

Title

Comment on “Worldwide evidence of a unimodal relationship between productivity and plant species richness”

Authors

Andrew T. Tredennick^{1*†}, Peter B. Adler^{1†}, James B. Grace^{2†}, W. Stanley Harpole^{3†}, Elizabeth T. Borer^{4†}, Eric W. Seabloom^{4†}, T. Michael Anderson⁵, Jonathan D. Bakker⁶, Lori A. Biederman⁷, Cynthia S. Brown⁸, Yvonne M. Buckley⁹, Chengjin Chu¹⁰, Scott Collins¹¹, Michael J. Crawley¹², Philip A. Fay¹³, Jennifer Firn¹⁴, Daniel S. Gruner¹⁵, Nicole Hagenah¹⁶, Yann Hautier¹⁷, Andy Hector¹⁸, Helmut Hillebrand¹⁹, Kevin Kirkman²⁰, Johannes M. H. Knops²¹, Ramesh Laungani²², Eric M. Lind⁴, Andrew S. MacDougall²³, Rebecca L. McCulley²⁴, Charles E. Mitchell²⁵, Joslin L Moore²⁶, John W. Morgan²⁷, John L. Orrock²⁸, Pablo L. Peri²⁹, Suzanne M. Prober³⁰, Anita C. Risch³¹, Martin Schütz³¹, Karina L. Speziale³², Rachel J. Standish³³, Lauren L. Sullivan⁴, Glenda M. Wardle³⁴, Ryan J. Williams³⁵, Louie H. Yang³⁶

Affiliations

¹Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main, Logan, UT 84322 USA.

²U.S. Geological Survey, Wetland and Aquatic Research Center, 700 Cajundome Boulevard, Lafayette, LA 70506, USA.

³Department of Physiological Diversity, Helmholtz Center for Environmental Research – UFZ, Permoserstr. 15, 04318 Leipzig, Germany.

⁴Department of Ecology, Evolution, and Behavior, University of Minnesota, St Paul, Minnesota 55108, USA.

⁵Department of Biology, Wake Forest University, Box 7325 Reynolda Station, Winston-Salem, NC, 27109, USA.

⁶School of Environmental and Forest Sciences, University of Washington, 3501 NE 41st St, Box 354115, Seattle, WA 98195 USA.

⁷Ecology, Evolution and Organismal Biology, Iowa State University, 251 Bessey Hall, Ames Iowa 50010, USA.

⁸Department of Bioagricultural Sciences and Pest Management, Colorado State University, 307 University Ave., Fort Collins, CO 80523 USA.

⁹School of Natural Sciences, Trinity College Dublin, University of Dublin, Zoology, Dublin 2, Ireland.

¹⁰School of Life Sciences, Sun Yat-sen University, Xingang Xi Road 135, Guangzhou, 510275, China.

¹¹Department of Biology, University of New Mexico, Albuquerque, NM 87131 USA.

¹²Department of Biology, Imperial College London, Silwood Park, Ascot, SL5 7PY, UK.

¹³Grassland, Soil, and Water Research Laboratory, USDA-ARS, 808 E. Blackland Road, Temple, TX 76502 USA.

* To whom correspondence should be addressed. Email: atredenn@gmail.com

† Core authors that led the analysis and wrote the paper. All other authors, listed alphabetically, are Nutrient Network members and/or co-authors of Adler et al. that sign our Comment in support to show consensus among the Nutrient Network.

