it is important to restore higher species diversity in restoration projects to favor the long-term persistence of planted species.

Zusammenfassung

Die Persistenz, d.h. die Fähigkeit einer Gemeinschaft Artenzusammensetzung und -diversität aufrechtzuerhalten, ist eine Komponente der Stabilität, die wichtig für die Restauration ist. Wir unterhielten ein Biodiversität–Ökosystemfunktions-Experiment über drei Jahre hinweg und stellten dann das Jäten für fünf bzw. sechs Jahre ein. Dies erlaubte uns zu überprüfen, ob höhere Artendiversität der Pflanzen und unterschiedliche Wuchshöhen bei hohem Einwanderungsdruck durch nicht einheimische Arten zu höherer Persistenz der Gemeinschaft führen. Unser Ansatz war einzigartig, weil im Experiment Artenzahl (eine oder vier Arten) und Evenness (drei Stufen plus Monokultur der dominanten Art) mit zwei Wuchshöhenvarianten (nur hochwüchsige Arten und hochwüchsige und niedrige Arten gemischt) in sechs räumlich-zeitlichen Blöcken variiert wurden. Die Persistenz wurde quantifiziert als in welchem Maße positive Produktivität–Diversitäts–Beziehungen, der Anteil gepflanzter einheimischer Arten und der Artenreichtum über die Zeit unverändert blieben. D.h. hohe Persistenzwerte zeigen geringe Einwanderung und lokales Aussterben an. Wir fanden, dass die positive Beziehung zwischen Diversitätsmaßen und Produktivität

*Corresponding author. Tel.: +1 515 294 0232; fax: +1 515 294 1337.

E-mail address: bwilsey@iastate.edu (B.J. Wilsey).

nach dem Ende der Jätarbeiten bestehen blieb. Der Anteil der gepflanzten Arten war in Mischkulturen um 32% höher als in Monokulturen. Dies besagt, dass die Einwanderung von nicht einheimischen Arten in Monokulturen höher war. Eine reduzierte Evenness beeinflusste die Persistenzmaße auf Flächen mit Pflanzen unterschiedlicher Wuchshöhe nicht, aber die Maßzahlen nahmen linear mit abnehmender Evenness ab, wenn auf den Flächen nur hochwüchsige Arten angepflanzt waren. Unsere Ergebnisse legen nahe, dass (1) die Beziehungen zwischen Persistenz und Diversität wahrscheinlich mit den Merkmalen der Arten, die selten werden und aussterben, variieren und dass (2) es wichtig ist, eine höhere Artendiversität in Restaurationsprojekten wiederherzustellen, um die langfristige Persistenz der gepflanzten Arten zu befördern.

© 2013 Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie.

Keywords: Invasive species; Dissimilarity; Resilience; Restoration; Evenness; Richness; Stability; Biodiversity–ecosystem function

Introduction

Theory predicts that declines in plant diversity will lead to reduced stability (Loreau 2010). Stability is a multi-faceted concept that includes resistance, resilience, persistence and invariability in community and ecosystem processes over time (Pimm 1984; Ives & Carpenter 2007). In terms of restoration, reduced stability may manifest itself in many ways, including higher invasion by non-native species (Kennedy et al. 2002), switches to alternate states dominated by non-native or weedy native species (Martin & Wilsey 2012), or greater variability in net primary productivity from year to year (Tilman, Reich, & Knops 2006). Over longer time frames, high invasion by non-native species or greater fluctuations in net primary productivity may lead to native communities that fail to persist if local extinctions occur and native species do not re-establish.

Establishing a persistent native-dominated community is one of the primary goals of restoration (Falk et al. 2006), yet, we have little information on what factors predict persistence. Persistence has been defined in general terms as the ability of a system to maintain itself through time (Pimm 1984), and community persistence has been defined more specifically as the constancy of abundance, abundance rankings and the presence of species over time (Rahel 1990). Of course, some year-to-year variation is normal in ecosystems, and restoration plans should reflect this. However, if native communities become heavily invaded by non-native species, or if planted species fail to establish reproducing populations, then persistence will be low. In this case, we will not see the target native community except when it is in transition to an invaded community state (Hobbs & Norton 1996). Restoring a diverse assemblage of native species that can persist over long time periods without further human intervention is an attribute of successfully restored ecosystems (Galatowitsch 2012). Thus, a restored community that has high persistence will have low levels of invasion, consistent levels of ecosystem process rates, and low levels of target species extinction. There are few long-term studies on persistence (Pfisterer, Joshi, Schmid, & Fischer 2004; Bezemer & van der Putten 2007; Roscher, Temperton, Buchmann, & Schulze 2009; Doherty, Callaway, & Zedler 2011), and persistence over multiple years in an unweeded setting is especially understudied.

