

## PERSPECTIVE

# We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data

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**Editor:** Franck Courchamp**Abstract**

Our current, empirical understanding of the relationship between biodiversity and ecosystem function is based on two information sources. First, controlled experiments which show generally positive relationships. Second, observational field data which show variable relationships. This latter source coupled with a lack of observed declines in local biodiversity has led to the argument that biodiversity-ecosystem functioning relationships may be uninformative for conservation and management. We review ecological theory and re-analyse several biodiversity datasets to argue that ecosystem function correlations with local diversity in observational field data are often difficult to interpret in the context of biodiversity-ecosystem function research. This occurs because biotic interactions filter species during community assembly which means that there can be a high biodiversity effect on functioning even with low observed local diversity. Our review indicates that we should not necessarily expect any specific relationship between local biodiversity and ecosystem function in observational field data. Rather, linking predictions from biodiversity-ecosystem function theory and experiments to observational field data requires considering the pool of species available during colonisation: the local species pool. We suggest that, even without local biodiversity declines, biodiversity loss at regional scales—which determines local species pools—may still negatively affect ecosystem functioning.

**KEYWORDS**

community assembly, ecosystem function, local species pool, realised diversity, regional species pool

**INTRODUCTION**

Does biodiversity matter to the functioning of the Earth's ecosystems? A considerable part of the ecological literature since the 1990s has examined this question in the light of rising extinction rates and ecosystem change (Cardinale et al., 2012; Loreau et al., 2001; Tilman et al., 2014). However, identifying what causes variation in ecosystem function has been challenging. First, there

are many hypothesised drivers such as the environment, species composition (i.e. the identity and abundance of species) and species diversity (predominantly species richness), (Diaz et al. 2007). Second, many of these hypothesised drivers covary and feedback on each other (Adler et al. 2011; Grace et al., 2016). Despite this complexity, there is a current consensus in the literature that species diversity is a major determinant of variation in ecosystem function at local spatial scales (Hooper et al.,

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2012; Tilman et al., 2012), where species interactions strongly affect species composition (McGill et al., 2015; Sax & Gaines, 2003).

The major source of evidence that species diversity increases ecosystem function comes from classic biodiversity-ecosystem function (BEF hereafter) experiments combined with ecological theory (reviewed in Tilman et al., 2014). When we refer to classic BEF theory and experiments, we refer to the substitutive design whereby different numbers of species are inoculated into local-scale habitat patches with similar environmental conditions whilst controlling for the overall abundance of inoculated species (Schmid et al., 2002). The communities assemble and, after some time, the relationship between some measure of species diversity (most commonly species richness, i.e. the number of inoculated species) and ecosystem function is examined. Several hundreds of these experiments have been conducted with different taxa, and in different habitat types. Multiple syntheses and meta-analyses confirm a general positive relationship between inoculated species richness and function (e.g. Balvanera et al., 2006; Cardinale et al., 2011). The form of the relationship is usually positive and saturating and is reasonably conserved across taxa and habitats (O'Connor et al., 2017). The results from these syntheses underpin the current consensus that, at local spatial scales (local hereafter), species diversity increases ecosystem function (Cardinale et al., 2012; Isbell et al., 2017).

## APPLYING BEF RESEARCH TO OBSERVATIONAL FIELD DATA FROM REAL-WORLD ECOSYSTEMS

The interpretation of the local BEF relationship is important because, as several recent studies have pointed out, local species diversity may not be declining with the same ubiquity as global-scale species diversity (reviewed in Chase et al., 2019; McGill et al., 2015). Analyses of time-series data from aquatic and terrestrial ecosystems across the globe show that, while local species composition is changing, there has been no systematic decline in local species richness over the last 100 years (Dornelas et al., 2014; Elahi et al., 2015; Blowes et al., 2019; but see Newbold et al., 2015; Gonzalez et al., 2016; Mentges et al., 2021). This has led some authors to question the relevance of BEF research to the current biodiversity crisis. For example both Vellend et al. (2013) and Wardle (2016) have, in some form, argued that BEF research may have little relevance for justifying conservation in the absence of declines in local species richness in real ecosystems (see also Schwartz et al., 2000; Srivastava & Vellend 2005 for further discussions).

In addition to questions about the relevance of BEF research to conservation and management in the current biodiversity crisis, the last decade has seen a marked increase in studies using observational field data (used

interchangeably with *field data* hereafter) to correlate local species diversity with some measure of ecosystem function (reviewed in van der Plas, 2019). Typically, these studies sample plots (i.e. local habitat patches) across a spatial species diversity gradient and relate variation in local species diversity to ecosystem function. The justification for examining BEF relationships in field data is frequently based on the results of BEF theory and experiments (e.g. Duffy et al., 2017). Many of these field studies aim to determine whether the results of short-term local BEF experiments are consistent at larger spatial scales with greater levels of environmental heterogeneity and more complex trophic structures (Duffy et al., 2017).

