

Corrections

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Community assembly and invasion: An experimental test of neutral versus niche processes

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Contributed by David Tilman, May 22, 2003

A species-addition experiment showed that prairie grasslands have a structured, nonneutral assembly process in which resident species inhibit, via resource consumption, the establishment and growth of species with similar resource use patterns and in which the success of invaders decreases as diversity increases. In our experiment, species in each of four functional guilds were introduced, as seed, into 147 prairie–grassland plots that previously had been established and maintained to have different compositions and diversities. Established species most strongly inhibited introduced species from their own functional guild. Introduced species attained lower abundances when functionally similar species were abundant and when established species left lower levels of resources unconsumed, which occurred at lower species richness. Residents of the C4 grass functional guild, the dominant guild in nearby native grasslands, reduced the major limiting resource, soil nitrate, to the lowest levels in midsummer and exhibited the greatest inhibitory effect on introduced species. This simple mechanism of greater competitive inhibition of invaders that are similar to established abundant species could, in theory, explain many of the patterns observed in plant communities.

biodiversity | invasibility | resource competition | functional guilds | ecological niche

Do communities have general and repeatable invasion and assembly processes (1–6), or are communities indistinguishable from random or neutral assemblages (7, 8)? Many ecological models assume that species differ in their traits, with interspecific tradeoffs such that no one species can be the best competitor for all resources, under all environmental conditions (e.g., refs. 2, 3, and 9). One feature common to these tradeoff-based models is that the inhibitory effect of one species on another is greater the more similar the species are, i.e., the closer they fall along an interspecific tradeoff curve (10). As a result, in the community assembly process, established (resident) species should more strongly compete with and inhibit the establishment of species that have resource requirements similar to the resident species. Because species in the same functional guild (11) should have similar resource requirements, we hypothesize that species in a given functional guild should most strongly inhibit invasion by species in their own guild (12). Such an assembly process need not impose a fixed upper limit on the number of species and would not necessarily mean that only certain combinations of species may co-occur. Rather, this process, in combination with environmental resource availabilities, would influence the probability that an invading species would establish and become abundant. Such a process, although stochastic, could cause communities to assemble toward specific relative abundances of different functional guilds.

Many of the central assumptions of theories of resource competition, succession, and community assembly (e.g., refs. 2, 3, and 6) were called into question by a neutral theory of community assembly (8). Neutral theory assumes that all species are competitively identical and that regional abundances are determined by random walks driven by demographic stochasticity (8). In the neutral model, local community assembly is a

random process driven by regional propagule abundances. Thus, once a propagule arrives at a site, the probability of its successful germination and growth is predicted, by neutral theory, to be independent of its traits relative to the traits of the species in the existing community. Thus, niche tradeoff models and neutral models make markedly different predictions about the community assembly process: niche tradeoff models predict that resident species will most strongly inhibit establishment and growth of species similar to them, whereas neutral models predict random assembly independent of species traits.

Whether communities are assembled randomly or with a repeatable process has broad implications for basic and applied ecology. Processes that depend on species increasing from rarity, such as invasion, coexistence, succession, and competition, may all be affected by the stronger within-guild interactions tested for in our experiment.

Some hypothesized community assembly processes have been interpreted as predicting patterns such as “forbidden pairs,” “checkerboards,” or “favored states” and have been tested by measuring abundance patterns in natural communities (see discussions in refs. 13 and 14). However, the difficulties of inferring process from pattern have generated debate and spurred the development of null models of community assembly (8, 15, 16). Here we use an approach that avoids this problem. We first experimentally manipulated both community functional composition and species number and subsequently added propagules of potential invading species to these communities after 3 years of establishment. As such, we were able to directly observe the effects of functional guild composition and diversity on community assembly.

We tested the hypothesis of stronger intrafunctional guild interactions with four functional guilds associated with the seasonality of growth and the timing, source, and efficiency of resource use. The four guilds were C3 (cool-season) grasses, C4 (warm-season) grasses, legumes, and non-nitrogen-fixing forbs. We also measured levels to which available resources (soil nitrate, soil water, and light) were reduced by the resident species. Thus, our experiment allows us to test whether there are stronger interactions among functionally similar species, and if responses of introduced functional guilds correspond with patterns of resource availability created by resident species.

