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

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Title: Worldwide Evidence of the Unimodal Relationship Between Productivity and Plant Species Richness

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One Sentence Summary: Empirical evidence from grasslands around the world demonstrates a humped-back relationship between plant species richness and biomass at the 1 m² plot scale.

Abstract: One of the central problems of ecology is the prediction of species diversity. The humped-back model (HBM) suggests that plant diversity is highest at intermediate levels of productivity; at low productivity few species can tolerate the environmental stresses and at high productivity a small number of highly competitive species dominate. A recent study claims to have comprehensively refuted the HBM. Here we show, using the largest, most geographically diverse dataset ever compiled and specifically built for testing this model that if the conditions are met, namely a wide range in biomass at the 1 m² plot level and the inclusion of plant litter, the relationship between plant biomass and species richness is hump shaped, supporting the HBM. Our findings shed new light on the prediction of plant diversity in grasslands, which is crucial for supporting management practices for effective conservation of biodiversity.

Main Text: The relationship between plant diversity and productivity is a topic of intense debate (1-6). The HBM states that plant species richness peaks at intermediate productivity, taking above-ground biomass as a proxy for annual net primary productivity (ANPP) (7-9). This diversity peak is driven by two opposing processes; in unproductive and disturbed ecosystems where there is low plant biomass, species richness is limited by either stress, such as insufficient water and mineral nutrients, or high levels of disturbance-induced removal of biomass, which few species are able to tolerate. In contrast, in the low disturbance and productive conditions that generate high plant biomass it is competitive exclusion by a small number of highly competitive species that is hypothesized to constrain species richness (7-9). Other mechanisms proposed to explain the unimodal relationship between species richness and productivity include disturbance (10), evolutionary history and dispersal limitation (11,12), and density limitation affected by plant size (13).

Different case studies have supported or rejected the HBM, and three separate meta-analyses reached different conclusions (14). This inconsistency may indicate a lack of generality of the HBM, or it may reflect a sensitivity to study characteristics including the type(s) of plant communities considered, the taxonomic scope, the length of the gradient sampled, the spatial grain and extent of analyses (14,15), and the particular measure of net primary productivity (16). Although others would argue (6), we maintain that the question remains 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 novel data from a globally-coordinated (17), distributed, scale-standardized and consistently designed survey, in which plant richness and biomass were measured in grasslands. This was replicated at 30 sites in 19 countries across 6 continents (Fig. 1). We sampled 64 square-meter quadrats within 8 m x 8 m grids (details in Supplemental Materials and Methods section and Fraser *et al.* (15)). At each site at least two, and as many as 14, grids were sampled resulting in 128 to 896 quadrats per site. Collectively, our samples spanned a broad range of biomass production (2 to 5,711 g m⁻²) and a variety of grassland community types, including natural and managed (pastures, meadows) grasslands over a broad range of climatic zones (from temperate to Mediterranean to tropical), and altitudes (lowland to alpine) (Appendix S1). In each square meter quadrat, we identified and counted all plant species, and harvested above-ground biomass and plant litter. Litter production is generally 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 (18,19), thus contributing to competitive exclusion quite as much as live plants. Indeed, the HBM was originally defined in terms of live plus litter material (7,8). In addition, plant litter provides clues to site disturbance history, such as grazing and fire in grasslands (20). The majority of the sites we sampled were subject to some form of management, usually livestock grazing or mowing. In this respect, our sites are representative of the vast majority 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 measures constitutes a reliable measure of annual net aboveground production in herbaceous plant communities (21).

Our results support the humped-back model of the richness-productivity relationship. As in the original HBM, the overall association takes the form of a unimodal relationship (across all sites, and using each square-meter quadrat as an observational unit; $N = 9,016$), which is characterized by a statistically significant concave-down quadratic regression (negative binomial generalized linear model) and a significant concave-down quantile regression (95% quantile; Fig. 2a). Of the 28 study sites, 17 are concave down, 3 are positive, 7 are negative, and one is concave up.

