

Worldwide Evidence of a Unimodal Relationship Between Productivity and Plant Species Richness

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One Sentence Summary: Empirical evidence from grasslands around the world shows a humped-back relationship between biomass production and plant species richness.

Abstract: 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, using data from coordinated surveys conducted throughout grasslands worldwide, and comprising a wide range of site productivities, we provide strong evidence in support of the HBM pattern, at both global and regional extents. The relationships described here provide a strong foundation for further research into the local, landscape, and historical factors that ensure the maintenance of biodiversity.

Main Text: Despite 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). While 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 question therefore remains 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 strength of the richness-productivity relationship using globally coordinated surveys (20), which yielded scale-standardized data, and were distributed across 30

sites in 19 countries and 6 continents (Fig. 1). Collectively, our samples spanned a broad range of biomass production (from 2 to 5,711 g m⁻²) and grassland community types, including natural and managed (pastures, meadows) grasslands over a wide range of climatic zones (temperate, Mediterranean and tropical), and altitudes (lowland to alpine) (table S1). Our protocol involved sampling sixty-four 1 m² quadrats within 8 m x 8 m grids (18, 21). At each site, between two and 14 grids were sampled, thus resulting in 128 – 896 quadrats per site. In each 1 m² 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 least three 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 humped-back model of the plant richness-productivity relationship. Using a global-extent regression model (N = 9631 1 m² 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; 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 m², 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: using grains of 1 m² up to 64 m², each time maintaining a global extent, we consistently found a significant concave-down relationship, though the proportion 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; 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 while those of Adler et al. (1), or 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 1,535 gm⁻² (ours was 3,374 gm⁻²) (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 re-ran our statistical analyses using random subsets of our data that were constrained to exhibit similar properties to those of the Adler et al. dataset. Specifically, after limiting the overall dataset to less than 1,535 gm⁻² 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 shown in Fig. 2B), the average proportion of significant concave-down, within-site regressions was 0.31 ± 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 non-significant 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: $P < 2.2 \times 10^{-16}$). Finally, the 48 within-site analyses of Adler et al. spanned, on average, a live biomass range of 428.7gm⁻²

± 38.36 (range: 89 – 1217 gm^{-2}). This is (i) less than half of the average range encompassed by our 28 site-level analyses shown in Fig. 2A (mean = 1,067.5 $\text{gm}^{-2} \pm 140.63$; range 286 to 3,256 gm^{-2}), and (ii) almost 50% narrower than the smallest average biomass range encompassed by our 500 random subset analyses (627.4 gm^{-2}) (fig. S6). Taken together, these findings 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+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 (1,011 samples were over 1,000 gm^{-2} , approximately 10% of the 9,631 samples; maximum 5,711 gm^{-2}), contributed considerably to the right-hand part of the fitted humped-back regression. This could be a reason why the dataset of Adler et al. (1) (in which only 0.5% of samples were over 1,000 gm^{-2} and a maximum of 1,534 gm^{-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 3,000 dry $\text{gm}^{-2} \text{yr}^{-1}$), and provides sufficient replication of quadrats along the productivity gradient.

Competitive exclusion has been cited as the primary factor driving low species numbers at 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, 29). 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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Acknowledgements: We are grateful to all of the people who helped in the collection and processing of the samples; including Liam Alabiso-Cahill, D Ariunzaya, Mariana R Ávila, Júlio C R Azambuja, Laura Bachinger, I Badamnyambu, Kathy Baethke, J Batbaatar, Sandro Ballelli, Kh Bayarkhuu, Gustavo Bertone, Vera Besnyői, Camila L Bonilha, Greg Boorman, Rafael A X Borges, Tanner Broadbent, Roberto Canullo, Josephine Carding, Brenda Casper, Karen Castillioni, Marco Cervellini, Grace Charles, Giovana Chiara, Elsa Cleland, Rachel Cornfoot, Gayle Crowder, András István Csathó, László Demeter, Maike Demski, Miranda Deutschlander, Sabina Donnelly, André L P Dresseno, S Enkhjin, O Enkhmandal, T Erdenebold, L Erdenechimeg, B Erdenetsetseg, Jean K Fedrigo, Ana Carolina Ferreira, Zoltan Foldvari, Louise Fourie, Bruce Fraser, Jonathan Galdi-Rosa, Elizabeth Gorgone-Barbosa, Ruth Greuel, Anaclara Guido, Éva György, David Hall, Ali Hassan, Judit Házi, Roi Henkin, Samuel Hoffmann, Teele Jairus, M Jankju, Ülle Jõgar, Tessa Jongbloets, Melinda Juhász, Cristiane F Jurinitz, Vahid Rahimi Kakroudi, Alpár Kelemen, T Khandarmaa, E Khash-Erdene, Christiane Koch, Cecília Komoly, Sam Kurukura, Pierre Liancourt, Simon Lima, Ariuntsetseg Lkhagva, M Lucrecia Lipoma, D Lkhagvasuren, Julio Lombardi, M Eugenia Marcotti, Jennifer McPhee, Bryana

McWhirter, Luciana Menezes, Justine McCulloch, M Mesdaghi, István Máthé, Mario Messini, Maia Mistral, Chandra Moffat, Mohamud Mohamed, Lutendo Mugwedi, Jeff Padgham, Priscila Padilha, Susanne Paetz, S Pagmadulam, Greg Pec, Chiara Peconi, Gabriella Péter, Sándor Piros, Vitor C Pistóia, Lysandra Pyle, Morgan Randall, Mariana Ninno Rissi, Rosângela G Rolim, Mandy Ross, Tina Salarian, Sh Sandagdorj, S Sangasuren, Carlo Santinelli, Colin Scherer, Graziela H M Silva, Mariana G Silva, Thomas Smith, Sh Solongo, Francesco Spada, Reinhold Stahlmann, John Steel, Monika Sulyok, Alex Sywenky, Gábor Szabó, Lányi Szabules, Vickey Tomlinson, Julien Tremblay-Gravel, Gergely Ungvari, O Urangoo, M Uuganbayar, Mariana S Viera, Cleúsa E Vogel, Dan Wallach, Rita Wellstein, Juan I Withworth Hulse, Zita Zimmermann. This work was supported in part by the Canada Research Chair Program, Canadian Foundation for Innovation (CFI), and a Natural Sciences and Engineering Research Council Discovery Grant (NSERC-DG) of Canada awarded to L.H.F., and Thompson Rivers University; a CFI and NSERC-DG awarded to J.P.; the University of Tartu, Estonia, and a European Regional Development Fund: Centre of Excellence FIBIR awarded to M.Z. and M.M.; a Hungarian National Science Foundation (OTKA K 105608) awarded to S.B.; Taylor Family-Asia Foundation Endowed Chair in Ecology and Conservation Biology and University of Mongolia's Support for High Impact Research program awarded to B.B.; the Rangeland Research Institute, University of Alberta, Canada; CONICET, Universidad Nacional de Córdoba, FONCyT and the Inter-American Institute for Global Change Research (IAI, with support of the US National Science Foundation) awarded to S.D., L.E., and M.C.; a NSERC-DG awarded to J.C.; State Nature Reserve "Montagna di Torricchio" and University of Camerino, Italy; Hungarian University of Transylvania, Romania; a Fundação Grupo Boticário, Brazil (0153_2011_PR) awarded to A.F.; a NSF DEB-1021158 and DEB-0950100 awarded to B.F.;

