



Biodiversity–ecosystem function experiments reveal the mechanisms underlying the consequences of biodiversity change in real world ecosystems

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Abstract

In a recent Forum paper, Wardle (*Journal of Vegetation Science*, 2016) questions the value of biodiversity–ecosystem function (BEF) experiments with respect to their implications for biodiversity changes in real world communities. The main criticism is that the previous focus of BEF experiments on random species assemblages within each level of diversity has ‘limited the understanding of how natural communities respond to biodiversity loss.’ He concludes that a broader spectrum of approaches considering both non-random gains and losses of diversity is essential to advance this field of research. Wardle’s paper is timely because of recent observations of frequent local and regional biodiversity changes across ecosystems. While we appreciate that new and complementary experimental approaches are required for advancing the field, we question criticisms regarding the validity of BEF experiments. Therefore, we respond by briefly reiterating previous arguments emphasizing the reasoning behind random species composition in BEF experiments. We describe how BEF experiments have identified important mechanisms that play a role in real world ecosystems, advancing our understanding of ecosystem responses to species gains and losses. We discuss recent examples where theory derived from BEF experiments enriched our understanding of the consequences of biodiversity changes in real world ecosystems and where comprehensive analyses and integrative modelling approaches confirmed patterns found in BEF experiments. Finally, we provide some promising directions in BEF research.

A brief history of the biodiversity–ecosystem functioning debate

The notion that biodiversity could be an important determinant of ecosystem functions stems from observations of natural communities (Elton 1958) as well as theoretical models (Tilman et al. 1997a; Yachi & Loreau 1999) and has been around for decades. The history of biodiversity–ecosystem functioning (BEF) research is peppered with debates on the design and interpretation of experiments as well as the validity and generality of the findings (e.g., Givnish 1994; Tilman et al. 1994; Aarssen 1997; Grime 1997; Huston 1997; Lepš 2004; Schmid & Hector 2004; Duffy 2009; Wardle & Jonsson 2010). One of the first BEF experiments used different concentrations of N addition and studied plant diversity and productivity responses (Tilman & Downing 1994), finding a positive biodiversity–stability relationship. This study was criticized because it did not manipulate biodiversity as an independent factor, meaning that stability of plant biomass production was likely (co-)determined by the N treatment (Givnish 1994). After the first ‘wave’ of scientific debate, Grime (1997) concluded that: ‘...neither evolutionary theory nor empirical studies have presented convincing evidence that species diversity and ecosystem function are consistently and causally connected.’

This stimulated experiments that directly manipulated biodiversity in random combinations to focus on plant species diversity effects on functioning (e.g., Tilman et al. 1997b; Hooper et al. 2005). The results were surprisingly significant: community biomass production increased with an increasing number of species (Hooper et al. 2005). However, these early experiments were criticized because of the limitation of their design to separate complementarity (whereby a high-diversity plant community can use resources more completely due to differences in resource acquisition among species) from sampling effects (elevated chance of including species of high productivity in high-diversity treatments; Aarssen 1997; Huston 1997), thus weakening their relevance for real world ecosystems.

The third generation of BEF experiments took this criticism into account by establishing complex experiments designed to separate complementarity from sampling effects and functional group from species richness effects (e.g., Reich et al. 2004; Roscher et al. 2004). Nonetheless, these experiments have also provoked debate over their realism, with some arguing that randomly assembled communities do not mirror real world assembly and disassembly, which are determined by the simultaneous interplay of abiotic and biotic filters in time and space (Götzenberger et al. 2012). To more specifically quantify differences between non-randomly and randomly assembled communities, and test concrete hypotheses regarding the

complementarity and redundancy of species in experimental and real world communities, more recent experiments focus less on the number of species *per se* and assess the functional and phylogenetic dissimilarity within species assemblages (Scherer-Lorenzen et al. 2007; Cadotte 2013; Ebeling et al. 2014). Other experiments have implemented a non-random biodiversity loss scenario and can compare the results with randomly assembled communities (e.g., Schlöpfer et al. 2005; Bruelheide et al. 2014). Debate about the relevance of BEF experiments to non-random biodiversity loss is not new (Lepš 2004; Schmid & Hector 2004; Duffy 2009; Wardle & Jonsson 2010). Some recent papers, however, have refueled this debate by highlighting that no consistent loss of biodiversity has been found at the local scale in real world ecosystems (Vellend et al. 2013; Wardle 2016).