If each species most strongly inhibits species that are most similar to it, then each added functional guild and added species should confer additional invasion resistance to a community. This may partially explain the negative relationship between diversity and invasibility observed in some experiments (17–21). The number of functional guilds planted in a plot (functional guild number) and the number of species planted in a plot (species number) are both measures of functional diversity. Functional guild number is a measure of large differences in functional diversity, whereas species number stands as a proxy for within-guild functional diversity. Thus, these two measures of the functional diversity of a system are complementary, and

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niche tradeoff models predict that higher values of both should lead to lower invasibility.

Methods

We used a biodiversity experiment at Cedar Creek Natural History Area, Minnesota (22) in which each 3 m × 3 m plot of vegetation-free soil in a plowed and disked field was randomly assigned to be planted with 1, 2, 4, 6, or 8 species (20 replicates each), 12 species (23 replicates), or 24 species (24 replicates). Species for each plot were randomly drawn from a pool of 24 grassland perennials. In May 1994, each plot received 10 g·m⁻² of seed, with equal masses of each species. Plots received about 30 mm of rainfall and irrigation, in total, each week of each growing season. This provided ≈150 mm of irrigation water between June 1 and August 31 in addition to precipitation of ≈350 mm. Weeds were removed by hand from elevated platforms three to four times per year.

In our experiment, viable seeds of 27 species that had not been planted in the biodiversity experiment but that already occurred at Cedar Creek Natural History Area were introduced into existing plots at the start of the fourth growing season (1997), by which time the established plants were mature flowering adults. The introduced species were both exotic and native and possess a range of traits. For each of the 27 introduced species, 1 g of seed of each was placed in a container, mixed, and then added to a 1 m × 0.5 m subplot in each plot on June 10, 1997. All nonexperimental species were manually removed the first week of July 1997, but subplots were not weeded subsequently. All seeds were planted dry, without scarification or stratification.

Percent cover of each species was visually estimated in late July/early August in each 0.5-m² subplot each year. Bare ground in 1997 (initial bare ground) is used as a measure of the availability of open space for germination. Because treatment effects became stronger through time as the added plants matured, we only report results for 1999, the third growing season. In addition, in mid-August 1999 all individuals of all added plant species in each subplot were clipped at ground level. The biomass of the five most abundant introduced species (one C3 grass, *Agropyron repens*; two forbs, *Oenothera biennis* and *Penstemon grandiflorus*; and two legumes, *Trifolium pratense* and *Desmodium canadense*) was sorted to species, dried, and weighed.

In mid-July, extractable soil nitrate (NO₃), soil H₂O, and light transmittance were measured within each 9-m² plot in areas where no introduced species were added. Soil nitrate was extracted with 0.01 M KCl from two 2.5-cm-diameter by 20-cm-deep soil cores per plot and analyzed on an Alpkem autoanalyzer (Astoria-Pacific, Clackamas, OR). Gravimetric soil H₂O was determined for these soil samples. The proportion of available light that reached the soil surface (light transmittance) was estimated with an AccuPAR Linear PAR/LAI ceptometer (Decagon, Pullman, WA) by taking 12 readings spaced approximately equally within each plot, within 2 h of solar noon.

Statistical analyses used SAS 6.12 or JMP 3.2.2 (SAS Institute, Cary, NC). When necessary, response variables were log transformed, log₁₀(variable + 1) to minimize unequal variances.

Results

On average across all plots, cover of introduced species differed greatly among the four added functional guilds (Fig. 1). Legumes had the greatest cover, followed by nonleguminous forbs, C3 grasses, and C4 grasses. Cover of each introduced functional guild decreased significantly and similarly with increasing resident functional guild richness (for all four regressions, $P < 0.05$). Compared with their average cover in plots with a single resident functional guild, in plots with all four functional guilds average cover of introduced legumes was reduced by 70% (from 10% to

