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## PLANT ECOLOGY

# Worldwide evidence of a unimodal relationship between productivity and plant species richness

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The search for predictions of species diversity across environmental gradients has challenged ecologists for decades. The humped-back model (HBM) suggests that plant diversity peaks at intermediate productivity; at low productivity few species can tolerate the environmental stresses, and at high productivity a few highly competitive species dominate. Over time the HBM has become increasingly controversial, and recent studies claim to have refuted it. Here, by using data from coordinated surveys conducted throughout grasslands worldwide and comprising a wide range of site productivities, we provide evidence in support of the HBM pattern at both global and regional extents. The relationships described here provide a foundation for further research into the local, landscape, and historical factors that maintain biodiversity.

**D**espite a long history of research, the nature of basic patterns between environmental factors and biological diversity remain poorly defined. A notable example is the relationship between plant diversity and productivity, which has stimulated a long-running debate (1–6). A classic hypothesis, the humped-back model (HBM) (7), states that plant species richness peaks at intermediate productivity, taking above-ground biomass as a proxy for annual net primary productivity (7–9). This diversity peak is driven by two opposing processes. In unproductive ecosystems with low plant biomass, species richness is limited by abiotic stress, such as insufficient water and mineral nutrients, which few species are able to tolerate. In contrast, in the productive conditions that generate high plant biomass, competitive exclusion by a small number of highly competitive species is hypothesized to constrain species richness (7–9). Other mechanisms that may explain the unimodal relationship between species richness and biomass include disturbance (7, 10), evolutionary history and dispersal limitation (11, 12), and the reduction of total plant density in productive communities (13).

Since its initial proposal, a range of studies have both supported and rejected the HBM, and three separate meta-analyses reached different

conclusions (14–17). Although this inconsistency may indicate a lack of generality of the HBM, it may instead reflect a sensitivity to study methodology, including the plant community types considered, the taxonomic scope, the range of site productivities sampled, the spatial grain and extent of analyses (17, 18), and the particular measure of net primary productivity used (19). The questions therefore remain open as to what the form of the relationship between diversity and productivity is, and whether the HBM serves as a useful and general model for grassland ecosystem theory and management.

We quantified the form and the strength of the richness-productivity relationship by using globally coordinated surveys (20), which yielded scale-standardized data and were distributed across 30 sites in 19 countries and six continents (Fig. 1). Collectively, our samples spanned a broad range of biomass production (from 2 to 5711 g m<sup>-2</sup>) and grassland community types, including natural and managed (pastures and meadows) grasslands over a wide range of climatic zones (temperate, Mediterranean, and tropical), and altitudes (lowland to alpine) (table S1). Our protocol involved sampling 64 1-m<sup>2</sup> quadrats within 8-m-by-8-m grids (18, 21). At each site, between 2 and 14 grids were sampled, thus resulting in 128 to 896 quad-

rats per site. In each 1-m<sup>2</sup> quadrat, we identified and counted all plant species and harvested above-ground biomass and plant litter. Litter production is a function of annual net primary productivity in grasslands and can have profound effects on the structure and functioning of communities, from altering nutrient cycling to impeding vegetative growth and seedling recruitment (22, 23), thereby also playing a major role in driving community structure. Indeed, the HBM was originally defined in terms of live biomass plus litter material (7, 8). Most of the sites in our survey were subject to some form of management, usually livestock grazing or mowing. In this respect, our sites are representative of most of the world's grasslands. Our sampling was conducted at

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least 3 months after the last grazing, mowing, or burning event and at the annual peak of live biomass, which, when coupled with litter, constitutes a reliable measure of annual net aboveground production in herbaceous plant communities (24).

Our results strongly support the HBM of the plant richness-productivity relationship. By using a global-extent regression model ( $N = 9631$  1-m<sup>2</sup> quadrats) (21), we found that plant richness formed a unimodal relationship with productivity (Fig. 2A) that is characterized by a highly significant concave-down quadratic regression [negative binomial generalized linear model (GLM); Table 1]. This relationship was not sensitive to the statistical model used; the hump-backed relationship was also evident when we used a negative binomial generalized linear mixed model (GLMM) that accommodated the hierarchical structure of our sampling design (grids nested within sites; Table 1 and fig. S1).

