

# Realistic Species Losses Disproportionately Reduce Grassland Resistance to Biological Invaders

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Consequences of progressive biodiversity declines depend on the functional roles of individual species and the order in which species are lost. Most studies of the biodiversity–ecosystem functioning relation tackle only the first of these factors. We used observed variation in grassland diversity to design an experimental test of how realistic species losses affect invasion resistance. Because entire plant functional groups disappeared faster than expected by chance, resistance declined dramatically with progressive species losses. Realistic biodiversity losses, even of rare species, can thus affect ecosystem processes far more than indicated by randomized-loss experiments.

Rapid biodiversity losses at both local and global scales disproportionately involve species with particular values of traits such as size, trophic position, rarity, distribution, and degree of specialization (1–5). While the evolutionary consequences of the nonrandomness of biodiversity loss have been explored recently (6), our understanding of the functional consequences of nonrandom loss remains limited mainly to studies of the declines of individual species (7, 8) [but see (9)]. These studies focus on keystone species or on species that were once widespread and abundant. However, most species in ecosystems—and most at-risk species—are less dominant and exert what influence they have on ecosystem functioning in relatively small numbers (10–12).

The prevailing experimental approach to testing the functional consequences of biodiversity change isolates the effects of species or functional group richness by (i) randomizing species composition and (ii) equalizing species abundances within each richness treatment (13–16). This approach provides little information about the importance of species loss order [“community disassembly” (5)] or relative species abundances for ecosystem processes. Recent studies generating nonrandom species losses through removals of rare and uncommon species from natural communities provide more insight about the effects of nonrandom loss on ecosystem functioning (17, 18), but local abundance or rarity alone is an imperfect predictor of species loss order (19) (Table 1).

Patterns of nonrandom change and variation in diversity can be better assessed with tools specifically designed for the measurement of extinction order, such as nested subset analysis (20, 21). Nested subset analysis

quantifies the degree to which species disappearances are ordered, most often across a series of habitat fragments of decreasing size or increasing isolation (22, 23). Although seldom extended in this way, nested subset analysis can also be used to quantify the order in which species are lost through space or time. It bases this order solely on observations of species occurrences across sites or dates rather than on assumptions about specific drivers of diversity loss or species characteristics thought

to be associated with species vulnerability to local extinction (20, 24). Nested subset analysis can thus provide an empirical species loss order through either space or time at a specified scale and for a particular community type.

We observed 4 years of spatial variation in the plant species richness of plots in a California grassland ecosystem to quantify the degree to which changes in richness occurred in a consistent, nested order (25). We treated nested patterns of species occurrences through space as indicators of a representative order of local extinction, because similar mechanisms appear to affect richness through space and time in our study system. Variation through space in species richness at our level, treeless site appears to reflect heterogeneous soil conditions resulting from gopher activity (up to present) and past mechanical soil disturbance and vehicular compaction (as recently as 30 years ago) (26). The resulting heterogeneity likely affects species richness both directly and indirectly through effects on productivity (27–29) and invasibility (30, 31). These mechanisms resemble important drivers of grassland biodiversity change in California and elsewhere, including soil disturbances associated with agriculture and livestock production, biological invasions, and increased productivity due to anthropogenic nitrogen fertilization (32, 33),

**Table 1.** Species compositions and traits comprising each experimental diversity level. Values are target numbers of stems for each species in a given treatment. Life history traits: early annual (E), indeterminate annual/late annual (L), biennial/perennial (P). Functional types were defined as early grasses, early forbs, nitrogen fixers, late forbs, and perennials based on groupings from previous California grassland studies (13, 38). Abundance ranks are means based on field observations of neighborhood relative abundances across plots of varying richness; 1 indicates most locally abundant species.

