Productivity Is a Poor Predictor of Plant Species Richness

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Productivity Is a Poor Predictor of Plant Species Richness


For more than 30 years, the relationship between net primary productivity and species richness has generated intense debate in ecology about the processes regulating local diversity. The original view, which is still widely accepted, holds that the relationship is hump-shaped, with richness first rising and then declining with increasing productivity. Although recent meta-analyses questioned the generality of hump-shaped patterns, these analyses have been criticized for failing to account for methodological differences among studies. We addressed such concerns by conducting standardized sampling in 48 herbaceous-dominated plant communities on five continents. We found no clear relationship between productivity and fine-scale (meters to kilometers) richness within sites, within regions, or across the globe. Ecologists should focus on fresh, mechanistic approaches to understanding the multivariate links between productivity and richness.

For more than three decades, ecologists have debated the role of primary productivity in regulating plant species richness at fine spatial scales (1, 2). Although some studies have advocated multivariate approaches (3–5), much of the debate remains focused on evidence for a single, general relationship between productivity and richness. This classic productivity-richness relationship (PRR) is hump-shaped, with richness increasing at low to intermediate levels of productivity and decreasing at high productivity (6). The mechanisms invoked to explain the decreasing phase of the PRR in terrestrial plant communities have attracted the greatest controversy and include disturbance (3, 7), competitive exclusion mediated by shifts in the identity or heterogeneity of limiting resources (8–10), and evolutionary history and dispersal limitation (11). However, the theoretical justification for a hump-shaped PRR has been challenged (12), and the empirical evidence is mixed. For example, recent meta-analytical syntheses concluded that evidence for a single, canonical pattern was weak (13–15). A large percentage of studies exhibited negative, U-shaped, or nonsignificant PRRs in addition to unimodal and positive linear patterns, and the frequency of these various patterns depended on taxon and spatial scale. Subsequent critiques of the meta-analyses argued that the apparent lack of generality in PRRs might simply reflect methodological inconsistencies among the field studies (16, 17). First, PRR studies vary widely in their choice of both the grain (the area of the sampling unit) and extent (the area over which sampling units are spread) (15, 18). Because of the strong effects of area and heterogeneity on richness, such differences in scale confound cross-study comparisons (19). Second, many of the studies included in PRR meta-analyses did not measure primary production directly but used weakly related surrogates such as latitude, temperature, or altitude (14).

We assessed the generality of the PRR and addressed previous methodological inconsistencies by conducting standardized, observational sampling in 48 herbaceous-dominated plant communities on five continents (Fig. 1 and table S1) (20). We sampled plant species richness in standard 1-m² quadrats located in blocks of 10 plots, holding grain constant and minimizing differences in extent across sites. In addition, we used the same protocol at all sites for estimating aboveground net primary production (ANPP) as peak-growing-season live biomass, an effective measure of ANPP in herbaceous vegetation (21), especially when consumption by herbivores is low (fig. S1).

Previous work indicated that the form of the PRR might vary with the spatial extent of sampling. Although significant PRRs have been observed at spatial extents ranging from individual
plots located within one community to means of sites spread across continents, the hump-shaped pattern has emerged most frequently in studies that cross community boundaries (14, 22). PRRs described within communities may be weaker because of the potential for limited variation in productivity among sampling plots as well as measurement error on individual samples (22) and because mechanisms involving variation in species pools and dispersal are excluded. We tested for scale-dependence by characterizing the shape of the PRR at three spatial extents: (i) The within-site extent compares richness and productivity sampled in individual plots; (ii) the regional extent compares site-level averages for 1-m² richness and productivity among sites occurring within a biogeographic province; and (iii) the global extent compares site-level averages for richness and productivity among all sites.

The 48 within-site PRRs took all possible shapes in parametric regressions of species richness on productivity (Fig. 2, fig. S2, and tables S2 and S3). The most common relationship was nonsignificant (34 sites), 5 sites had a positive linear pattern, 5 sites had a negative linear pattern, 3 sites were concave-up (U-shape), and 1 site was concave-down (the classical hump shape). Repeating this analysis with quasipoisson regression (20) gave similar results (34 nonsignificant, 5 positive linear, 6 negative linear, 2 concave-up, and 1 concave-down). We did not find factors that explained the variation in the shape of the within-site PRRs. For example, if unproductive sites had positive linear PRRs and highly productive sites had negative PRRs, then there should be a correlation between site-level productivity and the slope of the within-site linear relationship (18). We found no such pattern (correlation coefficient \( r = 0.07, df = 46, P = 0.62 \)), nor were sites that spanned larger ranges in productivity more likely to show significant PRRs. Specifically, the probability of finding a non-null PRR was unrelated to the range of ANPP within a site (logistic regression \( P = 0.20 \)).

