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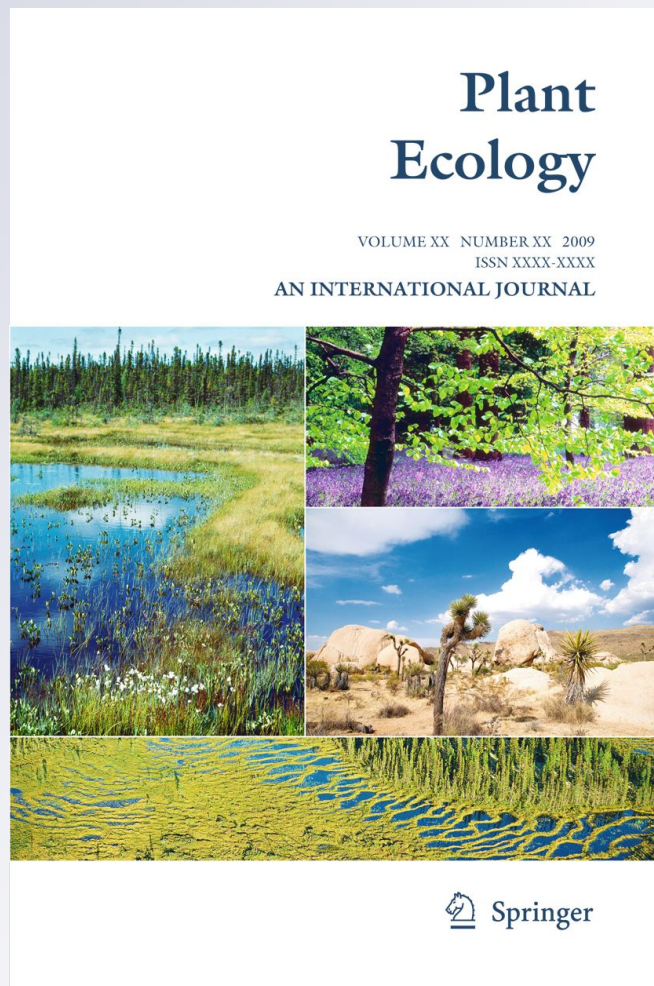
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Rapid biodiversity declines in both ungrazed and intensely grazed exotic grasslands

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Abstract Exotic-dominated ecosystems with low diversity are becoming increasingly common. It remains unclear, though, whether differences between native and exotic species (driver model), or changes in disturbances or resources (passenger model), allow exotics to become competitive dominants. In our field experiment, plant species origin (native or exotic), cattle grazing (ungrazed or intensely grazed once), and species composition treatments were fully crossed and randomly assigned to four-species mixtures and monocultures of grassland plants. We found that biodiversity declined more rapidly in exotic than in native species mixtures, regardless of our grazing disturbance treatment. Early declines in species evenness (i.e., increases in dominance) led to subsequent declines in species richness (i.e., local extinctions) in exotic mixtures. Specifically, Simpson's diversity was 29% lower after 1 year, and species richness was 15% lower after 3 years, in exotic than in native mixtures. These rapid biodiversity declines in exotic mixtures were partly explained by decreased complementarity (i.e., niche partitioning and facilitation), presumably because exotic species lack the coevolutionary history that can lead to complementarity and coexistence in native communities. Thus, our results suggest that exotic species can drive biodiversity declines in the presence or absence of a grazing disturbance, partly because exotic species interactions differ from native species interactions. This implies that restoring plant biodiversity in grasslands may require removal of exotic species, in addition to disturbance management.

Keywords Land use change · Novel ecosystems · Coexistence · Complementarity · Conservation

Introduction

Biodiversity is rapidly declining (Pimm et al. 1995); and these declines are often associated with global ecosystem changes, including changes in land use, exotic species, nutrient enrichment, and climate change (reviewed by Chapin et al. 2000). It is often difficult to determine which of these global changes actually drive biodiversity declines, though, because several changes often occur simultaneously. For example, low diversity exotic-dominated ecosystems have replaced high diversity native-dominated ecosystems in many places (reviewed by Hobbs et al. 2006; Seastedt et al. 2008; Hejda et al. 2009). It is possible that these increases in exotic dominance and

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decreases in biodiversity are explained by: (i) differences between native and exotic species (driver model) (Vitousek 1990; Wilsey et al. 2009), (ii) changes in disturbances or resource availability (passenger model) (Gurevitch and Padilla 2004; Didham et al. 2005; MacDougall and Turkington 2005), or (iii) both (Kimball and Schiffman 2003). Note that if the passenger model is correct, then restoring diversity might simply depend on altering disturbances or resources. In contrast, if the driver model is correct, then restoring diversity might also require removing exotic species.

Common garden experiments allow comparisons between natives and exotics, while controlling for potentially confounding variables, such as resource availability and disturbances (Wilsey et al. 2009). Using this approach in a previous study, we found that biodiversity declined more rapidly in mixtures of exotic species than in mixtures of native species that started at the same level of diversity (Wilsey et al. 2009). These previous results suggest that the passenger model cannot completely explain biodiversity declines. Our previous study controlled, but did not manipulate resources or disturbances. Thus, further study is needed to determine whether: (i) exotic species drive biodiversity declines in the presence of disturbances such as livestock grazing, which is common in exotic-dominated grasslands, and (ii) exotic species and livestock grazing synergistically drive biodiversity declines (Kimball and Schiffman 2003).

