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

Jason Pither,^{1*} Lauchlan H. Fraser,² Anke Jentsch,³ Marcelo Sternberg,⁴ Martin Zobel,⁵ James Cahill,⁶ Carl Beierkuhnlein,⁷ Sándor Bartha,^{8,9} Jonathan A. Bennett,^{5,6} Bazartseren Boldgiv,¹⁰ Leslie R. Brown,¹¹ Marcelo Cabido,¹² Giandiego Campetella,¹³ Cameron N. Carlyle,¹⁴ Stefano Chelli,¹³ Anna Mária Csergő,¹⁵ Sandra Diaz,¹⁶ Lucas Enrico,¹⁶ David Ensing,¹⁷ Alessandra Fidelis,¹⁸ Heath W. Garris,² Hugh A. L. Henry,¹⁹ Maria Höhn,²⁰ John Klironomos,¹ Kadri Koorem,⁵ Rachael Lawrence-Lodge,²¹ Peter Manning,²² Randall J. Mitchell,²³ Mari Moora,⁵ Valério D. Pillar,²⁴ Gisela C. Stotz,⁶ Shu-ichi Sugiyama,²⁵ Szilárd Szentes,²⁶ Radnaakhand Tungalag,¹⁰ Sainbileg Undrakhbold, Camilla Wellstein,²⁷ Talita Zupo¹⁸

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 log₁₀ 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 con-

straint 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

¹Department of Biology, University of British Columbia, Okanagan Campus, Kelowna, BC, Canada. ²Department of Natural Resource Sciences, Thompson Rivers University, Kamloops, BC, Canada. ³Department of Disturbance Ecology, BayCEER, University of Bayreuth, Bayreuth, Germany. ⁴Department of Molecular Biology and Ecology of Plants, Tel Aviv University, Tel-Aviv, Israel. ⁵Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia. ⁶Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada. ⁷Department of Biogeography, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany. ⁸Hungarian Academy of Sciences Centre for Ecological Research, Institute of Ecology and Botany, Vácrátót, Hungary. ⁹School of Plant Biology, University of Western Australia, Crawley, Australia. ¹⁰Ecology Group, Department of Biology, National University of Mongolia, Ulaanbaatar, Mongolia. ¹¹Department of Environmental Sciences, University of South Africa, Florida, South Africa. ¹²Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina. ¹³School of Biosciences and Veterinary Medicine, Plant Diversity and Ecosystems Management Unit, University of Camerino, Camerino, Italy. ¹⁴Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Canada. ¹⁵School of Natural Sciences, Trinity College Dublin, The University of Dublin, Dublin, Ireland. ¹⁶Instituto Multidisciplinario de Biología Vegetal (IMBIV), National Scientific and Technical Research Council and Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina. ¹⁷Department of Biology, Queen's University, Kingston, Ontario, Canada. ¹⁸Departamento de Botânica, UNESP – Universidade Estadual Paulista, Rio Claro, SP, Brazil. ¹⁹Department of Biology, University of Western Ontario, London, Ontario, Canada. ²⁰Department of Botany, Faculty of Horticultural Science, Corvinus University of Budapest, Hungary. ²¹Department of Botany, University of Otago, Dunedin, New Zealand. ²²Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, Germany. ²³Department of Biology, University of Akron, Akron, OH, USA. ²⁴Department of Ecology, Federal University of Rio Grande do Sul, Porto Alegre, Brazil. ²⁵Faculty of Agriculture and Life Science, Hirosaki University, Aomori, Japan. ²⁶Institute of Plant Production, Szent István University, Gödöllő, Hungary. ²⁷Faculty of Science and Technology, Free University of Bozen-Bolzano, Bolzano, Italy. *Corresponding author. E-mail: jason.pither@ubc.ca

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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