Studying the BEF relationship using field data has been criticised previously. In field data, the relationship between plant productivity (a commonly measured ecosystem function) and observed local species diversity can vary considerably (Mittelbach et al., 2001). For example, negative and unimodal productivity-species diversity relationships are reasonably common in field data (Adler et al., 2012; Fraser et al., 2015). This variation appeared to contradict the results from BEF experiments that typically found positive relationships between species diversity and productivity (Balvanera et al., 2006; Cardinale et al., 2011; Hooper et al., 2005). This paradox was resolved by recognising that studies using field data were examining the relationship between productivity and species diversity without controlling for differences in environmental conditions (e.g. nutrient availability, rainfall). In contrast, BEF experiments were directly manipulating local species diversity whilst experimentally controlling for environmental conditions (Bengtsson et al., 2002; Loreau et al., 2001; Schmid, 2002). Most recent studies using field data attempt to control for environmental variation and other potentially confounding factors (e.g. species or functional composition) with a set of covariates (e.g. Gamfeldt et al., 2013; Grace et al., 2016). Whilst controlling for covariates may partially resolve this problem, it is rare to have a complete set of covariates (Grace & Irvine 2020; Laubach et al. 2020). In addition, it remains unclear which set of covariates are required to isolate a possible effect of species diversity. However, setting aside the covariate issue, there is an additional fundamental problem with directly applying insights from BEF theory and experiments to observational field data which is the subject of this *Perspectives* article.

## REALISED DIVERSITY SHOULD NOT NECESSARILY CORRELATE POSITIVELY WITH ECOSYSTEM FUNCTIONING IN OBSERVATIONAL FIELD DATA

Both (1) the argument that BEF research is unimportant without declines in local species diversity and (2) the use

of field data to examine BEF relationships rely on a key assumption. They both assume that the number of species present at a given time (the realised diversity hereafter) is the driver of ecosystem functioning. However, this is not always the case. Classic BEF theory and experiments typically manipulate the number of species that are initially inoculated into different habitat patches (initial diversity hereafter), (Rychteká et al., 2014; Stachová & Lepš, 2010). Classic BEF theory shows that initial diversity then affects ecosystem functioning through two groups of mechanisms: selection and complementarity effects (Fox, 2005; Loreau & Hector, 2001). Whilst selection and complementarity effects can both increase functioning, the biotic processes driving these effects can have very different consequences for realised diversity.

Complementarity effects occur when interactions among coexisting (or co-occurring) species increase (or decrease) ecosystem function (Barry et al., 2019; Loreau, 2000; Tilman, 1999; Turnbull et al., 2013). For example positive complementarity effects can arise from local resource partitioning among species (Cardinale, 2011; Williams et al., 2017). Complementarity effects are highest when many species coexist (or co-occur) and contribute to ecosystem functioning (Godoy et al., 2020; Loreau & Hector, 2001; Turnbull et al., 2016). Therefore, when complementarity effects are strong, many species coexist and might, for example, partition resources locally or through time (Chesson et al., 2001; Gross & Cardinale, 2007; Turnbull et al., 2013). In this case, interactions among coexisting species increase ecosystem function relative to the monoculture expectations of the constituent species (Figure 1a; Barry et al., 2019; Godoy et al., 2020 provide an exemplary example).

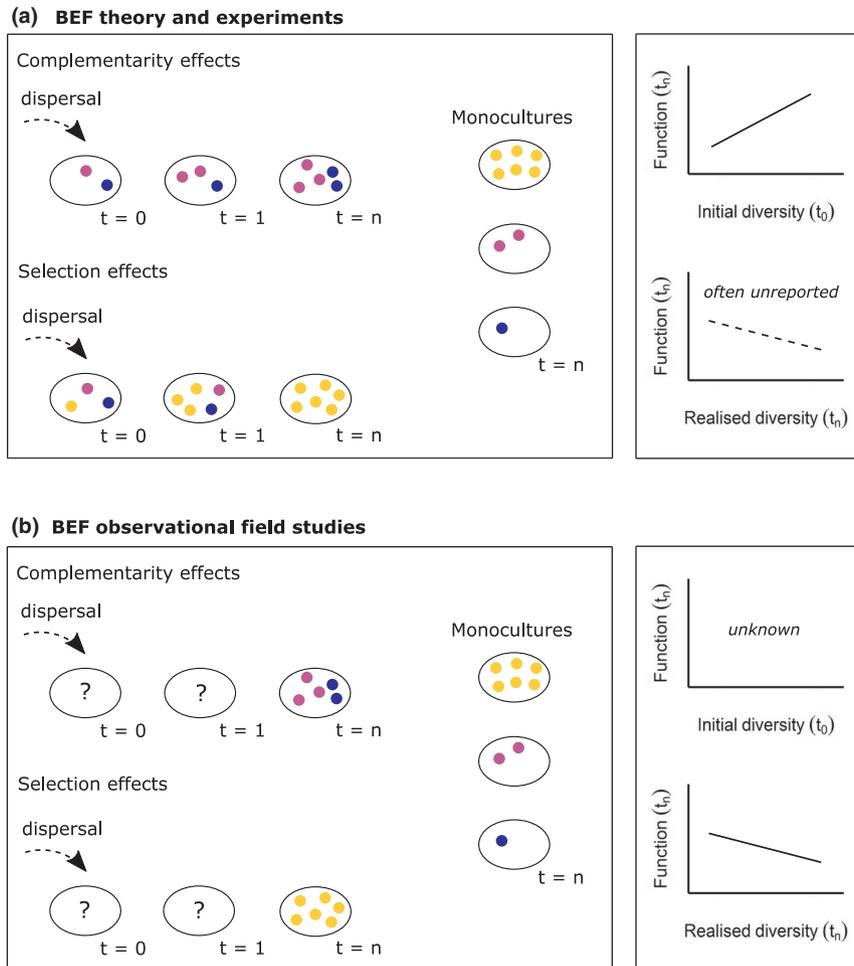
Selection effects occur when the community includes one (or several) competitive and highly functioning species that attain dominance through time (i.e. dominance *sensu* Fox, 2005 as selection effects *sensu* Loreau and Hector (2001) include an aspect of complementarity). Unlike complementarity effects, selection effects on ecosystem function are strongest when the highest functioning species outcompetes all other species in mixture. Therefore, when positive selection effects are strong, high functioning species attain high relative abundance and outcompete other species (Tilman, 1999; Chesson et al., 2001). This decreases realised diversity over time (see Creed et al., 2009; Doherty et al., 2011; Spaak & De Laender, 2021 for examples) but increases ecosystem function relative to the monoculture expectations of the constituent species (i.e. a positive net biodiversity effect, Figure 1a).

