# Response to 'Evidence against linking the biodiversity crisis to ecosystem collapse'

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### Abstract

Re-analyzing data from our study, Bruun & Ejrnaes (2022) show that key species to productivity are more abundant than species threatened by extinction. They therefore conclude that biodiversity loss hardly hampers ecosystem processes. Acknowledging the validity of the findings, we clarify why we believe their conclusions are drawn too far.

### Response to 'Evidence against linking the biodiversity crisis to ecosystem collapse'

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# Abstract

Re-analyzing data from our study, Bruun & Ejrnaes (2022) show that key species to productivity are more abundant than species threatened by extinction. They therefore conclude that biodiversity loss hardly hampers ecosystem processes. Acknowledging the validity of the findings, we clarify why we believe their conclusions are drawn too far.

# Main text

In a recent study (Brun *et al.* 2022), we used an empirical screening approach to identify species in the French Alps and Switzerland whose abundance (1) contributed most to ecosystem productivity given environmental conditions and (2) was positively associated with productivity. We then demonstrated that the top five of these key species jointly contributed more to explaining productivity than common measures of functional community composition and diversity, and that key species were typically tall and showed high specific leaf area. However, the relationships we identified are highly dependent on environmental context, with marked deviations in low-productivity environments.

Bruun & Ejrnaes (2022) point out that our results may allow inferring how many species can go extinct before ecosystems collapse, and that we missed evaluating our findings in this light. They therefore combine data from our analysis with information on red-listed species in the study area, and demonstrate that red-listed species have significantly lower occurrence frequencies and local abundances than key species and would thus contribute less to ecosystem productivity. From these findings, they conclude that few key species may suffice to maintain productivity, and ecosystem processes in general, and that most species can go extinct without hampering the efficiency of ecosystem processes.

We believe that these conclusions overinterpret our results. Although the contrasting occurrence frequencies between key species and red-listed species are striking, they are not surprising. We focused on the most important species at regional scale and assessed to which degree their abundance serves as a proxy for productivity after accounting for environmental conditions, and such species need to be common to a minimum degree. In order to be red-listed, on the other hand, species need to be geographically restricted or locally scarce (UNEP-WCMC and IUCN 2016), so by definition key species and red-listed species hardly overlap in occurrence frequency. Does this mean red-listed species are irrelevant to productivity and ecosystem functioning in general? Most of the red-listed species are part of the 83% least frequent species that we did not investigate. That red-listed species' contributions to productivity are smaller than those of key species can be expected, and our results are not even necessary to prove this. But this is just a ranking with regards to productivity that by no means implies that disappearing red-listed species hardly affect ecosystem processes in general, and especially on the long run.

A fair assessment of the contributions of rare and red-listed species should focus on per-abundance effects rather than per-species effects, and in this respect a large body of literature highlights that they often are disproportionately important. Geographically restricted and/or locally scarce species have been shown to be important drivers of grassland multifunctionality (Soliveres *et al.* 2016) and ecosystem stability (Säterberg *et al.* 2019). Moreover, rare and red-listed species disproportionately shape the functional structure of ecosystems (Leitão *et al.* 2016), as they often exhibit distinct combinations of traits (Mouillot *et al.* 2013; Loiseau *et al.* 2020). Such functionally distinct species further promote forest productivity in harsh environments (Delalandre *et al.* 2022) and ecosystem multifunctionality across biomes (Le Bagousse-Pinguet *et al.* 2021). Although per-species effects of rare species may currently be smaller than those of key species, relative abundances are dynamic (Loreau *et al.* 2003), and rare species today may become key in the changing world of tomorrow - as long as they manage to survive (Yachi & Loreau 1999).