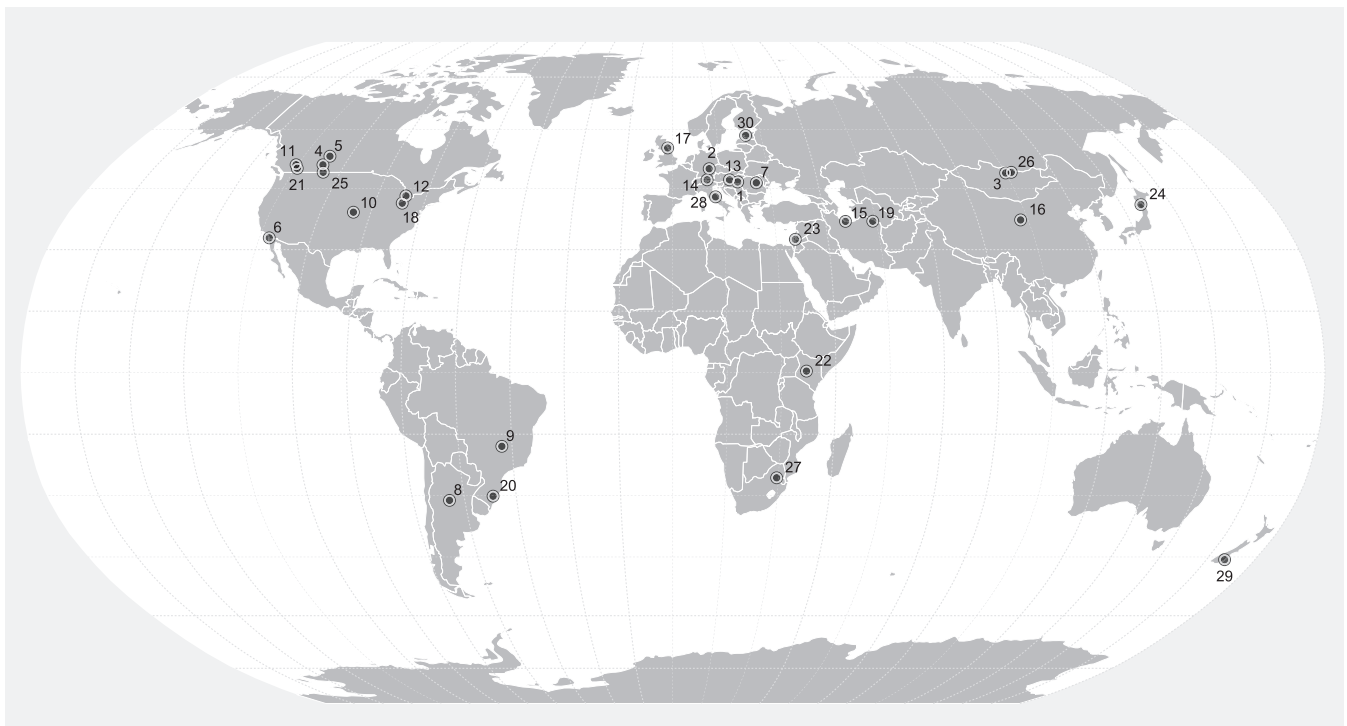
At a sampling grain of 1 m<sup>2</sup>, 19 of 28 site level analyses (68%) yielded significant concave-down relationships (table S2 and Fig. 2A). This contrasts markedly with the results of Adler *et al.* (1), who found only 1 of their 48 within-site analyses to be significantly concave-down. We also found the form of the productivity-diversity relationship to be robust to sampling grain: by using grains of 1 m<sup>2</sup> up to 64 m<sup>2</sup>, each time maintaining a global extent, we consistently found a significant concave-down relationship, although the proportion of variation explained tended to decrease with increasing grain (fig. S2).

The HBM predicts a boundary condition or upper limit to diversity that, in any given site,

may not be realized for a variety of reasons (18). Consistent with this view, our global-extent association is characterized by a significant concave-down quantile regression (95th percentile) (Table 1), below which considerable scatter exists (Fig. 2A). This pattern was also insensitive to the statistical method used; a hierarchical Bayesian analysis that accommodated the nested sampling design and that enabled both the mean and the variance of species richness to be modeled more accurately against (log-transformed) biomass also revealed a significant 95th percentile quantile regression (fig. S3). Likewise, we found a significant, concave-down quantile regression (95th percentile) between the maximum (quadrat-scale) richness found within a grid and the total biomass of the same quadrat (Table 1 and fig. S4). Each of these approaches to characterizing boundary conditions suggests the existence of a “forbidden space,” wherein high productivity precludes high local diversity. Furthermore, they suggest that extremely low-productivity sites rarely accommodate high diversity.

