

Reply to Byrnes et al.: Aggregation can obscure understanding of ecosystem multifunctionality

We manipulated soil animal communities in combination with nitrogen fertilization and found that individual grassland ecosystem functions had contrasting responses across the manipulations (1). We therefore cautioned against using a single multifunctionality index that aggregates individual functions to characterize overall ecosystem functioning (1).

Byrnes et al. (2) contend that this caution misinterprets the concept of ecosystem multifunctionality. They suggest that multifunctionality does not require positive correlation of multiple functions. Moreover, they advise that a multifunctionality framework must assess both individual functions and overall functionality. We agree with both of their points. However, both fail to address the caution raised by our study (1).

We argue that a summary index of multifunctionality will inappropriately characterize relationships between a driver and net ecosystem functioning whenever responses of the individual functions to drivers are context dependent. Our cautions then expressly relate to those cases where the underlying drivers of individual functions are process and/or context dependent. These criteria apply to our study and to most ecosystems.

The issue of aggregating contrasting variables is not limited to ecology and underlies a suite of logical (or inference) fallacies in statistics, such as Simpson's paradox, where statistical summarization changes the interpretation of a mean because a second factor modifies the effect of the first (3). Byrnes et al. (2) state that "No statistician would argue that variation in data invalidates estimates of a mean." This statement misrepresents our

argument and the broader issue of logical fallacies: the important question is what we can infer from the mean (3). Where the effects of a driver are context dependent, the resulting variation can invalidate conclusions based on mean estimates summarizing the influence of a single driver (3–5).

We believe the notion of multifunctionality is necessary to enhance ecosystem management. Otherwise, management for only a single ecosystem function is likely to lead to the degradation of co-occurring functions. Nevertheless, we contend that the challenge remains to develop multifunctionality indices that appropriately account for the aggregate effects of contrasting individual functions when their responses depend on multiple drivers that vary in their effects either in space or time. This is especially important as biodiversity-ecosystem functioning studies move toward assessing the relative importance of multiple drivers—not just biodiversity—on ecosystem functioning. Byrnes et al. (2) concluded that the study of ecosystem multifunctionality is about the forest as well as the individual trees. We agree with their conclusion and suggest that the way to understand the forest is to study the trees.

**Mark A. Bradford^{a,1}, Stephen A. Wood^b,
Richard D. Bardgett^c, Helaina I. J. Black^d,
Michael Bonkowski^e, Till Eggers^f,
Susan J. Grayston^g, Ellen Kandeler^h,
Peter Manningⁱ, Heikki Setälä^j,
and T. Hefin Jones^k**

^a*School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511;*

^b*Department of Ecology, Evolution, and*

Environmental Biology, Columbia University, New York, NY 10027; ^cFaculty of Life Sciences, The University of Manchester, Manchester M13 9PT, United Kingdom; ^dThe James Hutton Institute, Aberdeen AB15 8QH, Scotland, United Kingdom; ^eZoologisches Institute, University of Cologne, D-50674 Köln, Germany; ^fCentre for Population Biology, Department of Biological Sciences, Imperial College at Silwood Park, Berkshire SL5 7PY, United Kingdom; ^gDepartment of Forest Sciences, University of British Columbia, Vancouver, BC, Canada V6T 1Z4; ^hInstitute of Soil Science and Land Evaluation, University of Hohenheim, D-70593 Stuttgart, Germany; ⁱInstitute of Plant Sciences, University of Bern, CH-3013 Bern, Switzerland; ^jDepartment of Environmental Sciences, University of Helsinki, Helsinki 00014, Finland; and ^kSchool of Biosciences, Cardiff University, Cardiff CF10 3AX, United Kingdom

1 Bradford MA, et al. (2014) Discontinuity in the responses of ecosystem processes and multifunctionality to altered soil community composition. *Proc Natl Acad Sci USA* 111(40):14478–14483.

2 Byrnes J, et al. (2014) Multifunctionality does not imply that all functions are positively correlated. *Proc Natl Acad Sci USA* 111:E5490.

3 Gelman A, Shor B, Bafumi J, Park D (2007) Rich state, poor state, red state, blue state: What's the matter with Connecticut? *Quart J Poli Sci* 2:345–367.

4 Bradford MA, et al. (2014) Climate fails to predict wood decomposition at regional scales. *Nature Clim Change* 4:625–630.

5 Schmitz OJ (2010) *Resolving Ecosystem Complexity* (Princeton Univ Press, Princeton).

Author contributions: M.A.B., S.A.W., R.D.B., H.I.J.B., M.B., T.E., S.J.G., E.K., P.M., H.S., and T.H.J. wrote the paper.

The authors declare no conflict of interest.

¹To whom correspondence should be addressed. Email: mark.bradford@yale.edu.