Why do our data support the HBM while those of Adler et al. (1), or related studies (4,6), do not? We examined this question by sub-sampling our data to mimic the data used by Adler et al. Specifically, (1) we restricted our dataset to the same maximum biomass as observed by Adler et al. ($1,535 \text{ gm}^{-2}$), (2) we excluded litter from the calculation of biomass, and (3) we reduced the sample size to 30 quadrats per site. Although the general relationship is concave-down, the analyses by site shows inconsistent patterns between species richness and biomass (Fig. 2b), with as many linear negative (10) as concave-down (10) relationships, as well as 7 linear positive and 1 concave up. We also determined whether sites that span a larger range in productivity are more likely to display a unimodal relationship. Out of 500 sub-sampling iterations (each with 30 randomly selected quadrats per site), in 425 (85%) of them the mean biomass range (in log space) was the largest for the concave-down relationship, which suggests

that the range in productivity, measured as above-ground biomass and plant litter, influences the form of the relationship.

The HBM predicts a boundary condition. To test this prediction, we identified the highest species richness quadrat from each site, and related this value to the matching quadrat biomass using a quantile regression (Fig. 3). The relationship is concave-down and accounts for ca 35% of the variation. The quantile regression maps a clear boundary condition such that there are no plots in which high biomass sites contain high species richness, and it is rare to find low biomass sites with high species richness.

It has been suggested (2) that some previous studies, including the most prominent of recent studies (1), failed to support the HBM because they had excluded litter. Indeed, using only live plant material in the biomass estimates yielded weaker regression models across all sampling grains, with some relationships being non-significant (i.e. a flat, null relationship). It has also been suggested that previous surveys failed to properly represent high-productivity communities. Indeed, our high-biomass plots (981 samples were over 1,000 g m⁻², approximately 11% of the 9,016 samples; maximum 5,711 g/m²), contributed considerably to the right-hand part of the fitted humped-back regression; this could be one explanation why the dataset of Adler et al. (1) (which contained only 0.5% of samples over 1,000 g /m² and a maximum of 1,534 g m⁻²) failed to support the HBM. Our results therefore show that a robust test of the HBM in herbaceous plant communities yields the expected pattern; yet, it should

include an adequate range in biomass production (from 1 to at least 3,000 dry g m⁻² yr⁻¹), with wide representation along the range.

We have demonstrated that there is a general concave-down unimodal pattern in the form of the biomass-richness relationship for herbaceous grassland communities, and that it can be applied across geographic areas. However, there is a limitation to simply identifying a pattern without understanding the underlying processes, and more work is needed to determine those causal mechanisms (1,6,14,15). We found no reason to discard the theory, but we think that Adler et al. (1) made a very good point that we can agree with: that much more work is needed to understand the multivariate drivers of species richness. It is important to recognize that productivity in our study and many others explains a fairly low proportion of the overall variance in richness. There are clearly many other drivers of richness than productivity. So it is not only important to determine the causal mechanisms of the unimodal curve but important also to understand mechanisms driving richness in general – including those that are associated with productivity and those that are not.

Competitive exclusion has been cited as the primary factor driving low species numbers at high plant biomass (7,8). However, in the case of nitrogen addition the negative relationship between productivity and species richness has been shown to diminish over time (22). It may be that low species richness in high-productivity conditions is partly because most such habitats are human-induced, and there are few species in the local pool adapted to these conditions. If

so, it is possible that further species will eventually immigrate from distant pools, so that the right-hand part of the hump will then flatten out.

Owing to its global extent and regional representation, our study provides a strong foundation for further research into the local, landscape, and regional/historical factors that ensure the maintenance of biodiversity. Grasslands serve as ideal model ecosystems for biodiversity research, and here yielded results that are of general relevance. Worldwide, humans affect grasslands via disturbance, altering productivity, and through land use changes, all of which are among the most influential drivers of global biodiversity declines. Since productivity varies in response to disturbance such as grazing and burning, a better understanding of how productivity moderates plant species richness is essential to tailoring management practices for effective conservation of biodiversity, target species and ecological restoration. On a landscape scale, conserving biodiversity in order to retain ecosystem services is a major goal, and an understanding of what combination of conditions will promote high levels of species richness is fundamental to making correct management decisions.