- ¹⁴School of Earth, Environmental and Biological Sciences, Queensland University of Technology (QUT), Gardens Point, Brisbane, Queensland, Australia, 4001.
- ¹⁵Department of Entomology, University of Maryland, 4112 Plant Sciences, College Park, MD 20742 USA.
- ¹⁶School of Life Sciences, University of KwaZulu-Natal, 1 Carbis Road, Pietermaritzburg, 3201, South Africa.
- ¹⁷Department of Biology, Ecology and Biodiversity group, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands.
- ¹⁸Department of Plant Sciences, University of Oxford, South Parks Road, Oxford, OX1 3RB, UK.
- ¹⁹Institute for Chemistry and Biology of the Marine Environment, Carl-von-Ossietzky University Oldenburg, Schleusenstrasse 1, 26382 Wihlhemshaven, Germany.
- ²⁰School of Life Sciences, University of KwaZulu-Natal, 1 Carbis Road, Pietermaritzburg, 3201, South Africa.
- ²¹School of Biological Sciences, University of Nebraska, 211 Manter Hall, Lincoln, NE 68588, USA.
- ²²Biology Department, Doane College, 1014 Boswell Ave, Crete NE 68333 USA.
- ²³Department of Integrative Biology, University of Guelph, 50 Stone Rd, Guelph, Ontario, Canada N1G 2W1.
- ²⁴Department of Plant & Soil Science, University of Kentucky, N-222D Ag Science North, Lexington, KY 40546-0091 USA.
- ²⁵Department of Biology, University of North Carolina at Chapel Hill, CB#3280, Chapel Hill NC 27599 USA.
- ²⁶School of Biological Sciences, Monash University, Clayton Campus, Wellington Road, Clayton 3800, Victoria, Australia.
- ²⁷Department of Ecology, Environment and Evolution, La Trobe University, Kingsbury Drive, Bundoora 3086, Victoria, Australia.
- ²⁸Department of Zoology, University of Wisconsin, 430 Lincoln Drive, Madison, WI 53706 USA.
- ²⁹Department Forestry, Agriculture and Water, Southern Patagonia National University-INTA-CONICET, CC 332, (CP 9400), Río Gallegos, Santa Cruz, Patagonia, ARG.
- ³⁰CSIRO Land and Water, Private Bag 5, Wembley WA 6913 Australia.
- ³¹Community Ecology, Swiss Federal Institute for Forest, Snow and Landscape Research, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland.
- ³²Department of Ecology, INIBIOMA (CONICET-UNCO), Quintral 1250, Bariloche, (8400), Rio Negro, Argentina.
- ³³School of Veterinary and Life Sciences, Murdoch University, Perth, Western Australia, 90 South Street, Murdoch, Western Australia 6150
- ³⁴School of Biological Sciences, University of Sydney, Heydon-Laurence Building, A08, University of Sydney, Sydney, NSW, 2006, Australia.
- ³⁵Agricultural and Biosystems Engineering, Iowa State University, USA.
- ³⁶Department of Entomology and Nematology, University of California, Davis, One Shields Ave, Davis, CA 95616

Print Abstract

Fraser *et al.* (Reports, 17 July 2015, p. 302) report a unimodal relationship between productivity and species richness at regional and global scales, which they contrast with the results of Adler *et al.* (Reports, 23 September 2011, p. 1750). However, both data sets, when analyzed correctly, show clearly and consistently that productivity is a poor predictor of local species richness.

Online Main Text

Fraser *et al.* (1) collected a worldwide dataset to examine the relationship between productivity and species richness at global and local scales. They present their results as a direct contrast with the results of Adler *et al.* (2). However, their presentation obscures substantial areas of agreement, and where results between the two studies do differ, problems in Fraser *et al.*'s statistical analysis amplify the apparent differences.

The most important area of agreement is the low explanatory power of the “Humped Back Model” (HBM), in which species richness peaks at intermediate productivity and declines at low and high productivity. Fraser *et al.* fit a bivariate relationship between productivity and diversity that accounts for less than 1% of the observed variation in species richness in their data (Table 1; marginal R^2 s for Fraser *et al.* data set). The same is true for an analysis of the Adler *et al.* data set using a Generalized Linear Mixed Model (GLMM) with a block nested within site random effects structure (Table 1; marginal R^2 s for Adler *et al.* data set). Thus, the analyses in both Adler *et al.* and Fraser *et al.* demonstrate that productivity is an uninformative predictor of richness for most grasslands. A combined analysis using both data sets yields similar results (Table 1).