Exotic species and livestock grazing often occur together, and may synergistically drive biodiversity declines. Managed livestock grazing is currently the most extensive type of land use worldwide, covering more than 25% of earth's terrestrial surface (Asner et al. 2004). Exotic forage species are frequently introduced with livestock grazing (D'Antonio and Vitousek 1992; Kimball and Schiffman 2003; Asner et al. 2004), and intense livestock grazing can facilitate the spread of these and other exotic species (Kimball and Schiffman 2003; Parker et al. 2006; Best and Arcese 2009; HilleRisLambers et al. 2010). Interestingly, native herbivores tend to suppress exotic plants, while exotic herbivores tend to promote the abundance of exotic plants (Parker et al. 2006). Thus, it has been hypothesized that these two factors (i.e., exotic plant species and intense livestock grazing by exotic herbivores) synergistically drive

biodiversity declines (Simoes and Baruch 1991; Smith and Knapp 2001; Kimball and Schiffman 2003; Parker et al. 2006). New experiments that independently manipulate both plant species origin and livestock grazing are needed to test this hypothesis.

Exotic species and livestock grazing may drive biodiversity declines by decreasing complementarity. Here we use Loreau and Hector's (2001) definition of complementarity, which includes niche partitioning (e.g., partitioning resources or natural enemies) and interspecific facilitation. There is considerable evidence that complementarity is common in mixtures of grassland plant species (reviewed by Cardinale et al. 2007), and that these species interactions can be important for the maintenance of biodiversity (Chesson 2000; McKane et al. 2002; Harpole and Suding 2007; Isbell et al. 2009b; Levine and HilleRisLambers 2009). If complementarity results from coevolution, then complementarity may be reduced in exotic ecosystems, where species often lack an evolutionary history of interaction (Wilsey et al. 2009). Additionally, when grazing is intense and nonselective, it may decrease spatiotemporal resource partitioning by increasing the synchrony of plant species growth in space and time (Fuhlendorf and Engle 2001). Thus, complementarity may be reduced in exotic and intensely grazed communities.

The objectives of this study were to determine whether exotic species and a grazing disturbance have independent or synergistic effects on biodiversity, and to determine whether changes in plant species interactions explain these effects. Specifically, we hypothesized that biodiversity declines would be: (i) more rapid in exotic than in native plant species mixtures; (ii) most rapid in intensely grazed exotic mixtures; and (iii) explained by decreased complementarity.

Materials and methods

Study site

The biodiversity and grazing in exotic and native grasslands (BioGEN) field experiment (Isbell and Wilsey 2011) was conducted at Iowa State University's Western Research and Demonstration Farm in the loess hills region of Iowa, USA (42.06°N,

95.82°W). The study was established on a hill in an abandoned pasture dominated by *Bromus inermis* that had not been grazed for 5 years. The vegetation in the abandoned pasture was killed with glyphosate herbicide prior to the establishment of our experimental plots. The 30-year average annual temperature and precipitation are, respectively, 9.7°C and 782 mm. The mean annual temperature and precipitation were, respectively, 9.7°C and 561 mm during 2007; 8.0°C and 835 mm during 2008; and 8.3°C and 738 mm during 2009. Soils are fine-silty, mixed (calcareous), mesic Typic Udorthents, and calcareous loess is the dominant parent material.

Experimental design

We paired perennial native and exotic grassland plant species by taxonomic and functional groups (Table 1) (Isbell and Wilsey 2011). This allowed us to manipulate species origin while controlling for other differences between species that are already known to be important. We included all exotic species that could be paired with a native species that were known to be present in grasslands near the study site, and for which propagules could be collected or purchased. Thus, our study was designed to compare native and exotic grasslands (Wilsey et al. 2009), rather than testing the effect of particularly invasive exotic species. Most studies comparing natives and exotics have included only one species pair, and in many cases native and exotics have not been carefully paired (reviewed by Vila and Weiner 2004; Wilsey 2005). For example, it is difficult to determine whether native or exotic species are more competitive when exotic vines or trees are compared to native grasses (Vila and Weiner 2004).

Seedlings from eight native and eight exotic grassland plant species were grown in a greenhouse during spring 2007. Approximately, equal mass seedlings were transplanted into 1 by 1 m field plots on May 8–11, 2007. There were no differences in seedling biomass between any of the native and exotic species pairs at planting ($P > 0.05$, $N = 7$ randomly sampled transplants for each species). In each plot, 64 seedlings were randomly assigned to a location in an 8×8 grid using the same arrangement of functional groups (Table 1) in each plot. This seedling density was within the range of observed

Table 1 The native and exotic species used in this experiment were paired by functional and taxonomic groups