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FIGURE LEGENDS

Figure 1. Site locations. Approximate locations of 157 grids at 30 sites, 19 countries and 6 continents. Additional site details are provided in Appendix S1.

Figure 2. a) Biomass-species richness relationships for 28 sites. Solid black line: significant quantile regression (95%) of overall relationship (N=9,016 quadrats). Dashed black line: significant negative binomial GLM (N=9,016). Colored lines indicate significant GLM regressions (Poisson or quasi-Poisson). b) same as (a) but the data presented is a sub-sample of the complete dataset, with litter removed, plots with greater than 1,500 gm⁻² excluded, and only 30 plots per site included to reflect the data used by Adler et al.

Figure 3: Maximum richness of 1 m² plot within each 64 quadrat grid (N=141 grids) as a function of the matching plot total biomass among quadrats. The red line represents the least-squares regression that includes a highly significant quadratic term. The black line represents the quantile regression that determines the boundary condition.

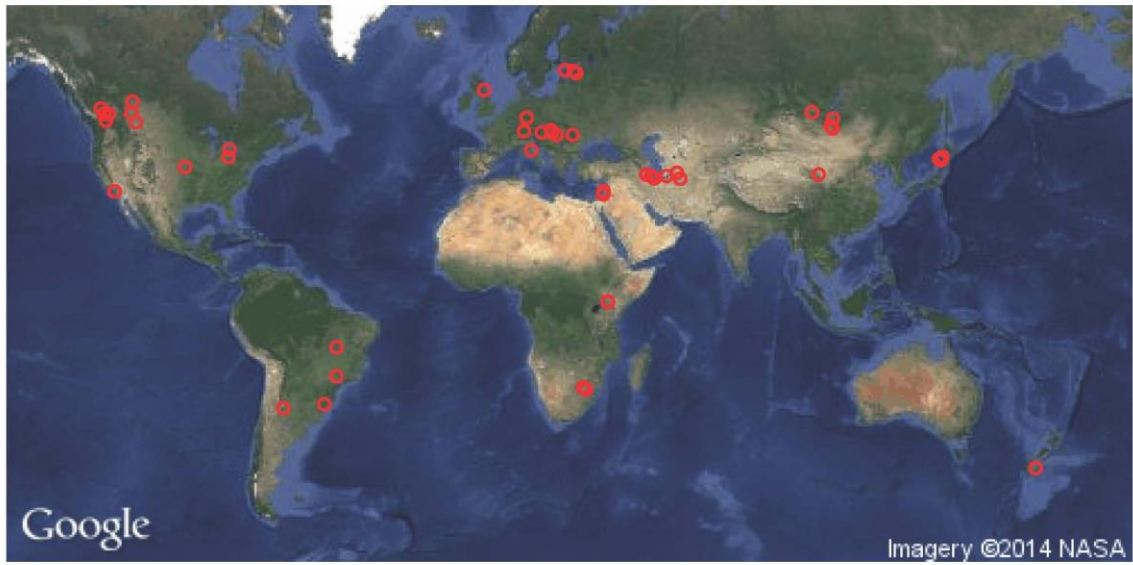


Figure 1

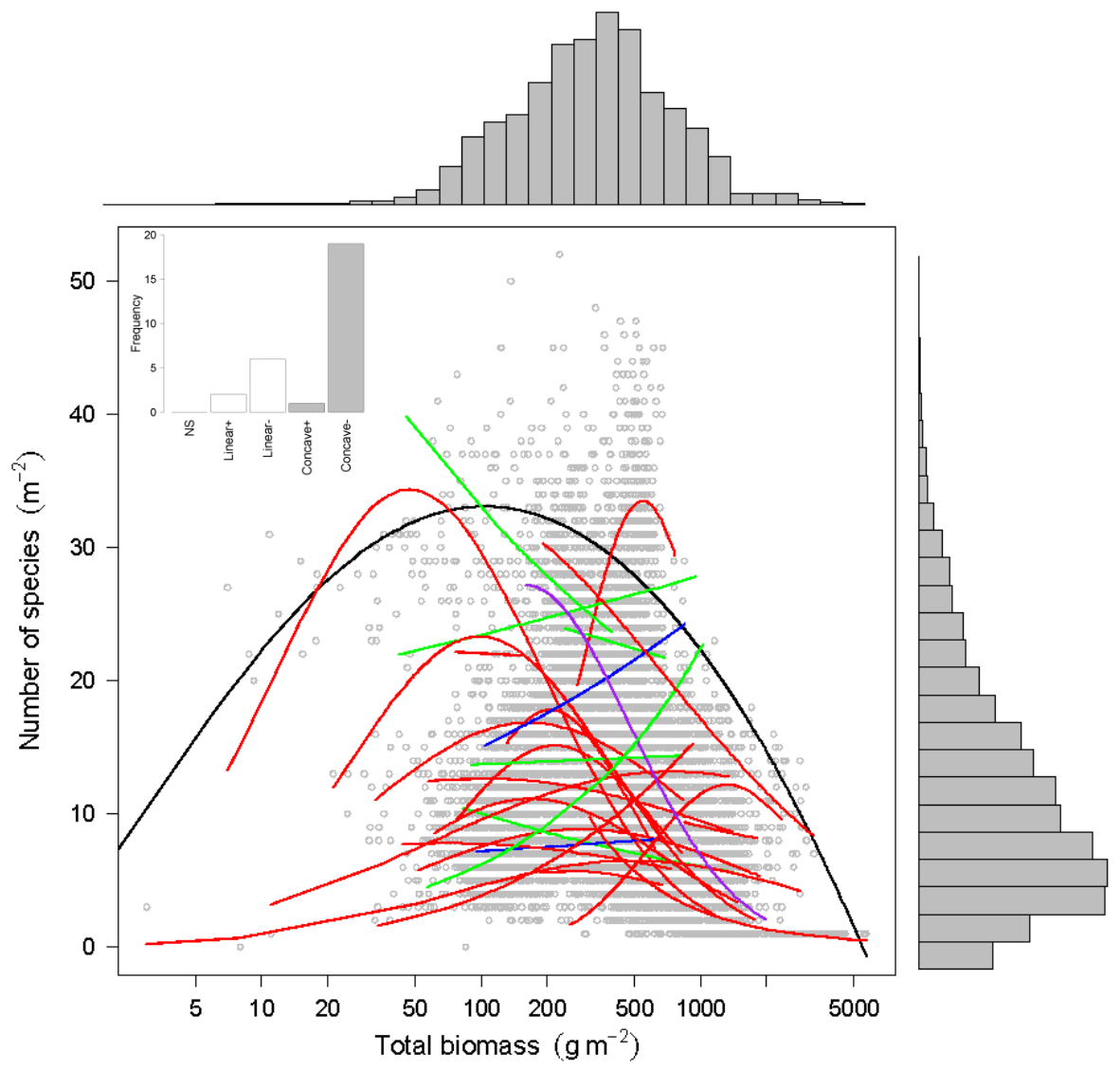


Figure 2a

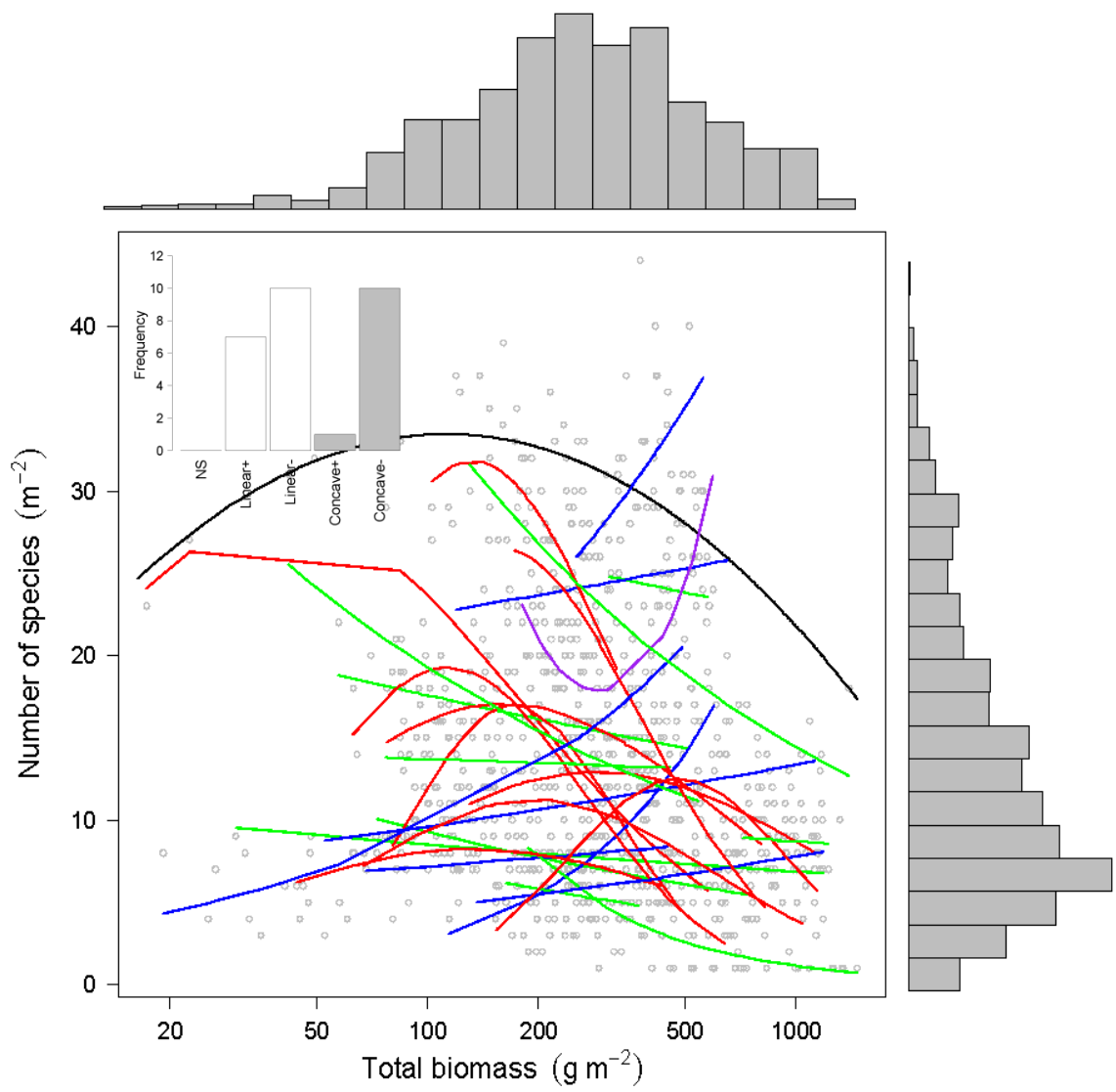


Figure 2b

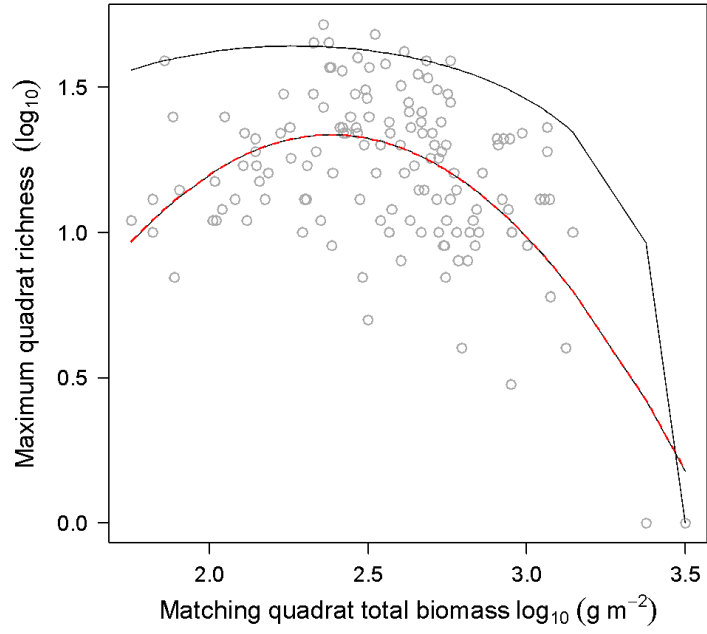


Figure 3

Supplementary Materials:

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 observations¹⁷. The full sampling design is detailed here and in ¹⁵. 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. All 29 sites included in the current analysis (Fig. 1) 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 recorded for future