Why do our data show a hump-backed relationship, whereas those of Adler *et al.* (1) and related studies (4, 6), do not? One possibility is that data limitations can thwart detection of the HBM (18). For example, the data used by Adler *et al.* differed from ours in the following potentially important ways: (i) They exhibited a maximum live biomass of only 1535 g<sup>-2</sup> (ours was 3374 g<sup>-2</sup>), (ii) litter was not included within the calculation of biomass, and (iii) sample size was limited to 30 quadrats per site (ours ranged from 128 to 894 quadrats per site; table S1). We conducted a form

of sensitivity analysis in which we reran our statistical analyses using random subsets of our data that were constrained to exhibit similar properties to those of the Adler *et al.* data set. Specifically, after limiting the overall data set to less than 1535 g<sup>-2</sup> and excluding litter, we randomly selected 30 quadrats per site 500 times, each time conducting the within-site regression analyses ( $N = 30$  for each of the 28 site-level GLMs conducted per subsampling iteration). For each iteration, we also calculated the average range of biomass spanned by the 28 site-level relationships. Across the 500 iterations (one example set of outcomes is shown in Fig. 2B), the average proportion of significant concave-down, within-site regressions was  $0.31 \pm 0.003$  (SEM), significantly less than our observed proportion of 0.68 (fig. S5). Moreover, when significant concave-down relationships were detected, they tended to span a broader range of biomass than the remaining forms (including nonsignificant relationships). Specifically, in 458 of the 500 iterations (92%), the mean biomass range of the concave-down regressions was larger than the mean of the remaining forms' biomass ranges (binomial test:  $P < 2.2 \times 10^{-16}$ ). Last, the 48 within-site analyses of Adler *et al.* spanned, on average, a live biomass range of  $428.7 \text{ g}^{-2} \pm 38.36$  (range of 89 to 1217 g<sup>-2</sup>). This is (i) less than half of the average range encompassed by our 28 site-level analyses shown in Fig. 2A (mean =  $1067.5 \text{ g}^{-2} \pm 140.63$ ; range of 286 to 3256 g<sup>-2</sup>) and (ii) almost 50% narrower than the smallest average biomass range encompassed by our 500 random subset analyses ( $627.4 \text{ g}^{-2}$ ) (fig. S6). Taken together, these findings



**Fig. 1. Site locations.** Locations of the geographic centroids of the 30 study sites, which include 151 sampling grids. Some points overlap and are therefore indistinguishable. Additional site details are provided in table S1. Map is displayed using the Robinson projection.