A second point of agreement is the difficulty of inferring process from bivariate patterns. The HBM can arise through a wide array of mechanisms (3-4), meaning that the detection of a unimodal pattern does not provide evidence for any particular mechanism. Adler *et al.* argued, “ecologists should focus on fresh, mechanistic approaches to understanding the multivariate links between productivity and richness” (2). Fraser *et al.* also concluded “more work is needed to determine the underlying causal mechanisms that drive the unimodal pattern” and called for “additional efforts to understand the multivariate drivers of species richness.”

The key disagreement between Fraser *et al.* and Adler *et al.* concerns the statistical significance of the quadratic term that determines the concavity of the richness-productivity relationship. Adler *et al.* found little evidence for a concave-down relationship at the site scale (2% of 48 sites; Adler *et al.*, figure 2), and at the global scale reported a significant effect but noted that it was sensitive to choices about which sites to include in the analysis (Adler *et al.*, figure 3). In contrast, Fraser *et al.* found that 68% of 28 site-level relationships were significantly concave-down (Fraser *et al.*, figure 2A), and in a global extent regression, across all sites, the negative quadratic term had a significant, and robust, P -value. However, their analysis at the site-level is flawed, and the presentation of the global regression in their main figure is misleading.

The site-level regressions reported by Fraser *et al.* and displayed in their figure 2A do not include the proper random effects structure. An important feature of the Fraser *et al.* design was explicitly selecting areas (i.e., grids) to sample across productivity gradients within sites, while Adler *et al.* located blocks of plots randomly with respect to local productivity gradients. To properly reflect their sampling design, in which each “grid” of quadrats was located at one point along the within-site productivity gradient, each site-level regression requires a random effect of “grid” to account for the inherent correlation among plots nested within a sampling grid. We re-ran the analysis of Fraser *et al.* with the grid random effect included (5), except for one site (6). When the proper statistical model is used, we find that only 29% of 28 site-level regressions are significantly concave-down (Fig. 1).

Fraser *et al.* correctly account for their sampling design at the global extent by using a GLMM with grid nested within site, as reported in their table 1. However, in their figure 2A they plot the much more compelling fit from the statistical model *without* the random effects. Although still significant ($P < 0.0001$), the valid relationship is much weaker than the relationship presented by Fraser *et al.* (Fig. 1, heavy black line; Table 1).

Despite Fraser *et al.*’s assertion that their results are diametrically opposed to those presented in Adler *et al.*, the degree of concordance is impressive. In both data sets, the variance explained by the addition of a quadratic term is virtually indistinguishable from that of a linear model (Table 1). In fact, in both data sets the random effects of site and grid (block for Adler *et al.*) explain much more of the variation in species richness than productivity, the supposed mechanistic driver of species richness (Table 1). Furthermore, with the appropriate statistical treatment, the main difference in our results, the strength of evidence for a significant quadratic term, appears smaller.

A continued focus on this bivariate relationship hinders progress toward understanding the underlying multivariate causal relationship (4) and the development of truly predictive models. It is time to focus on effect sizes and variance explained rather than just P -values. The title of Adler *et al.*’s paper, “Productivity is a poor predictor of plant species richness,” would be a perfectly appropriate title for the Fraser *et al.* paper, too.

References and Notes

1. L.H. Fraser *et al.*, Science 349, 6245 (2015)
2. P. B. Adler *et al.*, Science 333, 1750 (2011)
3. J.B. Grace *et al.*, Science 335, 6075 (2012)
4. J.B. Grace *et al.*, Func. Ecol. 28, 4 (2014)
5. We used the 'lme4' package in the statistical programming environment R to fit the GLMMs at the site and global extents. Some models struggled to converge on coefficient estimates, a well-known issue with mixed effects models. We conducted the analyses using different optimizers to make sure our results are robust (they are) and we did our own checks of model diagnostics to make sure the warnings could be ignored (they could). Lastly, we fit a hierarchical mixed effects model using a Bayesian approach to make sure we obtained consistent results (we did). All of our analyses and results can be found on GitHub at

- 179 <https://github.com/atredennick/prodDiv> and as release v0.1,
180 <https://github.com/atredennick/prodDiv/releases/tag/v0.1>
- 181 6. There are four sites, out of 28, that have only two grids. In only one case did this
182 result in inadequate fits of the GLMM model with a “grid” random effect. We
183 therefore fit that one site with GLM with no random effects.
- 184 7. Nakagawa and Schielzeth, *Methods Ecol. Evol.* 4, 2 (2013)
- 185 8. J. Lefcheck, R-squared for generalized linear mixed-effects models,
186 <https://github.com/jslefcche/rsquared.glmm>
187