Wardle (2016) concludes that BEF experiments have been ‘advocated and implemented at the expense of other approaches,’ and calls for a broader spectrum of experimental approaches in the future. He lists three main criticisms of BEF experiments to support his conclusion, which we will discuss in this paper.

1 Wardle (2016) sees ‘little evidence that species richness is consistently declining at local spatial scales’ by referring to two recent global analyses (Vellend et al. 2013; Dornelas et al. 2014a).

2 Wardle (2016) questions whether inconsistent findings in BEF experiments and context-dependencies of BEF relationships can be used in a meaningful way to understand the consequences of biodiversity loss in real world ecosystems.

3 Wardle (2016) states that BEF experiments cannot ‘mimic what happens in real world ecosystems either when local extinctions occur or when species losses are offset by gains of new species.’

Gains and losses in local biodiversity

A heated debate in ecology has recently developed around whether biodiversity is decreasing at local scales (Vellend et al. 2013; Dornelas et al. 2014a,b; Wright et al. 2014; McGill et al. 2015; Gonzalez et al. 2016). This topic and the underlying controversy are much more thoroughly covered in recent perspectives papers (e.g., Wright et al. 2014; McGill et al. 2015) and re-analyses of the respective data sets (Gonzalez et al. 2016). Our focus, here, is to discuss the criticism from Wardle (2016) over the use of BEF experiments to predict ecosystem functioning following species losses, despite the fact that many ecosystems may not in fact be losing species diversity.

Wardle (2016) emphasizes the results of Newbold et al. (2015) by stating that: ‘there is little evidence that species richness is consistently declining at local spatial scales

except where intensive land use and/or resource exploitation is taking place.' However, managed systems currently make up ~50% of all land (McGill et al. 2015), with the percentage being expected to increase in the future. While extensively managed systems may not experience significant biodiversity loss, intensively managed systems have been shown to lose species (Allan et al. 2015; Newbold et al. 2015).

Notably, results from Vellend et al. (2013) and Dornelas et al. (2014a) do not specifically demonstrate that biodiversity change does not occur at the local scale (Gonzalez et al. 2016). For example, an alarming outcome of Dornelas et al. (2014a) was that beta-diversity decreased substantially over time (Dornelas et al. 2014b), indicating directional shifts in community and trait composition. In fact, BEF experiments have tested a vast range of different community compositions at different diversity levels, and they show that species turnover and functional identities can have a strong influence on ecosystem functioning, particularly when diversity is low. An increasing number of BEF experiments manipulate the functional diversity and dissimilarity within assemblages (e.g., Scherer-Lorenzen et al. 2007; Ebeling et al. 2014), and the respective results may help to predict the consequences of non-random shifts in community and trait composition.

We agree with Wardle (2016) and others (e.g., Vellend et al. 2013; Dornelas et al. 2014a) that all scenarios of biodiversity change (no change, gain, loss) are found in nature. A plethora of different processes and biodiversity trajectories, however, underpin those changes (Fig. 1; McGill et al. 2015; Gonzalez et al. 2016). Detection and attribution of diversity changes to human drivers have not yet been well justified. For example, studies on biodiversity change need to consider the appropriate baseline measure of biodiversity. What is the reference point of the recent biodiversity change studies? When did anthropogenic activities start affecting ecosystems, and which drivers were most important at which points in time? These questions are extremely difficult to answer. By ignoring the 'point of departure' in biodiversity change studies, we are likely to mix several fundamentally different conditions, processes and biodiversity change trajectories (Fig. 1; Gonzalez et al. 2016). Furthermore, reported diversity changes have not been adequately associated with ecosystem functioning. This topic needs additional attention (Dornelas et al. 2014b) and requires experiments manipulating different facets of biodiversity and community composition in different global change scenarios (Cardinale et al. 2012).