Most stability studies have focused on plant biomass variability across years, or on communities' resistance and resilience to various forms of extrinsic disturbance (Ives & Carpenter 2007). Many experimental studies have found that ecosystem stability increased or exotic species invasion decreased when plant diversity increased (e.g. Kennedy et al. 2002; Tilman et al. 2006; Jiang, Zhang, & Wang 2007; Losure, Wilsey, & Moloney 2007). However, results are mixed overall when experimental and observational results are combined, with several observational studies finding no relationship or negative relationships between stability and diversity (e.g. Foster, Smith, Dickson, & Hildebrand 2002; Polley, Wilsey, & Derner 2007; Grman, Lau, Schoolmaster, & Gross 2010; Sasaki & Lauenroth 2011), and few have been done in a restoration context (Bullock, Pywell, Burke, & Walker 2001; Bullock, Pywell, & Walker 2007; Bezemer & van der Putten 2007). In a comparison of restorations and remnants, Polley et al. (2007) found that more diverse prairie remnants were equal or less stable over time than lower diversity restorations due to dominant species with high year-to-year stability in the restoration (Roscher et al. 2011). We suggest that results point to two important issues: (1) results vary depending on the measure of stability used (Ives & Carpenter 2007), and (2) both complementary resource use and the traits of dominant species can be important predictors of stability. Using this conceptual framework, we predict that positive relationships between stability, in this case quantified with persistence measures, and diversity will be found only in cases where niche partitioning is operating as a mechanism.

Finally, it is important to know whether relationships derived from well controlled short-term studies under artificial weeding (all important for straight-forward tests of theory) will translate to longer time frames, and to more realistic conditions where weeding no longer occurs (Bullock et al. 2001, 2007; Foster & Dickson 2004; Doherty et al. 2011). Relationships from weeded studies might weaken or disappear over longer time frames once weeds are allowed to invade (Pfisterer et al. 2004; Bezemer & van der Putten 2007). For example, Doherty et al. (2011) stopped weeding their plots for eleven years and found that the strong positive richness–productivity relationship that they observed earlier disappeared over time. They suggested that weeded experiments are not as relevant to restorations as previously thought and that species-rich plantings are unlikely to ensure

Table 1. Experimental design. Evenness was varied by changing the dominance of *Andropogon gerardii* to establish high (H), medium (M), and low (L) evenness treatments with a geometric distribution of relative abundance with different slopes for two dissimilarity types of four-species mixtures (i.e. dissimilar and tall). Planted relative abundances of each species are given for each treatment combination and for *Andropogon* monocultures.

Species	Height mean (cm) ^a	Mixture treatments						<i>Andropogon</i> monoculture
		All tall			Dissimilar			
		H	M	L	H	M	L	
<i>Andropogon gerardii</i>	133.2	0.31	0.53	0.72	0.31	0.53	0.72	1
<i>Salvia azurea</i>	94.5	0.26	0.27	0.21	0.26	0.27	0.21	
<i>Bouteloua gracilis</i>	44.6				0.24	0.14	0.06	
<i>Liatris punctata</i>	42				0.19	0.07	0.01	
<i>Schizachyrium scoparium</i>	84.6	0.24	0.14	0.06				
<i>Heterotheca villosa</i>	96.9	0.19	0.07	0.01				
Kirwan et al. (2007) evenness		0.99	0.86	0.58	0.99	0.86	0.58	0
C ₄ proportions		0.55	0.67	0.78	0.55	0.67	0.78	1
CV height ^a		0.21	0.19	0.18	0.52	0.42	0.37	

^aMean and coefficient of variation in heights are from Losure et al. (2007).

long-term restoration of functions. In some experiments, weeding extended the positive diversity–productivity relationships (Tilman et al. 2006; van Ruijven & Berendse 2009), while unweeded counterparts lost similar relationships in just two years (Pfisterer et al. 2004; Roscher et al. 2009). Thus, we suggest that we need further long-term tests of how planted communities, and positive relationships between diversity and productivity will persist over time in the face of invasions by non-native species. Our experiment, which took place in small plots in an exotic-dominated field with high invasive species propagule pressure, provides such a test.