testing and monitoring. Our study focused on grassland herbaceous community types. For each 1 m² plot, the number of species were identified and counted. Total above-ground biomass (including plant litter) at peak biomass was harvested dried and weighed by plot. Live biomass and litter was 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. When a woody plant was encountered the species was identified and added to species list and the height and canopy spread was measured. Cryptogams were not counted in the species richness nor were they included in the harvest for biomass.

The ideal level of participation for each investigator was to sample at least six grids, 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 ($>800\text{ g m}^{-2}$). Most sites had a history of grazing or fire and were currently under some form of management. Therefore, sampling was done at least three months after it was last grazed or burned.

Statistical analyses.

(1) Spatial autocorrelation

Using the R packages “*pgirmess*” and “*spdep*”, we determined whether richness and / or productivity exhibited evidence of significant autocorrelation within grids by examining Moran’s I values across inter-quadrat distances classes. We found evidence of significantly positive autocorrelation at distances of less than 2.8 m for both richness and biomass (Fig. S1). Thus, in subsequent analyses that use individual 1 m^2 quadrats as the observational grain size / unit of measurement, we used a more stringent alpha level of 0.01 (see Dale, M.R.T. & Fortin, M-J. 2002. Spatial autocorrelation and statistical tests in ecology. *Ecoscience* **9**: 162-167).