Native species	Functional group	Taxonomic group[a]	Compositions	Exotic species	Place of origin for exotic
Andropogon gerardii Vitman[b]	C₄ grass	Andropogoneae	*A, D, E, G*	*Miscanthus sacchariflorus* (Maxim.) Franch.[b]	East Asia
Sorghastrum nutans (L.) Nash	C₄ grass	Andropogoneae	*B, C, F, H*	*Miscanthus sinensis* Andersson	East Asia
Pascopyrum smithii (Rydb.) A. Löve	C₃ grass	Pooideae	*A, B, C, G*	*Bromus inermis* Leyss.	Eurasia
Elymus canadensis L.	C₃ grass	Triticeae	D, E, F, H	*Agropyron cristatum* (L.) Gaertn.	Northern Asia
Ratibida pinnata (Vent.) Barnhart	Forb	Asteraceae	*A, C, E, F*	*Leucanthemum vulgare* Lam.	Eurasia
Brickellia eupatoroides (L.) Shinners	Forb	Asteraceae	*B, D, G, H*	*Cichorium intybus* L.	Eurasia
Astragalus canadensis L.	Legume	Fabaceae	*C, E, G, H*	*Coronilla varia* (L.) Lassen	Mediterranean
Dalea purpurea Vent.	Legume	Fabaceae	*A, B, D, F*	*Trifolium repens* (L.)	Europe

For example, composition *A* native mixtures included *A. gerardii*, *P. smithii*, *R. pinnata*, and *D. purpurea*. Composition *A* exotic mixtures were also established, and included the four exotic species that were paired with these native species. Each mixture included one species from each of the four functional groups; each species was present in four of the eight unique species compositions; and each pair of species was present in two of the eight compositions. Compositions *F* and *H* were randomly chosen for sampling niche overlap in aboveground space

[a] Forbs were paired by family, grasses were paired by subfamily or tribe

[b] Seedlings from this species pair were vegetatively propagated, all others were propagated from seed

plant densities in a nearby native prairie remnant (Losure et al. 2007). Seedlings that did not survive the first week were replaced. Planting plots with equal mass seedlings, rather than seeds, allowed us to control the assembly process so that we could carefully study the disassembly process (Wilsey and Polley 2004; Wilsey et al. 2009), and have equal species diversity and functional group diversity across treatments at the time of planting. Temporal changes in biodiversity were monitored to determine the effect of our intense livestock grazing and species origin treatments on biodiversity. All weeds (i.e., non-planted species) were removed monthly during the growing season. Plots were separated by 1.1-m alleys.

Grazing experiments can vary the intensity, frequency, or height of the foliage removal; however, varying all these factors in one experiment can become unmanageable. Most previous experiments that have compared the effects of grazing on native and exotic species have clipped biomass to simulate defoliation (e.g., Kimball and Schiffman 2003). Our experiment included aspects of grazing that clipping studies are unable to simulate, such as trampling. The grazing treatment was applied as a single event during mid-June because all the plant species were actively growing at this time. This also allowed us to accurately quantify consumption, resistance, and resilience for each plant species in each plot (Isbell and Wilsey 2011). Half of the plots were intensely grazed by twenty 450-kg Angus steers (*Bos taurus*) during June 10–11, 2008. Cattle consumed 74% of the standing crop biomass in one 24-h period, which was 40% of annual aboveground productivity (Isbell and Wilsey 2011). This grazing treatment is comparable to some common grazing regimes (e.g., flash grazing or infrequent but intense grazing by migratory grazers), but differs considerably from other grazing regimes (e.g., continuous grazing). The Iowa State University Institutional Animal Care and Use Committee approved all experimental protocols.

The experiment consisted of 128 plots, including 64 four-species mixtures and 64 monocultures. Mixtures had a full-factorial treatment structure for three factors: 2 grazing treatments (ungrazed or intensely grazed) × 2 species origins (native or exotic) × 8 species compositions (Table 1) × 2 true replicates = 64 mixtures. Species compositions were systematically chosen to balance the frequency of pair-wise species interactions (Table 1). Monocultures also had a full-factorial treatment structure for three factors: 2 grazing treatments × 2 origins × 8 species pairs (Table 1) × 2 true replicates = 64 monocultures. An exclosure fence was constructed for each of the ungrazed plots. Unfortunately, one of these grazing exclosures was misplaced. Consequently, one of the two replicate "ungrazed" monocultures for *C. varia* was intensely grazed, and one of the two replicate "intensely grazed" composition B (Table 1) exotic mixtures was not grazed (Isbell and Wilsey 2011). The planted proportions of functional groups in our study were based on the relative biomass of each functional group observed in native and exotic grasslands near the study site (Table 2). We did not plant equal proportions of each species because there is now considerable evidence that changes in species richness (Wilsey and Polley 2004) and ecosystem functioning (reviewed by Hillebrand et al. 2008) can depend on species evenness.

Table 2 Relative biomass of four plant functional groups in three types of grasslands that are common near our study site

	Native remnant grassland[a]	Native restored grassland[a]	Exotic grassland[b]	Mean relative biomass	Seedlings planted per mixture
C_3 grass	0.229	0.225	0.974	0.476	30
C_4 grass	0.273	0.560	0.002	0.278	18
Forb	0.439	0.199	0.024	0.221	14
Legume	0.059	0.016	0.000	0.025	2

The species mixtures in our experiment were planted with the mean of these values

[a] Native grasslands were sampled by Martin et al. (2005)

[b] We sampled an abandoned pasture near the study site by clipping biomass in 10 randomly located quadrats (100 × 50 cm), sorting by species, categorizing by functional group, drying to constant mass, and weighing. Note that one exotic C_3 grass, *Bromus inermis*, produced nearly all (i.e., 97.4%) of the biomass in the abandoned pasture