Here, we tested whether increased diversity (both richness and evenness) and dissimilarity in height would lead to increased community persistence over 5–6 years in the face of high invasion pressure by mostly non-native species (i.e. without weeding). We varied niche partitioning by comparing plantings with different height dissimilarities, a predictor of productivity in Naeem, Thompson, Lawler, Lawton, and Woodfin (1994) and Wilsey and Potvin (2000). Losure et al. (2007) and Isbell, Losure, Yurkonis, and Wilsey (2008) reported on invasion and diversity–productivity relationships during the three years that plots were weeded. We tested the hypotheses: (1) positive relationships between diversity and productivity will persist under high invasion pressure; (2) communities with higher diversity, either richness or evenness, will be more persistent than plots with lower diversity; and (3) communities containing plants that are dissimilar in height will be more persistent than those with similar heights due to greater niche partitioning. To address the first hypothesis, we measured how well the previously documented positive diversity–productivity relationships persisted through time. To address the last two hypotheses, we measured how well the initial proportion of native target species persisted (planted biomass/planted species plus invader biomass), and then whether fewer extinctions occurred in plots planted with higher diversity than in

plots planted with lower diversity. High native species proportions and low extinction rates are indicative of lower invasive species impact.

Methods

Experimental design

The study was conducted in the Loess Hills in an abandoned pasture at Iowa State University's Western Research Farm in Iowa, USA (42°1'N, 95°8'W). We used six native species in our plots: *Andropogon gerardii*, a tall, deeply rooting C₄ grass; *Schizachyrium scoparium*, a tall (in our area), shallowly rooting C₄ grass; *Bouteloua gracilis*, a short, shallowly rooting C₄ grass; *Heterotheca villosa*, a tall, shallowly rooting forb; *Salvia azurea*, a tall, deeply rooting forb; and *Liatris punctata*, a short, shallowly rooting forb. Six spatiotemporal blocks, each consisting of 12.1 × 1 m plots, were established in a randomized block design on three hillsides (SW, E, and N aspects) in two trials (2003 and repeated in 2004).

For each plot, we grew plants from seed and then planted 72 roughly equal-sized transplants in either four species mixtures, or monocultures of each of the six species (Table 1). Mixture plots were planted with three levels of species evenness crossed with two levels of height dissimilarity (all tall species or having tall and short species combined, Table 1) in a factorial treatment arrangement. Evenness was varied by changing the level of *A. gerardii* dominance, a grass species that commonly dominates tallgrass prairies and is especially problematic in restorations (Collins, Knapp, Briggs, Blair, & Steinauer 1998; Howe 2000). In both tall and dissimilar plots, we controlled rooting depth by selecting species based on availability of published heights and rooting depths using subordinate species that are rare in tallgrass prairies of the

Table 2. ANOVA results for planted species biomass (g/m^2) and proportion of planted species biomass (planted/[planted + invader biomass]) across treatments that varied evenness crossed with two mixture types (i.e. dissimilar vs. all tall plots). ‘Trial’ and ‘Aspect’ were blocking terms. *F*-values are for type III SS. Dominance contrast coefficients were based on relative abundance of *Andropogon gerardii*, and included its monoculture.

Source	DF	Peak biomass		Proportion	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Trial	1	1.04	0.31	4.50	0.04
Aspect	2	1.12	0.33	4.69	0.01
Treatment	11	6.55	<0.0001	13.35	<0.0001
Error	56				
<i>A priori</i> linear contrasts					
Species richness	1	18.11	<0.0001	54.74	<0.0001
Tall vs. dissimilar	1	3.66	0.06	4.58	0.04
<i>A. gerardii</i> dominance in tall	1	6.89	0.01	4.39	0.04
<i>A. gerardii</i> dominance in dissimilar	1	0.21	0.65	0.16	0.69

area (Wilsey, Martin, & Polley 2005). Alleyways, which were seeded with *Bouteloua curtipendula* and mowed in the first three years of the study, were not mowed during the years of the current study.

Three characteristics of our study led to high invasive species propagule pressure. First, the plots were embedded in an exotic-dominated field (Isbell & Wilsey 2011). Second, we stopped weeding plots after the third year, so plots have been subjected to invasion by non-native weedy species over the last five (2003 trial) or six (2004 trial) years. Third, the plots and blocks were small compared to the size of the surrounding fields, which enabled us to test for persistence in the face of heavy invasion over a six-year time frame. Invader species were primarily exotic in origin, although there was a small amount of spreading of planted native species to other plots and by the species (*B. curtipendula*) that was originally seeded in alleyways.

Persistence measures

Persistence was quantified as to how well: (1) positive productivity–diversity relationships, (2) proportion of planted species, and (3) species richness remained constant over the time during which plots were no longer weeded (i.e. by the end of the six-year time frame). Primary productivity was assessed using peak aboveground biomass in September 2011 in all spatiotemporal blocks. Plant material was clipped to 2-cm height in the center 50 cm × 50 cm of all plots, and was then sorted by species, or grouped as standing dead. Plant material was dried at 65 °C in an oven for 48 h and weighed.

We used the following equations to estimate the persistence of both planted species biomass and richness after 5–6 years of invasion: (1) Peak aboveground biomass across treatments of planted species in 2011 compared to earlier estimates in 2005/2006 from Isbell et al. (2008). (2)

Proportion of planted species remaining in plots = planted species biomass in 2011 / (planted species biomass in 2011 + invader species biomass in 2011). (3) Persistence of species richness = number of planted species that went locally extinct between 2005/2006 and 2011, with low values denoting high persistence.