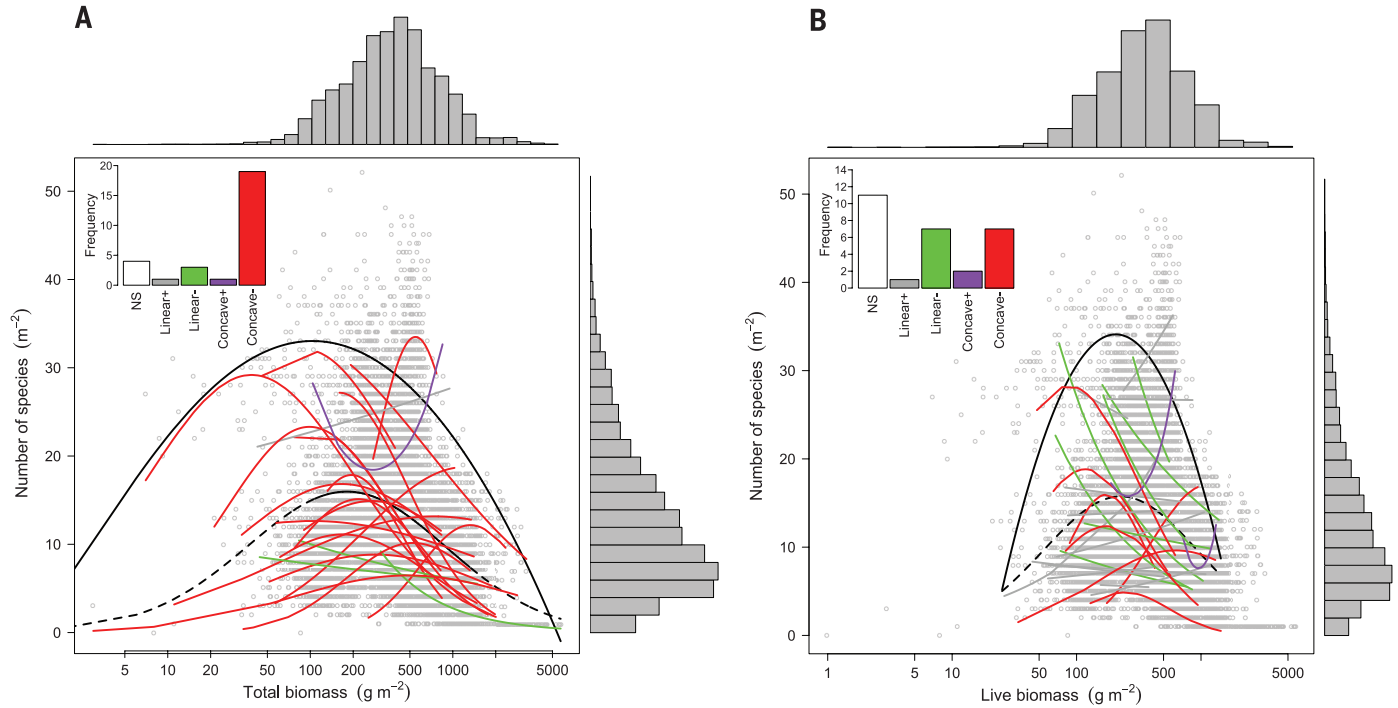
strongly suggest that we were able to detect more concave-down relationships because of the greater sample sizes and biomass ranges in our analysis.

It has been suggested (2) that some previous studies, including Adler *et al.* (1), failed to support the HBM because they excluded litter. Although we do find a significant concave-down relationship at the global extent using only live biomass (Table 1), a comparison of models using biomass versus biomass and litter (both  $N = 9,631$ ) shows

total biomass to provide a far better fit [residual deviance = 10,105 (live) versus 10,037 (total); Vuong  $z$ -statistic for comparing non-nested models:  $-13.4$ ;  $P < 0.001$ ]. It has also been suggested that previous surveys failed to adequately represent high-productivity communities. Indeed, our high-biomass quadrats (1011 samples were over  $1000 \text{ g}^{-2}$ ,  $\sim 10\%$  of the 9631 samples; maximum of  $5711 \text{ g}^{-2}$ ) contributed considerably to the right-hand part of the fitted humped-back regression. This could be a reason why the data set of Adler *et al.* (1) (in

which only 0.5% of samples were over  $1000 \text{ g}^{-2}$  with a maximum of  $1534 \text{ g}^{-2}$ ) failed to support the HBM. Our results therefore show that a test of the HBM in herbaceous plant communities yields the expected pattern when it is robust and comprehensive, spans a wide range of biomass production (from 1 to at least  $3000 \text{ dry g}^{-2} \text{ year}^{-1}$ ), and provides sufficient replication of quadrats along the productivity gradient.

Competitive exclusion has been cited as the primary factor driving low species numbers at



**Fig. 2. Biomass production as a function of species richness.** (A) Biomass production-species richness relationships for 28 study sites. Solid black line indicates significant quantile regression (95th percentile) of overall relationship (quadratic coefficient  $P < 0.001$ ;  $N = 9631$  quadrats). Dashed black line, significant negative binomial GLM (quadratic coefficient  $P < 0.001$ ;  $N = 9631$ ). Colored lines indicate significant GLM regressions (Poisson or quasi-Poisson), with  $N$  ranging from 128 to 894 quadrats.

(Inset) The frequencies of each form of relationship observed across study regions. NS, not significant. (B) Same as (A) but the results are derived from the analysis of an example, random subsample of the complete data set that satisfies the following criteria: litter biomass excluded, quadrats with biomass  $>1534 \text{ g}^{-2}$  excluded, and including 30 (randomly selected) quadrats per site (total  $N = 840$ ). These criteria match the characteristics of the data set used by Adler *et al.* (1).

**Table 1. Regression results.** Results of regression analyses of the relationship between productivity and species richness, measured at a global extent and a sampling grain of  $1\text{-m}^2$  quadrat. Total biomass = live biomass + litter biomass. All linear and quadratic term coefficients were highly significant ( $P < 0.001$ ).