The difference between complementarity and selection effects means that initial diversity can positively affect ecosystem function when realised diversity is high (i.e. if complementarity effects dominate) or when realised diversity is low (i.e. if selection effects dominate), (Figure 1a). However, in both cases, the trait variation associated with high initial diversity is predicted to

increase ecosystem function (Loreau, 2000). Thus, based on BEF theory and experiments, initial diversity is expected to consistently increase ecosystem functioning irrespective of the observed realised diversity at some time point. Indeed, the consistent positive effect of initial diversity on ecosystem function through a combination of selection and complementarity effects has indeed been confirmed in several large meta-analyses of BEF experiments (Balvanera et al., 2006; Cardinale et al., 2011; O'Connor et al., 2017). However, the relationship between realised diversity and ecosystem function may not be so straightforward.

The complexity in the relationship between realised diversity and ecosystem function was demonstrated by Jan Lepš and colleagues. First, Stachová and Lepš (2010) used Lotka–Volterra models to simulate a classic BEF experiment (i.e. varying initial diversity among patches and calculating ecosystem function at some later time). The model generated a positive relationship between initial diversity and ecosystem function similar to those commonly observed in BEF experiments (Figure 2a). Because realised diversity was positively correlated with initial diversity (Figure S1), the relationship between realised diversity and ecosystem function was also positive. However, when considering subsets of the data for which initial diversities were equal, the results changed. Depending on the level of initial diversity that was supplied, the relationship between realised diversity and ecosystem function was either neutral, negative or positive (Figure 2b). Later, Rychteká et al. (2014) showed that these results were consistent with data from the Jena biodiversity experiment (Weigelt et al., 2016; Weisser et al., 2017). They found a positive relationship between initial diversity and community biomass (Figure 2c). However, within any given initial diversity treatment, the relationship between realised diversity and community biomass was variable (Figure 2d). Most notably, in the 16 species initial diversity treatment of the Jena experiment, ecosystem function was considerably higher in the patches with the lowest realised diversity within that treatment (yellow points, Figure 2d).

These patterns are not specific to the Jena experiment but are also found in data from the eight BIODEPTH sites (Spehn et al., 2005, 2016) that we reanalysed. BIODEPTH was a pan-European experiment that manipulated the initial diversity of plant species in experimental grasslands in different European countries. From these datasets, we extracted realised diversity and biomass data from initial diversity treatments where the difference in realised diversity among patches was at least one and had sufficient replication (see Supplementary material for details). Within these treatments with equal initial diversity, we examined the relationship between realised diversity and ecosystem function (as per Rychteká et al., 2014, see Figure 2b and d above). As with the Jena experiment, the relationship between realised diversity and function was variable within initial diversity treatments.