Data collection

Aboveground peak biomass was quantified for each species in each plot during years 1 (August 31–September 1, 2007), 2 (August 27–28, 2008), and 3 (August 20–21, 2009) using a nondestructive point-intercept sampling method calibrated with biomass. Point-intercept pins were dropped vertically through holes in a frame that was above the vegetation canopy within the 0.64 m^2 center of each plot (i.e., avoiding the 10-cm wide strip at the edge). The frame had 81 evenly spaced holes, 10-cm apart, in a 9 by 9 grid. All contacts with pins (i.e., hits) were recorded, and a value of 0.5 was recorded for each species that was present, but not in contact with any of the pins. In each plot, pins were systematically dropped through half (i.e., 40) of the holes in the grid, alternating so that not two neighboring holes were sampled. Peak biomass was harvested after point-intercept sampling during year two. All aboveground biomass in all plots was clipped to 3 cm above the soil surface, sorted by species, dried to constant mass, and weighed. Aboveground biomass was strongly linearly correlated with the number of point-intercept hits (R^2 for each species ranged from 0.72 to 0.97). After measurements were made, clipped biomass was returned to the plot it came from to avoid removing nutrients and litter.

Simpson's diversity index ($1/D$, where $D = \sum p_i^2$, and p_i is the relative biomass of species i) was quantified for each mixture within each year. Diversity includes both richness and evenness components, and both components are important for explaining variation in diversity (Wilsey et al. 2005). Furthermore, declines in evenness often precede declines in richness because rare species are more likely to become locally extinct (Wilsey and Polley 2004). Thus, we also quantified species richness (S = the number of species) to separately consider the richness and evenness components of diversity that are combined in Simpson's index.

The complementarity and selection effects were quantified for each mixture plot within each year using Loreau and Hector's (2001) additive partition of the net biodiversity effect (NBE):

$$\text{NBE} = S\overline{\Delta RY}\,\overline{M} + S\,\text{cov}(\Delta RY, M), \tag{1}$$

where S is species richness, ΔRY is the difference between the observed and expected relative yield, and

M is monoculture peak biomass. In Eq. 1, the first (average) term on the right side of the equation is the complementarity effect and the second (covariance) term is the selection effect. The observed relative yield for species i was calculated as Y_{oi}/M_i, where Y_{oi} and M_i are the observed mixture and monoculture aboveground peak biomass values for species i, respectively. The expected relative yield was taken as the planted relative biomass for year 1, and the previous relative biomass for years 2 and 3 (Loreau and Hector 2001). A species overyields (i.e., positive ΔRY) when the net effect of individual interactions is more favorable in mixtures than in monocultures (Harper 1977). A species underyields (i.e., negative ΔRY) when the net effect of individual interactions is more favorable in monocultures than in mixtures (Harper 1977). Positive complementarity effects indicate that species in a mixture overyield on average, which indicates niche partitioning or facilitation (Loreau and Hector 2001). Positive selection effects indicate that the most productive species overyield most in mixture (Loreau and Hector 2001), and can lead to biodiversity declines (Isbell et al. 2009b). To determine which native and exotic species contributed most to the selection effect, we compared species' monoculture peak biomass (M_i) and mixture yielding behaviors (ΔRY_i).

In addition to quantifying the complementarity effect as an integrative measure of niche partitioning and facilitation, we also quantified aboveground space partitioning as a more specific measure that may be affected by our grazing disturbance. Niche overlap in aboveground space was quantified for all pairs of species that were present in a subset of mixtures (Table 1) during the year 2 point-intercept sampling. Aboveground space was divided into three vertical classes: 0–50 cm, 51–100 cm, and 101–150 cm. The number of contacts between the point-intercept pins and each species was recorded for each vertical class. This allowed us to quantify the percent of biomass for each species in each vertical class. These values were then used to quantify niche overlap in aboveground space between each pair of species in each mixture, using the proportional similarity method (Schoener 1970).

Data analyses

We used linear models in SAS (version 9.2; SAS Institute Inc., Cary, NC, USA) to determine the effect

of our treatments in species mixtures. We tested treatment effects on biodiversity, the complementarity effect, the selection effect, M_i, and ΔRY_i during year 1, before the grazing event, with a general linear model (PROC GLM) that included both main effects and the interaction for two fixed factors: origin and composition. We tested treatment effects on these same response variables during years 2 and 3 with repeated measures general linear models (PROC MIXED). These models contained all main effects and interactions for four factors: grazing, origin, species composition, and year. Year was modeled with a compound symmetry (i.e., split-plot in time) covariance structure. We tested treatment effects on species richness during year 3 with contingency table analyses (PROC FREQ). We tested treatments effects on niche overlap during year 2 with a general linear model (PROC GLM) that included all main effects and interactions for three fixed factors: grazing, origin, and composition. To meet model assumptions, M_i and ΔRY_i were natural logarithm transformed; the complementarity and selection effects were square-root transformed, keeping original positive or negative signs. Non-significant interactions $(P > 0.15)$ were pooled into the error terms.

