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

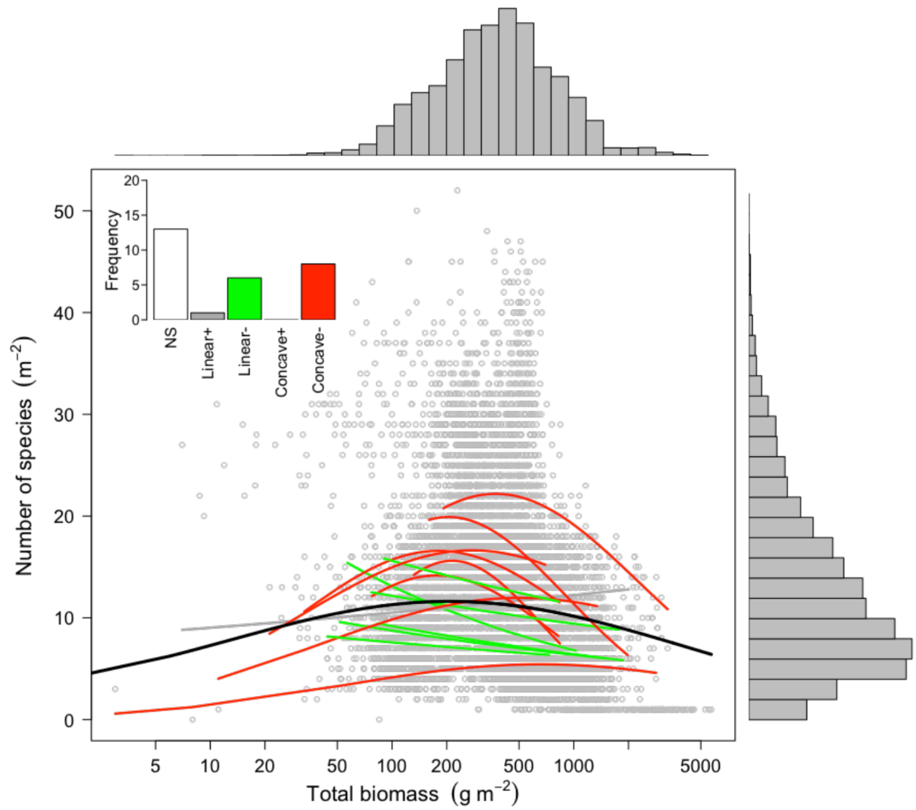

Fig. 1. Species richness as a function of biomass production at the site level (colored lines) and at the global extent (heavy black line). These regressions are the same as presented by Fraser *et al*. except that we included a grid random effect for the site-level regressions, and we show the proper 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.

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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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TECHNICAL RESPONSE

PLANT ECOLOGY

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

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Tredennick *et al*. criticize one of our statistical analyses and emphasize the low explanatory power of models relating productivity to diversity. These criticisms do not detract from our key findings, including evidence consistent with the unimodal constraint relationship predicted by the humped-back model and evidence of scale sensitivities in the form and strength of the relationship.

Tredennick *et al.* (*1*), among them many contributors to the original Adler *et al.* study (*2*), argue that our findings (*3*) align closely with those of Adler *et al.* once their criticisms (described below) are addressed. This is not the case. Tredennick *et al.* fail to acknowledge key findings of ours that remain at odds with those of Adler *et al.*, including (i) a significantly concave-down, global-extent relationship between productivity and richness; (ii) a significantly concave-down, global-extent quantile regression, consistent with the constraint prediction of the humped-back model (HBM); and (iii) our finding that patterns consistent with the HBM appear more evident when a broad range of productivity is sampled.

Tredennick *et al.* present three main criticisms of our study: (i) the analyses of the within-site productivity-diversity relationship should have included sample "grid" as a random effect, thereby accounting for our nested sampling design; (ii) our analyses focused too much on the significance of the quadratic term and not enough on the limited explanatory power of the models; and (iii) our figure 2A (*3*) was "misleading" and should have included a line representing the mixed-effects model for the global-extent relationship. We address each of these in turn.

(i) We agree that including "grid" as a random effect within mixed-effects models would be a reasonable approach. In our within-site analyses, we intentionally replicated the within-site analyses of Adler *et al.*, who did not accommodate the nestedness inherent to their sampling design. In hindsight, we regret not including the results of mixed-effects models for our within-site analyses in the supplementary materials, as we did for all other analyses. We made our data publicly available, which enabled Tredennick *et al.* to conduct analyses of their own, finding that 8 (29%) rather than 19 (69%) of the 28 within-site analyses yielded a significant concave-down relationship when "grid" is included as a random effect. Crucially, these revised analyses by Tredennick *et al.* have no effect on the global models we presented that form the main conclusion of the study. Also, thanks to Tredennick *et al.* making their data and analyses publicly available, we found that the 8 sites that did exhibit a significantly concave-down relationship in their analyses encompassed a significantly larger range of productivity (on the $\log_{10}$ scale) than the 13 sites where no association was found (permutation test on the difference in mean productivity; 9999 permutations; Z score = 2.09; P = 0.039). Moreover, the probability of detecting a concave-down relationship (i.e., significant quadratic term) over no relationship using the mixed-effects modeling approach tended to increase with increasing biomass range (logistic regression; residual deviance = 22.6 on 19 df; P = 0.078).

(ii) We recognize that regressions modeling the mean trend between productivity and richness yield limited explanatory power, and stated so in our Report (*3*). We suggest that Tredennick *et al.*'s focus on the mean trend is misplaced because, provided one samples a sufficiently broad range of productivity, the HBM predicts a constraint relationship, whereby richness is constrained to low levels at very low and very high productivity. Our study provided evidence of this, in the form of a significantly concave-down, global-extent quantile regression (both with and without random effects included). Adler *et al.* also tested for such a constraint relationship (without random effects) but failed to detect it, possibly because of limits to their sampling (*3*). For our analyses of mean trends, we focused on the form of the relationship, and hence the significance of the quadratic term, because this—not explanatory power—lies at the heart of the debate surrounding the HBM (*4*, *5*). Our sampling design and sampling scope allowed us to test the sensitivity of the form of the relationship to varying sampling grains and extents.

(iii) We formatted our figure 2A (*3*) with the objective of making it directly comparable to the results presented by Adler *et al.* (*2*), specifically their figure 2, and their global-extent regression, which was displayed in their figure 3. Adler *et al.* did not account for nested sampling structure in any of their analyses (i.e., using mixed-effects models), including within their global-extent analysis that yielded a significantly concave-down

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relationship. We therefore opted to show our analogous regression results in figure 2A (*3*). We showed the results of our mixed-effects model for the global relationship in figure S1 (*3*).

We encourage future research to (i) explore why low species richness (per unit area) is found at the extreme ends of the productivity gradient and (ii) determine the processes that suppress species richness below its potential at intermediate levels of productivity.

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