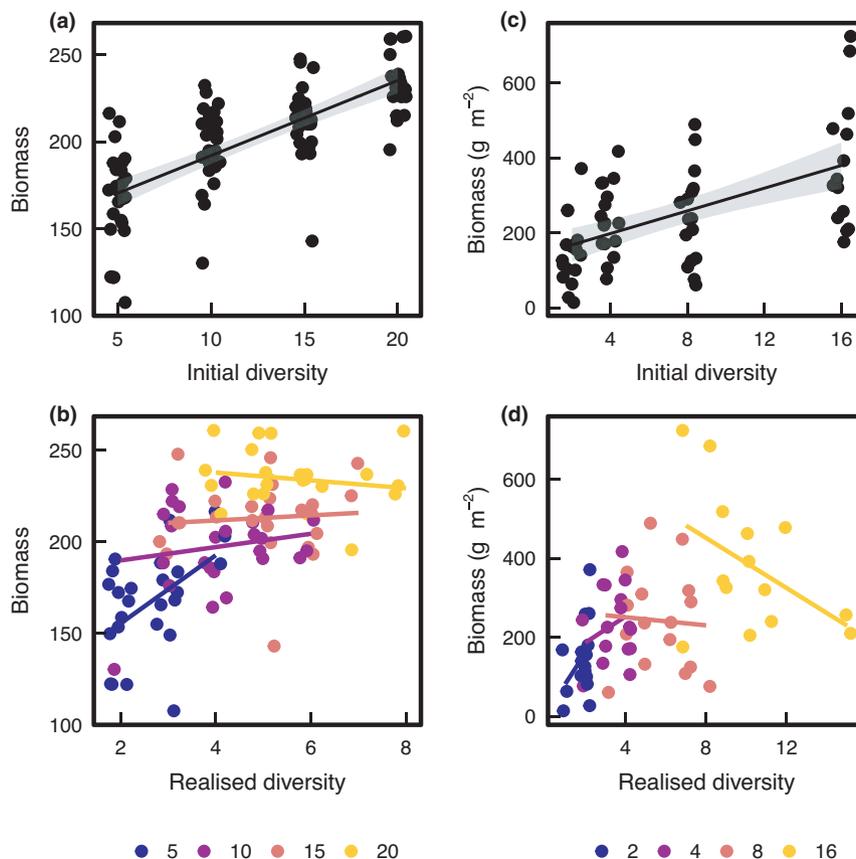
**FIGURE 1** (a) In BEF theory and experiments, a set of species (akin to a regional species pool) is used to inoculate environmentally similar patches with a different initial diversity. In each patch, the inoculated species coexist or go locally extinct. After some arbitrary length of time, the ecosystem function is measured (i.e. function  $t_n$ ). At this time point ( $t_n$ ), the realised diversity (i.e. the number of remaining species) might be the same or different than was initially inoculated. Usually, in BEF experiments, the relationship between initial diversity ( $t_0$ ) and function at  $t_n$  is then examined and this relationship is frequently positive as predicted by theory. The relationship between realised diversity and ecosystem function is often not reported (but see e.g. Tilman et al. 2001; Reich et al., 2012). This is different from BEF studies using observational field data (b). In observational field data, we can only measure realised diversity and ecosystem function at some arbitrary time-point ( $t_n$ ). Unless detailed time-series data are available, the history of community assembly remains unknown. Thus, field data may suggest a strong effect of individual species when positive effects of initial diversity on function are unobserved

Positive relationships dominated slightly but negative relationships were also common (Figure 3a and b).

It is important to note that we are not claiming that positive relationships between realised diversity and functioning have not been found in BEF experiments. Although meta-analyses of BEF experiments have typically not considered realised diversity in the analyses, many well-known BEF studies have examined realised diversity–function relationships and found qualitatively similar results to initial diversity–function relationships (Tilman et al. 2001; Reich et al., 2012). This occurs because complementarity effects in these experiments are common and frequently strong (Tilman et al. 2001; Marquard et al., 2009) and because there is generally a positive correlation between initial and realised diversity (Figure S1–S3; e.g. Tilman et al. 2001; Doherty et al., 2011; Jochum et al., 2020). We are, however, claiming

that if a set of habitat patches have the same or similar levels of initial diversity, the resulting realised diversity–function relationships may be variable (e.g. Figure 2b and d, Figure 3). This can occur if the biotic interactions causing selection and complementarity effects differ among the replicate patches (Stachová & Lepš, 2010) or if sampling error results in many species not being recorded. Thus, whilst the difference between initial and realised diversity may not necessarily be important for interpreting many BEF experiments, it can be important when applying insights from BEF research to observational field data.

The difference between initial and realised diversity is important for BEF studies using observational field data because the positive effects of initial diversity on ecosystem functioning may not be observed if only realised diversity is available. This is a critical point because, in



**FIGURE 2** The relationship between initial diversity (measured as species richness) and ecosystem function (in this case total community biomass) is positive in both (a) Stachová and Lepš' (2010) model and in (b) the Jena biodiversity experiment. This changes when considering subsets of the data with equal initial diversity. In this case, the relationship between realised diversity and ecosystem function varies between neutral, positive and negative in the (c) model and (d) the Jena biodiversity experiment. These results are an independently produced summary of those reported in Stachová and Lepš (2010) and Rychteká et al. (2014) with slight modifications (see Supplementary material for details). The legend at the bottom shows the different levels of initial diversity. Relationships between initial diversity and realised diversity for the model and Jena experiment are presented in the supplementary material (Figure S1 and S2 respectively)