UHURU: NSERC and CFI awarded to J.R.G and the University of Wyoming; an NSERC-DG awarded to H.A.L.H.; an NSERC-DG awarded to J.K.; a National Natural Science Foundation of China grant (No. 41171417) awarded to R.L.; Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Brazil (n. 307719/2012-0) awarded to S.M.; CNPq, Brazil (grants 403750/2012-1 and 307689/2014-0) awarded to V.P.; University of Florida and a NSF DEB 1149980 awarded to T.P.; Princeton Environmental Institute and a NSF DEB 1355122 awarded to R.M.P.; a CONYCIT Becas-Chile Scholarship awarded to G.C.S. Data and R scripts associated with this paper are deposited in the Dryad Repository (<http://datadryad.org/>).

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 1m² 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 (95 th 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

FIGURE LEGENDS

Figure 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.

Figure 2. A Biomass production-species richness relationships for 28 study sites. Solid black line: significant quantile regression (95th percentile) of overall relationship (quadratic coefficient $P < 0.001$; $N = 9,631$ quadrats). Dashed black line: significant negative binomial GLM (quadratic coefficient $P < 0.001$; $N = 9,631$). Colored lines indicate significant GLM regressions (Poisson or quasi-Poisson), with N ranging from 128 to 894 quadrats. The inset bar graph presents the frequencies of each form of relationship observed across study regions; B Same as A but the results are derived from the analysis of an example, random sub-sample of the complete dataset, that satisfies the following criteria: litter biomass excluded, quadrats with biomass $>1,534 \text{ gm}^{-2}$ excluded, and including 30 (randomly selected) quadrats per site (total $N = 840$). These criteria match the characteristics of the dataset used by Adler et al. (1).

