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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