TECHNICAL COMMENT

PLANT ECOLOGY

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

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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.

Fraser *et al.* (*1*) collected a worldwide data set 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^2s for the 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^2s for the 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, "[e]cologists 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 downward 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) [figure 2 in (*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 [figure 3 in (*2*)]. In contrast, Fraser *et al.* found that 68% of 28 site-level relationships were significantly concave-down [figure 2A in (*1*)], 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, whereas 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

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Table 1. Results from global-extent GLMMs 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 *et al.*	Linear	0.00007	0.84	8.5
Fraser *et al.*	Quadratic	0.009	0.84	8.3
Adler *et al.*	Linear	0.0007	0.79	7.7
Adler *et al.*	Quadratic	0.001	0.78	7.7
Combined	Linear	0.00005	0.82	8.4
Combined	Quadratic	0.003	0.82	8.3

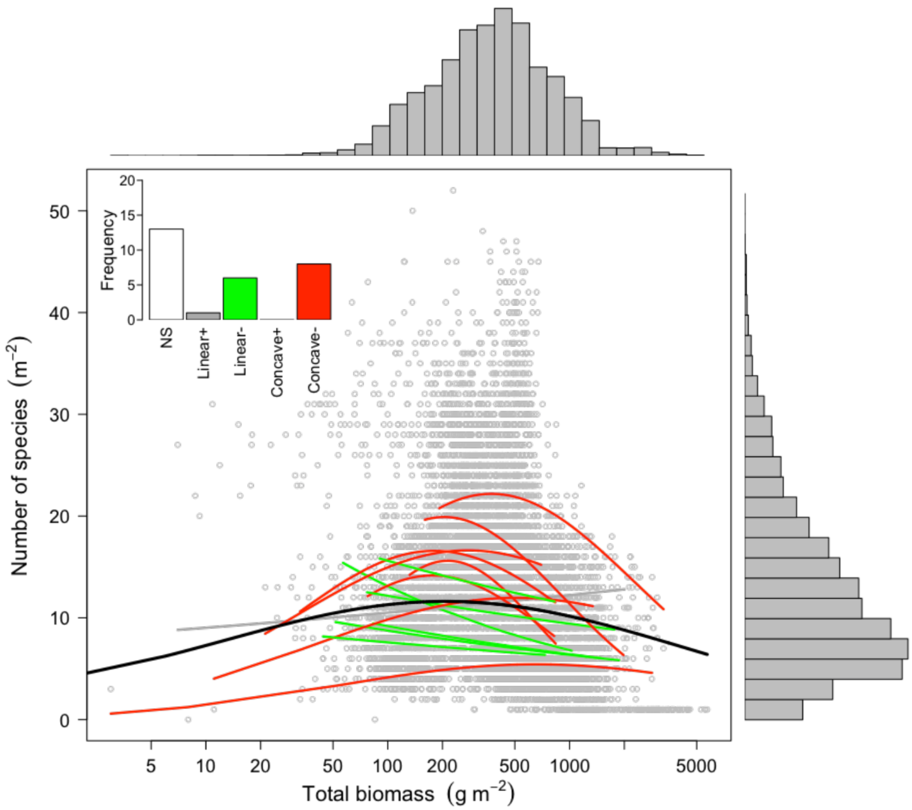

Fig. 1. Species richness as a function of biomass production at the site level (colored lines) and at the global extent (heavy black line). These regressions are the same as presented by Fraser *et al.* except that we included a grid random effect for the site-level regressions, and we show the proper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

regression requires a random effect of "grid" to account for the inherent correlation among plots nested within a sampling grid. We reran 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, and 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

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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 that our results are robust (they are), and we did our own checks of model diagnostics to make sure that 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 http://github.com/atredennick/prodDiv and as release v0.1, https://github.com/atredennick/prodDiv/tag/v0.1
6. There are four sites, out of 28, that have only two grids. In only one case did this result in inadequate fits of the GLMM model with a "grid" random effect. We therefore fit that one site with a generalized linear model with no random effects.
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