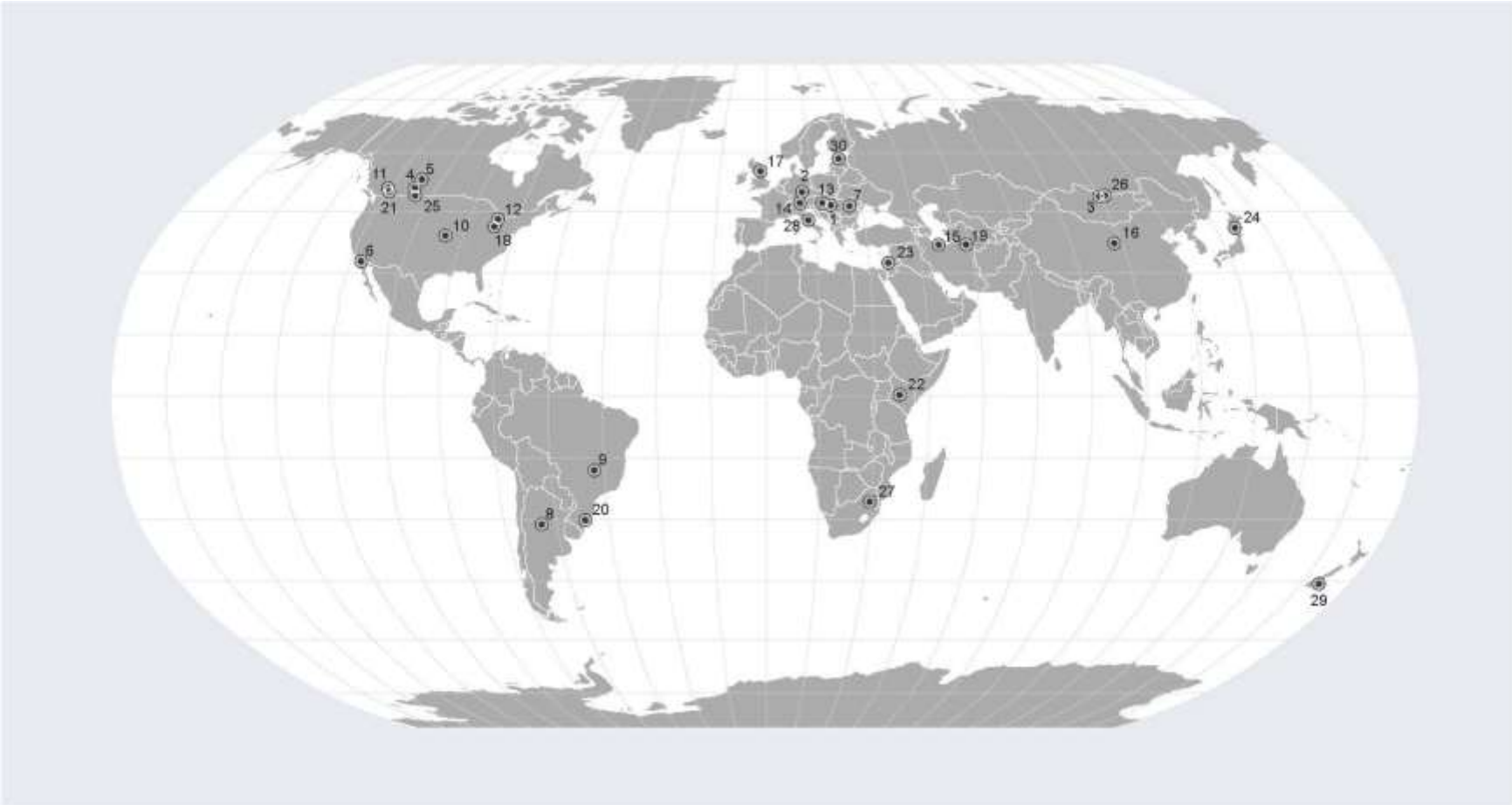


Figure 1

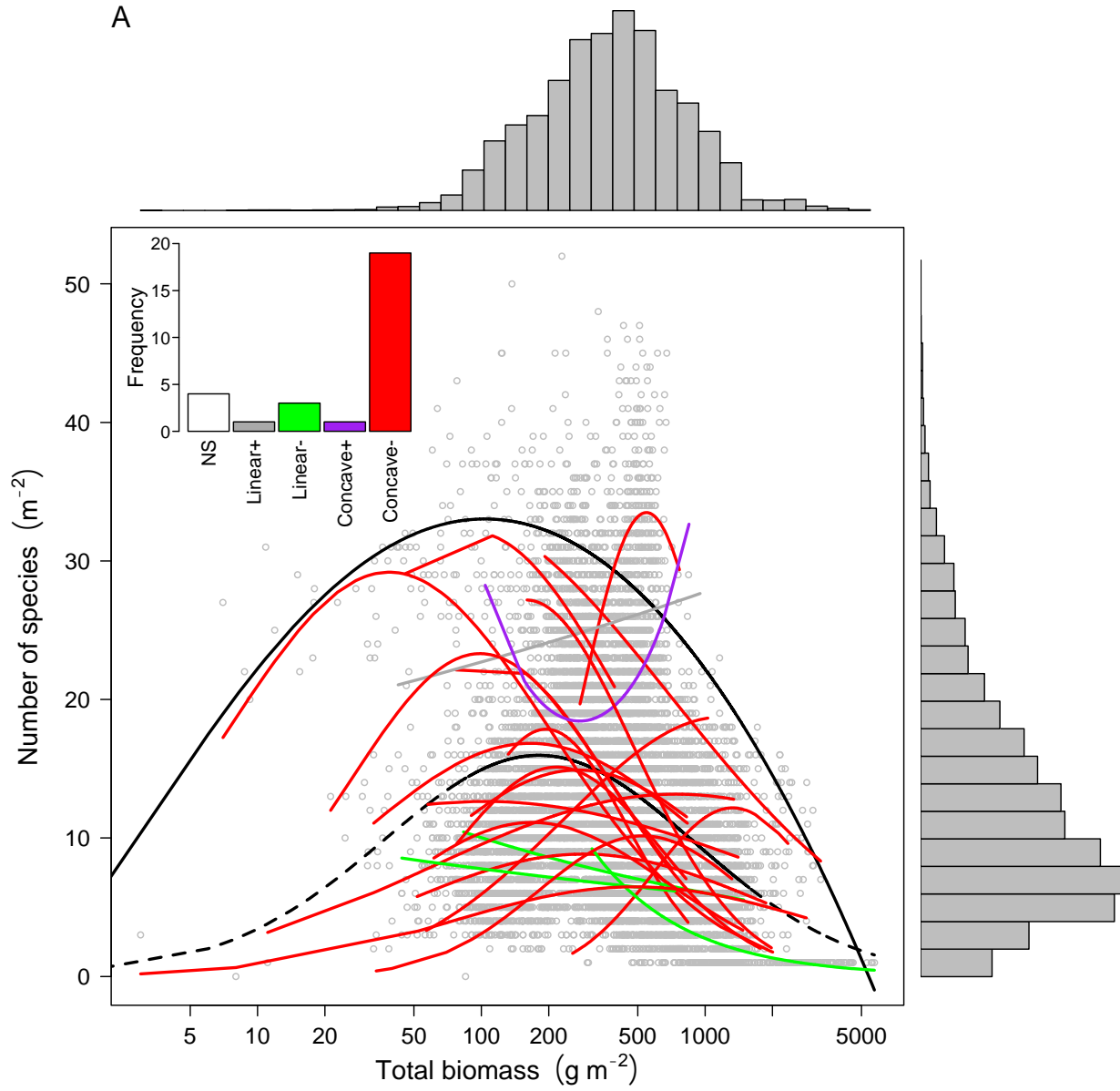


Figure 2A

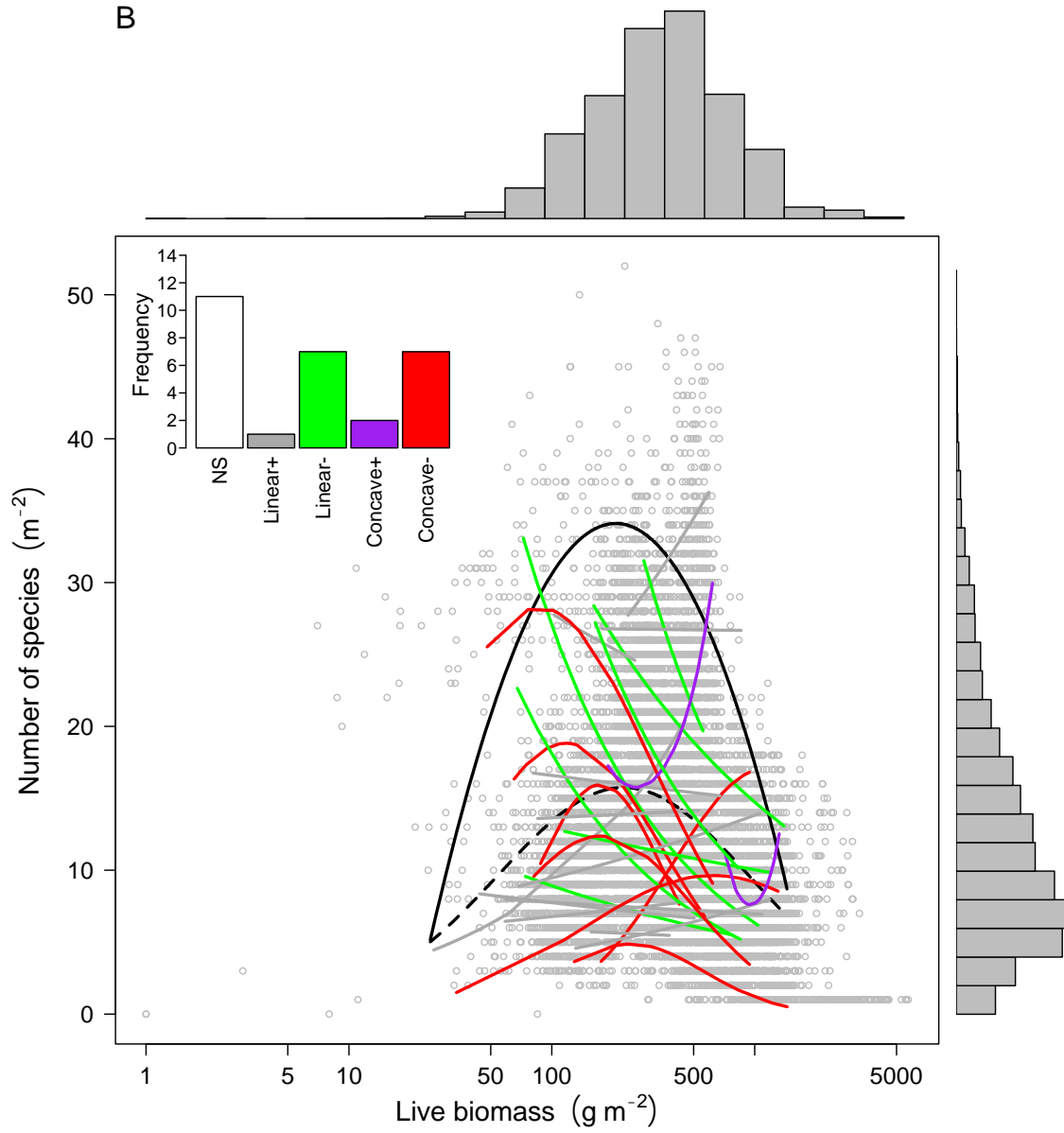


Figure 2B

Supplementary Materials for

Materials and Methods

Site selection: The Herbaceous Diversity Network (HerbDivNet) is a network of researchers working at herbaceous grassland sites in 19 countries located on 6 continents performing coordinated distributed experiments and observations (20). The full sampling design is detailed here and in Fraser et al. (18). All HerbDivNet sites are located in areas dominated by herbaceous vegetation representing the regional species composition.

Sampling protocol: The design is an 8 x 8 meter grid containing 64 1 m² plots. Within all 30 sites included in the current analysis (Fig. 1) we collected biomass and species richness data from at least two and up to fourteen 8 x 8 m grids. All grids were marked and GPS coordinates were recorded for future use. Our study focused on herbaceous grassland community types. For each 1 m² plot, all species were identified and the number counted. In the rare instances where species were unidentifiable, morphotypes were assigned. Total above-ground biomass (including plant litter) at peak biomass was harvested, dried and weighed by plot. Live biomass and litter were separated prior to drying and weighing. We did not separate biomass by species. Sampling was restricted to herbaceous plant communities; however, the occasional small woody plant was found within a sample area, which was noted but not included in the analyses. Cryptogams were not included in either measures of species richness, or biomass.

The ideal level of participation for each investigator was to sample at least six grids of 64 quadrats, two each at three relatively different levels of productivity from low ($\sim 1\text{-}300\text{ g m}^{-2}$) to medium ($\sim 300\text{-}800\text{ g m}^{-2}$) to high ($>800\text{ g m}^{-2}$). However, logistical constraints meant this was not possible at all sites and some sites had as few as two grids, taken at the low and high ends of the gradient. Most sites had a history of grazing or fire and were currently under some form of management. Therefore, sampling was performed at least three months after the last grazing or burning event.

Supplementary Text 1

Assessing the richness-productivity relationship at the global extent:

In the main text we present the results of generalized linear model (GLM) analysis, in which species richness was modeled as a function of total biomass (\log_{10} transformed) using a negative binomial GLM. We complement this analysis with a generalized linear mixed model (GLMM) analysis, which accommodates the spatially nested structure of our sampling design (grids nested within sites). Regression diagnostics revealed a negative binomial distribution to be appropriate again (as in the main GLM analyses), with grids nested within sites, both coded as random effects, and \log_{10} -transformed total biomass as the fixed effect. This was achieved using the “glmmADMB” package in R (31). The predicted association from this regression is shown in Figure S1 below.