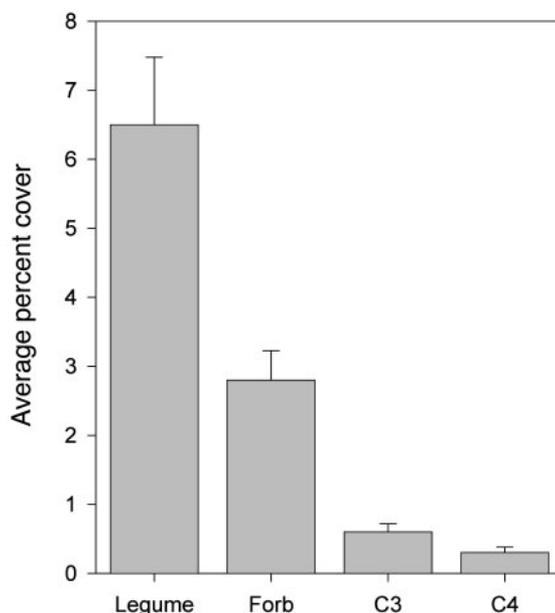


Fig. 1. Average cover of introduced functional guilds.

3%), forbs by 78% (from 5% to 1%), C3 grasses by 72% (from 1.4% to 0.4%), and C4 grasses by 75% (from 0.35% to 0.08%).

The number, cover, and biomass of introduced species decreased with both increasing species richness (Fig. 2) and increasing functional guild richness ($P < 0.0001$ for all three regressions) in univariate regressions. Because functional and species richness are correlated in this experiment ($r^2 = 0.50$ for regression of functional guild richness on species richness), we also ran multiple regressions based on conservative type III sums of squares. Both species and functional guild richness uniquely and simultaneously explained a significant amount of the variation in log invader biomass ($P < 0.01$ for each predictor), supporting the hypothesis that both species and functional diversity increased invasion resistance. In addition, log of invader biomass was significantly dependent on species richness, functional guild richness, and midsummer soil nitrate ($P < 0.05$ for each predictor) when all three were included in a similar multiple regression. Invader biomass declined with increases in functional and species richness and increased with increases in soil nitrate.

In a multiple regression, the total biomass of introduced species was positively correlated with levels of available (unconsumed) resources, specifically nitrate, initial bare ground, and light transmittance (P values were 0.0003, 0.0086, and 0.0149, respectively). Because resource levels were measured in areas of each plot where seed of introduced species had not been added (initial bare ground was measured in the seed addition plots, but at the start of experiment), this supports the hypothesis that invader abundance depends on the amounts of resources left unconsumed by resident species.

Each of the added functional guilds had a different pattern of dependence on the levels of unconsumed resources, as measured by using the total cover of all species in each guild (Table 1). Positive associations between a resource and the cover of a guild suggest that the guild was limited by the resource. Introduced forbs and introduced C3 grasses, but not introduced legumes or introduced C4 grasses, were positively correlated with midsummer soil nitrate. Forbs and C4 grasses, but not legumes and C3 grasses, were positively correlated with initial bare ground. C3 and C4 grasses, but not forbs or legumes, were

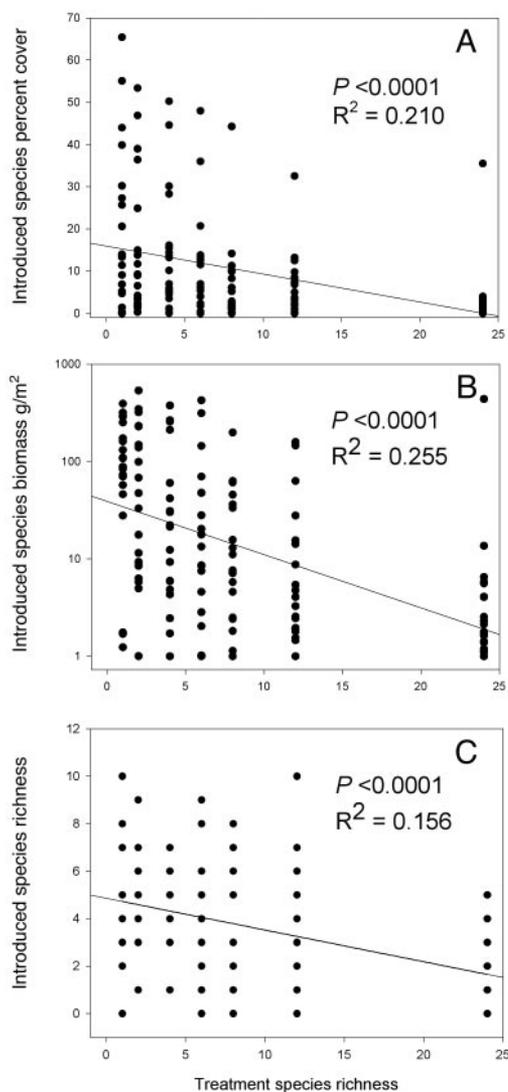


Fig. 2. Relationship between species richness treatment and performance of introduced species. The lines are the best-fit simple linear regressions. Percent cover and biomass of introduced species were log transformed before statistical analysis.

positively correlated with light. For none of the guilds was soil water significantly correlated with total cover.