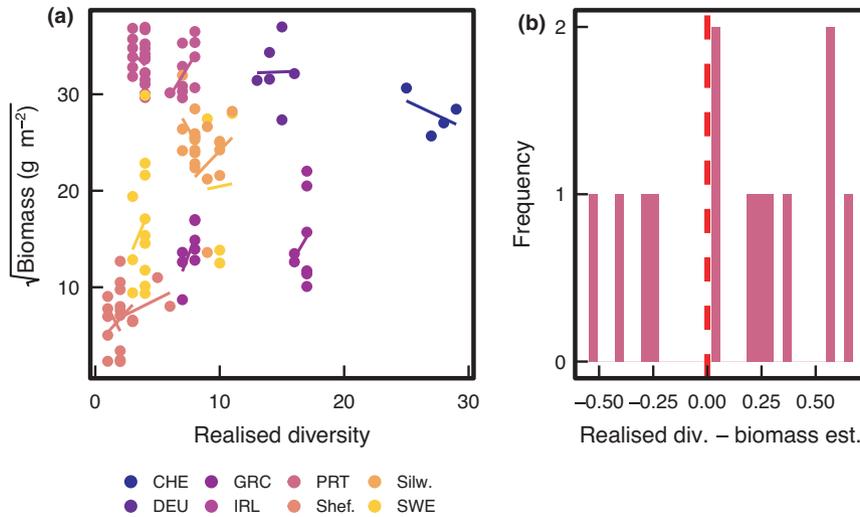
BEF studies conducted with observational field data, we can only observe realised diversity (Figure 1b; Leibold et al., 2017; Rychteká et al., 2014; Stachová & Lepš, 2010). Unless detailed time-series data are available, the initial diversity and process of community assembly remains unknown. As a result, a positive effect of initial diversity on ecosystem function may not be observed in field data when only realised diversity data are available which is commonly the case (Figure 1b). Therefore, in our view, there is no reason to expect positive realised diversity–function relationships in observational field data based on the results of BEF theory and experiments.

It is worth noting that a range of ecological models also do not predict positive realised diversity–function relationships. Whilst models employed in BEF theory typically vary initial diversity (and consequently also realised diversity), several other ecological models have explicitly examined how realised diversity affects functioning. The general conclusion from these models is that positive realised diversity–function relationships are only predicted for certain parameter combinations (e.g. Leibold et al., 2017; Mouquet et al., 2002; Thompson

et al., 2020). For example, several models show that when realised diversity is maintained by immigration and species compete for the same resource, the realised diversity–function relationship is either negative or neutral (Mouquet & Loreau, 2003; Bond & Chase, 2002; see also Thompson et al., 2020 for other examples). Thus, whilst realised diversity may correlate with functioning in BEF experiments manipulating initial diversity, this may not be the case in observational field data. Rather, in our view, applying insights from BEF research to observational field data will likely require considering an appropriate analogue to initial diversity.

## THE LOCAL SPECIES POOL CONCEPT

What is the analogue of initial diversity in observational field data? As others have previously noted, the quantity most analogous to initial diversity in natural systems is the diversity of the local species pool (Hector et al., 2007; Rychteká et al., 2014; Stachová & Lepš, 2010). Here, the



**FIGURE 3** (a) The relationship between realised diversity and ecosystem function (square root of biomass) within initial diversity treatments with a realised diversity gradient of at least one and sufficient replication (see Supplementary material). Data are from the eight BIODDEPTH experiment sites (different colours, see Table S1 for a list of the abbreviations). (b) Histogram of the standardised, regression slopes for the relationship between realised diversity and ecosystem function. The red dashed line is centred on zero. The relationship between initial diversity and realised diversity can be found in the supplementary material (Figure S3)

local species pool of a habitat patch can be defined as the subset of the regional species pool that can (1) tolerate the local conditions, and (2) be expected to disperse into the habitat patch over ecologically relevant timescales (filtered species pool *sensu* Cornell & Harrison, 2014). In similar conceptual frameworks, the local species pool of a habitat patch comprises the species currently occupying the patch, and the species in the surrounding landscape/region that could tolerate the local conditions in that patch: the so-called dark diversity (Partel et al. 2011) or the regional diversity in a metacommunity framework (Leibold et al., 2017). The local species pool concept has the potential to link predictions made by BEF theory and experiments more directly to observational field data.

As we have argued so far, BEF research shows that we should expect local species pool diversity to correlate positively with functioning. However, a realised diversity gradient in field data can be challenging to interpret. Ambiguity in data interpretation occurs when there is limited local species pool diversity variation between patches (Rychteká et al., 2014; Stachová & Lepš, 2010), and (1) biotic interactions causing selection and complementarity effects differ among patches (Stachová & Lepš, 2010) or (2) if sampling error results in incorrect species diversity estimates. Of course, realised diversity and local species pool diversity in natural systems are not independent. The diversity of the local species pool sets the upper limit on realised diversity. In cases where they correlate strongly (like in many BEF experiments, Figure S1–S3; e.g. Tilman et al. 2001; Jochum et al., 2020), the difference between local species pool and realised diversity will be trivial. However, empirical relationships between realised diversity and local species pool diversity can be surprisingly variable. A recent meta-analysis

of studies measuring diversity at local and regional scales showed that more than 30% of studies found no discernible relationship between realised diversity and local species pool diversity (Szava-Kovats et al., 2013). These results suggest that local species pool diversity is not always strongly correlated with realised diversity in field data.