Research on biodiversity and ecosystem functioning advances by better understanding the system, not by debating about the validity of established hypotheses. In our analysis, we identified high importance of key-species abundance to explain ecosystem productivity and we found support for the 'mass ratio hypothesis' (Grime 1998), but we also found that trait diversity has a positive association with productivity, in line with the 'complementary resource use hypothesis' (Naeem *et al.* 1994). A joint relevance of both hypotheses has been found repeatedly for productivity (Sonkoly *et al.* 2019; Gao *et al.* 2021) and other ecosystem processes (García-Palacios *et al.*2017; Le Bagousse-Pinguet *et al.* 2021), and countless studies exist that support each of these two hypotheses individually. It therefore appears appropriate to view the 'mass ratio hypothesis' and 'complementary resource use hypothesis' as independent axioms in the context of multifunctionality: some ecosystem functions are driven more by averages of traits while others primarily respond to trait diversity or complementarity. What matters is our ability to understand ecosystem processes and how species are contributing to them, and this ability is unnecessarily limited by presuming that the main question is mass ratio or complementarity.

# References


Le Bagousse-Pinguet, Y., Gross, N., Saiz, H., Maestre, F.T., Ruiz, S., Dacal, M., *et al.* (2021). Functional rarity and evenness are key facets of biodiversity to boost multifunctionality. *Proc. Natl. Acad. Sci.* , 118.

Brun, P., Violle, C., Mouillot, D., Mouquet, N., Enquist, B.J., Munoz, F., *et al.* (2022). Plant community impact on productivity: Trait diversity or key(stone) species effects? *Ecol. Lett.* , 25, 913–925.

Bruun, H.H. & Ejrnaes, R. (2022). Evidence against linking the biodiversity crisis to ecosystem collapse. *Ecol. Lett.*

Delalandre, L., Gauzere, P., Thuiller, W., Cadotte, M., Mouquet, N., Mouillot, D., *et al.* (2022). Functionally distinct tree species support long-term productivity in extreme environments. *Proc. R. Soc. B Biol. Sci.* , 289.

Gao, W., Lei, X., Gao, D. & Li, Y. (2021). Mass-ratio and complementarity effects simultaneously drive aboveground biomass in temperate Quercus forests through stand structure. *Ecol. Evol.* , 11, 16806–16816.

Garcia-Palacios, P., Shaw, E.A., Wall, D.H. & Hattenschwiler, S. (2017). Contrasting mass-ratio vs. niche complementarity effects on litter C and N loss during decomposition along a regional climatic gradient. *J. Ecol.* , 105, 968–978.

Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* , 86, 902–910.

Leitao, R.P., Zuanon, J., Villeger, S., Williams, S.E., Baraloto, C., Fortunel, C., *et al.* (2016). Rare species contribute disproportionately to the functional structure of species assemblages.*Proc. R. Soc. B Biol. Sci.* , 283, 20160084.

Loiseau, N., Mouquet, N., Casajus, N., Grenie, M., Gueguen, M., Maitner, B., *et al.* (2020). Global distribution and conservation status of ecologically rare mammal and bird species. *Nat. Commun.* , 11, 5071.

Loreau, M., Mouquet, N. & Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci.* , 100, 12765–12770.

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., *et al.* (2013). Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. *PLoS Biol.* , 11, e1001569.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems.*Nature* , 368, 734–737.

Saterberg, T., Jonsson, T., Yearsley, J., Berg, S. & Ebenman, B. (2019). A potential role for rare species in ecosystem dynamics.*Sci. Rep.* , 9, 11107.

Soliveres, S., Manning, P., Prati, D., Gossner, M.M., Alt, F., Arndt, H., *et al.* (2016). Locally rare species influence grassland ecosystem multifunctionality. *Philos. Trans. R. Soc. B Biol. Sci.* , 371, 20150269.

Sonkoly, J., Kelemen, A., Valko, O., Deak, B., Kiss, R., Toth, K.,*et al.* (2019). Both mass ratio effects and community diversity drive biomass production in a grassland experiment. *Sci. Rep.* , 9, 1848.

UNEP-WCMC and IUCN. (2016). *Protected Planet Report 2016* . Cambridge UK and Gland, Switzerland.

Yachi, S. & Loreau, M. (1999). Biodiversity and Ecosystem Productivity in a Fluctuating Environment: The Insurance Hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* , 96, 1463–1468.