To explore the effects of resident functional guilds on the abundances attained by the introduced species, we examined partial correlation coefficients from four multiple regression

Table 2. Partial correlations from four multiple regression models in which the response of the log(cover + 1) of each introduced functional guild in 1999 was regressed on the log(cover + 1) of all four resident functional guilds in 1999

Resident functional guild	Introduced functional guild			
	Nonlegume forb	C3 grass	C4 grass	Legume
Nonlegume forb	-0.36***	-0.05	-0.12	-0.03
C3 grass	-0.11	-0.23**	0.01	-0.14
C4 grass	-0.47***	-0.32***	-0.48***	-0.24**
Legume	0.01	0.09	0.005	-0.12
Overall r^2	0.30	0.14	0.24	0.11
Overall P	<0.0001	0.0003	<0.0001	0.002

Significance levels were determined by using sequential Bonferroni (22) corrections for four multiple regressions (i.e., smallest P value < 0.0125, next smallest P < 0.0167, then P < 0.025, and the remainder P < 0.05). Uncorrected significance levels are presented for statistics that meet the sequential Bonferroni criteria: *, P < 0.05; **, P < 0.01; ***, P < 0.001.

models. In each model, the log cover of each introduced functional guild was regressed on log cover of each of the four resident functional guilds (Table 2). Partial correlations indicate the strength of associations between two selected variables when all other variables are held constant, thus removing effects of other variables in the model. Log transformations minimized inequality of variances.

We detected two strong patterns. First, each resident functional guild had its most negative impact on the total cover attained by introduced species of its own functional guild. This can be seen by evaluating each row in Table 2. For example, resident forbs inhibited forbs more than they inhibited any other guild (Table 2). Similarly, resident C3 grasses most inhibited introduced C3 grasses, and resident C4 grasses most inhibited introduced C4 grasses (Table 2). The pattern was qualitatively similar for legumes, with the estimate of the effect of resident legumes on introduced legumes being negative and with the estimates for the effect of legumes on the other three functional guilds being positive, although none of the partial correlation coefficients were significant (Table 2). Conservative, nonparametric analyses using ranked data (24) and analyses on the subset of introduced species for which biomass was sorted to species (one C3 grass, two forbs, and two legumes) yielded similar results.

Second, resident C4 grasses had significant negative effects on all four introduced functional guilds (Table 2). Evaluating each of the four columns in Table 2 reveals that the C4 grass resident functional guild was the one that most strongly inhibited each of the four introduced functional guilds.

In another test, we used the proportional cover of introduced species (i.e., introduced functional guild cover divided by total

Table 1. Parameter estimates for four multiple regressions of introduced functional guild cover against resource levels

Source of variation	df	Log introduced forb cover	Log introduced C3 cover	Log introduced C4 cover	Log introduced legume cover
Soil nitrate	1	1.75***	0.711**	0.319 [†]	0.233
Initial bare ground	1	0.00779***	0.00148 [†]	0.00227***	0.00151
Light	1	0.091	-0.227*	0.213**	0.258
Soil H ₂ O	1	-0.00523	0.0367	-0.0455	0.1206
Overall r^2	0.47	0.12	0.22	0.04	
Overall P	<0.0001	<0.0008	<0.0001	0.186	

Bare ground was measured in 1997, and other variables were measured in 1999. Variance inflation factors for response variables are < 1.5, indicating that they are not appreciably collinear. [†], P < 0.1; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

cover of all introduced species) for each functional guild. This measures the relative success of each functional guild. We then asked whether relative success depended on resident functional guild proportional cover by testing for correlations between introduced and resident proportional cover within a functional guild. The rank correlation of introduced and resident proportional cover was significantly negative for all four functional guilds (for one-tailed tests, $P = 0.040, 0.024, 0.023,$ and <0.0001 for legumes, forbs, C3 grasses, and C4 grasses respectively). These results show that an introduced functional guild was relatively less successful when resident members of that functional guild were relatively more abundant in a plot.