There are certain conditions that cause realised diversity to correlate more strongly with local species pool diversity (see Cornell & Harrison, 2014 for a review). First, there needs to be variation between patches in the local species pool diversity. For this to occur, patches need to cover a sufficiently large spatial extent (i.e. the total area encompassed by all sampling patches, Chase & Knight, 2013), a threshold which is likely to vary considerably depending on the dispersal abilities of different species (Germain et al., 2017). Second, processes like disturbance which enhance the colonisation success of dispersing species have been shown to make realised diversity more similar to local species pool diversity (Myers & Harms 2011). Finally, factors that typically enhance local coexistence such as habitat heterogeneity and spatial grain (Hart et al., 2017; Stein et al., 2014) will likely increase the correlation between realised diversity and local species pool diversity and, therefore, make positive BEF relationships more likely (Thompson et al., 2020). However, it is not always straightforward to determine which combination of these factors is important for a given set of study patches. This makes it difficult to make clear predictions regarding the relationship between realised diversity and local species pool diversity in any given field dataset.

Considering the preceding discussion and the conceptual framework of local species pools does, however, lead

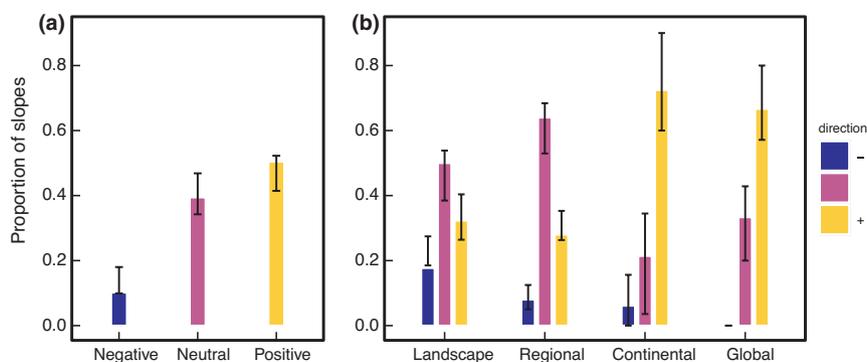
to two general expectations regarding realised diversity–functioning relationships in field data. First, given that the local species pool is generally unknown in field data (Figure 1b) and is frequently unrelated to local species pool diversity (Szava-Kovats et al., 2013), we expect that realised diversity–function relationships will be variable in field data. Second, if the diversity of the local species pool does not vary among focal habitat patches, then we do not necessarily expect any consistent realised diversity–function relationship. Without variation in local species pool diversity among patches, examining a realised diversity–function relationship would be akin to studying a single initial diversity treatment of a BEF experiment (i.e. Figure 2c, d, Figure 3). This latter case is more likely at small spatial extents where local species pools are less likely to vary (Germain et al., 2017). Thus, we expect that realised diversity–function relationships will be especially variable in field data at small spatial extents.

To test these predictions, we used data from a recent systematic review to examine 246 relationships between local realised diversity and concurrently measured productivity-related ecosystem functions in field data across a range of taxa and habitats while controlling for environmental covariates (see van der Plas, 2019 and Supplementary material for details). As reported by van der Plas (2019) and reproduced here, the slope of the relationship between realised diversity and ecosystem function varied considerably between studies. Together, neutral and negative BEF relationships were as common as positive relationships (Figure 4a). This contrasts with meta-analyses of experimental BEF studies which have generally found positive BEF relationships (e.g. Balvanera et al., 2006; Cardinale et al., 2011; O’Connor et al., 2017). Therefore, by this comparison, BEF relationships may be more variable in natural systems compared to experimental systems (although direct comparisons are not straightforward), (van der Plas, 2019).

We then tested whether the frequency of negative, neutral and positive relationships varied with the spatial extent of the study. To do this, we classified the BEF relationships in van der Plas’ (2019) systematic review into four categorical spatial extents: landscape, regional, continental and global (e.g. based on reported coordinates, study site maps, etc., see Supplementary Information for details). As predicted, the results show that, at small spatial extents (i.e. landscapes and regions), neutral and negative BEF relationships were more common than positive BEF relationships (Figure 4b). These results strongly concur with a meta-analysis that showed that realised diversity did not limit ecosystem function in grasslands at landscape spatial extents (Grace et al., 2007). Moreover, as expected, at continental and global spatial extents, where variation among patches in the local species pool is likely larger, positive BEF relationships were more common (Figure 4b). However, whether this is a local species pool effect or an effect of other, unmeasured environmental drivers that also vary more at large spatial extents cannot be determined using these data.

## CORRELATING REALISED DIVERSITY WITH ECOSYSTEM FUNCTION MAY UNDERESTIMATE THE IMPORTANCE OF BIODIVERSITY FOR ECOSYSTEM FUNCTION

Examining the relationship between realised diversity and functioning in field data may lead us to underestimate the importance of biodiversity to ecosystem function. This is likely for two reasons. First, as we have argued, neither BEF research nor ecological theory necessarily predict that realised diversity should be positively related to ecosystem function at local scales in field data. Therefore, recent BEF studies using field