Assessing the diversity-productivity relationship at the spatial extent of sites:

A total of 28 sites were analyzed, keeping sampling grain fixed (1 m^2) with the number of sample quadrats ranging from 128 to 894 (Table S1). For these regressions we followed the methods of Adler et al. (1) as closely as possible. Specifically:

- (i) Scatterplots between species richness and productivity were inspected to flag potential violations of regression assumptions.
- (ii) Because species richness data comprises counts, we first modeled richness using a Poisson regression in a GLM framework. We used the “AER” package (32) in R to test whether the dispersion parameter differed significantly from the assumed value of 1 (either under- or over-dispersed). If it was, we used a quasi-GLM model to adjust the standard errors (33).
- (iii) For each regression, we fit species richness as both a linear and quadratic function of biomass, and inspected regression diagnostics including leverage values and residual plots.
- (iv) If the inclusion of the quadratic term did not result in a significant reduction in residual deviance (at $\alpha = 0.10$) then it was removed from the model. If the remaining single-term model was no better than the null (based on deviance), then the model was designated “not significant” (NS). These results were identical when we judged significance based on the coefficient estimate (not shown).

The results of these analyses are presented in Figure 2A, and in Table S2.

Assessing the richness-productivity relationship across different sampling grains:

Using the entire global dataset as the extent of analysis, we evaluated how the richness-productivity association varied across increasing sampling grain, from 1 m² to 64 m². For each of the 8 grain sizes, we equated richness with the number of unique species encountered in the given area, and productivity with the total biomass (live biomass+litter) across the area. Thus, in each regression analysis, each sampling grid provided one data point. Missing biomass values for 31 individual quadrats reduced the number of grids for some analyses. We used normal least-squares regression, as a Gaussian error distribution was found to be suitable. Examination of regression diagnostics also led us to eliminate 2 grids with high leverage (with low richness and extremely high biomass), though results were qualitatively identical otherwise. Thus, final sample sizes ranged between N = 133 and 149. For the first suite of 8 regressions, we used quadrats “grown” in size from one consistent corner of the grid. We then constructed three new regression models, each time using data from a different starting grid corner and thus orientation. Parameter estimates and coefficients of determination were averaged across the 4 orientations for each grain size. We used alpha = 0.05 throughout. The results of this analysis are presented in Figure S2, below.