Productivity measure	Type of regression	Sample size	Test of model fit	Intercept estimate $\pm$ SEM	Linear term coefficient $\pm$ SEM	Quadratic term coefficient $\pm$ SEM
Total biomass	negative binomial GLM (log-link function)	9631 quadrats	likelihood ratio stat. = 1602.2	$-2.52 \pm 0.235$	$4.69 \pm 0.186$	$-1.04 \pm 0.037$
Total biomass	negative binomial GLMM (log-link function) random effects: grid nested in site	9631 quadrats 151 grids 28 sites	likelihood ratio stat. = 114.0	$0.91 \pm 0.191$	$1.33 \pm 0.133$	$-0.29 \pm 0.028$
Total biomass	quantile (95th percentile)	9631 quadrats	pseudo- $F$ statistic = 179.1	$-12.9 \pm 7.159$	$45.6 \pm 5.833$	$-11.3 \pm 1.173$
Live biomass	negative binomial GLM (log-link function)	9644 quadrats	likelihood ratio stat. = 950.3	$-2.03 \pm 0.212$	$4.27 \pm 0.178$	$-0.96 \pm 0.037$



high plant biomass (7, 8, 25). However, in the case of nitrogen addition the negative relationship between productivity and species richness has been shown to diminish over time [(26), but see (27, 28)]. It may be that low species richness in high-productivity conditions arises in part because most such habitats are anthropogenic, and there are few species in the local pool adapted to these conditions (11, 12). If so, it is possible that species will eventually immigrate from distant pools, so that the right-hand part of the hump will then flatten out.

We have shown a global-scale concave-down unimodal relationship between biomass production and richness in herbaceous grassland communities. However, the original HBM (7) is vaguely articulated by the standards of modern ecological theory, and it is clear that more work is needed to determine the underlying causal mechanisms that drive the unimodal pattern (1, 6, 17, 18). We recognize that, in our study and many others, productivity accounts for a fairly low proportion of the overall variation in richness and that many other drivers of species richness exist (28–30). Accordingly, we echo the call of Adler *et al.* (1) for additional efforts to understand the multivariate drivers of species richness.

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#### SUPPLEMENTARY MATERIALS

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Materials and Methods  
Supplementary Text  
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#### ICE SHEETS

## Reverse glacier motion during iceberg calving and the cause of glacial earthquakes

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Nearly half of Greenland’s mass loss occurs through iceberg calving, but the physical mechanisms operating during calving are poorly known and in situ observations are sparse. We show that calving at Greenland’s Helheim Glacier causes a minutes-long reversal of the glacier’s horizontal flow and a downward deflection of its terminus. The reverse motion results from the horizontal force caused by iceberg capsizing and acceleration away from the glacier front. The downward motion results from a hydrodynamic pressure drop behind the capsizing berg, which also causes an upward force on the solid Earth. These forces are the source of glacial earthquakes, globally detectable seismic events whose proper interpretation will allow remote sensing of calving processes occurring at increasing numbers of outlet glaciers in Greenland and Antarctica.

One-third to one-half of Greenland’s total mass loss occurs through iceberg calving at the margins of tidewater-terminating glaciers (1, 2). Recent rapid changes in glacier dynamics are associated with increased calving rates (3–5) and increased rates of glacial earthquakes (6). At large glaciers with near-grounded termini, calving typically occurs when buoyancy forces cause icebergs that are the full thickness of the glacier to capsize against the calving front (6–9). This type of calving is associated with glacial earthquakes (6, 7, 10), long-period seismic emissions of magnitude ~5 that are observed globally (11). These earthquakes have expanded northward and increased sevenfold in number during

the past two decades (6, 12, 13), tracking changes in glacier dynamics, the retreat of glacier fronts, and increased mass loss (6, 14). Buoyancy-driven calving represents an increasingly important source of dynamic mass loss (6–8) as glacier fronts throughout Greenland have retreated to positions near their grounding lines (15). However, because of the difficulty of instrumenting the immediate near-terminus region of these highly active glaciers, few direct observations of the calving process are available, limiting development of the deterministic calving models required for improved understanding of controls on dynamic ice-mass loss. Detailed knowledge of the glacial earthquake source would allow quantification of calving processes for a large



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