Statistical analysis

Peak biomass of planted species and proportion of planted species biomass were analyzed with PROC GLM in SAS, with *a priori* contrasts between the two types of mixture plots and among evenness treatments that included the *A. gerardii* monocultures (Littell, Stroup, & Freund 2002). Biomass values were square root-transformed to meet the assumptions of ANOVA. In *A. gerardii* dominance contrasts, the coefficient values were 0.71 in the *A. gerardii* monocultures and 0.16, –0.21, and –0.65 in the low, medium and high evenness mixture plots, respectively. These coefficients were based on planted rank-abundance slopes and *A. gerardii* dominance. The proportion of planted species biomass was normally distributed ($w = 0.97$, $P = 0.09$) and was not transformed before analysis.

Persistence of species richness over time was analyzed in mixtures among treatments with a non-parametric approach using a generalized linear model with a multinomial distribution (PROC GENMOD in SAS). Multinomial models apply to cases where an observation can fall into *k* categories, in this case three categories of 0 (no local extinctions), 1 or 2 species. Linear and quadratic relationships were tested within each mixture type treatment using *a priori* contrasts. Monoculture extinctions were compared across species using a binomial ($k = 2$, extinct or not) model in PROC GENMOD in SAS for species that went extinct in at least one plot.

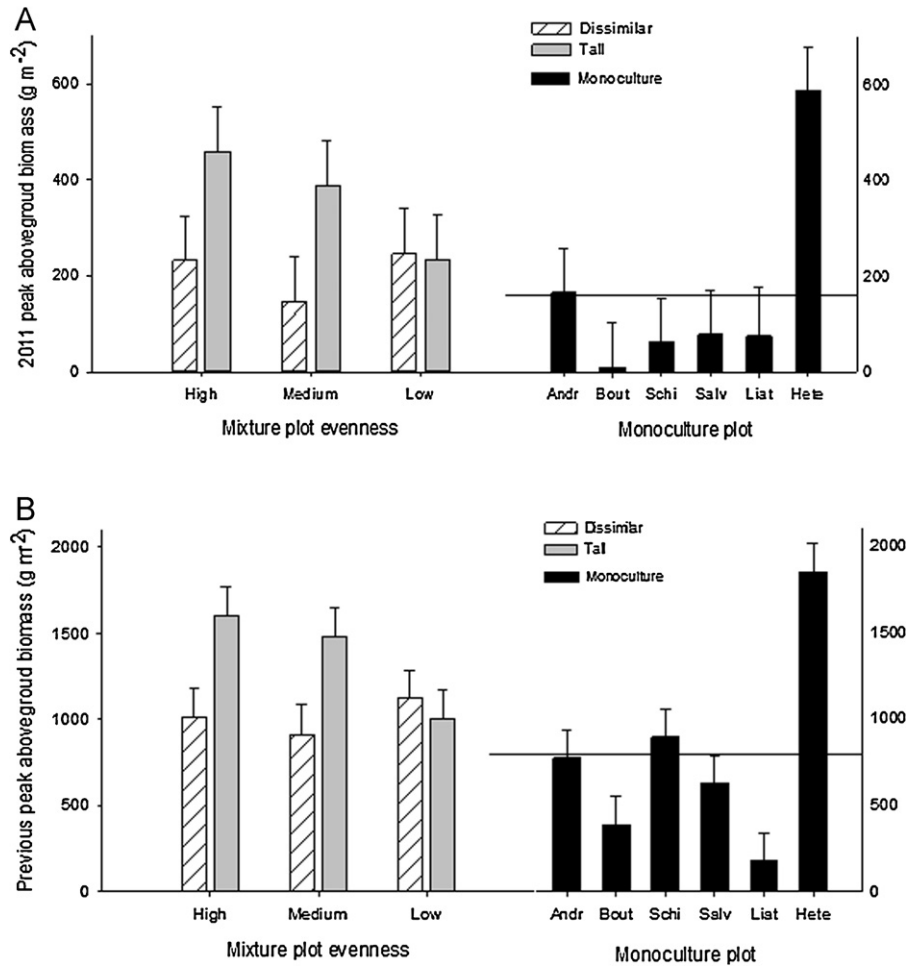


Fig. 1. Planted-species biomass for mixture and monoculture plots in 2011, 5–6 years after weeding stopped (A), and in a previous year prior to cessation of weeding (B, from Isbell et al. 2008, figured used with permission from *Oikos*). The horizontal line is the average of monoculture plots. Peak biomass (LS-means + 1 SE) in 2011 did not differ among evenness treatments in dissimilar plots, but significantly decreased with increased dominance of *Andropogon* in tall plots (linear contrast, $P=0.01$). Species abbreviations: *Andr* = *A. gerardii*, *Salv* = *S. azurea*, *Bou* = *B. gracilis*, *Liat* = *L. punctata*, *Schi* = *S. scoparium*, *Hete* = *H. villosa*.

