Received: 25 October 2022 | Accepted: 25 October 2022

DOI: 10.1111/1365-2656.13836

RESEARCH HIGHLIGHTS

Journal of Animal Ecology
BRITISH ECOLOGICAL SOCIETY

Variation in diversity–function relationships can be explained by species interactions

Daniel Montoya[1,2]

[1]Basque Centre for Climate Change (BC3), Leioa, Spain

[2]IKERBASQUE, Basque Foundation for Science, Bilbao, Spain

Correspondence
Daniel Montoya
Email: daniel.montoya@bc3research.org

Funding information
Eusko Jaurlaritza, Grant/Award Number: BERC 2022-2025; H2020 European Research Council, Grant/Award Number: 101043548; Ministerio de Ciencia e Innovación, Grant/Award Number: MDM-2017-0714 and RYC2020-028780-I

Handling Editor: Mariano Rodriguez-Cabal

Abstract

***Research Highlight*:** Wu, D., Xu, C., Wang, S., Zhang, L., & Kortsch, S. (2022). Why are biodiversity–ecosystem functioning relationships so elusive? Trophic interactions may amplify ecosystem function variability. *Journal of Animal Ecology*, https://doi.org/10.1111/1365-2656.13808. There is consensus that average trends of ecosystem functions increase with species diversity. However, large variations in ecosystem function (VEF) in systems with similar diversity levels are commonly observed, yet not understood. In this study, Wu et al. (2022) integrate empirical aquatic food webs with a multitrophic model to show that VEF generally shows a hump-shaped pattern along the species richness gradient. This pattern is related to changes in taxa composition across trophic levels—the proportion of consumer species relative to basal species—along the gradient of species richness. Thus, VEF dependence on species diversity is driven by both bottom-up and top-down control that regulate taxa composition and taxa dominance. These results are corroborated with an independent food web dataset from the Gulf of Riga. An important implication of this study is that biodiversity loss may not only reduce the mean levels of ecosystem functioning, but also increase unpredictability of functions by generating greater function variability.

KEYWORDS
biodiversity, consumer:resource ratio, ecosystem functioning, stability, trophic interactions

The last three decades of Biodiversity and Ecosystem Functioning (hereafter BEF) research have demonstrated that biodiversity is key to the functioning of ecosystems. Models and controlled experiments, that prevent or minimize potential drivers of ecosystem functioning other than the number of species, show that the impact of biodiversity is positive and becomes stronger when we move from single to multiple functions (Cardinale et al., 2012; Hector & Bagchi, 2007), and when we expand the spatial and temporal scales of analysis (Isbell et al., 2011; Maestre et al., 2012; Zavaleta et al., 2010). However, even though average trends of ecosystem function increase with species diversity, large variations in ecosystem function (VEF) are often observed across ecosystems with similar diversity levels. This VEF remains poorly understood.

The vast majority of BEF studies have defined biodiversity taxonomically, that is, the number of species, and have usually focused on single trophic levels (but see Duffy, 2003; Duffy et al., 2007; Thébault & Loreau, 2003; Wang & Brose, 2018). In addition, most studies are based on small-scale experimental manipulations of biodiversity, and so the extent to which the nature and architecture of species interactions determine functionality in ecosystems remains unclear. The study by Wu et al. (2022) integrates the complexity of natural multitrophic communities into the framework of BEF. More specifically, it significantly contributes to BEF research by (i) providing a mechanistic understanding of VEF, (ii) adopting a food web approach and (iii) considering real-world, uncontrolled communities.

In this study, Wu et al. (2022) use a multitrophic food web model parameterized with eight aquatic food webs and five ecosystem functions. Importantly though, the results presented below are corroborated with an independent 34-year (1981–2014) food web dataset from the Gulf of Riga ecosystem in the Baltic Sea (Kortsch et al., 2021). Wu et al. (2022) find a consistent positive effect of increasing species richness on ecosystem functioning, although the rates of increase (i.e. steepness of the BEF curve) differ across individual functions. Also, substantial variation in the mean provision of ecosystem functions, measured by the coefficient of variation of ecosystem functions, is reported. These first two results confirm previous knowledge of BEF relationships (e.g. Eisenhauer et al., 2019; Gonzalez et al., 2020; O'Connor et al., 2017; Tilman et al., 2014). The first unexpected, novel outcome of this study comes from the observation that VEF shows a general hump-shaped pattern along the species richness gradient (Figure 1). This pattern in VEF contrasts with the saturating and linear relationships of average functional trends versus species richness often documented in BEF experiments, and also reported in this work. While the magnitude of VEF varies with ecosystem type—ecosystems with large biodiversity range show larger variations of ecosystem function in response to species richness—the peak in function variability depends both on the ecosystem type and the function considered.