Results

Biodiversity

Consistent with our first hypothesis, biodiversity declined more in exotic than in native mixtures. Early declines in species evenness led to subsequent declines in species richness in exotic mixtures. After one growing season, Simpson's diversity was 29% lower in exotic than in native mixtures (origin: $F_{1,48} = 51.97$, $P < 0.0001$) (Fig. 1a); and this difference was similar across species compositions (origin × composition: $P > 0.10$). Biodiversity declines during year 1 were largely due to declines in evenness, because species richness remained near the planted values in both native and exotic mixtures (Fig. 1b). By year 3, species richness was 15% lower in exotic than in native mixtures (origin: $\chi^2 = 7.51$, $P = 0.023$ for year 3 richness) (Fig. 1b). Specifically, after three growing seasons, eight exotic and eight native mixtures had lost one species, and five exotic and zero native mixtures had lost two species. The

exotic mixtures that lost two species were dominated by *B. inermis* (3 mixtures) or *L. vulgare* (2 mixtures). Three of the eight native species were lost from at least one mixture: *A. canadensis* (6 mixtures), *D. purpurea* (1 mixture), and *A. gerardii* (1 mixture). Three of the eight exotic species were lost from at least one plot: *M. sinensis* (8 mixtures), *T. repens* (8 mixtures), and *C. varia* (2 mixtures). Simpson's diversity increased in exotic mixtures during years 2 and 3 (Table 3; Fig. 1a), because species evenness increased as species richness decreased (Fig. 1b). Contrary to our second hypothesis, our intense grazing treatment had no significant effect on Simpson's diversity (Table 3; Fig. 1a) or richness (grazing: $\chi^2 = 0.16$, $P = 0.922$ for year 3 richness) (Fig. 1b).

Species interactions

Consistent with our third hypothesis, exotic mixtures and intensely grazed mixtures exhibited decreased complementarity. There was a significant interaction between origin and grazing effects on the complementarity effect (Table 3), indicating that the complementarity effect was greatest in the ungrazed native mixtures (Fig. 1c). During year 1, the complementarity effect did not differ between native and exotic mixtures $(P > 0.10$ for main effects and the interaction) (Fig. 1c). However, the complementarity effect was smaller in exotic than in native mixtures during years 2 and 3 (Table 3; Fig. 1c). Additionally, intense grazing decreased the complementarity effect during year 2, when the grazing event occurred, and this effect persisted through the following growing season (Table 3; Fig. 1c). Interestingly, there was a positive correlation $(r = 0.25, P = 0.049)$ between the mean complementarity effect, averaged across all three years, and the total change in biodiversity from planting to year 3. This indicates that biodiversity declined (i.e., negative change in biodiversity) most rapidly in mixtures with the least niche partitioning and facilitation (i.e., lowest complementarity effect).

Canopy overlap in aboveground space was greater in exotic mixtures than in native mixtures (origin: $F_{1,79} = 6.27$, $P = 0.014$) (Fig. 2). It was also greater in grazed mixtures than in ungrazed mixtures (grazing: $F_{1,79} = 13.78$, $P = 0.0004$) (Fig. 2). There was no interaction between origin and grazing effects on canopy overlap (origin × grazing: $P > 0.10$). These

Fig. 1 Temporal trends in Simpson's diversity (**a**), species richness (**b**), the complementarity effect (**c**), and the selection effect (**d**), in native (*circles*) and exotic (*triangles*) mixtures that were either ungrazed (*filled*) or intensely grazed (*unfilled*) by cattle. **a**, **b** The initial planted values are shown on the *y*-axis. *Arrows* when the intense livestock grazing event occurred. *Error bars* 1 s.e.m. The complementarity and selection effects were square-root transformed, keeping the original positive or negative sign
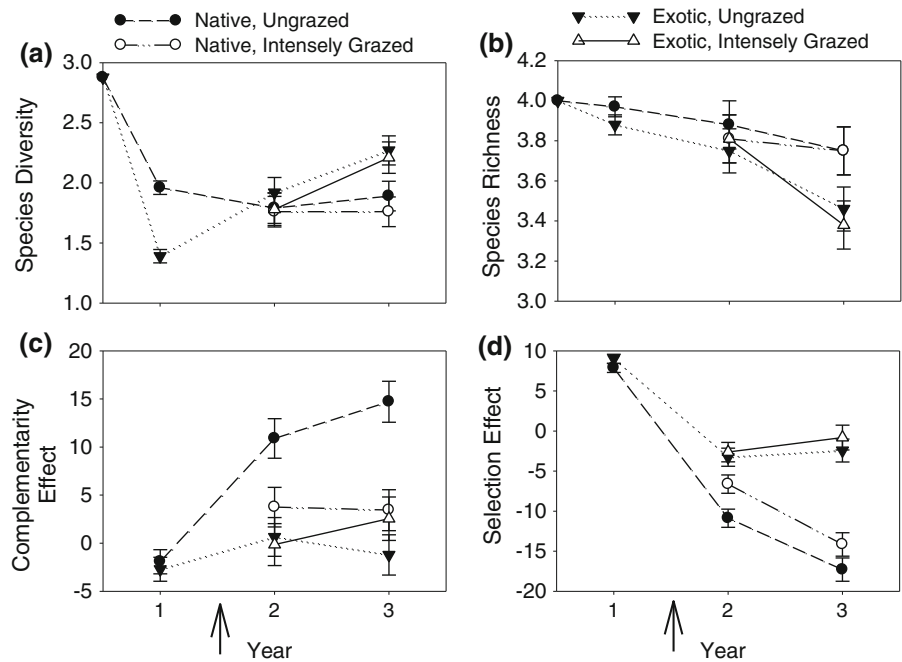