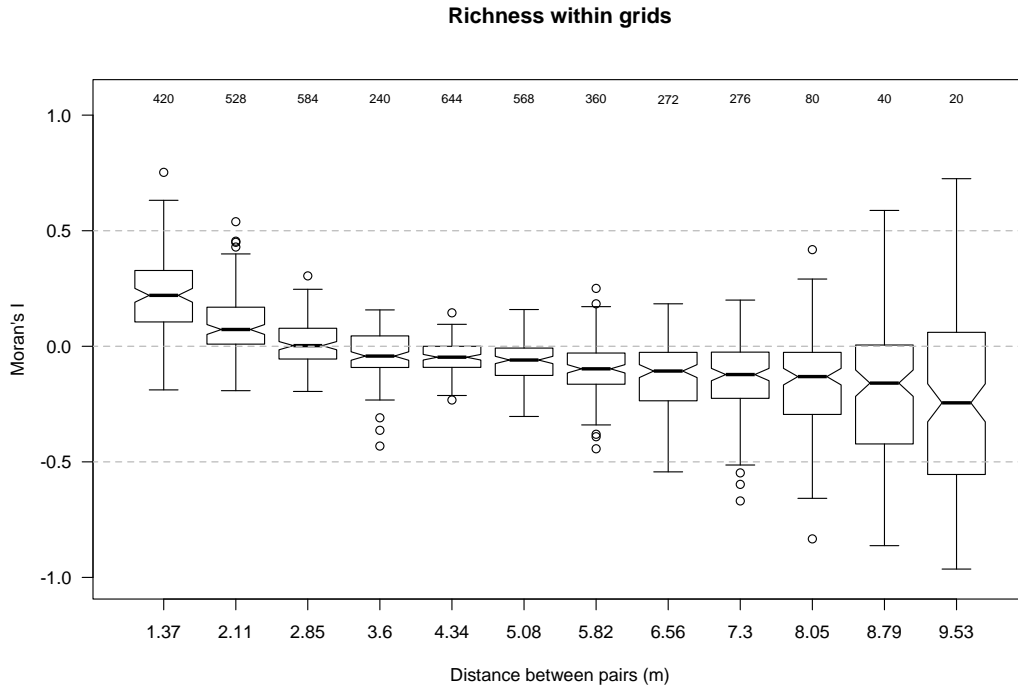


Fig. S1a: Moran's I values for richness variation among quadrats within 8x8 m grids.

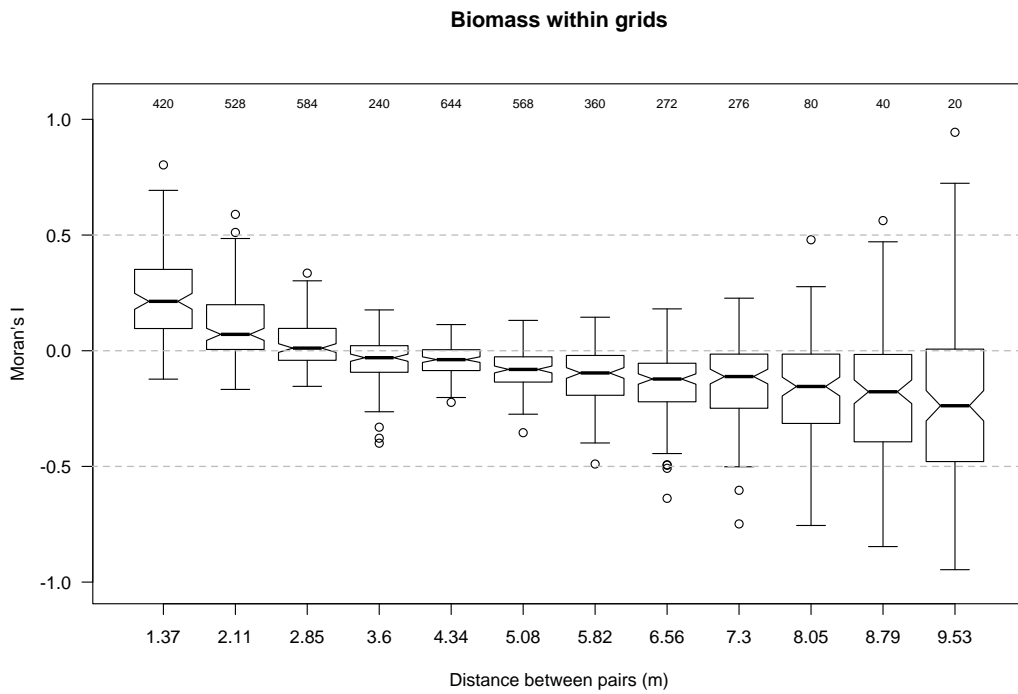


Fig. S1b: Moran's I values for total biomass variation among quadrats within 8x8 m grids.

(2) Regression analyses

(A) The richness-productivity relationship across different extents

We explored the form and strength of the richness-productivity relationship across the following different organizational extents, in every case using the 1 m² quadrat as the observational grain: (i) the entire global dataset; (ii) within geographic study areas used by each investigator (Total of 28 regressions; N varying from 128 to 896); and, (iii) using a subset of the entire global dataset (no plots with greater than 1,500 g m⁻², litter removed from biomass, and a random sample of 30 plots per site [equivalent to principal investigator]).

(B) The richness-productivity relationship at grid focus

Using the global dataset as the extent of analysis, we examined the richness-productivity relationship using the sample grid as the “focus”, with maximum plot richness and associated plot biomass as the response and predictor variables, respectively.

For all regression analyses the following procedure was followed.