Contrary to Wardle's (2016) claim, we would like to point out that BEF experiments are not conducted at the expense of experiments that consider non-random diversity changes. Indeed, there has been an explosion of

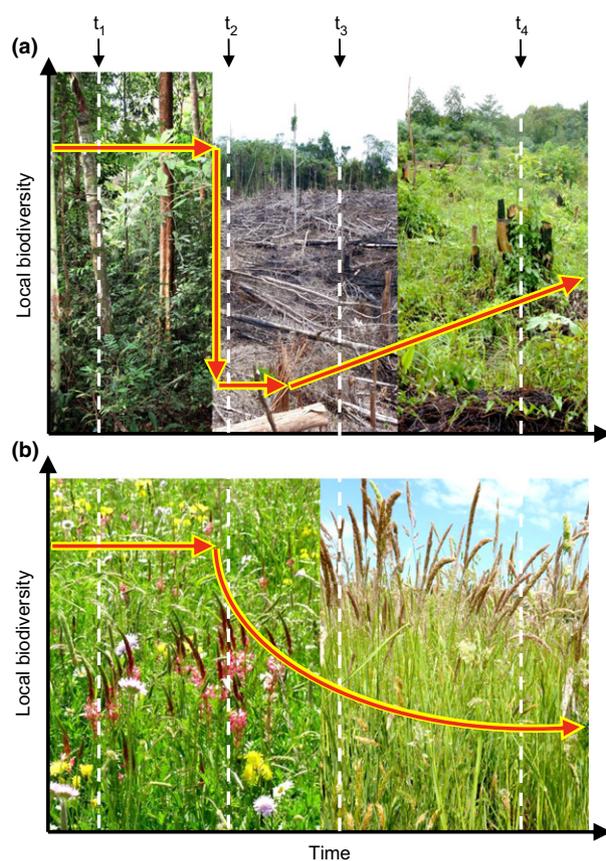


Fig. 1. Two selected scenarios of local biodiversity change over time due to human activities. **(a)** A pristine rain forest was clear-cut and then recovered slowly. **(b)** Fertilization of a species-rich meadow slowly decreased plant diversity over time. Biodiversity was assessed four times (t_1 – t_4). Note that there are also many cases where anthropogenic activities have increased local biodiversity, and the examples presented here are not intended to provide an exhaustive overview, but to introduce the methodological difficulties in current biodiversity research. If we believe that those two habitats had not been disturbed by human activities before, we could comfortably submit that time point t_1 is the adequate reference point ('baseline measure of biodiversity'). In both examples, a comparison of t_1 and t_4 would lead us to conclude that human activities decreased local biodiversity because $t_4 - t_1 < 0$. However, it is extremely hard to find adequate baseline measurements in the few time series data sets that exist today. Thus, it is likely that such data sets contain many situations where the first sampling was conducted after the anthropogenic disturbance had occurred (Gonzalez et al. 2016), and the difference between a trend and an oscillation will depend on the temporal scale that the observations take place. That is, if we now compare t_2 with t_3 , we would conclude that biodiversity has not changed significantly over time in (a), while it decreased in (b). Comparing t_2 with t_4 would suggest that biodiversity increased over time in (a), but decreased in (b). This simple example shows that it is very likely to observe all possible changes in biodiversity over time when we ignore the context (baseline, biodiversity change driver) of the measurement or argue that all change scenarios are of equal explanatory power. Photo credit: Stefan Scheu (a), Alexander Fergus (b, left), Anne Ebeling (b, right).

highly influential experiments focused on understanding the influences of different global change drivers on biodiversity and BEF relationships (e.g., Nutrient Network, Borer et al. 2014; Drought-Net, <http://wp.natsci.colostate.edu/droughtnet/>; Zostera Experimental Network, <http://zenscience.org/about-zen/>), which account for non-random changes in species assemblages. Comparisons between experiments that directly and indirectly manipulate diversity in combination with multiple global change drivers are emerging and reflect promising future directions (Hautier et al. 2014). Such experiments will help to identify the resulting global change impacts on mechanisms that mediate the regulation of ecosystem functions under different biodiversity scenarios.

Do we need consistent BEF findings to gain mechanistic insights?

A wealth of studies has provided compelling evidence for positive BEF relationships (Tilman et al. 2014; Isbell et al. 2015), but this cannot be found for all studies (Isbell et al. 2015) or all functions (Lefcheck et al. 2015). Do those contrasting results undermine the relevance of BEF experiments? We suggest that the exact opposite is true. Case studies and meta-analyses exploring and synthesizing BEF relationships across different experimental contexts have provided mechanistic insights into relationships found in nature by identifying the contexts under which specific mechanisms are likely to regulate ecosystem properties. In this way, such inconsistencies in the results of BEF experiments can effectively identify important context-dependencies, allowing us to better understand how biodiversity will affect ecosystem functioning in a range of real world scenarios.