Hierarchical Bayesian analyses of the boundary richness-productivity relationship:

We used a hierarchical Bayesian modeling approach, in which both the mean and variance of species richness were modeled nonlinearly against (log-transformed) biomass, and that included

Fraser et al. Productivity-diversity relationship

random effects to account for the nested spatial structure of the dataset. Posterior distributions for upper quantiles (envelope) of richness were calculated from normal distributions of estimated means and variances across the biomass gradient.

Because we expected nonlinear relationships for both the mean and variance of richness against biomass, we included quadratic expressions for the mean and variance of richness in the following way:

$$\text{Species richness}_i \sim N(\mu_i, \sigma_i^2)$$

$$\mu_i = \beta_0 + \beta_1 * \text{Biomass}_i + \beta_2 * \text{Biomass}_i^2 + N(0, \sigma_{study}^2) + N(0, \sigma_{grid}^2)$$

$$\sigma_i = \alpha_0 + \alpha_1 * \text{Biomass}_i + \alpha_2 * \text{Biomass}_i^2$$

where the richness of quadrat i is distributed normally with mean μ and variance σ^2 , and mean richness includes random intercept effects of study site and grid-within-study. To generate posteriors for an upper quantile, we used fitted mean and variance estimates to calculate the value of the 95th quantile for each MCMC iteration:

$$q95_i = \text{qnorm}(0.95, \text{mean}=\mu_i, \text{variance}=\sigma_i^2)$$

Models were fit via Markov chain Monte Carlo optimization as implemented in JAGS (34) run from R 3.03 (31) in the R2jags package (35). We ran three parallel MCMC chains for 10,000 iterations after a 500-iteration burn-in, and evaluated model convergence with the Gelman & Rubin statistic (36) such that chain results were indistinguishable. We used flat normal priors for β and α coefficients, with the exception of uniform positive priors for α_1 to ensure positive variance estimates.

Fraser et al. Productivity-diversity relationship

Fitted 95th quantiles and associated 95% credible intervals for biomass including litter are shown below (Fig. S3). Note that we did not attempt to include richness observations at extremely low (< 50 g; 0.7% of the data) or high biomass values (> 1500 g; 3% of the data, half of which were richness values of 1) due to low sample sizes that precluded envelope calculations.

Assessing the boundary richness-productivity relationship using maximum grid richness as the response, and employing quantile regression:

Using the global dataset as the extent of analysis, we quantified the upper boundary of the richness-productivity relationship using maximum richness observed in a grid (among the 1m² quadrats) as the response variable, and the total biomass associated with the quadrat of maximum richness as the predictor variable. We employed quantile regression, using the 95th percentile. For comparison, we include the results of a least-squares regression. The results of this analysis are presented below in Figure S4.

Examining the sensitivity of the richness-productivity relationship to biomass range, measures of productivity, and sample size:

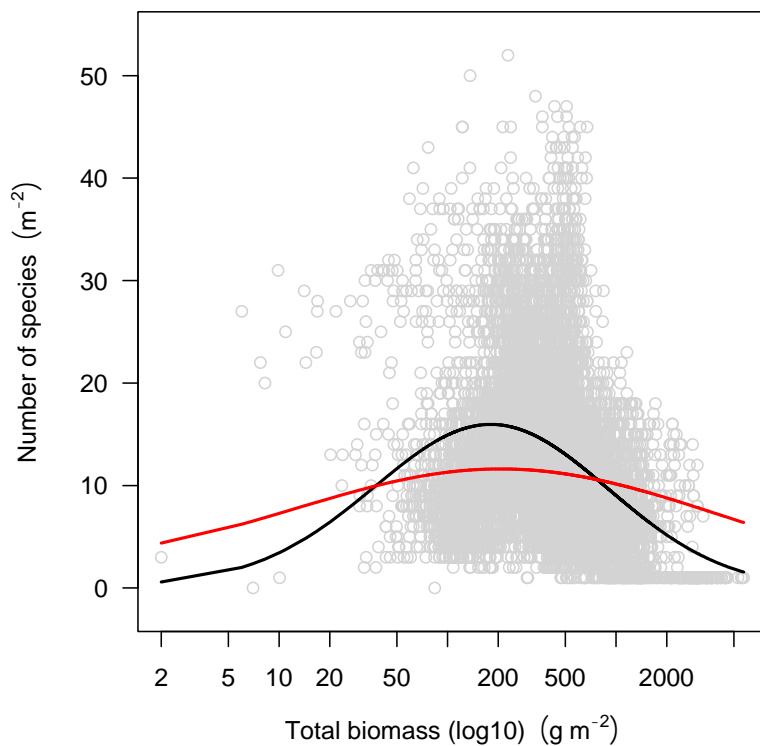
The goal of this suite of analyses was to mimic the properties of the dataset used by Adler et al. (1), and to re-analyze this subset of data using the same methods employed to produce Figure 2A. The details of the subsampling procedure are described in the main document, and the