Table 3 Results from the repeated measures analyses which tested treatment effects on biodiversity, the complementarity effect, and the selection effect during years 2 and 3

	Biodiversity	Complementarity effect	Selection effect
Grazing (G)	$F_{1,54} = 0.68$	$F_{1,39} = 4.36*$	$F_{1,32} = 5.44*$
Origin (O)	$F_{1,54} = 5.25*$	$F_{1,39} = 17.54***$	$F_{1,32} = 92.01***$
Composition (C)	$F_{7,54} = 7.99***$	$F_{7,39} = 2.03$	$F_{7,32} = 3.99**$
G × O		$F_{1,39} = 8.38**$	
G × C		$F_{7,39} = 1.83$	$F_{7,32} = 5.03***$
O × C		$F_{7,39} = 3.72**$	$F_{7,32} = 4.60**$
G × O × C			$F_{8,32} = 2.95*$
Year (Y)	$F_{1,41} = 11.06**$	$F_{1,25} = 1.10$	$F_{1,32} = 11.62***$
Y × G			
Y × O	$F_{1,41} = 6.22*$		$F_{1,32} = 25.09***$
Y × C		$F_{7,25} = 2.04$	$F_{7,32} = 2.41*$
Y × G × O		$F_{2,25} = 2.49$	
Y × G × C		$F_{7,25} = 2.30$	
Y × O × C	$F_{21,41} = 1.70$		$F_{7,32} = 2.96*$
Y × G × O × C		$F_{21,25} = 1.67$	$F_{16,32} = 1.66$

Non-significant ($P > 0.15$) interactions were pooled into the error terms to determine the minimally adequate models

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

effects were also similar across species compositions ($P > 0.10$ for all composition interactions).

Our species origin and grazing treatments had independent influences on the selection effect (Table 3). During year 1, the selection effect did not differ between native and exotic mixtures on average (origin: $F_{1,48} = 2.07$, $P = 0.157$) (Fig. 1d),

although some native compositions exhibited slightly greater or smaller selection effects than their exotic counterparts (origin × composition: $F_{7,48} = 3.56$, $P = 0.004$). However, after year 1, the selection effect was greater in exotic than in native mixtures, especially during year 3 (Table 3; Fig. 1d). Furthermore, intense grazing increased the selection effect during year 2, when

the grazing event occurred, and this grazing effect persisted through the following growing season (Table 3; Fig. 1d). The selection effect was not correlated with the total change in biodiversity ($r = 0.01$, $P = 0.93$).

Species' biomass production in monocultures and yielding behavior in mixtures

To determine which native and exotic species contributed most to the selection effect, we compared monoculture peak biomass and yielding behaviors across species. During year 1, some native species exhibited greater peak monoculture biomass than the exotic species they were paired with (origin × species pair: $F_{7,48} = 4.35$, $P = 0.001$) (Fig. 3a); and some exotic species exhibited greater overyielding or underyielding than the native species they were paired with (origin × species pair: $F_{7,240} = 12.64$, $P < 0.0001$) (Fig. 3b). In general, though, the productive forbs tended to overyield and the unproductive C_3 grasses tended to underyield similarly in native and exotic mixtures (Fig. 3a, b). This partly explains why selection effects were positive in both native and exotic mixtures during year 1 (Fig. 1c).

During years 2 and 3, there was a significant four-way interaction for monoculture peak biomass (year × grazing × origin × species pair: $F_{7,32} = 3.32$, $P = 0.009$) (Fig. 3c, e) and species yielding behaviors (year × grazing × origin × species pair: $F_{7,164} = 3.56$, $P = 0.001$) (Fig. 3d, f), indicating complex and inconsistent treatment effects on these response variables. Generally, C_3 grasses continued to exhibit

low monoculture peak biomass, but started overyielding (Fig. 3). At the same time, two forbs, *R. pinnata* and *L. vulgare*, continued to exhibit high monoculture peak biomass, but started underyielding (Fig. 3). These trends partly explain why the selection effect decreased across years in most mixtures (Fig. 1d). During years 2 and 3, the yielding behaviors of the other two forbs, *B. eupatoroides* and *C. intybus*, diverged (Fig. 3d, f), partly explaining why the selection effect diverged in native and exotic mixtures (Fig. 1d).

Discussion

Grazing can have positive, negative, or neutral effects on biodiversity, often depending on the intensity of grazing, the local climate, soil fertility, and whether the plants evolved with grazing (Milchunas and Lauenroth 1993; Proulx and Mazumder 1998; Huston 2004). In some ecosystems, intense continuous livestock grazing and exotic species appear to synergistically drive biodiversity declines (Kimball and Schiffman 2003; Parker et al. 2006; Best and Arcese 2009). However, we found that exotic species and a grazing disturbance did not synergistically drive declines in biodiversity. Instead, biodiversity declines were more rapid in exotic than in native mixtures, regardless of the grazing treatment. Surprisingly, our grazing treatment did not influence biodiversity, even though it had large influences on biomass, light interception, and nutrient uptake (Isbell and Wilsey 2011). Interestingly, decreased complementarity seemed to explain biodiversity declines in exotic, but not in intensely grazed plots. Here, we elaborate on each of these findings and discuss the mechanisms that might explain them.