In this vein, experiments using simple model communities have been established to directly test context-dependent mechanisms (e.g., Jousset et al. 2011). Habitat complexity and environmental stress are two such contexts that likely give rise to apparent inconsistencies in BEF relationships. Complex and heterogeneous environments provide a larger variety of niches, i.e. a larger habitat space, than simple and homogenous environments, thereby determining the strength and direction of BEF relationships (Loreau et al. 2003; Cardinale 2011; Jousset et al. 2011). Indeed, Tylianakis et al. (2008) demonstrate this phenomenon in a real world system, showing that niche complementarity strongly increases with resource heterogeneity. In another recent study, Craven et al. (2016) highlighted the context-dependency of complementarity effects and provided important insights regarding where biodiversity effects should be more or less pronounced. They show that, across ten plant diversity experiments with an orthogonal manipulation of nutrient addition, this

perturbation did not alter BEF relationships but decreased plant complementarity effects at high plant diversity (Craven et al. 2016). From these studies we see that inconsistencies in results revealed by meta-analysis can allow us to identify the nature of context-dependent results. Results from several BEF studies thus suggest that the way humans transform real world ecosystems will determine how species interact and influence the strength and form of BEF relationships. This topic is of particular importance as climate extremes are likely to increase in frequency and magnitude in the future, and one essential function of biodiversity may be the stabilizing effect of multiple species on ecosystem responses to climate variability (MacArthur 1955; McNaughton 1977; Isbell et al. 2015).

BEF experiments unravel the mechanisms to understand real world ecosystem responses

In line with Wardle (2016), we agree that 1:1 comparisons between BEF experiments and real world ecosystems can be misleading, raising the critical question: what can BEF experiments tell us about real world communities? Based on recent comprehensive comparisons of results of BEF experiments and real world communities, we suggest that BEF experiments can inform us about the mechanisms underlying ecosystem responses to biodiversity change. This means that BEF experiments provide unique and indispensable mechanistic information, which cannot be derived from observations in real world and/or removal experiments alone (Box 1; Fig. 2). We will discuss several examples substantiating this statement.

A critical consideration for the results of BEF experiments is whether similar patterns can also be found in real world ecosystems. Recent studies have shed new light on the complex relationship between biodiversity and productivity in real world ecosystems (Wardle & Zackrisson 2005; Isbell et al. 2013; Grace et al. 2016). Specifically, Grace et al. (2016) used structural equation modelling to take into account the many drivers of biodiversity and productivity, such as climatic variables, disturbances and environmental heterogeneity (Fig. 3). By acknowledging the complex network of causal relationships operating in ecological systems, they confirmed the positive relationship between plant species richness and productivity found in many BEF experiments. Similarly, Isbell et al. (2013) separated effects of N addition on plant biomass production from effects on plant diversity, as well as the effects of N addition-induced changes in plant diversity on biomass production, which had not been explicitly separated in an earlier, criticized study (Tilman & Downing 1994). As suggested by Wardle (2016), N addition caused non-random biodiversity loss, particularly of dominant C₄ grasses. Interestingly, the loss of these species caused stronger declines

Box 1: The interplay of theory, experimentation and observation advance BEF research

Ecological understanding is not a black and white issue that can be classified by one approach. Independent theoretical, experimental and observational studies often address overlapping ecological questions, and their results consequently inform the next generation of studies. The many shades of grey reflect integration of scientists from different fields of study and schools of thought, who hone existing theories and develop new ones (Fig. 2). Similarly, BEF studies cannot be categorized with one approach: the relationship between biodiversity and ecosystem functioning has been tested widely in experimental (Hooper et al. 2005) and observational (Grace et al. 2016; van der Plas et al. 2016) settings and theory-based modelling approaches (Tilman et al. 1997a; Yachi & Loreau 1999). Results from these studies have both generalized knowledge regarding the importance of biodiversity change and generated new, broader questions integrating ideas from other fields in ecology, including disease ecology (Civitello et al. 2015), ecosystem services (Cardinale et al. 2012), food web ecology (Hines et al. 2015) and evolutionary ecology (Zuppinge-Dingley et al. 2014). Findings from these studies are not strictly limited to the BEF experimental model: a multitude of studies test for BEF relationships in real world ecosystems (e.g., Winfree et al. 2015; Grace et al. 2016; van der Plas et al. 2016) to gain insights into ecological mechanisms and their relationships to ecosystem process. Thus, BEF will contribute to and benefit from interactions with other fields in ecology, advancing biodiversity science on multiple fronts.