**FIGURE 4** (a) Observed proportion of negative, neutral and positive slopes between realised diversity and biomass/productivity-related ecosystem functions (usually biomass or productivity) among studies reviewed by van der Plas (2019). (b) Observed proportion of negative, neutral or positive slopes for studies conducted at different spatial extents. Spatial extent, in this classification, increases from: landscape ( $n = 96$ ), to regional ( $n = 25$ ), to continental ( $n = 98$ ) and finally, to global ( $n = 12$ ). Error bars are between the maximum and minimum slope proportion when considering one slope from each study in 1000 randomisations to account for potential non-independence when studies reported several slopes (see Supplementary material for details)

data that fail to find positive relationships between realised diversity and ecosystem function do not contradict BEF experiments and theory as is sometimes claimed (e.g. Schoolmaster et al., 2020). Secondly, and perhaps more importantly, even if local species diversity is not declining (e.g. Blowes et al., 2019; Dornelas et al., 2014; Elahi et al., 2015) this does not mean that there will be no consequences for ecosystem functioning. Rather, in our interpretation, BEF research suggests that regional extinctions and habitat fragmentation will negatively affect ecosystem function by preventing local ecosystems from receiving a diverse set of colonists from local species pools irrespective of any changes in realised diversity (see also Hector et al., 2007; Leibold et al., 2017).

## APPLYING BEF THEORY TO OBSERVATIONAL FIELD DATA: FUTURE DIRECTIONS

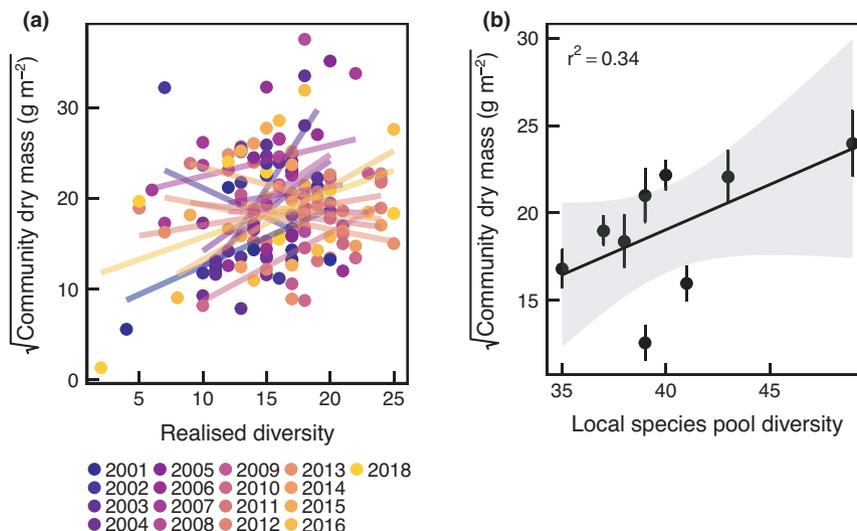
To make progress in BEF research using field data, we suggest that we must distinguish between two separate but related questions. First, are the results of BEF theory and experiments consistent with field data from natural systems? So far, this has been tested by correlating realised diversity with ecosystem function in field data (Figure 1b). However, as we and others have argued, it is arguably more suitable to test predictions from BEF theory in field data using the diversity of the local species pool, not realised diversity. Second, how do observed changes in species diversity and composition due to anthropogenic change (e.g. land-use change, pollution, etc.) affect ecosystem function? BEF research has generally focused on species diversity loss. However, a decline in local species diversity is just one potential consequence of anthropogenic change (McGill et al., 2015). Anthropogenic change can affect species diversity and composition in many ways, each with potentially considerable consequences for ecosystem functioning (Mayfield et al., 2010; Spaak et al., 2017). Therefore, if we want to predict how anthropogenic change will affect ecosystem functioning, we need to understand how different pathways of change in species diversity and composition affect ecosystem functioning in response to different drivers (Hillebrand and Matthiessen 2009; see De Laender et al., 2016 for a review).

The first question, testing whether results from BEF theory and experiments are consistent with field data, can be approached in at least two different ways. The first and perhaps simplest way is to use model systems to test the effect of local species pool diversity on ecosystem function. As with many questions in ecology, island systems (i.e. relatively closed systems that lack species sustained by dispersal influxes *sensu* Rosenzweig, 1995) may be useful models in this regard. Specific habitat types (e.g. mesic grasslands, ponds, etc.) on islands typically have reasonably well-defined regional species pools (i.e. all

species associated with a given habitat type on the island). Habitat patches in these systems are largely colonised by species from those regional species pools. Thus, habitat-specific regional species pools of islands are probably reasonable estimates of local species pools and have clear similarities to initial diversity used in BEF theory and experiments. Therefore, examining the relationship between regional diversity and ecosystem function in habitat patches from islands with different regional diversities but with similar environmental conditions may closely approximate the ecological scenario studied in classic BEF models. Islands may differ in regional diversity due to, for example area or connectivity (Warren et al., 2015), thereby providing a natural local species pool diversity gradient. Working with island systems has been successfully used to understand how local species pools affect local species composition (e.g. Karger et al., 2015). Whilst islands have been the subject of important BEF work (e.g. Kardol et al., 2018), they have, to our knowledge, not been used to compare the effects of realised diversity and local species pool diversity on ecosystem functioning.

