Science AAAS

Comment on "Productivity Is a Poor Predictor of Plant Species Richness"

Jason D. Fridley *et al.*

Science **335**, 1441 (2012);
DOI: 10.1126/science.1215042

Comment on "Productivity Is a Poor Predictor of Plant Species Richness"

Jason D. Fridley,[1]* J. Philip Grime,[2] Michael A. Huston,[3] Simon Pierce,[4] Simon M. Smart,[5] Ken Thompson,[2] Luca Börger,[6] Rob W. Brooker,[7] Bruno E.L. Cerabolini,[8] Nicolas Gross,[6] Pierre Liancourt,[9] Richard Michalet,[10] Yoann Le Bagousse-Pinguet[10]

Adler *et al*. (Reports, 23 September 2011, p. 1750) reported "weak and variable" relationships between productivity and species richness and dispute the "humped-back" model (HBM) of plant diversity. We show that their analysis lacks sufficient high-productivity sites, ignores litter, and excludes anthropogenic sites. If corrected, the data set of Adler *et al*. would apparently yield strong HBM support.

The humped-back model (HBM) of plant diversity, describing a unimodal relationship between annual production (standing biomass and litter) and maximum species richness for herbaceous vegetation, was proposed nearly four decades ago (*1*) and is among the preeminent theories of plant community organization (*2*–*5*). The conclusion of Adler *et al*. (*6*) that relationships between productivity and richness are "weak and variable," based on an analysis of a global-scale data set, casts doubt on the utility of this model. However, even cursory examination of the data and methods of Adler *et al.* reveals that it is an inadequate basis for rejecting the HBM for several reasons.

First, it is deficient in its range of productivity values, including only a handful of sites above 500 g/m^2. In one of the earliest extensive descriptions of the HBM, Al-Mufti *et al*. (*7*) found consistently low species richness at productivity levels of 800 g/m^2 or higher, which is broadly consistent with subsequent studies conducted at this scale (*8*–*11*). With so few high-productivity sites, Adler *et al*. have no statistical basis for expecting a maximal unimodal curve to emerge from their data, an artifact of a limited range of productivity values that has been acknowledged repeatedly in the literature (*4*, *5*, *12*).

Second, although never clearly stated, Adler *et al*. apparently did not include litter in their productivity measurements. (Statistical testing involved "live biomass," although the methods refer to the collection of "recently senescent material"; whether this would include production from early phenological species is unclear, but presumably it ignores accumulated litter.) Data collected to evaluate the HBM have routinely included plant litter along with standing biomass in estimates of productivity, because dead plant material is an important component of productivity and has an important role as a mechanism of competitive suppression (*13*). This means that plots shown by Adler *et al*. as being of intermediate productivity are likely much higher, which would likely shift the peak of maximum species richness found by Adler *et al*. from 300 to 400 g/m^2 closer to the 500 to 600 g/m^2 range observed by Al-Mufti *et al*. (*7*).

Third, the statistical inadequacy of the data set at high levels of productivity is compounded when the authors dismiss "anthropogenic" sites without sufficient scientific basis. The authors treat anthropogenicity as if it were a categorical factor, either human-derived or not. This may provide a basis for them to then delete anthropogenic sites, but this assignment is not justified in their paper and is not logical given the continuum of variation in productivity and the gradual way natural ecosystem productivity is augmented by human inputs. Due to eutrophication associated with agricultural activities, anthropogenic sites are often of high productivity, and, as the HBM predicts, are typically of low richness due to dominance by large plants of high competitive ability (*14*). It is unfortunate that Adler *et al*. dismiss such sites, because one of the main applications of the HBM is to show how eutrophication reduces local richness in terrestrial communities, which has been of much import to the conservation community (*5*, *15*). Had the data set been gathered with the intent of addressing local production-richness relationships across a broad productivity gradient, we have no doubt that "natural" herbaceous assemblages of high production—such as salt marshes, meadows of rich substrate, and herbaceous floodplains, all of which are characterized by high dominance and low species richness—would reveal the classic HBM pattern of declining richness at high levels of productivity. Adler *et al*. also omit one (high biomass, low richness) wetland site, without explanation.

Finally, despite the clear deficiencies in the data for testing the HBM, it is remarkable that the data in their figures 2, 3, and S3 show a clear peak of maximum species richness that comes close to both the production and richness values at the peak (30 to 40 species at about 400 g/m^2) found by Al-Mufti *et al*. (*7*). If these data were to include litter and a larger sample of high productivity sites, regardless of their anthropogenic influence, it is reasonable to conclude that a clear HBM would emerge.

The HBM is a cornerstone of plant ecology, backed by decades of careful mechanistic analysis and used extensively by plant conservationists and restoration ecologists, as well as by theoretical ecologists. It would be imprudent to abandon this important concept on the basis of one unsuitable data set.

[1]Department of Biology, Syracuse University, Syracuse, NY 13244, USA. [2]Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK. [3]Department of Biology, Texas State University, San Marcos, TX 78666, USA. [4]Department of Plant Production, University of Milan, Via Celoria 2, Milan, Italy. [5]Centre for Ecology and Hydrology, Lancaster Environment Centre, Lancaster, LA1 4AP, UK. [6]Centre d'Etudes Biologiques de Chizé, CNRS (UPR1934) and INRA (USC1339), 79360 Beauvoir sur Niort, France. [7]The James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK. [8]Department of Structural and Functional Biology, University of Insubria–Varese, via Dunant 3, I-21100 Varese, Italy. [9]Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA. [10]Université Bordeaux 1, UMR 5805 EPOC, Avenue des Facultés, 33405 Talence, France.

*To whom correspondence should be addressed. E-mail: fridley@syr.edu

References

1. J. P. Grime, *Nature* **242**, 344 (1973).
2. M. A. Huston, *Am. Nat.* **113**, 81 (1979).
3. D. Tilman, *Resource Competition and Community Structure* (Princeton Univ. Press, Princeton, NJ, 1982).
4. J. B. Grace, *Perspect. Plant Ecol. Evol. Syst.* **2**, 1 (1999).
5. P. A. Keddy, *Ann. Bot.* **96**, 177 (2005).
6. P. B. Adler *et al*., *Science* **333**, 1750 (2011).
7. M. M. Al-Mufti, C. L. Sydes, S. B. Furness, J. P. Grime, S. R. Band, *J. Ecol.* **65**, 759 (1977).
8. D. R. J. Moore, P. A. Keddy, *Vegetatio.* **79**, 99 (1989).
9. B. D. Wheeler, S. C. Shaw, *J. Ecol.* **79**, 285 (1991).
10. L. Gough, J. B. Grace, K. L. Taylor, *Oikos* **70**, 271 (1994).
11. O. Kull, A. Aan, *Ecography* **20**, 146 (1997).
12. M. L. Rosenzweig, *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, 1995).
13. J. M. Facelli, S. T. A. Pickett, *Bot. Rev.* **57**, 1 (1991).
14. S. M. Smart *et al*., *J. Appl. Ecol.* **43**, 1128 (2006).
15. D. R. J. Moore, P. A. Keddy, C. L. Gaudet, I. C. Wisheu, *Biol. Conserv.* **47**, 203 (1989).

10 October 2011; accepted 15 February 2012
10.1126/science.1215042