The unimodal relationship between VEF and species richness suggests that there is something else beyond the number of species that influences VEF. Wu et al. (2022) investigate the role of trophic interactions in shaping such variation in ecosystem function. By looking at taxa composition across trophic levels (characterized by the proportion of primary producers, decomposers and consumers), the analysis reveals changes in the proportion of trophic-level species along the gradient of species richness. This means that taxa composition across trophic levels does not remain constant as the number of species increases. The VEF curve can be divided into two sections (Figure 1). In the first section of the curve, at low taxa richness levels, the increase in species richness of the entire community mainly results from a fast increase in basal taxa (i.e. primary producers). Within the same species diversity, this elevates VEF by (i) enhancing the resource pool and diversifying energy channels for consumer taxa, and/or by (ii) weakening top-down pressure from consumers and the subsequent variation in taxa dominance, a mechanism reported elsewhere (Maureaud et al., 2020). It is worth to note that decomposers, not widely considered in food web studies, play a similar trophic role as primary producers and diversify resources for top consumers, which, in turn, promotes vertical diversity and ecosystem functioning.

The second section of the VEF curve is characterized by a saturation of basal taxa richness and an increase in consumer species. One main effect of this consumer dominance is that it enhances trophic complexity by adding more omnivore interactions. Omnivory can buffer the cascading effects of top-down control resulted from higher consumer: resource ratios, and this reduces variation of basal taxa composition and their associated functions (Figure 1). Therefore, the end result of increased consumer richness in this part of the curve is a reduction of VEF within the entire food web. Collectively, these results show that the observed nonlinearities in VEF can be mapped onto the nonlinear changes in the proportion of consumer species relative to basal species along the gradient of species richness. These results reconcile a seemingly contradictory evidence of BEF relationships. That is, the large variation in BEF relationships of observational and experimental studies with low replication is not merely driven by community assembly processes (e.g. biotic filtering; Hagan et al., 2021); rather, it is also a consequence of the variation in taxa composition along species diversity gradients.

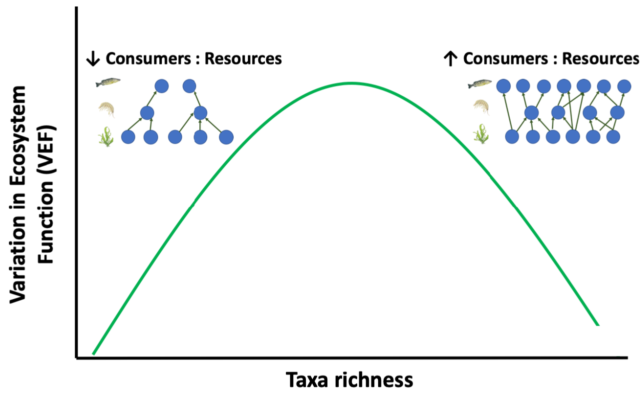

FIGURE 1 Variation in ecosystem function (VEF, measured as the coefficient of variation in ecosystem function) against taxa richness. The curve shows the general hump-shaped pattern observed across eight aquatic food webs and independently corroborated by the Gulf of Riga ecosystem. This pattern is mechanistically linked to changes in taxa composition across trophic levels—the proportion of consumer species relative to basal species represented by the two example food webs drawn—along the gradient of species richness.

This study has several important implications. First, in contrast to what was previously thought (McGrady-Steed et al., 1997; Naeem & Li, 1997), higher species diversity does not necessarily decrease VEF. This observation results from analysing multiple trophic levels and the relative proportion of basal and consumer species, an approach that differs from that used in single trophic-level studies. Therefore, a food web approach provides additional mechanistic insights into BEF relationships. The second important implication of this study is that the mean and variability in the provision of ecosystem functions can change independently with species diversity. Although this result is not novel (e.g. Montoya et al., 2019, 2021), to my knowledge it is observed in food webs for the first time, and emphasizes that biodiversity loss may not only reduce the mean levels of ecosystem functioning, but also increase unpredictability of functions by generating greater function variability. Given the ongoing high rates of biodiversity loss, this raises alarm over the potential for major losses in ecosystem functions and their stability (inverse of variability).

Scientific studies often raise more questions than those targeted. For example, how generalizable the results obtained by Wu et al. (2022) are? Will they hold in terrestrial food webs and for mutualistic interactions with their associated ecosystem functions? Aside from taxa composition across trophic levels, other food web properties change along the species richness gradient (e.g. connectance). Do such properties play a role in determining VEF? What is the effect of species interaction strengths on VEF? These and other questions will feed current and future research to further our understanding of BEF relationships. The findings by Wu et al. (2022) provide a step forward towards a more mechanistic understanding of variation in BEF relationships, and call for further investigation in this field.

ACKNOWLEDGEMENTS

I would like to acknowledge the financial support provided by María de Maeztu excellence accreditation 2018-2022 (MDM-2017-0714), funded by MCIN/AEI/http://doi.org/10.13039/501100011033/; the Basque Government through the BERC 2022-2025 program; the Spanish Ministry of Science & Innovation and by the European Social Fund through the Ramón y Cajal Program (RYC2020-028780-I) and the ERC (ERC Consolidator Grant RECODYN 101043548).

CONFLICT OF INTEREST

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

Data have not been archived because this article does not use data.