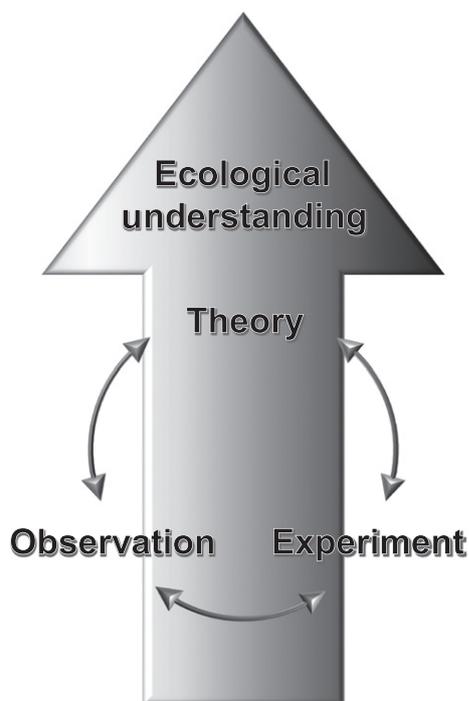


Fig. 2. Graphic depiction of the non-linearity of scientific discovery evolving via interactions among theory, experimentation and observation. The parallel use of different approaches is indicated by the different shades of grey in the arrow.

in plant biomass production than found in an adjacent BEF experiment (Isbell et al. 2013); an effect that can be understood and predicted when accounting for the functional composition of the plant communities in the BEF experiment. The authors concluded that long-term effects

of anthropogenic drivers on ecosystem functions are contingent upon how the respective drivers influence biodiversity as well as the functional composition of communities.

Notably, BEF theory does not predict biogeographic patterns of productivity–diversity relationships and does not claim that ecosystems with more species should have higher productivity than ecosystems with fewer species as biodiversity and productivity may be driven by environmental factors (Fig. 3). However, BEF theory predicts that local biodiversity changes within an ecosystem should have significant consequences for the functioning of that given ecosystem after accounting for other external variables, such as environmental heterogeneity (Fig. 3). The findings of Isbell et al. (2013) and Grace et al. (2016) substantiate the general predictions from BEF experiments by demonstrating that the often-reported discrepancies in results between experimental and real world BEF studies may in fact be due to multiple interacting and unexplained drivers typically operating in real world systems.

Further support for the application of results from BEF experiments has recently come to light by testing BEF theory in naturally assembled and experimentally manipulated plant communities. Specifically, theory derived from BEF experiments predicts that biodiversity should increase temporal stability of ecosystem functioning (Isbell et al. 2015) via the asynchrony in the performance of different species (de Mazancourt et al. 2013). Indeed, Hautier et al. (2014) showed that plant diversity increases stability of plant biomass production through elevated species asynchrony at high plant diversity, generalizing results from the BIODDEPTH experimental network to real world grasslands of a global network of plant observation plots