Results

Net primary productivity of planted species

Peak biomass of planted species was significantly greater in mixtures than in monocultures in 2011, after 5 or 6 years of invasion (Table 2 and Fig. 1A). There tended to be greater biomass in tall plots than in dissimilar plots ($P=0.06$, Table 1 and Fig. 1A). As the dominance of *A. gerardii* increased across tall mixtures, peak biomass linearly decreased (Table 2 and Fig. 1A). However, there was no difference in peak biomass among evenness treatments in dissimilar plots. These trends were highly consistent with trends reported in year 3 before weeding ceased (Fig. 1B, from Isbell et al. 2008). Biomass values were lower on average in 2011 than in the earlier sampling period, possibly due to the age of the plots, or to the fact that invaders were present but not included in the calculations for 2011.

In monocultures, *H. villosa* was the most productive species, similar to the species rankings before weeding was halted (Isbell et al. 2008). By 2011, it remained the most productive species, but importantly, it did not competitively displace other native species in tall plots.

Persistence of planted species

Proportion of biomass that was from planted species was 80% higher in mixtures than in monocultures (Table 2 and Fig. 2), i.e. the amount of invasion was lower in mixtures than monocultures. The top four invader species by frequency were the exotics *Bromus inermis* (which invaded 71 plots), *Poa pratensis* (55 plots), *Coronilla varia* (21 plots), and the native *Bouteloua curtipendula* (33 plots). All of these species are perennials. Proportion of planted species was also significantly greater in tall plots than in dissimilar ones (Table 2 and

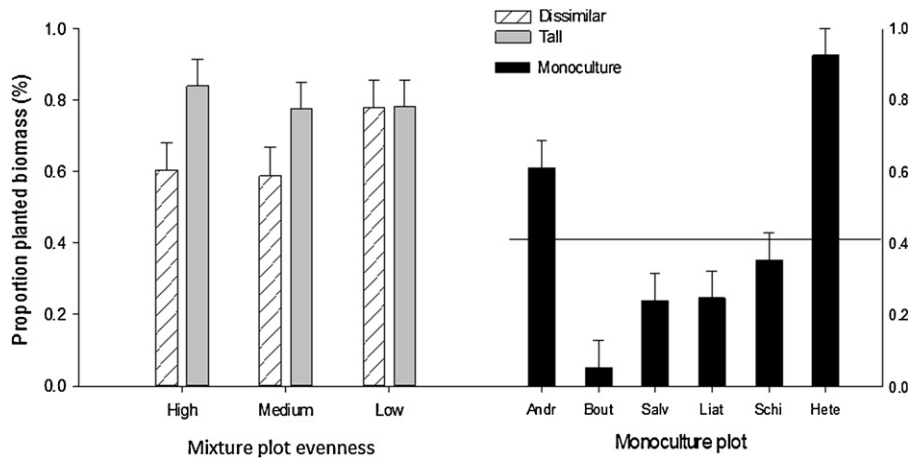


Fig. 2. Proportion of planted biomass (1-proportion of invaders) for mixture and monoculture plots after 5–6 years of not weeding. The horizontal line is the average of monoculture plots. Proportions (LS-means + 1 SE) did not differ among evenness treatments in dissimilar plots, but declined linearly with decreased evenness (and increased dominance by *Andropogon*) in tall plots (linear contrast, $P = 0.04$). Species abbreviations are found in Fig. 1 legend.

Fig. 2). As dominance of *A. gerardii* increased in tall plots (i.e. evenness decreased), proportion of planted species declined linearly. Proportion of planted biomass did not change significantly with increased *A. gerardii* dominance in dissimilar plots (Table 2 and Fig. 2).

There were also large differences in proportion of planted species biomass among monocultures. One short species, *B. gracilis*, was highly susceptible to invasion and almost went extinct in all plots in which it was originally planted, including several monocultures (Fig. 1A). *B. gracilis* was frequently replaced by the exotic invader *Poa pratensis*.