Our results indicate that the passenger model cannot completely explain differences in diversity between native and exotic grasslands. The passenger model (Gurevitch and Padilla 2004; Didham et al. 2005; MacDougall and Turkington 2005) would predict similar changes in biodiversity in both native and exotic experimental communities, because other drivers, such as resources or disturbances, are experimentally controlled. In contrast, the driver model (Vitousek 1990; Wilsey et al. 2009) would predict more rapid biodiversity declines in exotic than in native experimental communities, because of
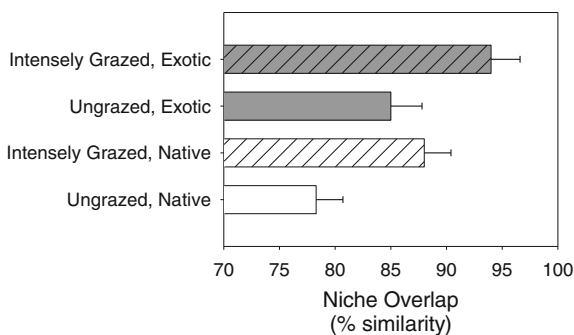

Fig. 2 Niche overlap in aboveground space for native and exotic species mixtures that were either ungrazed or intensely grazed once by cattle. Niche overlap was quantified as the percent similarity of biomass production in three vertical regions of aboveground space between all pairs of species in mixtures. *Error bars* 1 s.e.m

Fig. 3 Peak biomass in monocultures (**a**, **c**, **e**) and species yielding behaviors in mixtures (**b**, **d**, **f**) during years 1 (**a**, **b**), 2 (**c**, **d**), and 3 (**e**, **f**). *Error bars* 1 s.e.m. *Asterisks* significant ($P < 0.05$) overyielding or underyielding. For clarity, one value is not shown: the change in relative yield for *B. eupatoroides* in ungrazed mixtures during year three was 2.76 ± 0.16 (mean ± s.e.m.)
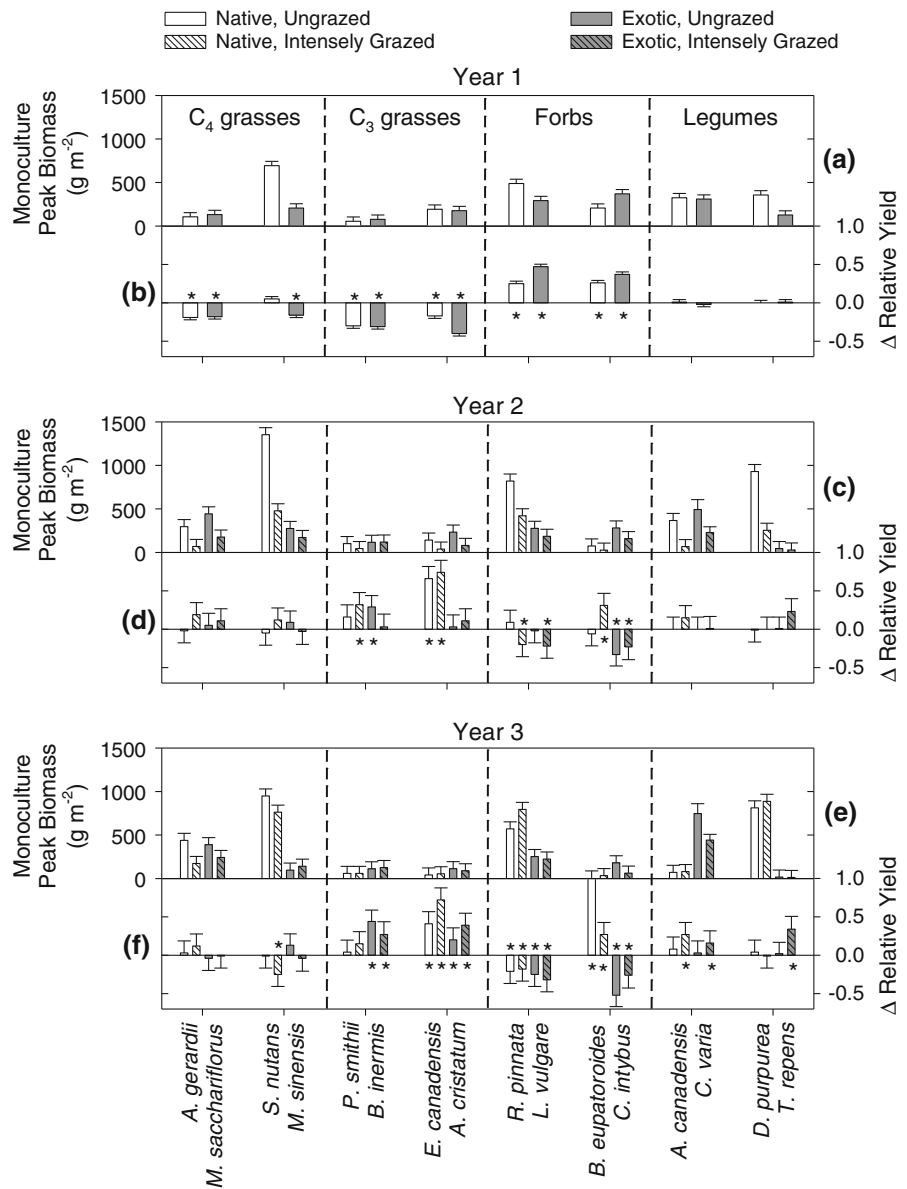
differences between native and exotic species. Our results are not consistent with the passenger model.