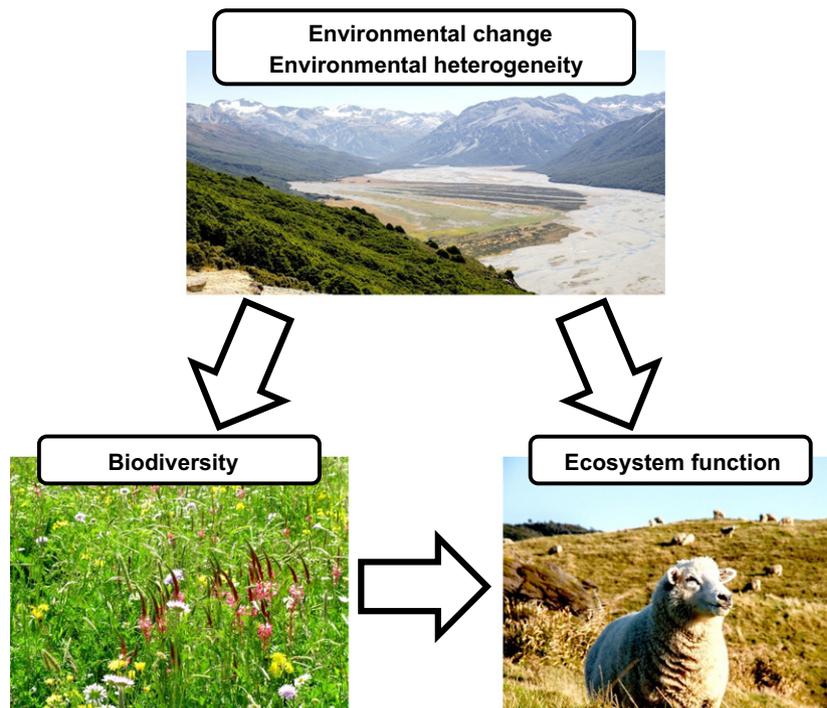


Fig. 3. Environmental change and heterogeneity determine the biodiversity and the functioning of ecosystems. In addition, changes in biodiversity can have significant effects on ecosystem functioning, which can be masked by strong environmental gradients (Isbell et al. 2013). Only by accounting for environmental heterogeneity can the role of biodiversity for ecosystem functioning be wholly realized (Grace et al. 2016). Figure modified after Isbell et al. (2013).

(Nutrient Network). Hautier et al. (2014) observed that eutrophication reduces stabilizing effects of biodiversity, a result that is similar to the weaker complementarity effects with nutrient addition found by Craven et al. (2016) in a synthesis of BEF experiments. Considered together, these results support the view that a complex resource environment can enhance biodiversity effects (Tylianakis et al. 2008; Jousset et al. 2011), and that a reduction in niche dimensionality can decrease BEF relationships (Jousset et al. 2011).

Several studies in real world ecosystems found strong BEF relationships (e.g., Mora et al. 2011); however, others also found weaker and/or context-dependent biodiversity effects (Wardle & Zackrisson 2005). While context-dependent BEF relationships are discussed above, one likely explanation for stronger BEF relationships in nature is the higher number of species interactions in real world ecosystems (Flombaum & Sala 2008; Eisenhauer 2012; Mora et al. 2015). Indeed, understanding species interactions may be the key to appreciating the consequences of biodiversity change. For instance, in BEF experiments, considering plant species interactions has been shown to increase the predictive power of statistical models (e.g., Connolly et al. 2011). Further, several recent studies have highlighted the role of multitrophic interactions in shaping BEF relationships (Hines et al. 2015). Wagg et al. (2011)

observed in a BEF experiment that a higher number of mycorrhizal species increases complementary nutrient uptake by plants, a mechanistic link that is likely to also be of high importance in natural grasslands (van der Heijden et al. 1998). Conversely, BEF studies show that high-diversity plant communities are better protected against soil-borne pathogens by facing a higher diversity but lower density of pathogens through a dilution effect (Fig. 4; Civitello et al. 2015; Johnson et al. 2015). In a recent meta-analysis, Civitello et al. (2015) observed significant and consistent effects of host diversity on parasite abundance. Notably, diversity effects did not differ between experiments and observational studies, suggesting that the patterns and mechanisms found in BEF experiments are valid in real world ecosystems (Johnson et al. 2015) and agricultural systems (Smith et al. 2015). Indeed, farmers have long been aware of the accumulation of soil-borne pathogens in crop monocultures and have implemented management strategies, like crop rotation, to increase 'temporal plant diversity' and crop yield (Eisenhauer 2012; Smith et al. 2015).