Fraser et al. Productivity-diversity relationship

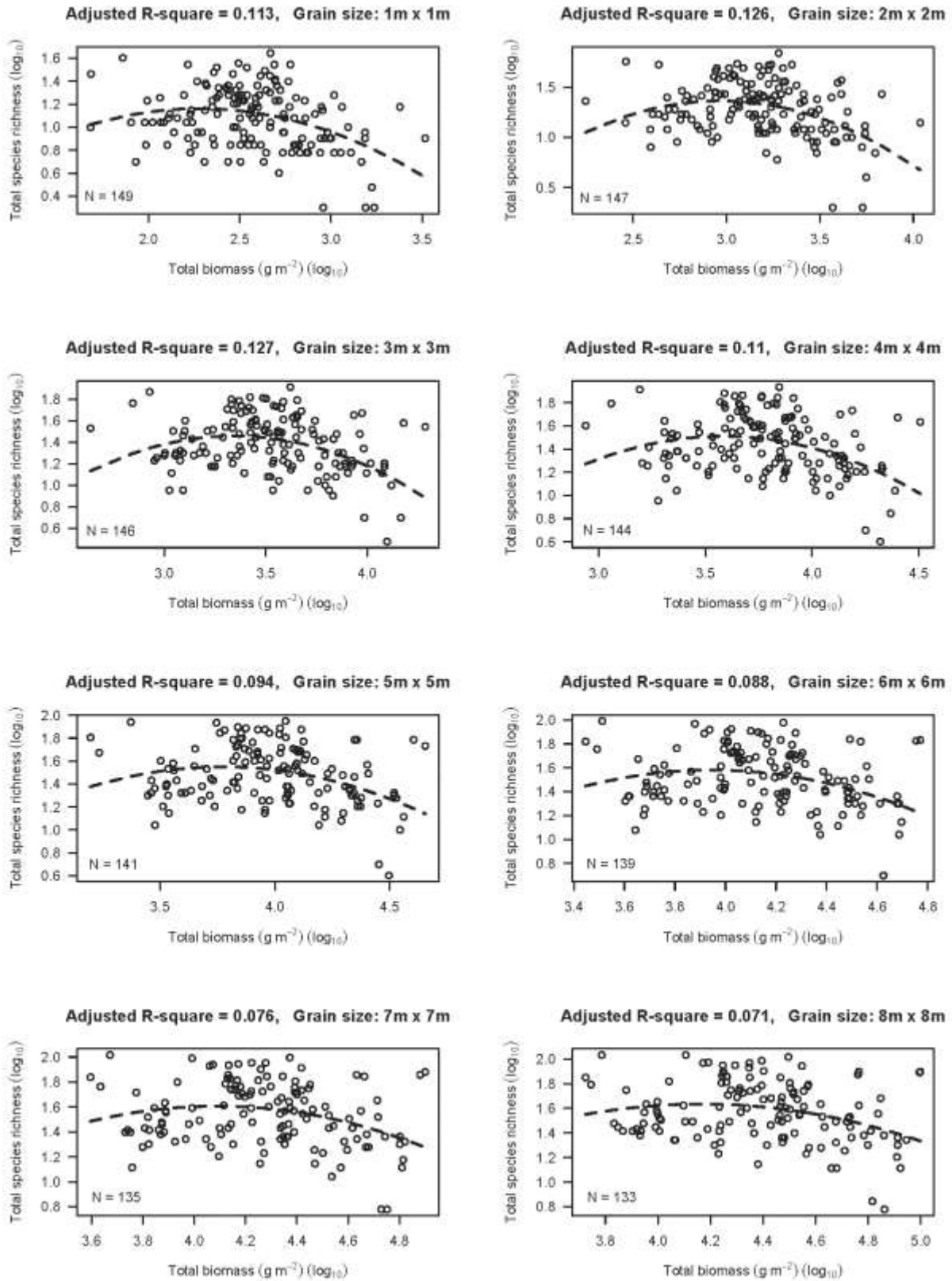
regression methods we used are identical to those described in section “C” above. For the GLM analysis conducted on each of the 500 random subsets of data (see main document), we calculated the proportion of the within-site regressions (out of 28 total) falling into each of the five categories of form. In Figure S5 below we show how these proportions compare to our observed proportions.

Lastly, for each iteration, we calculated the range of biomass encompassed by each site (based on its random sample of 30 quadrats). We then calculated the average of these biomass ranges across the 28 site-level analyses, for each iteration. Figure S6 below shows a histogram of the resulting 500 average biomass ranges, along with the average biomass range encompassed by the 48 site-level analyses of Adler et al. (data kindly provided by Jim Grace, and is housed at the Nutrient Network website: <http://nutnet.umn.edu/data>).

Supplementary Figures

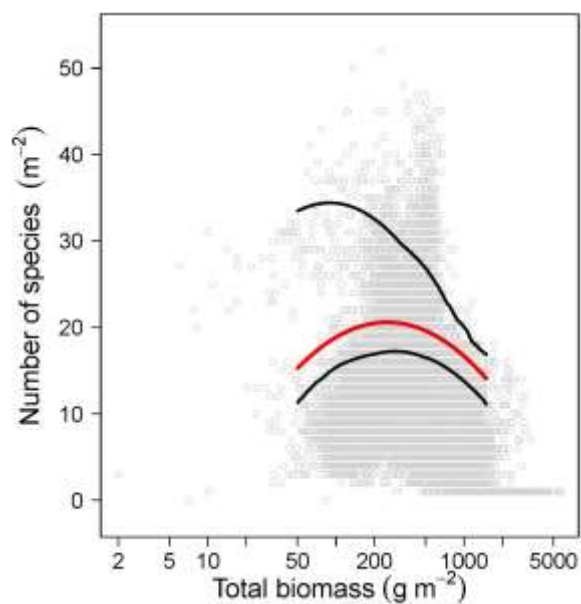


Supplementary Figure 1: The unimodal productivity-richness relationship. Superimposed over the individual quadrat values (light grey points; $N = 9631$) are the regression lines from the negative binomial GLM (black line; see Table 1) and the negative binomial GLMM in red (population level prediction), in which grids ($N = 151$) are nested within sites ($N = 28$), both as random effects (Log-likelihood = -23097.9; quadratic term coefficient = -0.29, Z -value = -10.4, $P < 0.001$).

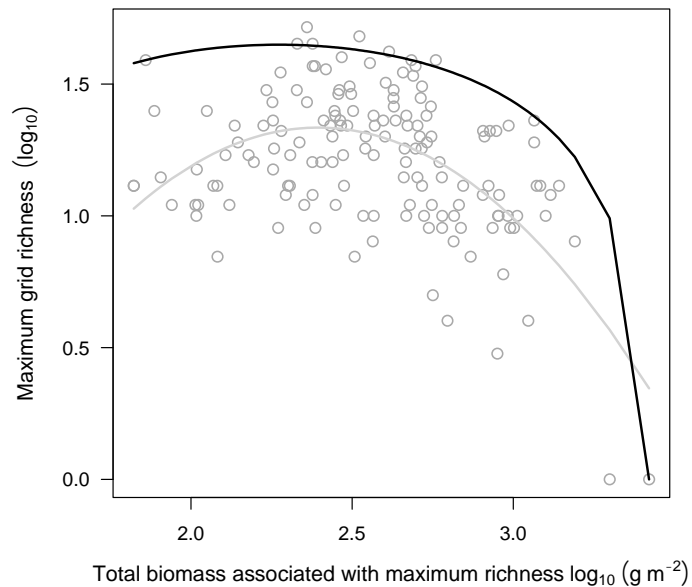


Supplementary Figure 2: Biomass-species richness relationship as it relates to scale.