Discussion

Our experiment revealed a significant, nonrandom, nonneutral pattern of community assembly. In particular, each of four plant functional guilds had its strongest negative effect on the cover attained by introduced species of the same functional guild in a partial correlation coefficients analysis (Table 2). In another test of the same hypothesis, we found that introduced and resident proportional cover were negatively rank correlated for all four functional guilds. To our knowledge, these are the first experimental results that show the strongest inhibitory effects of resident plants are on introduced plants of the same functional guild.

We found that resident functional guilds most strongly inhibited members of their own functional guild and that C4 grasses were the resident functional guild that most inhibited all of the added functional guilds (Table 2). These results are in no way contradictory but rather give added insight into the assembly process. Previous work has shown that C4 grasses are the best competitors for nitrogen on these low-nitrogen soils (25) and are the most abundant functional guild in nearby native grasslands. Their ability to strongly competitively inhibit all invaders is a likely explanation for their high abundance. However, because they most strongly inhibit establishment and growth of other C4 grasses, it is possible for species in other functional guilds to become established and coexist with them, albeit at lower densities than those attained by the C4 grasses. Indeed, the invasion experiment shows that each of the functional guilds can invade near-equilibrium communities of varying compositions, but that each is more successful when its own functional guild is rare. Such mutual invasibility when rare is the classical mechanism needed for stable coexistence (26).

There are a variety of plausible mechanisms that could cause resident functional guilds to most strongly inhibit members of their own functional guild. Indeed, any of a wide variety of niche-based mechanisms of multispecies coexistence could be responsible. Based on earlier studies at this site (25, 27, 28), we suggest that C4 grasses are the best competitors for soil nitrogen during the hot summer months and that other species are niche-differentiated by accessing nitrogen earlier (C3 grasses), deeper (many forbs), or from the air (legumes). Thus, C3 grasses may more strongly inhibit other C3 grasses by reducing early-season nitrogen availability, forbs by reducing nitrogen availability in deep soils, and legumes by reducing some other resource for which they have a relatively high requirement, such as water, phosphorus, or molybdenum. Although nitrogen and water are the two main limiting resources at Cedar Creek (29, 30), other processes, such as functional-guild-specific herbivores or pathogens, are also possible but, as yet, untested.

Several lines of evidence support the mechanisms we hypothesize. First, cover of introduced forbs and C3 grasses was positively associated with midsummer soil nitrate, consistent with our hypothesis of strong competition for this resource. Second, C4 grasses are strong nitrogen competitors in our system (25) and have many traits that make them dominant competitors for nitrogen. C4 grasses have higher nutrient-use efficiencies,

greater water-use efficiencies (31, 32), and lower tissue nitrogen concentrations (32) than C3 grasses. At Cedar Creek Natural History Area, a comparison of two C4 and three C3 grass species showed that C4 grasses more strongly reduced midsummer soil nitrate (27), had lower tissue nitrogen concentration, greater nitrogen-use efficiency, greater net productivity, and greater proportion of biomass below ground (33). In our experiment, C4 grasses reduced midsummer soil nitrate concentrations to lower levels than any other functional guild. In a comparison of plots with only one functional guild, midsummer soil nitrate concentrations varied significantly among functional guilds ($F_{3,22} = 4.89, r^2 = 0.40, P = 0.009$). Plots planted with only legume species had significantly higher soil nitrate ($0.65 \pm 0.09, n = 3$) than plots planted to only C4 grasses ($0.21 \pm 0.04, n = 13$) ($P < 0.05$ Tukey–Kramer highly significant difference), whereas plots planted with only C3 grasses ($0.31 \pm 0.15, n = 1$) or forbs ($0.27 \pm 0.05, n = 9$) were intermediate. Similar patterns were observed in the monocultures of an adjacent biodiversity experiment (refs. 34 and 35; unpublished data). In addition, in our experiment, soil nitrate was negatively related to cover of resident C4 grasses ($F_{1,145} = 23.12, r^2 = 0.14, P < 0.0001$) and uncorrelated with cover of other resident functional guilds ($P > 0.1$ for all three functional guilds).