Persistence of species richness

Planted species evenness and height dissimilarity both significantly affected the persistence of planted species richness (i.e. local extinctions). Local extinction was higher in plots with dissimilar heights than it was in plots with all tall species ($\lambda^2 = 7.21$, $P = 0.007$, Table 3). Local extinction also increased linearly as evenness declined in plots with tall species (dissimilarity \times evenness interaction: $\lambda^2 = 6.01$, $P = 0.049$; evenness main effect: $\lambda^2 = 3.27$, $P = 0.195$, Table 3, linear contrast within tall: $\lambda^2 = 12.4$, $P < 0.001$, quadratic $P = 0.27$). In dissimilar plots, there was no relationship between evenness and extinction (linear contrast, $\lambda^2 = 0.7$, $P = 0.41$, quadratic $P = 0.17$).

Species in monocultures went locally extinct in 4 of 6 *B. gracilis*, 1 of 5 *L. punctata*, and 1 of 6 *S. scoparium* plots, and this difference was significant across species ($\lambda^2 = 18.9$, $P < 0.01$ when all species were included, $\lambda^2 = 7.4$, $P = 0.02$ when only the species with extinctions were included). None of the other species went locally extinct in monocultures.

Discussion

Tallgrass prairie ecosystems are among the most endangered ecosystems in the world, and intact prairies are exceptionally diverse (Leach & Givnish 1996; Wilsey et al. 2005). Here we used a small part of that diversity to test hypotheses about species persistence when subjected to non-native propagule pressure. We found that persistence was greater in diverse plots on average, but that local extinction probability differed between the dissimilarity types. Restorations that are planted with a diverse seed mix or using a diverse set of transplants are predicted to be more likely to persist in the face of invasion (Middleton, Bever, & Schultz 2010).

Species evenness increased the persistence of native species in tall plots, but not in dissimilar-height plots. This result did not support our hypothesis of having greater persistence with high height dissimilarity at high evenness levels. In the tall plots, when *A. gerardii* dominance was low and *H. villosa* abundance was high, persistence of native plants was highest. We found earlier that light levels were much lower under mixtures with the C₃ forb *H. villosa* early in the spring when invasion is heaviest in this system (Losure et al. 2007). Conversely, light capture was low and invasion rate was higher in plots dominated by the C₄ grass *A. gerardii* (Losure et al. 2007). Thus, our results are inconsistent with the idea that niche partitioning in space aboveground is the mechanism behind increased persistence with diversity. Temporal components of niche partitioning were found to be important in Losure et al. (2007) and deserve further study (Hooper & Dukes 2004; Flombaum & Sala, 2012). We provide some support for the hypothesis that high evenness plantings had greater persistence than plots planted with low evenness, which supports the observational results of Leach and Givnish (1996) and Fischer and Stocklin (1997).

Table 3. Local extinction frequencies (number of plots) in dissimilar and tall communities across planted evenness treatments (high, medium or low) after 5–6 years of not weeding, which was tested with a non-parametric approach using a multinomial distribution model. Extinction was significantly higher in ‘dissimilar’ than ‘all tall’ plots, and was significantly higher as evenness declined in the ‘all tall’ treatment ($\lambda^2 < 0.05$).

Evenness	Extinctions (number of species lost)						Total
	All tall			Dissimilar			
	0	1	2	0	1	2	
High	4	2	0	0	1	4	11
Medium	2	4	0	2	1	2	11
Low	0	4	2	0	4	2	12
Total	6	10	2	2	6	8	34

Proportion of planted species was also different between the two community dissimilarity types. We hypothesized that mixtures containing tall and short species would be more persistent than mixtures with only tall species due to complementarity in light capture, but we found no support for this. To the contrary, proportion of plant species biomass remaining in tall communities was higher than in dissimilar communities. This can be explained by the persistence of species monocultures (Fig. 2). The two tall species persisted more than the two short species; *H. villosa* had the highest proportion of planted biomass remaining. *B. gracilis* went nearly extinct in all dissimilar plots and monocultures, primarily due to invasion and complete replacement by *Poa pratensis*. Thus, plots with all tall species persisted much better than plots with tall and short-statured species. Observational studies have found that the loss of short-statured species like *B. gracilis* is greater than loss of tall-statured plant species in the prairie remnants in the central United States (Leach & Givnish 1996). Here, we present carefully controlled experimental results that are consistent with these observational ones.

Keeping short-statured species in restoration projects remains a challenge, and mowing, grazing or summer fires should be studied in the future as possible ways to keep them in the system (Dermer & Hart 2007). Daßler, Roscher, Temperton, Schumacher, and Schulze (2008) found that short-statured species had increased leaf area and specific leaf area in mixed stands, and this, along with mowing twice per year allowed the short-statured species to maintain themselves in mixed canopies. Conservation areas in the U.S. rarely include mowing or ungulate grazing, both of which may help to maintain short-statured species in the community (e.g. Belsky 1992; Anderson, Ritchie, & McNaughton 2007). Research should continue on how to incorporate mowing or grazing into projects as well as the responses of short-statured species to competition from taller species in mixed stands (Daßler et al. 2008).

