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Local-scale changes in plant diversity: reassessments and implications for biodiversity–ecosystem function experiments

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The recent meta-analysis by Vellend et al. (2013) was an important step towards understanding average changes in local-scale plant biodiversity. The meta-analysis included studies that have assessed changes in biodiversity at small spatial scales and provided evidence that, on average, biodiversity is not changing. Past work has indicated that while biodiversity is decreasing globally but increasing regionally (Sax & Gaines 2003), it may be decreasing, neutral, or increasing locally (Vellend et al. 2013). The abundance of observational studies examining changes in biodiversity at small scales makes a local-scale biodiversity meta-analysis both

important and timely. We agree with the need for such an assessment, yet we think it may be helpful to clarify the underlying logic and reassess the data in several ways.

Firstly, the underlying logic of Vellend et al. (2013) argues that biodiversity–ecosystem function (BEF) experiments are conducted at small spatial scales and, therefore, the results from such experiments only inform us about what happens to ecosystem functions *when species are lost at such scales*. If biodiversity *is not lost* at small spatial scales, then the results from these experiments are not relevant for making conservation decisions. The emphasis above (*italics*) brings attention to the two points in this argument that we believe introduce some confusion into the conversation about biodiversity in general, and BEF experiments in particular.

1. *The issue of scale*: If the BEF relationships that are currently studied at small spatial scales are similar to BEF relationships at larger spatial scales, then loss at larger spatial scales will also indicate the utility of such experiments for informing management decisions. Notably, BEF experiments were designed to assess relationships between biodiversity and

ecosystem function at small spatial scales due to the infeasibility of assessing these relationships at larger scales. We agree that certain mechanisms behind these relationships may affect ecosystem functioning more strongly at small spatial scales, but other mechanisms may not. For example, niche complementarity may impact species coexistence more heavily in a localized neighborhood and therefore be more important at small spatial scales (Loreau et al. 2001). However, the likelihood of including species that significantly affect ecosystem function (selection effects) may be constrained by regional scale processes such as dispersal distances and evolutionary history (Loreau et al. 2001). Nonetheless, without manipulations of biodiversity at larger spatial scales, these small-scale BEF experiments give us the only controlled experimental context for understanding changes in biodiversity at any scale. To address this gap in our understanding, we emphasize the importance of pursuing mechanistic BEF experimentation (mentioned briefly in the final paragraph of Vellend et al. 2013). Focusing on mechanisms will help determine the extent to which small-scale experiments can inform BEF relationships, and the implications of changes in biodiversity, at larger-scales. Current research is addressing these mechanistic underpinnings in terms of changes in species richness associated with compositional changes (Reich et al. 2004, Ebeling et al. 2014), genetic changes (Scherer-Lorenzen et al. 2007, Jousset et al. 2011), non-random species additions (Roscher et al. 2005) and removals (Diaz et al. 2003), and species evenness vs. diversity relationships (Scherer-Lorenzen et al. 2007). We see much promise in the potential to understand how biodiversity is related to ecosystem function at any scale, via mechanistic hypothesis-driven BEF experiments in the future.

2. *Biodiversity loss*: Vellend et al. (2013) posits that if biodiversity is not *lost* at small spatial scales, the results of BEF experiments are not useful for making conservation decisions. Importantly, this is only one side of the BEF argument, as BEF experiments also inform our understanding of how ecosystems should be managed when biodiversity *increases* at small spatial scales. In fact, BEF experiments demonstrate that when biodiversity *increases or decreases* we would expect a corresponding increase or decrease in ecosystem functioning (Isbell et al. 2011, Reich et al. 2012). Indeed, almost a quarter of the studies assessed in Vellend et al. (2013) reported increases or decreases in biodiversity that were greater than

20%. As argued in Vellend et al. (2013), changes of this magnitude will almost certainly have large implications for ecosystem function (Hooper et al. 2012). There are even more datasets included in this meta-analysis that demonstrate losses or gains of <20% (Vellend et al. 2013, Supporting Information, Fig. S2), and previous BEF experiments have demonstrated that even small changes in biodiversity have important implications for ecosystem function (Reich et al. 2012). It is important to consider that while an average can tell us something about the central tendency in a dataset, in this particular case, it does not reflect the large number of results where the change in biodiversity was not equal to zero. Regardless of the global average, a significant gain in biodiversity in one area does not compensate locally for a significant loss in biodiversity in a different area.

Finally, the conclusions of Vellend et al. (2013) rely heavily on the studies that were selected for the meta-analysis. Depending on the studies included, and the distribution of studies that have been published in the literature, certain types of drivers, habitats, and continents can have a disproportionately large effect on the results in a meta-analysis that is conducted in this way (Powers et al. 2011). For example, in their analysis there was a large representation of drivers that are expected to increase biodiversity (post-disturbance and post-fire) with an underrepresentation of other important drivers that often result in biodiversity loss (e.g. nitrogen deposition and habitat fragmentation). In fact, a closer examination of the data (Vellend et al. 2013, Supporting Information, Dataset S1) demonstrates that while nitrogen deposition is a known driver of biodiversity loss (Tilman 1987) it is lumped with air pollution and acidification in a total of eight studies on just two continents that fall under the broad heading of “pollution”. Habitat fragmentation appears to have been left out of the analysis completely. A larger representation of drivers across a range of conditions is important, as some drivers, such as nitrogen deposition, may cause significant loss of diversity in one ecosystem (Tilman 1987) but not in another (Lu et al. 2010). We suggest that a future analysis of this same dataset should assess the significant drivers and driver-habitat interactions that control local scale changes in biodiversity, before extrapolating to a global scale (Powers et al. 2011). Currently this may be difficult, as these types of biodiversity assessments are likely non-randomly

distributed in the literature (e.g. there are very few in African forests), which points to the urgent need for this type of biodiversity assessment across a wider range of systems in the future.

Overall, we agree with some of the conclusions made by the authors. For example, as the authors make implicitly clear, the lack of BEF experiments at large spatial scales means we need to establish experiments that address the mechanistic underpinning of the BEF relationship across scales. This type of work will help inform our understanding of the implications of species loss, or gain, at any scale (Cardinale 2012). We are excited about the discussion that this type of work inspires within the ecological community. However, we believe that their conclusions should be revisited based on a careful assessment of (1) how BEF experiments function mechanistically across scales, (2) how BEF experiments inform management decisions in all instances of biodiversity loss *or* gain, and (3) how their meta-analysis may be implemented differently and how this may lead to different conclusions. We think that there is great potential to use such meta-analyses to make clear recommendations for how to direct biodiversity research in the future.

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