1. Scatterplots between richness and productivity were inspected to flag potential violations of regression assumptions.
2. Because richness comprises counts, we first modeled richness using a Poisson regression in a GLM framework. We used the “AER” package in R to test whether the dispersion parameter differed significantly from the assumed value of 1 (either under- or over-dispersed). If so, we re-implemented the regression using the quasi-Poisson approach.

3. For each regression, we fit richness as both a linear and quadratic function of biomass, and inspected regression diagnostics including leverage values and residual plots.

4. If the quadratic term was not significant at $\alpha = 0.05$ (or 0.01 when all quadrats were used), then it was dropped. If the remaining linear term was also non-significant, then the model was designated “not significant” (NS).

We repeated all of the above analyses using quantile regression, using quantiles 0.95, 0.9, and 0.8. We implemented quantile regressions using the “quantreg” package in R.

Finally, we repeated all of the above analyses using only live biomass.

Appendix S1: 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 “No. of Grids” representing each grassland type. “No. of Grids” indicates the number of 64 m² sampling grids at each site. “*” indicates that no plant litter was collected at these sites, thus these sites were excluded from total biomass analyses, but included in live biomass analyses.

Site #	Country	Continent	Grassland type	Lat.	Long.	No. of Grids	Mean plot mass (g m ⁻²)	Mean plot richness (m ⁻²)
1	Canada	N Amer.	Temp(12)/Wet(2)	50.760	-120.435	14	488.9	7.8
2	Germany	Europe	Temp	49.902	11.575	6	410.1	13.9
3	Mongolia	Asia	Temp(2)/Wet(4)	51.023	100.765	10	304.1	15.3
4	Canada	N Amer.	Temp	50.873	-111.929	6	473.7	7.6
5	Canada	N Amer.	Temp	53.084	-111.564	6	293.8	13.2
6	USA	N Amer.	Med	32.892	-117.09	2	314.3	14.3
7	Romania	Europe	Alpine	46.409	25.949	4	494.6	31.8

8	Brazil	S Amer.	Trop	-13.673	-47.848	4	781.9	8.8
9	USA	N Amer.	Temp	39.058	-95.191	4	515.6	12.2
10	Iran	Asia	Med(6)/Alpine(5)	37.177	48.951	11	431.4	12.0
11	Canada	N Amer.	Temp	43.193	-81.317	2	390.8	5.4
12	Hungary	Europe	Temp	46.893	16.247	4	494.0	22.4
13	Austria	Europe	Alpine	47.146	10.698	6	324.8	25.0
14	China	Asia	Alpine	37.207	102.773	4	308.2	15.3
15	UK	Europe	Temp	55.218	-1.684	4	568.4	10.9
16	USA	N Amer.	Temp(4)/Wet(2)	41.359	-81.603	6	1592.7	2.8
17	Iran	Asia	Temp	36.149	59.536	6	298.9	7.0
18	Brazil	S Amer.	Trop	-30.101	-51.681	2	215.8	27.6
19	Canada	N Amer.	Alpine	49.358	-119.917	4	280.7	14.0
20	Kenya	Africa	Trop	0.281	36.865	6	812.8	6.0
21	Israel	Asia	Med	32.091	35.471	6	288.2	16.7
22	Japan	Asia	Temp(4)/Wet(2)	40.670	140.949	6	550.3	8.7
23*	Canada	N Amer	Temp	49.049	-110.441	2	105.3	8.1
24	South Africa	Africa	Temp	-26.005	30.078	6	533.4	8.0

25	Italy	Europe	Alpine	42.954	13.017	6	365.3	19.9
26	New Zealand	Australia	Temp	-45.680	170.623	2	1238.0	8.7
27	Estonia	Europe	Temp	58.579	23.557	10	479.0	19.1
28	Hungary	Europe	Temp	46.875	19.398	4	358.8	11.7
29	Argentina	S Amer.	Temp	-31.127	-64.426	4	959.5	20.3
30*	Mongolia	Asia	Temp	49.772	107.278	4	282.3	16.1