ORCID

Daniel Montoya https://orcid.org/0000-0002-5521-5282

REFERENCES

Cardinale, B. J., Duffy, J., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*, 59–67. https://doi.org/10.1038/nature11148

Duffy, J. E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*, *6*, 680–687.

Duffy, J. E., Cardinale, B. J., France, K. E., McIntyre, P. B., Thébault, E., & Loreau, M. (2007). The functional role of biodiversity in ecosystems: Incorporating trophic complexity. *Ecology Letters*, *10*, 522–538.

Eisenhauer, N., Schielzeth, H., Barnes, A. D., Barry, K. E., Bonn, A., Brose, U., Bruelheide, H., Buchmann, N., Buscot, F., Ebeling, A., Ferlian, O., Freschet, G. T., Giling, D. P., Hättenschwiler, S., Hillebrand, H., Hines, J., Isbell, F., Koller-France, E., König-Ries, B., … Jochum, M. (2019). A multitrophic perspective on biodiversity–ecosystem functioning research. *Advances in Ecological Research*, *61*, 1–54. https://doi.org/10.1016/bs.aecr.2019.06.001

Gonzalez, A., Germain, R. M., Srivastava, D. S., Filotas, E., Dee, L. E., Gravel, D., Thompson, P. L., Isbell, F., Wang, S., Kéfi, S., Montoya, J., Zelnik, Y. R., & Loreau, M. (2020). Scaling-up biodiversity-ecosystem functioning research. *Ecology Letters*, *23*, 757–776. https://doi.org/10.1111/ele.13456

Hagan, J. G., Vanschoenwinkel, B., & Gamfeldt, L. (2021). We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. *Ecology Letters*, *24*, 2537–2548.

Hector, A., & Bagchi, R. (2007). Biodiversity and ecosystem multifunctionality. *Nature*, *448*, 188–190.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Stanley Harpole, W., Reich, P. B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., Zavaleta, E. S., & Loreau, M. (2011). High plant diversity is needed to maintain ecosystem services. *Nature*, *477*, 199–202. https://doi.org/10.1038/nature10282

Kortsch, S., Frelat, R., Pecuchet, L., Olivier, P., Putnis, I., Bonsdorff, E., Ojaveer, H., Jurgensone, I., Strāķe, S., Rubene, G., Krūze, Ē., & Nordström, M. C. (2021). Disentangling temporal food web dynamics facilitates understanding of ecosystem functioning. *Journal of Animal Ecology*, *90*, 1205–1216. https://doi.org/10.1111/1365-2656.13447

Maestre, F., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M. A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., … Zaady, E. (2012). Plant species richness and ecosystem multifunctionality in global drylands. *Science*, *335*, 214–218. https://doi.org/10.1126/science.1215442

Maureaud, A., Andersen, K. H., Zhang, L., & Lindegren, M. (2020). Trait-based food web model reveals the underlying mechanisms of biodiversity-ecosystem functioning relationships. *Journal of Animal Ecology*, *89*, 1497–1510.

McGrady-Steed, J., Harris, P. M., & Morin, P. J. (1997). Biodiversity regulates ecosystem predictability. *Nature*, *390*, 162–165.

Montoya, D., Haegeman, B., Gaba, S., De Mazancourt, C., Bretagnolle, V., & Loreau, M. (2019). Trade-offs in the provisioning and stability of ecosystem services in agroecosystems. *Ecological Applications*, *29*, e01853. https://doi.org/10.1126/science.1215442

Montoya, D., Haegeman, B., Gaba, S., De Mazancourt, C., & Loreau, M. (2021). Habitat fragmentation and food security in crop pollination systems. *Journal of Ecology*, *109*, 2991–3006.

Naeem, S., & Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, *390*, 507–509.

O'Connor, M. I., Gonzalez, A., Byrnes, J. E. K., Cardinale, B. J., Duffy, J. E., Gamfeldt, L., Griffin, J. N., Hooper, D., Hungate, B. A., Paquette, A., Thompson, P. L., Dee, L. E., & Dolan, K. L. (2017). A general biodiversity–function relationship is mediated by trophic level. *Oikos*, *126*, 18–31.

Thébault, E., & Loreau, M. (2003). Food web constraints on biodiversity-ecosystem function relationships. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 14949–14954.

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 471–493.

Wang, S., & Brose, U. (2018). Biodiversity and ecosystem functioning in food webs: The vertical diversity hypothesis. *Ecology Letters*, *21*, 9–20.

Wu, D., Xu, C., Wang, S., Zhang, L., & Kortsch, S. (2022). Why are biodiversity-ecosystem functioning relationships so elusive? Trophic interactions may amplify ecosystem function variability. *Journal of Animal Ecology*.

Zavaleta, E., Pasari, J. R., Hulvey, K. B., & Tilman, D. (2010). Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 1443–1446. https://doi.org/10.1073/pnas.0906829107

How to cite this article: Montoya, D. (2023). Variation in diversity–function relationships can be explained by species interactions. *Journal of Animal Ecology*, *92*, 226–228. https://doi.org/10.1111/1365-2656.13836