The second and more direct way to compare the results from BEF theory and experiments to field data is to estimate local species pool diversity in different habitat patches. Existing methods for directly estimating local species pool diversity are not straightforward, and appropriate methods differ based on the focal taxa, scale of inference, and available data. Nonetheless, several solutions exist. At the most basic level, estimating local species pool diversity will require observing a habitat patch over relevant timescales (Brown et al., 2001). For example in the Jena dataset, the number of species observed across all sampling years closely approximates initial diversity but any given local sample does not (Allan et al., 2011). Such longer term local species pool diversity estimates can then be correlated with long-term mean ecosystem function which may more closely approximate the ecological scenario studied in BEF theory and experiments (see Figure 5a and b and caption for an example of this approach). When long-term data are unavailable, species pool estimation procedures can be used and are becoming more common. For example methods for estimating probabilistic species pools from a variety of data sources (e.g. species distributions, traits, etc.) are becoming more accessible with the proliferation of data availability and computational power (reviewed in Karger, 2016) as are novel estimation procedures (e.g. Shen et al., 2017). Indeed, Craven and colleagues (2020) recently used the former approach on North American forest data and found that local species pool diversity was a better predictor of productivity than realised diversity. Regardless of the approach, directly estimating local species pool diversity and comparing it to realised diversity may be a profitable avenue to understand how BEF theory and experiments relate to real-world ecosystems.

If we are instead interested in predicting how anthropogenic change will affect local ecosystem function, current



**FIGURE 5** (a) The relationship between realised diversity and community dry mass ( $\text{g m}^{-2}$ , square root transformed) of macroalgae observed at nine sites in 17 different years between 2001 and 2018 (colours are different years). As predicted, the realised diversity–function relationships are highly variable between years. All fitted lines are simple linear regressions. (b) The relationship between local species pool diversity of algae (all species observed over 17 years) and mean  $\pm$  SE community dry mass ( $\text{g m}^{-2}$ , square root transformed) for the nine sites across the 17 years. Despite considerable variation, the relationship is positive as would be expected based on BEF theory and experiments. Data are from kelp forests off the coast of California (see Supplementary materials for details). Fitted line is a simple linear regression (intercept  $\text{CI}_{95\%} = [-27.7 \text{ to } 24.5]$ ; slope  $\text{CI}_{95\%} = [-0.13 \text{ to } 1.2]$ )

BEF research which relies heavily on random manipulations of initial diversity must be expanded (Bannar-Martin et al., 2018; Wardle, 2016). Anthropogenic changes alter species diversity and composition in a variety of ways from species losses, species gains (Sax & Gaines, 2003), shifts in relative abundances (Blowes et al., 2019; Dornelas et al., 2014), increases in population density, to changes in *per capita* ecosystem function contributions (De Laender et al., 2016). Thus, to understand and predict the functional consequences of anthropogenic change, two separate but related approaches are required. First, we need to clearly characterise how species diversity and composition are changing in local communities in natural systems through time (e.g. Dornelas et al., 2014; Elahi et al. 2015; Blowes et al., 2019) and in response to different anthropogenic drivers (e.g. Newbold et al., 2015; Sol et al., 2020). Then, we need to understand the consequences of these observed changes in species diversity and composition for different ecosystem functions in different taxa and in different habitats. To this end, some progress has already been made (e.g. De Laender et al., 2016; Bannar-Martin et al., 2018; Smith et al., 2020; Benkwitt et al., 2020) and should continue. Combining these approaches will undoubtedly contribute to quantitatively predicting the effects of anthropogenic change on ecosystem function, a major goal in ecology (Currie, 2019).

## CONCLUSIONS

In this *Perspectives* article, we emphasised two points that are present (Hector et al., 2007; Stachová & Lepš, 2010; Rychteká et al., 2014; Leibold et al., 2017; Ladouceur et al.

2020), but, in our view, under-appreciated in the current ecological literature. First, the positive effects of initial diversity on ecosystem functioning may not be observed if only realised diversity is considered. BEF studies using field data often do not appreciate this point. Second, currently, BEF research does not necessarily make clear predictions about how and under which conditions realised diversity should affect ecosystem function in natural systems, especially in response to anthropogenic change. There are many possibilities, and the BEF relationship will likely depend on a combination of environmental characteristics, species traits and species interactions at a variety of scales (Grace et al., 2016; Ladouceur et al., 2020; Leibold et al., 2017; Mouquet et al., 2002; Thompson et al., 2020). More importantly, even if local species diversity is not declining, the arguments made in this paper warn that the loss of local species pool diversity through, for example, regional extinctions and habitat fragmentation will likely have negative long-term consequences for ecosystem functioning. The strength and ubiquity of these effects are, at present, understudied.

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## AUTHORSHIP

JGH, BV and LG conceived the idea. JGH performed various analyses. JGH wrote the manuscript with input from BV and LG.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13874>.

## OPEN RESEARCH BADGES



This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at: <https://doi.org/10.6084/m9.figshare.15178248.v1> and [https://github.com/haganjam/bef\\_experiment\\_observational](https://github.com/haganjam/bef_experiment_observational).

## DATA AVAILABILITY STATEMENT

Existing data used are available from the original publishers. New data are published on Figshare: <https://doi.org/10.6084/m9.figshare.15178248.v1>. The scripts used to produce the analysis can be found at: [https://github.com/haganjam/bef\\_experiment\\_observational](https://github.com/haganjam/bef_experiment_observational).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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