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Reply to: Data do not support large-scale oligotrophication of terrestrial ecosystems

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REPLYING TO Hiltbrunner, E., Körner, C., Meier, R., Braun, S. & Kahmen, A. *Nature Ecology & Evolution* https://doi.org/10.1038/s41559-019-0948-5 (2019).

Hiltbrunner et al.[1] apply a reductionist approach to argue that the evidence for widespread terrestrial oligotrophication[2] should be replaced with a two-factor explanation (growth dilution and depositional signatures) that does not invoke reductions in N availability, that is, the supply of N relative to plant demand. Contrary to any "adjustment of leaf photosynthetic capacity and a widening of leaf C:N ratios," there is little evidence that observed declines in foliar [N] are caused solely by photosynthetic downregulation. Photosynthetic downregulation is not universal and probably could be caused by reduced N availability[3]. A comprehensive synthesis of data on responses of plant productivity and N acquisition to elevated CO_2 in free-air carbon dioxide enrichment (FACE) experiments demonstrated that there were declines in N uptake in low-N ecosystems as a result of decreased 'access' to N, not reduced demand[4]. The growth dilution hypothesis was 'refuted' as an explanation for these declines[4].

There are many reasons that the isotopic signature of deposited N is unlikely to be causing the declines in plant $\delta^{15}N$. Although our analysis of foliar $\delta^{15}N$ was limited to after 1980, declines in foliar, tree-ring and sediment $\delta^{15}N$ (refs. [5,6,7]) pre-date the onset of widespread inorganic N fertilizer use, as well as any timing of shifts to more reduced forms of N in deposition that Hiltbrunner et al. posit. Also, despite variation in the isotopic signatures of N deposition and its sources[8], there is no evidence currently that the signature of atmospheric N deposition has been declining over time. A global, comprehensive dataset on the signature of N deposition does not exist and would be helpful to generate. Yet, even if the isotopic signature of N deposition has been declining, changes in N availability can have a stronger influence on plant $\delta^{15}N$ than the signature of added N (ref. [9]).

In asserting the importance of N deposition globally, Hiltbrunner et al. ignore or misrepresent the literature that supports the use of [N] and plant $\delta^{15}N$ as proxies for N availability and the consequences of elevated CO_2 on the N cycle. For example, multiple studies show positive relationships between soil N availability and $\delta^{15}N$ (ref. [10]), which is central to the use of $\delta^{15}N$ as a proxy for N availability. In addition, the authors characterize the global decline in foliar $\delta^{15}N$ of 0.6–1.6‰ as 'minute', yet the typical N availability gradient that ecologists measure in studies averages only 3.6‰ (ref. [10]). Our observation of declining $\delta^{15}N$ and its link to elevated CO_2 also matches the long-known observation that elevated CO_2 typically decreases foliar $\delta^{15}N$ (refs. [11,12]).

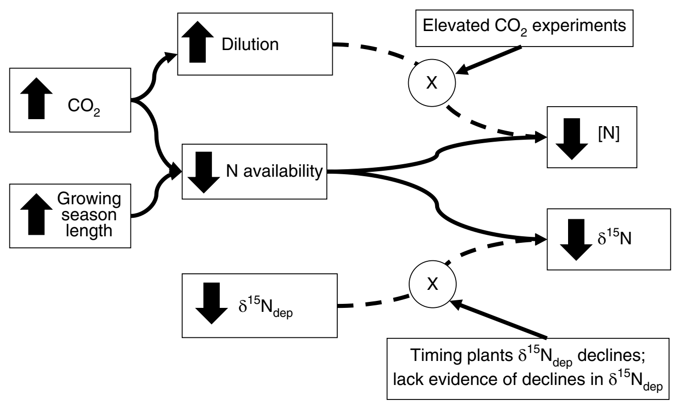

Fig. 1 | Parsimony diagram representing the relative evidence for different explanations behind declines in foliar [N] and $\delta^{15}N$. Results from elevated CO_2 experiments reduce the likelihood of declines in foliar [N] being caused by growth dilution. The timing of reduction in plant $\delta^{15}N$ from paleo-reconstructions is the main reason to downweight the role of a depositional (dep) signature. Declining N availability remains the most parsimonious explanation for global declines in foliar [N] and $\delta^{15}N$.

Overall, evidence of declining N availability in unfertilized terrestrial ecosystems continues to accumulate and extends beyond plant N concentrations and $\delta^{15}N$ (refs. [13–21]). We agree with Hiltbrunner et al. that the N cycle is complex, but complexity does not preclude the principles of parsimony. The declines in foliar [N] and $\delta^{15}N$ at the global scale are consistent with expectations of declining N availability. Declining N availability is the most parsimonious explanation for global declines in foliar [N] and $\delta^{15}N$ (Fig. 1). Most evidence supports widespread global terrestrial oligotrophication, not eutrophication, in the least anthropogenically

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affected regions, probably as a result of elevated atmospheric CO_2 and/or increased growing season length. We currently have no contemporaneous global maps of foliar [N], long-term records of soil N availability are rare, tree-ring and herbarium records of foliar [N] and $\delta^{15}N$ are not comprehensive and are largely restricted to Europe and North America, and global maps of the isotopic signature of N deposition do not exist. These gaps need to be filled if we are to better understand the pattern of global changes in N availability.

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Competing interests

The authors declare no competing interests.

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