Successfully restored communities should have minimal species extinctions in the face of invasion. Pfisterer et al. (2004) and Roscher et al. (2009) found that communities can fail to persist over time without hand-weeding. Doherty et al. (2011) investigated the relationship between richness and productivity and found that the loss of positive

relationships began soon after they stopped weeding. However, in our system, the positive diversity–productivity relationship remained after 5–6 years with no weeding. This suggests that persistence in the face of invasion may differ among systems, and richness–productivity relationships may be more persistent in lower productivity systems like ours than in systems such as the salt marshes of Doherty et al. (2011). Another difference is that our study was replicated over two years and three aspects, which increases the probability that at least some of the plantings will persist and will include the contexts necessary for a variety of species to have positive effects on ecosystem functioning (Isbell et al. 2011). An important caveat for interpreting our study is that we used four-species mixtures, and four species per m² is lower than in most grasslands. A relatively small number of species was used in this study due to its focus on dominance and evenness, and further research should be done with more species-rich communities (e.g. Bullock et al. 2001, 2007; Daßler et al. 2008).

In conclusion, we found that more diverse communities continued to have higher productivity than less diverse ones after 5–6 years of invasion. Positive relationships between evenness and persistence were found, but they tended to be stronger in plots of all tall species. The relatively high level of persistence in diverse plots suggests that they will persist successfully in the face of heavy invasion if they arrive and fully establish before invaders arrive (Martin & Wilsey 2012). Our results suggest that a diverse stand of tall species may be better at resisting invasion than a less diverse stand, but our management regime (or lack thereof) failed to keep short species in the system. More research should be done on how to incorporate realistic disturbance regimes that mimic the effects of ungulate grazers to foster the persistence of short native species, thus increasing the native plant diversity of prairie grasslands.

Acknowledgements

We thank David Losure for all his help. This work was partially supported by a grant from the NSF (DEB-0639417) and the China Scholarship Council.

