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

Lauri Laanisto* and Michael J. Hutchings

Fraser et al. (Reports, 17 July 2015, p. 302) report that a hump-backed model describes the worldwide relationship between productivity and plant species richness in grassland communities. We reanalyze their data from a larger-scale perspective, using local species pool. This influences richness far more strongly than productivity, and, when this is taken into account, the hump-backed richness-productivity relationship disappears.

Since it was first proposed more than 40 years ago, the unimodal relationship [hump-backed model (HBM)] between plant species richness and productivity has been one of the most persistent models in plant ecology (1). Although it has been confirmed many times at a local scale, there are still debates (1–8). While the HBM certainly applies in some regions and habitats, such as high-altitude grasslands (3), richness-productivity relationships tend to be positive in tropical areas (2–4). It is known that ecosystem stability and regional dispersal patterns influence diversity at different productivities (2) and that species/habitat productivity preferences are often determined by phylogenetic niche conservatism (4). Consequently, the plant species richness-productivity relationship is strongly contingent upon large-scale historical and biogeographical differences between habitats and species (2, 3, 9). However, such factors have so far been poorly integrated into richness-productivity models (2, 7, 10, 11). Only after assessing their influence on richness should the influence of more localized ecological processes, such as competition, be taken into consideration.

The case for adopting a different approach to assessment of the relationship between plant species richness and productivity locally and globally follows from numerous metastudies that have shown a diversity of empirical relationships between species richness and environmental parameters, including productivity, in different geographical regions. These different relationships have been attributed to divergent species pool dynamics and differences in evolutionary history (2–4, 9, 10). Thus, the shape of local richness-productivity relationships appears to be primarily dependent on large-scale processes, with local-scale interactions having less influence (3).

The HBM has been subjected to several regional and global meta-assessments, with contradictory outcomes. This has mainly been interpreted as a consequence of methodological inconsistencies between case studies included in the meta-data (1, 6, 12). A logical step to address this problem is to conduct meta-experiments using consistent methodology (1, 5, 12), but the results of two recent global-scale HBM meta-experiments, using very similar methods, have also been contradictory; one found no relationship between plant species richness and productivity (5), whereas the other found a hump-backed relationship (1).

The raw data of the latter study has been made available (13), and the results presented here are based on further analysis of these data.

The sampling design of Fraser et al.’s study (1) is based on 8-m-by-8-m grids, with each containing 64 1-m² plots. Altogether, there were 157 grids (15). Living and standing dead biomass and species richness data were collected from each plot from every grid (1). Collection of species pool data was optional for contributors to the meta-experiment (12), and species pool data were not used in Fraser et al.’s analysis, even though comparison of absolute values of species richness on a global scale for different habitats is considered problematic at best, and the use of species pool data has been recognized as preferable (9, 11). To estimate local species pool sizes, we extracted data from the total number of species recorded in each grid. There was a strong positive correlation between the size of the local species pool and the mean species richness of the plots within each of the grids (Fig. 1). Local species pool size had a much stronger effect on mean species richness (r² = 0.74) (Fig. 1) than productivity (r² values ranging from 0.071 to 0.127, depending on spatial scale of analysis) (see figure S2 in (1)).

We then calculated the mean living + dead biomass per plot in each grid (productivity, sensu Fraser et al.) and the mean percentage of the local species pool that was recorded in the plots in each grid. The relationship between mean percentage of the local species pool recorded in the plots and mean productivity was not significant, and there was no evidence of a hump-backed relationship between these variables (Fig. 2).

![Graph showing the relationship between local species pool and number of species](http://example.com/graph.png)

**Fig. 1.** Relationship between the mean number of species found in the plots of a single grid (number of species) and the total number of species found in that grid (local species pool). Each dot (n = 157) represents one 8- by 8-m grid containing 64 1-m² plots. [Data from (9)]
This analysis shows the critical role of large-scale factors—in this case, the size of the local species pool—in determining plant species richness (9) and that the inclusion of pertinent (macro) ecological context in the analysis significantly improves the explanatory power of the data and changes the shape of the relationship between plant species diversity and productivity.

The question of whether there are general laws and principles in ecology has been long debated and remains open. One point of view is that historical contingency, and the complexity of ecological phenomena, prevent the existence of generalizations that amount to laws in ecology (14). Another view is that ecological laws do exist, but with many exceptions (15), making it very difficult to find models that apply to all or even most ecological systems (2, 3, 14). A possible exception is the positive correlation between the size of the local species pool and local species richness. This appears to be one of very few consistent patterns in ecology, despite all the contingent processes and interactions involved in the assembly of ecological communities (15), suggesting that studies of species richness conducted at large spatial scales and across many habitat types should consider species pool size as potentially the most influential determinant of local species richness (9). The analysis presented here demonstrates that it has far more power than productivity for explaining plant species richness at a global scale. This contribution shows a simple way of including local species pool sizes in species richness-productivity studies when it is not possible to undertake complete species inventories.

**REFERENCES AND NOTES**

13. Data from (3); Dryad Digital Repository; http://dx.doi.org/10.5061/dryad.038j8 (2015).

**ACKNOWLEDGMENTS**

This research was supported by Estonian Research Council’s grants IUT 21-1, IUT 8-3, and PUT 607. Author contributions: L.L. designed the study and performed analysis, and L.L. and M.J.H. wrote the paper.

18 September 2015; accepted 4 November 2015 10.1126/science.aad4836
Comment on "Worldwide evidence of a unimodal relationship between productivity and plant species richness"
Lauri Laanisto and Michael J. Hutchings

*Science* 350 (6265), 1177.
DOI: 10.1126/science.aad4836