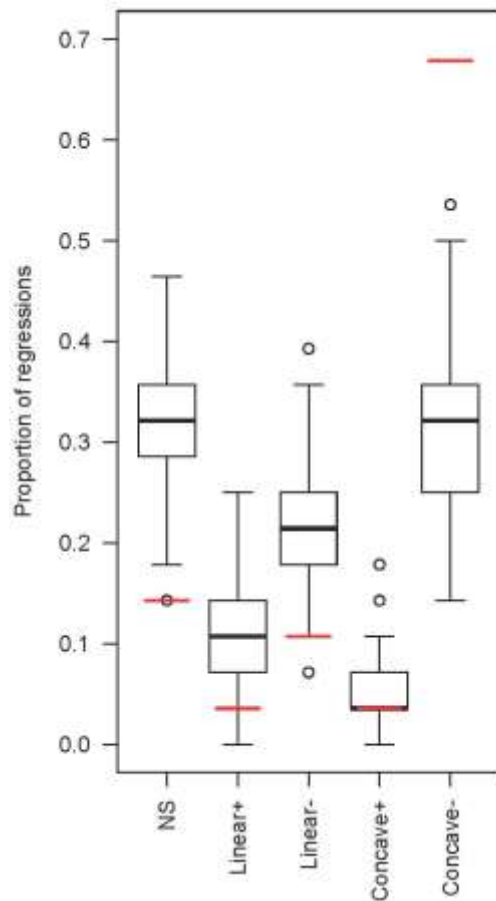
Varying the sampling grain (maintaining global extent) does not change the general form of the relationship between species richness and biomass, though the amount of variation accounted for by the model (see adjusted R^2 values) generally decreases with increasing grain. At every scale, the quadratic term was significant ($P < 0.05$). Dashed lines indicate the least-squares regression.



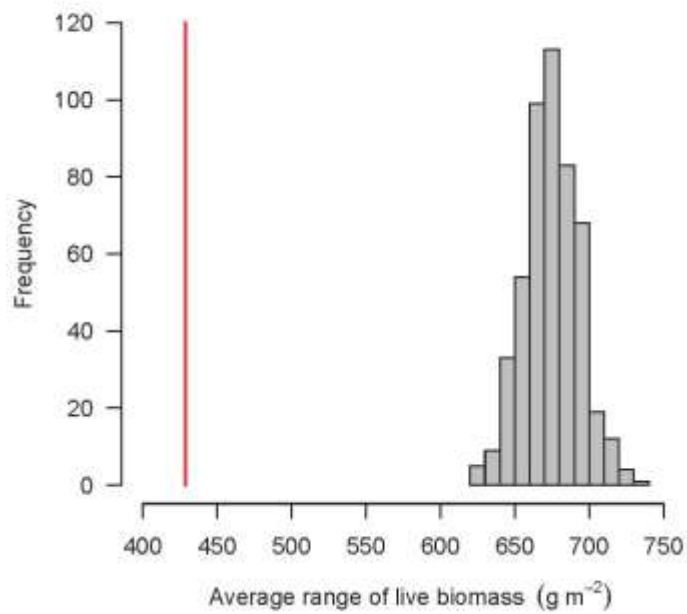
Supplementary Figure 3: Bayesian model results. Posteriors of the 95th quantile of species richness along a biomass gradient (mean and 95% credible intervals) from the Bayesian models.



Supplementary Figure 4: Estimating the upper boundary of richness in relation to productivity. Individual points show the maximum richness observed among 1 m² quadrats within a grid (N = 151 grids) paired with its associated total biomass. The solid black line represents the 95th percentile quantile regression that determines the boundary condition (quadratic term coefficient = -37.77, SE = 13.36, P = 0.005; pseudo R² = 0.14). The grey line represents the least-squares regression that includes a highly significant quadratic term (quadratic term coefficient = -0.94, SE = 0.14, P < 0.001; adjusted R² = 0.33). Excluding the two points with zero richness (bottom right) did not affect the significance of the quadratic term in either regression, though for the least-squares regression the adjusted R² was reduced to 0.16.



Supplementary Figure 5: Proportion of the 28 GLM regressions within study regions that correspond to the different forms. Each box includes $N = 500$ proportions, derived from the analyses of the 500 random subsets of data. The red lines correspond to our observed proportions (see inset of Figure 2A in main document). Our observed proportions differed significantly from those expected, based on the subsampled data ($\chi^2 = 11.54$; $P = 0.009$). None of the 500 analyses yielded proportions of “concave down” relationships as large as our observed proportion.



Supplementary Figure 6: Histogram of the average biomass range observed within each of the 500 iterations of site-level analyses. For comparison, the red line shows the average biomass range (428.7 gm⁻²) encompassed by the 48 site-level analyses of Adler et al. (1).

Supplementary Tables

Supplementary Table 1: Herbaceous Diversity Network sites. Grassland type is separated into 5 categories (Temp = temperate; Wet = temperate wet meadow; Med = Mediterranean; Trop = tropical and subtropical; and Alpine), with numbers in parentheses indicating number of grids within each grassland type. A grid represents one 8 x 8 m² sampling area. Coordinates are provided in decimal degrees, and use the WGS84 datum.