TABLES

Table 1. Results from global-extent Generalized Linear Mixed Models for both data sets. Results from regressions with and without a quadratic effect of productivity on species richness across all sites. Both models include a random effects structure of grid nested within site (Fraser *et al.*) or block nested within site (Adler *et al.*). Marginal and conditional R^2 values estimated using (7-8). For the combined analysis, we use the same grid (or block) nested within site random effects structure, and also include a “study” random effect.

Data set	Model type	Marginal R^2 (variance explained by fixed effects)	Conditional R^2 (variance explained by fixed + random effects)	Root Mean Square Error (in units of species number)
Fraser <i>et al.</i>	Linear	0.00007	0.84	8.5
Fraser <i>et al.</i>	Quadratic	0.009	0.84	8.3
Adler <i>et al.</i>	Linear	0.0007	0.79	7.7
Adler <i>et al.</i>	Quadratic	0.001	0.78	7.7
Combined	Linear	0.00005	0.82	8.4
Combined	Quadratic	0.003	0.82	8.3

FIGURES

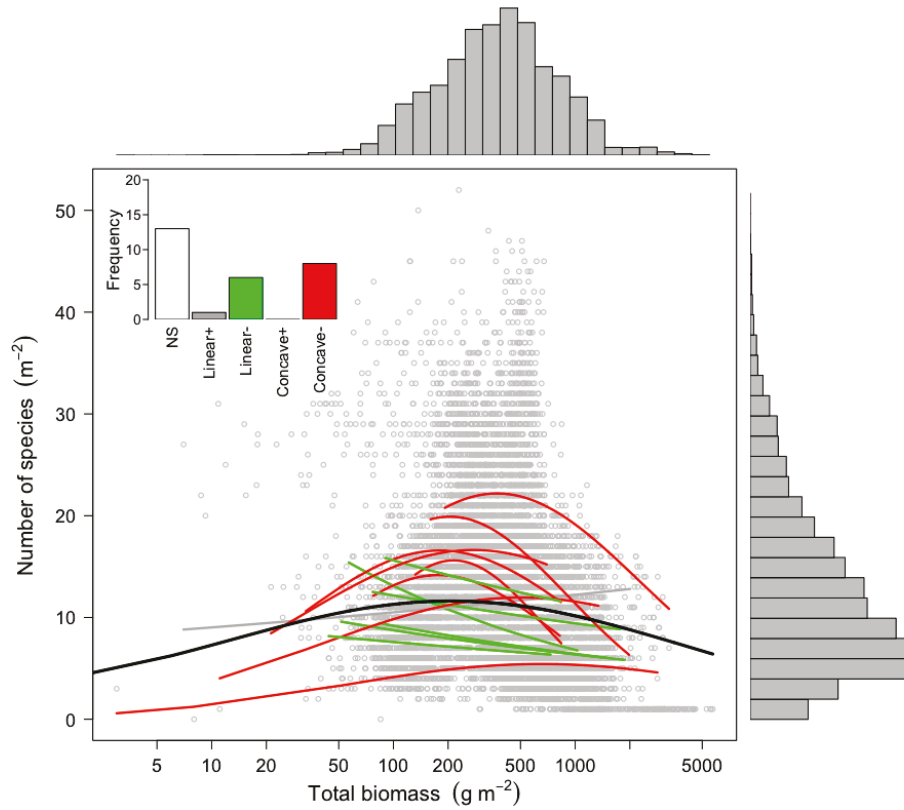


Fig. 1: Species richness as a function of biomass production at the site-level (colored lines) and at the global extent (heavy, black line). These regressions are the same as presented by Fraser *et al.* except we included a grid random effect for the site-level regressions and we show the proper global extent regression line from a Generalized Linear Mixed Model with grid nested within site. Non-significant regression fits are not plotted.