

TECHNICAL RESPONSE

PLANT ECOLOGY

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

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Laanisto and Hutchings claim that the local species pool is a more important predictor of local plant species richness than biomass and that when the species pool is considered, there is no hump-backed relationship between biomass and richness. However, we show that by calculating a more appropriate measure of species pool, community completeness, both regional and local processes shape local richness.

Species diversity varies from habitat to habitat. Because species diversity has been related to ecological processes and ecosystem functions, it is important to predict whether species diversity may be high or low in any given environment (1). Our recent Report (2) provides evidence from data collected from grasslands in 19 countries and six continents of a unimodal relationship between herbaceous species richness and aboveground plant biomass plus plant litter, such that the maximum potential species richness occurs at intermediate levels of biomass production. We tackled the question of the diversity-productivity relationship because of its foundational role in ecological research and its controversial history (2–7). The data were collected at the 1-m² scale, within 8-m-by-8-m grids, so that we could test linear and quadratic regressions at 1, 2, 4, 9, 16, 25, and 64 m² scales. At each scale, the best descriptor of the relationship was a concave quadratic regression, but explanatory power diminished with increasing scale (2).

We point to the relevance of our findings and the scaling approach in our analysis because it provides a comparative to Laanisto and Hutchings (8). Through a reanalysis of our data, Laanisto and Hutchings (8) argue that the local species pool has a stronger effect on species richness than primary productivity. We are in agreement that large-scale processes play a role in governing local-scale diversity, but it is challenging to account for large-scale processes in

an empirical study such as ours. Thus, instead of addressing whether it is more reasonable to seek for a relationship between species richness and primary productivity, or local species pool, we would rather ask what the relative role of local and regional factors is in shaping the em-

pirically observed relationship between diversity and productivity.

Laanisto and Hutchings emphasize geographic variation in the shape of the response curve (“While the HBM [hump-backed model] certainly applies in some regions and habitats, such as high-latitude grasslands ... richness-productivity relationships tend to be positive in tropical areas”). In fact, there are two confounding aspects in this statement: geographical region (with different biogeographic history) and ecosystem type (grassland versus forest). Positive relationships come predominantly from forests (9). We chose to avoid mixing different ecosystems because of the different processes that may be acting.

In their figure 1, Laanisto and Hutchings’s regression of local richness versus species pool is problematic because these two variables are inherently related, not independent, and local richness cannot exceed species pool size (10). Furthermore, all species recorded in an 8-m-by-8-m grid underestimates the local species pool. There are some techniques to overcome this problem—for example, estimating species pool size using Chao estimations (11). When applying this technique, we achieve a more complete estimate (Fig. 1A).

In figures 1 and 2 in (8), the analysis used by Laanisto and Hutchings could be more mathematically correct by calculating community completeness. When plotting richness against species pool, there is an upper limit where we do not have

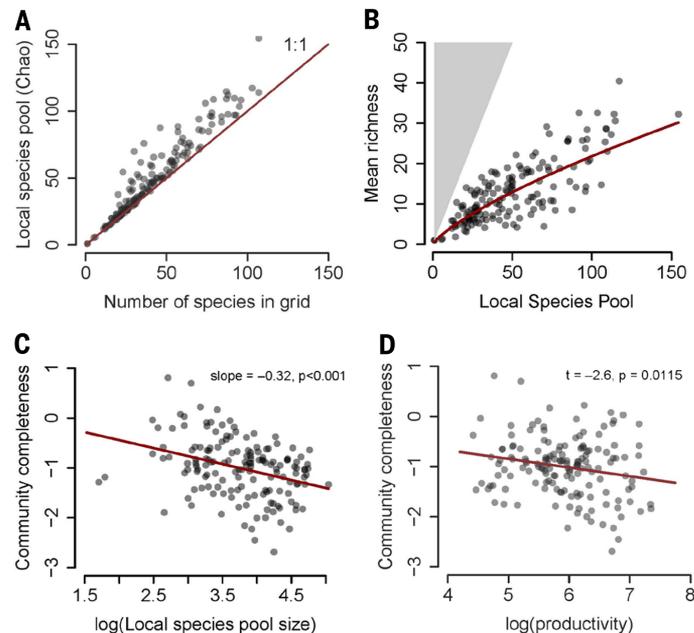


Fig. 1. Regional and local processes shape local species richness in globally distributed grasslands. The relationship between (A) the Chao estimation of local species pool found in the plots of a single grid [local species pool (Chao)] and the total number of species found in that grid; (B) the mean number of species found in the plots of a single grid (mean richness) and the local species pool (the shaded area represents impossible values where no data points can be found); (C) the log(richness/dark diversity) (community completeness) and the log(local species pool); and (D) the community completeness and the mean biomass found in the plots of a single grid [log(Productivity)]. Each dot ($n = 157$) represents one 8- by 8-m grid containing 64 1-m² plots [data from (14)]. Semitransparent dots are used to indicate overlapping revealed as a darker shade.

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data points because richness cannot be larger than the pool. We can, however, apply a recently developed technique to model the overall trend between pool and richness using a log-ratio method of community completeness: $\log(\text{local richness}/\text{dark diversity})$, dark diversity includes species that belong to the species pool but are currently not present locally (I0, I2, I3). We cannot calculate completeness for sites where there is no dark diversity—i.e., two monoculture sites were excluded, but these two points were outliers in any event. When we back-transform the trend line, we can see that the local richness is indeed positively related to local species pool size (Fig. 1B). The trend line, however, has a significant curvature. Curvature can be measured as the negative slope between community completeness and log species pool size (Fig. 1C). Thus, local richness is not a constant proportion of species pool, and when the size of the species pool increases, relatively fewer species are represented in 1-m² plots. This means that there are likely some local processes limiting richness.

Community completeness is a better way to express how the local species pool is realized in local plots than percentage (there are no upper and lower limits), and it works in log scale. Community completeness is negatively related to site productivity (log total biomass) (Fig. 1D). Here, the species pool effect has been taken into account, but we still see that, at high productivity, the species pool is realized less in local plots compared with low productivity. This can be due to competition. Thus, both regional and local processes shape local richness, but local processes are probably more important at high productivity.

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ACKNOWLEDGMENTS

We thank the Herbaceous Diversity Network (HerbDivNet) for the data set that has generated insights into plant diversity patterns and processes. This work was supported by a Natural Sciences and Engineering Research Council Discovery Grant Canada awarded to L.H.F. and J.P., the Estonian Research Council (20-28, 20-29), and a European Regional Development Fund Centre of Excellence Frontiers in Biodiversity Research awarded to M.P. and M.Z.

28 September 2015; accepted 4 November 2015
10.1126/science.aad4874

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Science **350** (6265), 1177.
DOI: 10.1126/science.aad4874

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