Species	Diversity level						Type	Life history	N fixer	Abundance rank
<i>No. species</i>	3	6	9	12	15	21				
<i>No. functional types</i>	2	3	3	4	4	5				
<i>Avena barbata</i>	206	149	110	98	74	24	Grass	E		1
<i>Bromus hordeaceus</i>	41	41	41	41	41	41	Grass	E		2
<i>Geranium dissectum</i>	21	20	21	20	21	21	Forb	E		6
<i>Bromus diandrus</i>		13	13	12	12	12	Grass	E		7
<i>Lolium multiflorum</i>		35	28	24	18	7	Grass	E		5
<i>Vicia sativa</i>		10	10	10	10	10	Forb	L	yes	8
<i>Avena fatua</i>			34	33	34	33	Grass	E		4
<i>Erodium botrys</i>			9	9	9	9	Forb	E		9
<i>Vulpia microstachys</i>			2	2	2	2	Grass	E		17
<i>Anagallis arvensis</i>				10	27	63	Forb	L		3
<i>Briza minor</i>				7	10	15	Grass	E		10
<i>Epilobium brachycarpum</i>				2	3	5	Forb	L		14
<i>Crepis vesicaria</i>					2	2	Forb	P		19
<i>Torilis arvensis</i>					3	3	Forb	L		13
<i>Trifolium hirtum</i>					2	2	Forb	L	yes	18
<i>Danthonia californica</i>						5	Grass	P		12
<i>Hemizonia congesta</i>						2	Forb	L		16
<i>Hordeum murinum</i>						2	Grass	E		15
<i>Medicago polymorpha</i>						2	Forb	L	yes	21
<i>Phalaris aquatica</i>						2	Grass	P		20
<i>Rumex acetosella</i>						6	Forb	P		11

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although they might capture less well species loss orders likely to be associated with other drivers of grassland biodiversity change, such as woody encroachment and climate change.

Species-by-site occurrence matrices at our study location were significantly nested in all years ( $T = 19.4^\circ$  to  $23.4^\circ$ ,  $P \ll 0.001$ ) (34). Local rarity was an inconsistent predictor of loss order, with some abundant species absent from low-richness plots and some uncommon species present in plots of both high and low richness (table S1). The most abundant species in our richest plots, *Anagallis arvensis* (Primulaceae), seldom occurred at all in plots below the median richness level (Table 1). All of the 38 species at our site maintained their approximate ranked positions in the nested order of diversity changes across years as individual plots increased or declined in species richness (table S1). This indicated that the order of species losses and gains through space from grassland patches is robust to interannual variability and change at our site. We used this observed nested order of species loss and gain to design a test of how these ordered changes in species richness influence grassland resistance to invasion, an ecosystem function of growing conservation relevance as invasions accelerate (35).

We constructed outdoor microcosm communities by planting locally collected seeds at six levels of species richness to reflect (i) the observed, nested order of local-scale variation in species richness and (ii) variation in relative species abundances that accompanied variation in species richness at our site (Table 1). At all species richness levels, species abundance ranks followed a log series-like distribution (11), with abundances varying by two orders of magnitude and most species

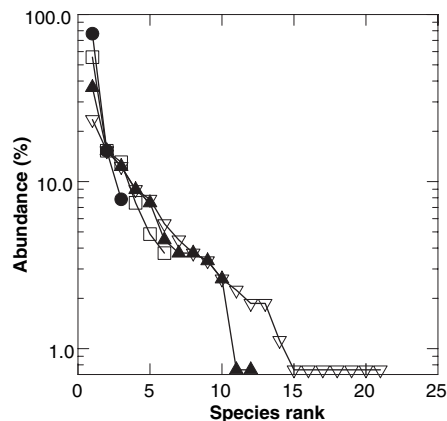
rare as observed in our field plots (Fig. 1). Constructed communities differed in the degree of dominance (dominance was higher in more species-poor treatments) but not the identity of the most abundant species. This allowed us to distinguish the effects of progressive changes in species richness from effects associated with the identity of the dominant species (17, 36). We invaded half of the communities at each richness level with *Centaurea solstitialis* L. (yellow starthistle), an expanding California grassland exotic that has already caused considerable ecological and economic damage (37).