Differences between natives and exotics likely explain the rapid biodiversity declines and decreased complementarity in exotic mixtures. Exotic species have frequently been nonrandomly selected and introduced for particular uses (Mack et al. 2000), including forage production. Consequently, exotic species can exhibit greater aboveground productivity under favorable conditions (Wilsey and Polley 2006; Wilsey et al. 2009), and greater resilience after intense grazing (Simoes and Baruch 1991; Kimball

and Schiffman 2003; Best and Arcese 2009; HilleRisLambers et al. 2010; Isbell and Wilsey 2011), than native species. Furthermore, species in native communities have had greater opportunity to coevolve than species in communities with novel combinations of exotic species (Hobbs et al. 2006; Seastedt et al. 2008), and this might explain why there can be greater complementarity in native than in exotic communities (Wilsey et al. 2009). The exotic species in our study came from Europe and Asia (Table 1), and in many cases their native ranges were separated by physical barriers, such as mountain ranges. Thus,

these differences between native and exotic species (due to nonrandom selection of exotic species), and between native and exotic communities (due to a relatively brief history of interaction among exotic species), likely explain the rapid biodiversity declines and decreased complementarity effects in exotic mixtures.

The legumes became locally extinct more frequently than the other species in our experimental communities. This is consistent with long-term observations in natural grasslands (Leach and Givnish 1996). Overyielding was uncommon for all the species that became locally extinct (i.e., *A. gerardii*, *M. sinensis*, and the four legumes) (Fig. 3). This is consistent with previous studies, which have found that the conditions for overyielding are similar to those for coexistence (Vandermeer 1981; Loreau 2004; Isbell et al. 2009b). Thus, rare species that consistently underyield, or rarely overyield, are unlikely to persist.

Interestingly, intense grazing decreased complementarity, but did not decrease biodiversity. Uniquely, our study considered the effects of grazing on both intraspecific interactions in monocultures and interspecific interactions in mixtures. It is necessary to consider interactions in both mixtures and monocultures because stabilizing mechanisms maintain biodiversity by decreasing interspecific competition *relative to* intraspecific competition (Chesson 2000). Thus, even when grazing decreases competition (Olff and Ritchie 1998), it may stabilize or destabilize species interactions, depending on whether it decreases interspecific competition more or less than intraspecific competition, respectively. We found that intense grazing decreased the complementarity effect, which indicates that intense grazing decreased interspecific competition less than intraspecific competition. Thus, intense grazing changed plant species interactions in a manner that would have negative, not positive, effects on biodiversity. Why, then, didn't grazing decrease biodiversity? Note that coexistence depends on both stabilizing interactions and fitness differences between species (Adler et al. 2007; Harpole and Suding 2007). We hypothesize that our grazing treatment did not decrease biodiversity because it destabilized species interactions and decreased fitness differences. We encourage future studies to determine the effects of various grazing regimes on both species interactions and fitness differences.

Global ecosystem changes that decrease complementarity may have long-term consequences for biodiversity, ecosystem functioning, and ecosystem stability. Our findings that the complementarity effect became increasingly positive, and the selection effect became increasingly negative, across years in the ungrazed native mixtures are consistent with several previous studies (Cardinale et al. 2007; Fargione et al. 2007; Isbell et al. 2009b; van Ruijven and Berendse 2009). In previous studies, these trends in species interactions have promoted productivity (Cardinale et al. 2007; Fargione et al. 2007; Isbell et al. 2009a; van Ruijven and Berendse 2009), biodiversity maintenance (Isbell et al. 2009b), and ecosystem stability (Isbell et al. 2009a). Uniquely, we also found that the complementarity effect was decreased in both exotic and intensely grazed mixtures. Together these results suggest that converting native grasslands to exotic grasslands or pastures can change plant species interactions in ways that may subsequently decrease biodiversity and ecosystem services. Future studies could similarly consider whether other global ecosystem changes commonly influence biodiversity, ecosystem functioning, and stability by decreasing complementarity. It will also be necessary for future studies to identify the specific biological processes that explain coexistence, ecosystem functioning, and ecosystem stability. We suspect that several mechanisms are often important, including spatiotemporal resource partitioning (McKane et al. 2002) and natural enemy partitioning (Petermann et al. 2008).

Conclusion

We found that biodiversity declined more rapidly in exotic than in native species mixtures, regardless of our grazing disturbance. Additionally, complementarity was decreased in both exotic and intensely grazed mixtures. These results suggest that converting native grasslands to exotic grasslands or pastures can change species interactions in ways that may lead to subsequent changes in biodiversity and ecosystem services, and that restoring biodiversity in grasslands may require removal of exotic species.

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