In fact, terrestrial BEF experiments closely mimic agriculture cropland systems where species assemblages, i.e. intercropping, are consistently selected and maintained for the production of particular crop species (Wardle 2016). Croplands now make up a large proportion of the Earth's

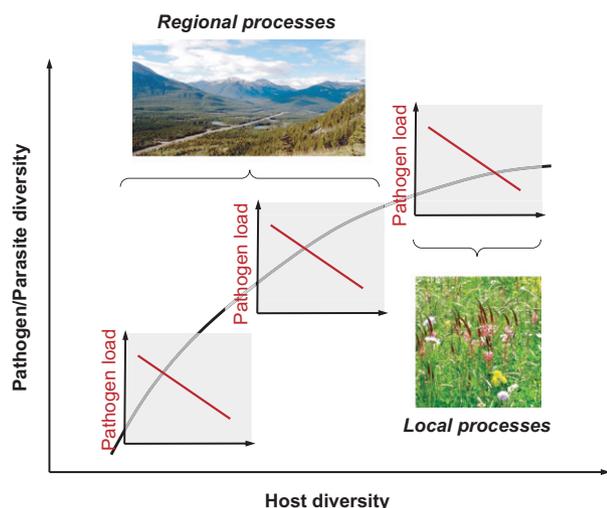


Fig. 4. The relationship between host diversity and pathogen or parasite diversity is positive across different communities, but the pathogen load per host individual is locally reduced with a higher diversity of hosts through a dilution effect (Civitello et al. 2015; Johnson et al. 2015). Figure modified after Johnson et al. (2015).

terrestrial ecosystems, with recent global estimates at around 12% of ice-free land (1.53 billion ha; Foley et al. 2011), and this could increase by as much as ~10% by 2030 (Lambin & Meyfroidt 2011). These novel ecosystems, resulting from human manipulation, comprise a range of diversity levels with important differences in ecosystem functioning. For example, intercropping – a common low-intensity practice of growing multiple crop species within the same agricultural plot – has been shown to increase yields beyond those of monocultures (e.g., Li et al. 2007). Clear links between BEF experiments and cropland diversity and agricultural intensity (Li et al. 2007) have been made before, highlighting the directly transferable results of BEF experiments to these globally important novel ecosystems.

Conclusion

We agree with Wardle (2016) that different complementary approaches are promising to advance our mechanistic understanding of BEF relationships in real world ecosystems by, for example, considering the role of different facets of biodiversity (e.g., Díaz et al. 2003; Scherer-Lorenzen et al. 2007; Cadotte 2013; Ebeling et al. 2014), meta-community processes (Leibold et al. 2004) and compositional changes caused by non-random biodiversity gains and losses (Dornelas et al. 2014b). This is needed particularly to scale up findings from the plot to management- and policy-relevant scales (Fig. 4; Cardinale et al. 2012; Tilman et al. 2014; Burley et al. 2016; van der Plas

et al. 2016). By incorporating spatial scaling of BEF relationships, BEF experiments could play a pivotal role in merging the principles of community ecology with those of macroecology (Spasojevic et al. 2016). Further, we have to embrace the complexity of multitrophic communities in BEF experiments to mechanistically link biodiversity to the multi-functionality of ecosystems (Barnes et al. 2014; Allan et al. 2015; Hines et al. 2015). However, this complexity can only be understood by experimentally controlling for part of the complexity in nature, to identify the relevance of particular mechanisms (Lawton 1995). Experiments will always come with some limitations and simplifications in comparison to nature (e.g., Lawton 1996), and ecologists have to be careful when relating the findings in experiments to observations in real world communities (Grace et al. 2016). However, BEF experiments have substantially advanced our appreciation of the role of biodiversity for the functioning of ecosystems; while three decades ago many ecologists questioned the functional importance of biodiversity, its significance for the functioning of ecosystems is well established, and we currently are in the midst of the exciting quest for the underlying mechanisms. BEF experiments have provided many promising hypotheses that need to be tested in future experiments and in real communities and at different spatial scales. While results from real world BEF studies remain inconsistent (e.g., Wardle & Zackrisson 2005; Allan et al. 2015), several recent analyses of data sets of observational studies (e.g., Hautier et al. 2014; Civitello et al. 2015; Grace et al. 2016) indicate that patterns found in real world ecosystems can now be better understood when applying BEF theory. Therefore, we second Wardle's (2016) proposal to utilize a high diversity of experimental approaches. Just as high species diversity elevates functioning of ecological communities, high diversity of approaches elevates functioning of scientific communities. Considered together, these approaches allow us to better comprehend the consequences of anthropogenic biodiversity change.

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