Starthistle biomass increased with progressive species loss by more than 100% from the most diverse to the least diverse communities ( $F = 5.58$ ,  $P = 0.002$ ,  $R^2 = 0.59$ ) (Fig. 2). Starthistle production and flower number were strongly correlated (Pearson coefficient = 0.790, Bartlett's  $\chi^2 = 33.8$ ,  $P < 0.001$ ), such that starthistle reproduction also increased with declining richness. Lost species effects on invader performance were highly disproportionate to their abundance in the community. For example, mean starthistle biomass was >60% lower in 20-species than in 15-species communities, even though the additional 5 species in the 20-species communities together comprised <4% of resident production and <3% of the total number of stems. Similarly, mean starthistle biomass was >70% lower in 20-species than in 12-species communities, while the 8 additional species made up <5% of resident production and <7% of total stems.

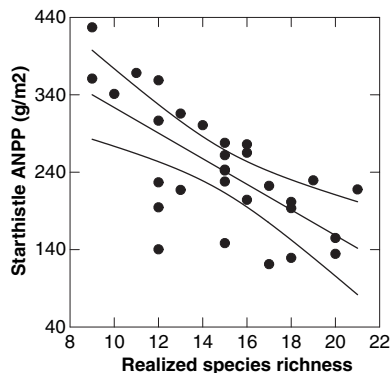
Our findings differ from the results of studies at the same site testing the effects of randomized changes in species richness on starthistle (38). In this earlier work, no differences in invader production occurred among

diversity treatments with >1 species. Functional group number was held constant across diversity levels with >1 species in the earlier study. Our nested subset analyses show, however, that in our study system, progressive diversity declines are not evenly distributed across species varying in key functional traits (Table 1). In our system, species-poor assemblages contain mainly early annuals, with no or few indeterminate, late-season, nitrogen-fixing, or perennial species that overlap strongly with starthistle in the location or timing of resource uptake. Progressively richer communities gain late-season annual forbs and perennial species, the former of which were shown to compete effectively against starthistle (which is also a late-season annual forb) in monoculture (38). The effects of reducing species richness while holding functional group number constant, while theoretically important, thus do not represent the effects of real biodiversity variation. Consequently, the incorporation of realistic species loss order into our experimental design profoundly altered the observed relation between diversity and invasibility.

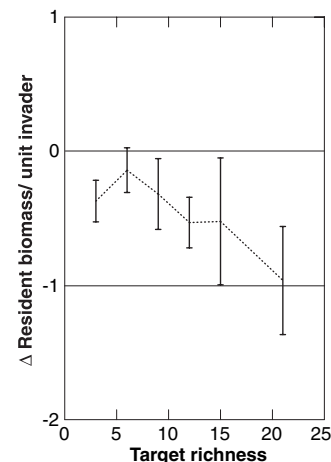
The decline in functional diversity that accompanies realistic species losses can also influence the degree to which invasions affect ecosystem processes. Starthistle increased total biomass (resident + starthistle) more at low than at high resident species richness levels ( $F = 6.77$ ,  $P = 0.01$ ,  $R^2_{\text{adj}} = 0.17$ ), reflecting greater total starthistle biomass in the more species-poor communities. The per-unit impact of starthistle on resident biomass, in contrast, increased with species richness, from <0.3 to nearly 1 g resident biomass lost per g starthistle present ( $F = 4.79$ ,  $P = 0.04$ ) (Fig. 3). Most likely,



**Fig. 1.** Target rank-abundance curves for 3- (closed circles), 6- (open squares), 12- (closed triangles), and 21-species (open triangles) treatments. Target treatment compositions display log series-like patterns of relative abundance, with most species relatively uncommon and a single dominant species across all diversity levels.