References

- Anderson, T. M., Ritchie, M. E., & McNaughton, S. J. (2007). Rainfall and soils modify plant community response to grazing in Serengeti National Park. *The American Naturalist*, *88*, 1191–1201.
- Belsky, A. J. (1992). Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science*, *3*, 187–200.
- Bullock, J. M., Pywell, R. F., Burke, M. J. W., & Walker, K. J. (2001). Restoration of biodiversity enhances agricultural production. *Ecology Letters*, *4*, 185–189.
- Bullock, J. M., Pywell, R. F., & Walker, K. J. (2007). Long-term enhancement of agricultural production by restoration of biodiversity. *Journal of Applied Ecology*, *44*, 6–12.
- Bezemer, T. M., & van der Putten, W. H. (2007). Ecology: Diversity and stability in plant communities. *Nature*, *446*, E6–E7.
- Collins, S. L., Knapp, A. K., Briggs, J. M., Blair, J. M., & Steinauer, E. M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, *280*, 745–747.
- Daßler, A., Roscher, C., Temperton, V. M., Schumacher, J., & Schulze, E. D. (2008). Adaptive survival mechanisms and growth limitations of small-stature herb species across a plant diversity gradient. *Plant Biology*, *10*, 573–578.
- Derner, J. D., & Hart, R. H. (2007). Grazing-induced modifications to peak standing crop in Northern mixed-grass prairie. *Rangeland Ecology & Management*, *60*, 270–276.
- Doherty, J. M., Callaway, J. C., & Zedler, J. B. (2011). Diversity–function relationships changed in a long-term restoration experiment. *Ecological Applications*, *21*, 2143–2155.
- Falk, D. A., Palmer, M. A., & Zedler, J. B. (Eds.). (2006). *Foundations of restoration ecology*. Washington, DC: Island Press.
- Fischer, M., & Stocklin, J. (1997). Local extinctions of plant in remnants of extensively used calcareous grasslands 1950–1985. *Conservation Biology*, *11*, 727–737.
- Flombaum, P., & Sala, O. E. (2012). Effects of plant species traits on ecosystem processes: Experiments in the Patagonian steppe. *Ecology*, *93*(2), 227–234.
- Foster, B. L., & Dickson, T. L. (2004). Grassland diversity and productivity: The interplay of resource availability and propagule pools. *Ecology*, *85*, 1541–1547.
- Foster, B. L., Smith, V. H., Dickson, T. L., & Hildebrand, T. (2002). Invasibility and compositional stability in a grassland community: Relationships to diversity and extrinsic factors. *Oikos*, *99*, 300–307.
- Galatowitsch, S. M. (2012). *Ecological Restoration*. Sunderland, Massachusetts, USA: Sinauer Associates, Inc., pp. 27–28.
- Grman, E., Lau, J. A., Schoolmaster, D. R., & Gross, K. L. (2010). Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecology Letters*, *13*, 1400–1410.
- Hobbs, R. J., & Norton, D. A. (1996). Towards a conceptual framework for restoration ecology. *Restoration Ecology*, *4*, 93–110.
- Hooper, D. U., & Dukes, J. S. (2004). Overyielding and plant functional groups in a long-term experiment. *Ecology Letters*, *7*, 95–105.
- Howe, H. F. (2000). Grass response to seasonal burns in experimental plantings. *Journal of Range Management*, *53*, 437–441.
- Isbell, F. I., Losure, D. A., Yurkonis, K. A., & Wilsey, B. J. (2008). Diversity–productivity relationships in two ecologically realistic rarity–extinction scenarios. *Oikos*, *117*, 996–1005.
- Isbell, F. I., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., et al. (2011). High plant diversity is needed to maintain ecosystem services. *Nature*, *477*, 199–203.
- Isbell, F. I., & Wilsey, B. J. (2011). Rapid biodiversity declines in both ungrazed and intensely grazed grasslands. *Plant Ecology*, *212*, 1663–1674.
- Ives, A. R., & Carpenter, S. R. (2007). Stability and diversity of ecosystems. *Science*, *317*, 58–62.
- Jiang, X. L., Zhang, W. G., & Wang, G. (2007). Biodiversity effects on biomass production and invasion resistance in annual versus perennial plant communities. *Biodiversity and Conservation*, *16*, 983–1994.
- Kennedy, T. A., Naeem, S., Howe, K. M., Knops, J. M. H., Tilman, D., & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, *417*, 636–638.
- Kirwan, L., Lüscher, A., Sebastia, M. T., Finn, J. A., Collins, R. P., Porqueddu, C., et al. (2007). Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. *Journal of Ecology*, *95*, 30–539.
- Leach, M. K., & Givnish, T. J. (1996). Ecological determinants of species loss in remnant prairies. *Science*, *273*, 1555–1558.
- Littell, R. C., Stroup, W. W., & Freund, R. J. (2002). *SAS for linear models*. Cary, NC: SAS Publishing.
- Loreau, M. (2010). *From populations to ecosystems: Theoretical foundations for a new ecological synthesis*. Princeton, USA: Princeton University Press.
- Losure, D. A., Wilsey, B. J., & Moloney, K. A. (2007). Evenness–invasibility relationships differ between two extinction scenarios in tallgrass prairie. *Oikos*, *116*, 87–98.
- Martin, L. M., & Wilsey, B. J. (2012). Assembly history alters alpha and beta diversity, exotic-native proportions, and ecosystem functioning of restored prairie plant communities. *Journal of Applied Ecology*, *49*, 1436–1445.
- Middleton, E. L., Bever, J. D., & Schultz, P. A. (2010). The effect of restoration methods on the quality of the restoration and resistance to invasion by exotics. *Restoration Ecology*, *18*, 181–187.
- Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H., & Woodfin, R. M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, *368*, 734–736.
- Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, *307*, 321–326.
- Pfisterer, A. B., Joshi, J., Schmid, B., & Fischer, M. (2004). Rapid decay of diversity–productivity relationships after invasion of experimental plant communities. *Basic and Applied Ecology*, *5*, 5–14.
- Polley, H. W., Wilsey, B. J., & Derner, J. D. (2007). Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos*, *116*, 2044–2052.
- Rahel, F. J. (1990). The hierarchical nature of community persistence: A matter of scale. *American Naturalist*, *136*, 328–344.
- Roscher, C., Temperton, V. M., Buchmann, N., & Schulze, E. D. (2009). Community assembly and biomass production in regularly and never weeded experimental grasslands. *Acta Oecologica*, *35*, 206–217.

- Roscher, C., Weigelt, A., Proulx, R., Marquard, E., Schumacher, J., Weisser, W. W., et al. (2011). Identifying population- and community-level mechanisms of diversity–stability relationships in experimental grasslands. *Journal of Ecology*, *99*, 1460–1469.
- Sasaki, T., & Lauenroth, W. K. (2011). Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia*, *166*, 761–768.
- Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*, 629–632.
- van Ruijven, J., & Berendse, F. (2009). Long-term persistence of a positive plant diversity–productivity relationship in the absence of legumes. *Oikos*, *118*, 101–106.
- Wilsey, B. J., & Potvin, C. (2000). Biodiversity and ecosystem functioning: Importance of species evenness in an old field. *Ecology*, *81*, 887–892.
- Wilsey, B. J., Martin, L. M., & Polley, H. W. (2005). Predicting plant extinction based on species–area curves in prairie fragments with high beta richness. *Conservation Biology*, *19*, 1835–1841.

Available online at www.sciencedirect.com

SciVerse ScienceDirect