We tested the regional relationship between site-level-average species richness (meters\(^{-2}\)) and average biomass production in the three biogeographic provinces of North America in which we had more than four sites (Fig. 3). For the 11 Pacific coast sites, located west of the Cascade/Sierra Mountain ranges and dominated by non-native species (along with one salt

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**Fig. 1.** Locations of the 48 Nutrient Network sites that provided data for this study. Numbers correspond to the “code” column in table S1. Colors and symbols represent the distinct biogeographic regions also shown in Fig. 3 (see Fig. 3 for key).

**Fig. 2.** Within-site relationships between productivity, measured as peak live biomass (dry weight) and species richness. The inset shows the frequencies of relationships that were nonsignificant (NS, thin dashed lines), positive or negative linear (thick dashed lines), and concave-up (+) or -down (–) (solid curves). Statistical results and separate figures for each of the 48 sites are available in table S2 and fig. S1, respectively. The marginal histograms show the frequency of species richness and peak live biomass across all sites.
Fig. 3. Global relationship between mean productivity, measured as peak live biomass (dry weight), and mean species richness (meters$^2$) at each site. White dots indicate managed sites (burned regularly or grazed by domestic livestock) and crosses indicate sites of anthropogenic origin (pastures, old fields, and restored prairies). The solid curve shows the quadratic relationship between productivity and richness with all sites included; the dotted line shows the linear relationship that remains when the anthropogenic sites are removed; and the dashed line shows the 0.95 quantile regression with all sites included. N. Am., North America.

rather than investing continued effort in attempting to identify a general PRR, ecologists should focus on more sophisticated approaches already available for investigating the complex, multivariate processes that regulate both productivity and richness (5, 25, 26). Coordinated, global networks represent a research approach that will be invaluable not only for addressing longstanding debates about the generality of empirical patterns but also for testing the underlying mechanisms.

References and Notes

20. Materials and methods are available as supporting material on Science Online.

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African Wild Ungulates Compete with or Facilitate Cattle Depending on Season

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Savannas worldwide are vital for both socioeconomic and biodiversity values. In these ecosystems, management decisions are based on the perception that wildlife and livestock compete for food, yet there are virtually no experimental data to support this assumption. We examined the effects of wild African ungulates on cattle performance, food intake, and diet quality. Wild ungulates depressed cattle food intake and performance during the dry season (competition) but enhanced cattle diet quality and performance during the wet season (facilitation). These results extend our understanding of the context-dependent—competition-facilitation balance, in general, and are critical for better understanding and managing wildlife-livestock coexistence in human-occupied savanna landscapes.

Weight gain of cattle within treatment plots they accessed exclusively (C) and those they shared foraging areas with wild ungulates, excluding or in combination with megaherbivores (African elephant Loxodonta africana and giraffe Giraffa camelopardalis) compete with cattle in a savanna ecosystem in Kenya. Specifically, we hypothesized that if these ungulates compete with cattle, food availability and quality should decrease in the shared foraging areas, resulting in reductions in food intake, diet quality, and most importantly, weight gain of cattle. Additionally, we hypothesized that these effects would reduce after experimental exclusion of megaherbivores, especially elephants, because of their documented seasonal resource overlap with cattle (10). Last, we expected greater competitive effects during the dry season, when food is less abundant.

We compared cattle weight gain, organic matter food intake (OMI), diet selection, dietary digestible organic matter (DOM), crude protein (CP), DOM/CP ratio, and herbage cover in treatment plots that cattle accessed exclusively and those they shared with wild ungulates, excluding or including megaherbivores, during wet and dry seasons (11). Consistent with our hypothesis, cattle experienced depressed weight gain when they shared foraging areas with wild herbivores during the dry season (Fig. 1A), providing evidence of competition. In contrast, this pattern was reversed in the wet season, with increased cattle performance in the shared treatments (Fig. 1B), demonstrating a surprising facilitative interaction that was nearly great enough to overcome the preceeding season’s competition.

Competition was associated with depressed food intake in the shared treatments (Table 1), which corresponded with reductions in cover and selection by cattle of Pennisetum stramineum (Fig. 2, A to C), suggesting that wild and cattle competed for this grass. For all other major herbaceous species, cover was not significantly different among herbivore treatments (Table S1). Relative bites on Themeda triandra increased in the treatment accessible to all three guilds of herbivores during wet season, but no other major plant species showed treatment effects on either relative bites or selection by cattle (tables S2 and

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Reports: “Productivity is a poor predictor of plant species richness” by P. B. Adler et al. (23 September, p. 1750). Scott L. Collins’s affiliation was listed incorrectly. He is at the Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, NM 87131, USA. He is not affiliated with The University of Queensland in Australia.