**Fig. 2.** The relation between realized species richness and starthistle aboveground net primary production (ANPP). Realized richness values reflect effects of negative (species that failed to establish) and positive (unplanted volunteers) deviations from treatment richness levels. Target diversity  $F = 5.58$ ,  $P = 0.002$ ,  $R^2 = 0.59$ ; realized deviations  $F = 7.85$ ,  $P = 0.01$ . 95% confidence limits are shown.



**Fig. 3.** Effect of species richness on per-unit invader impact (change in resident biomass/gram of starthistle biomass)  $\pm$  1 SE. This metric = 0 when resident biomass is unaffected by starthistle invasion and -1 when 1 g of resident biomass is displaced by each g of establishing starthistle.  $N = 5$ ,  $F = 4.79$ ,  $P = 0.04$ ,  $R^2_{\text{adj}} = 0.12$ .

this reflects more complete use of certain resources by the more species-rich assemblages. As a result, starthistle added substantial biomass to species-poor communities while mainly displacing resident biomass in species-rich communities. Invasibility can thus decline while per-unit invader impact on the resident community increases, underscoring the importance of measuring both.

This study helps bridge the gap between our understanding of general biodiversity-function relations and the role of extinction order in determining the consequences of biodiversity loss. Additional experiments are needed to assess the consequences of ordered species losses for other ecosystems and ecosystem functions, as well as to expand research designs to incorporate species losses occurring through time at larger spatial scales. If, as we found, important functional traits disappear more rapidly than expected by chance in other communities, the ecosystem consequences of real biodiversity losses—even of rare species—will often exceed expectations based on randomized diversity studies.

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#### Supporting Online Materials

[www.sciencemag.org/cgi/content/full/306/5699/1175/DC1](http://www.sciencemag.org/cgi/content/full/306/5699/1175/DC1)

Materials and Methods

Table S1

References

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## Extinction and Ecosystem Function in the Marine Benthos

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Rapid changes in biodiversity are occurring globally, yet the ecological impacts of diversity loss are poorly understood. Here we use data from marine invertebrate communities to parameterize models that predict how extinctions will affect sediment bioturbation, a process vital to the persistence of aquatic communities. We show that species extinction is generally expected to reduce bioturbation, but the magnitude of reduction depends on how the functional traits of individual species covary with their risk of extinction. As a result, the particular cause of extinction and the order in which species are lost ultimately govern the ecosystem-level consequences of biodiversity loss.

Marine coastal ecosystems are among the most productive and diverse communities on Earth (1) and are of global importance to climate, nutrient budgets, and primary productivity (2). Yet, the contributions that coastal ecosystems make to these ecological processes are compromised by human-induced stresses, including overfishing, habitat destruction, and pollution (3–5). These stressors particularly impact benthic (bottom-living) invertebrate communities because many species are sedentary and cannot avoid disturbance. Thus, marine coastal ecosystems are likely to experience a large proportional change in bio-

diversity should present trends in human activity continue (6–8).

Given these prospects, researchers have recently asked how the loss of biodiversity might alter the functioning of marine coastal ecosystems. Like most studies to date, these experiments have manipulated diversity by assembling random subsets of species drawn from a common pool of taxa (9–11). This approach (12, 13) may be useful for understanding the theoretical consequences of diversity loss but is unrealistic in the sense that it assumes species can go extinct in any order. Extinction, however, is generally a nonran-

dom process (14) with risk determined by life-history traits such as rarity, body size, and sensitivity to environmental stressors like pollution (15–18). Interspecific differences in extinction risk have implications for the ensuing changes in trophic interactions and community structure (18, 19), such that the ecosystem-level consequences of random versus ordered extinctions are likely to be fundamentally different (14, 20–22).

Here we explore how various scenarios of extinction for marine benthic invertebrates are likely to influence bioturbation (the biogenic mixing of sediment)—a primary determinant of sediment oxygen concentrations which, in turn, influences the biomass of organisms, the rate of organic matter decomposition, and the regeneration of nutrients vital for primary productivity (23, 24).

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