Third, C3 grasses attain peak biomass in the cool times of year, i.e., spring and fall (32, 36), whereas C4 grasses grow most actively in the hot summer months (31). These differences are attributable to their different photosynthetic pathways (31, 32). At Cedar Creek Natural History Area, biomass of C3 grasses increased from April to mid-June and again from mid-August through September, whereas C4 grasses had a single, midseason peak of above-ground biomass in July and August (36).

Fourth, legumes can avoid competition for nitrogen with C4 grasses and other species by accessing atmospheric nitrogen. Legumes are functionally unique because they fix atmospheric nitrogen, which reduces competition for soil nitrogen (37, 38). However, legumes are limited by other resources, such as light, water, phosphorus, or trace metals (39). In our experiment, legumes were not significantly associated with any of the measured resources (light, nitrogen, initial bare ground, and water). Although not significant, legumes had a stronger relationship, based on parameter estimates, with light and water than did other functional guilds (Table 1).

Fifth, many forb species, but not all, have tap root systems that proliferate at levels below many grasses (40) and reach maximum depths greater than grasses (41). Forbs and legumes tend to have thicker roots than grasses (40, 42). In another experiment at Cedar Creek Natural History Area, we found that functional guilds differed in their root-distribution patterns ($F_{3,39} = 9.77, r^2 = 0.43, P < 0.0001$). As quantified by the negative slope of root biomass with increasing depth (g of root per m^2/cm soil profile), roots of legumes were most evenly distributed ($0.020 \pm 0.003, n = 4$), followed by forbs ($0.023 \pm 0.001, n = 23$), C3 grasses ($0.030 \pm 0.003, n = 4$), and C4 grasses ($0.032 \pm 0.001, n = 12$).

Clearly, other functional classification systems are possible (e.g., refs. 42–44), and collecting the additional species trait data necessary to apply them would likely yield additional insights. A comparison of categorical and continuous classifications found that our categorical functional guilds were significantly differentiated from each other (42). Our hypothesis that established species will more strongly deter introduced species with similar resource-use patterns should generally apply to any functional grouping, as long as species within groups have resource-use patterns more similar than species in different groups.

Few studies have used experimental manipulations to compare interguild vs. intraguild responses. Heske *et al.* (45) showed stronger intraguild response to small rodent removal in a long-term experiment. Fowler (46) found weak responses in the abundance of other plants to single-species removals in a mown

grassland and no evidence of stronger intraguild interactions. Perhaps experimental additions or removals that measure inter- and intraguild abundance responses will provide a more sensitive test of the hypothesized community assembly process than attempts to detect patterns in species presence and absence.

Although few direct comparisons are available, our results are consistent with a large body of ecological research on community assembly (e.g., refs. 47 and 48), resource competition (e.g., ref. 2), succession (e.g., refs. 49 and 50), and invasion (e.g., refs. 17, 20, and 51), all of which are consistent with the hypothesis that invasion is influenced by effects of resident species on resources, and that invaders perform better when their traits, and thus presumably their patterns of resource use, differ from those of resident species. Thus, our results suggest that a mechanistic, resource-competition-based approach may help better explain many aspects of community ecology, including the dynamics and impacts of exotic species.

Conclusion

This experiment demonstrates a significantly nonrandom, non-neutral assembly process in which resident species more strongly inhibit new (invading) species that are functionally similar to the resident species. The critical assumptions of the community

assembly process we propose are that (i) resource competition occurs, i.e., species reduce levels of resources that are limiting to other species, (ii) species can be meaningfully grouped based on differences in their spatial and temporal demands on different limiting resources, and (iii) there are interspecific and interguild tradeoffs such that species better at dealing with one constraint are poorer at dealing with another. Given these three assumptions, it follows that resident species should most strongly inhibit species within their own functional guild. This should result in a pattern of community assembly that tends toward specific relative abundances of functional guilds, and not in neutral assembly driven by random sampling from regional species pools. Processes that depend on populations of species increasing from rarity in the presence of established species, including stable coexistence, invasion, succession, and community assembly, can all be given repeatable structure by the stronger-within-functional-guild competitive effects observed in this study.

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