Region	Country	Grassland type	Number of grids	Centroid longitude	Centroid latitude	Mean total biomass (gm ⁻²)	SD total biomass (gm ⁻²)	Mean species richness (m ⁻²)	SD species richness (m ⁻²)
1	Hungary	Temp	4	20.1885	46.6159	358.8	267.15	11.7	6.39
2	Germany	Temp	6	11.5636	49.9169	412.7	305.22	13.9	8.92
3	Mongolia	Temp (2) / Wet (4)	6	105.0168	48.8515	317.8	111.90	14.7	4.51
4	Canada	Temp	6	-111.9590	50.8912	473.7	317.65	7.6	1.94
5	Canada	Temp	6	-111.5615	53.0848	293.9	159.08	13.2	4.33
6	USA	Med	2	-117.1685	32.8839	314.2	121.90	7.7	1.62

Fraser et al. Productivity-diversity relationship

Region	Country	Grassland type	Number of grids	Centroid longitude	Centroid latitude	Mean total biomass (gm ⁻²)	SD total biomass (gm ⁻²)	Mean species richness (m ⁻²)	SD species richness (m ⁻²)
7	Romania	Alpine	4	25.9518	46.4089	495.1	87.18	31.8	6.94
8	Argentina	Temp	4	-64.4257	-31.1287	959.5	779.13	20.3	7.49
9	Brazil	Trop	4	-47.8668	-17.9540	781.9	318.12	8.8	5.95
10	USA	Temp	4	-95.1912	39.0575	515.6	268.09	12.2	6.79
11	Canada	Temp (12) / Wet (2)	14	-120.5730	50.9167	489.4	459.69	7.8	2.68
12	Canada	Temp	2	-81.3175	43.1930	390.8	84.79	5.4	1.44
13	Hungary	Temp	4	17.7028	47.1466	494	82.09	22.4	3.90
14	Austria	Alpine	6	10.7048	47.1456	324.9	112.83	25.0	7.35
15	Iran	Med (6) / Alpine (5)	11	50.9557	36.8583	431.4	291.03	12.0	4.32
16	China	Alpine	4	102.7787	37.2012	308.2	179.09	15.3	3.34
17	UK	Temp	4	-1.6837	55.2172	568.4	355.13	10.9	2.05

Fraser et al. Productivity-diversity relationship

Region	Country	Grassland type	Number of grids	Centroid longitude	Centroid latitude	Mean total biomass (gm ⁻²)	SD total biomass (gm ⁻²)	Mean species richness (m ⁻²)	SD species richness (m ⁻²)
18	USA	Temp (4) / Wet (2)	6	-81.6034	41.3593	1592.7	1173.77	2.8	2.58
19	Iran	Temp	6	59.0169	36.8936	300.7	184.50	7.0	1.94
20	Brazil	Trop	2	-51.6823	-30.1011	215.8	53.01	27.6	5.87
21	Canada	Alpine	4	-119.4263	50.0118	280.7	161.03	14.0	3.30
22	Kenya	Trop	6	36.8911	0.3882	812.8	451.06	6.0	3.61
23*	Israel	Med	6	35.5334	32.5213	288.2	169.03	16.7	8.32
24	Japan	Temp (4) / Wet (2)	6	140.9299	41.0162	545.5	282.98	8.7	4.02
25*	Canada	Temp	2	-110.4423	49.0361	105.3	37.15	8.1	2.47
26*	Mongolia	Temp	4	106.9060	49.0153	282.3	94.80	16.1	3.74
27	South Africa	Temp	6	29.4935	-25.6213	533.4	327.50	8.0	3.24
28	Italy	Alpine	6	13.0179	42.9542	365.3	120.93	19.9	4.92

Fraser et al. Productivity-diversity relationship

Region	Country	Grassland type	Number of grids	Centroid longitude	Centroid latitude	Mean total biomass (gm ⁻²)	SD total biomass (gm ⁻²)	Mean species richness (m ⁻²)	SD species richness (m ⁻²)
29	New Zealand	Temp	2	170.6227	-45.6794	1277	189.75	8.7	1.92
30	Estonia	Temp	10	24.7988	58.4634	479	344.14	19.1	8.32

* plant litter was not collected at these sites, so these were excluded from total biomass analyses, but included in live biomass analyses.

Supplementary Table 2: Regression coefficients from the GLM analyses (Poisson or quasi-Poisson approach) of the relationship between total biomass and species richness.

Regressions were conducted at the study site extent (28 sites, site numbers corresponding to those in Table S1). All coefficients are significant at $P < 0.001$, except as follows: ** $P < 0.01$; * $P < 0.05$. “NA” = not available. Forms are “CD” concave down; “NEG” negative linear; “POS” positive linear, and “NS” not significant.

Site	N	Linear term		Quadratic term		% Deviance explained	Form
		Coefficient	SE	Coefficient	SE		
1	256	6.03	1.258	-0.98	0.259	71.6	CD
2	373	3.03	0.304	-0.95	0.072	68.7	CD
3	382	17.25	2.538	-3.77	0.516	43.6	CD
4	384	-0.51	0.029	NA	NA	45.5	NEG
5	383	10.66	1.434	-2.28	0.3	16	CD
6	128	NA	NA	NA	NA	1.6	NS
7	253	33.07	8.824	-6.04	1.648	12.1	CD
8	256	1.8*	0.79	-0.49	0.138	76	CD
9	256	24.24	6.409	-3.88	1.106	23.3	CD
10	256	6.65**	2.422	-1.64	0.466	46.2	CD
11	894	3.78	0.416	-0.77	0.082	11.1	CD
12	128	NA	NA	NA	NA	2	NS
13	256	NA	NA	NA	NA	0.9	NS
14	382	0.2**	0.096	NA	NA	1.1	POS
15	704	2.45	0.549	-0.43	0.11	9.7	CD
16	256	3.79	0.736	-0.85	0.156	18.7	CD
17	256	1.18	0.56	-0.29**	0.107	37.5	CD
18	384	-2.39	0.128	NA	NA	54.2	NEG
19	380	-0.27	0.038	NA	NA	11.4	NEG
20	128	4.2	2.125	-1.07*	0.475	13.2	CD
21	256	5.33	1.337	-1.1	0.277	6.1	CD
22	382	3.89**	1.376	-0.72**	0.252	3.8	CD
23	384	5.94	0.76	-1.49	0.173	34.9	CD

Fraser et al. Productivity-diversity relationship

24	378	12.45	1.667	-2.29	0.318	22.7	CD
25	384	6.04	0.852	-1.36	0.171	46.9	CD
26	384	-11.67	1.993	2.39	0.391	15.2	CU
27	128	NA	NA	NA	NA	1.6	NS
28	640	9.45	1.023	-2.15	0.193	76.2	CD

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Fraser et al. Productivity-diversity relationship

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