Establishing causal links between aquatic biodiversity and ecosystem functioning: Status and research needs

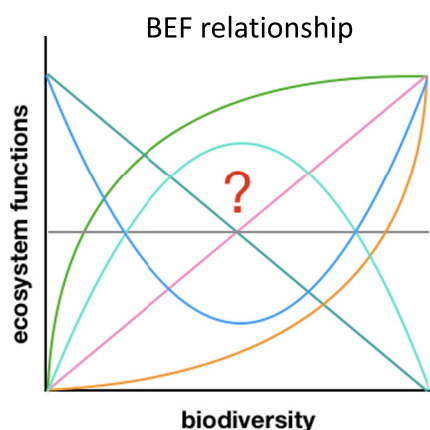Michiel A. Daam [1], Heliana Teixeira, Ana I. Lillebø, António J.A. Nogueira *

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HIGHLIGHTS

- Current research limitations and needs in aquatic BEF studies are reviewed.
- Most aquatic BEF relationships can be described by power functions.
- BEF relationships may not be directly extrapolated across ecosystem types.
- Meta-analysis and modelling approaches to study BEF relationships are recommended.

GRAPHICAL ABSTRACT

ABSTRACT

Understanding how changes in biodiversity affects ecosystem functioning is imperative in allowing Ecosystem-Based Management (EBM), especially when addressing global change and environmental degradation. Research into the link between biodiversity and ecosystem functioning (BEF) has indeed increased considerably over the past decades. BEF research has focussed on terrestrial ecosystems and aquatic ecosystems have received considerably less attention. Due to differences in phylogenetic diversity, ecological processes and reported BEF relationships, however, it may at least be questionable whether BEF relationships are exchangeable between these ecosystems (i.e. terrestrial and aquatic). The aim of the present paper was therefore to pinpoint key areas and bottlenecks in establishing BEF relationships for aquatic ecosystems (freshwater, transitional, and marine). To this end, the available literature with special emphasis on the last 10 years was assessed to evaluate: i) reported mechanisms and shapes of aquatic BEF relationships; ii) to what extent BEF relations are interchangeable or ecosystem-specific; and iii) contemporary gaps and needs in aquatic BEF research. Based on our analysis, it may be concluded that despite considerable progress in BEF research over the past decades, several bottlenecks still need to be tackled, namely incorporating the multitude of functions supported by ecosystems, functional distinctiveness of rare species, multitrophic interactions and spatial-temporal scales, before BEF relationships can be used in ecosystem-based management.

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1. Introduction

Concerns have been raised in the past decades about the rate of biodiversity decline and the consequences this may have for the functioning of ecosystems and the ecosystem services they provide (Tilman et al., 2014). Several international initiatives, like the *European Biodiversity Strategy to 2020* and the *Intergovernmental Platform on Biodiversity and Ecosystem Services* (*IPBES*), were initiated to safeguard healthy ecosystems and the essential services they provide to society. The understanding of how biodiversity influences ecosystem functioning (EF) also plays a key role in allowing ecosystem-based management (EBM) especially when addressing climate change and environmental degradation (Yasuhara et al., 2016).

Scientific research into the link between biodiversity and ecosystem functioning (BEF) and between biodiversity and ecosystem services (BES) has also increased in the past decades. Experimental and observational BEF studies, and meta-analyses of data generated by such studies, have been conducted to test the hypothesis that ecosystems with species-poor communities are also functionally poorer, less resistant (capacity to resist change) and resilient (capacity to recover from change) to disturbance than systems with species-rich communities (Covich et al., 2004; Stachowicz et al., 2007; Strong et al., 2015). Examples supporting this hypothesis include a possible alteration in decomposition with a decline in the diversity of invertebrates processing detritus may alter decomposition rates and nutrient cycling (Dirzo et al., 2014; Gessner et al., 2010); and that algal diversity losses may affect the ecosystem's capacity in sequestering nutrients (Cardinale, 2011; Truchy et al., 2015).

After reviewing the available BEF literature at the time, Cardinale et al. (2012) concluded that "There is now unequivocal evidence that biodiversity loss reduces the efficiency by which ecological communities capture biologically essential resources, produce biomass, decompose and recycle biologically essential nutrients." Despite the vast number of existing BEF studies, several authors have disputed the fact that not all ecosystem types have so far received an equal amount of attention. BEF research, and hence evidence for the existence of BEF relationships, has mostly focussed on terrestrial ecosystems like grasslands and forests (e.g. Castagneyrol et al., 2013; Duncan et al., 2015; Gagic et al., 2015; Messmer et al., 2014). Aquatic ecosystems have thus received comparatively little attention, and it may be disputed as to whether evidence of BEF relationships attained from studying terrestrial ecosystems can be extrapolated to aquatic realms (Duncan et al., 2015; Gamfeldt et al., 2014; Strong et al., 2015; Vaughn, 2010). In addition, different aquatic realms appear not to have received the same amount of BEF research effort. Gamfeldt et al. (2014), for example, discussed that, as compared to other aquatic realms, significant progress has been made in the marine realm, including manipulative marine experiments. In line with this, Strong et al. (2015) concluded that there is general consensus that biodiversity and ecosystem function relationships do exist in the marine environment, and that negative and positive effects of increasing biodiversity have been noted on several marine ecosystem functions (Cardinale et al., 2012; Gamfeldt et al., 2014; Jiang et al., 2008; Stachowicz et al., 2007; Worm et al., 2006). Significant knowledge gaps, however, have been reported for our understanding on how biodiversity decline influences ecosystem function in both estuarine/transitional water (Pinto et al., 2014) and freshwater (Bardgett and van der Putten, 2014; Vaughn, 2010) ecosystems. There is thus an urgent need for assessing BEF relationships in these understudied ecosystems, also to allow moving forward to understanding and predicting the impacts of biodiversity change on the provisioning of ES (Duncan et al., 2015).

To advance the evaluation of the links between biodiversity and ecosystem functions in aquatic realms (i.e., freshwater, coastal and marine), key areas and bottlenecks in existing knowledge need to be identified. The aim of the present paper was therefore to review i) reported mechanisms and shape of aquatic BEF relationships; ii) whether BEF relations are generalisable across ecosystems or whether they are ecosystem-specific; and ultimately iii) research limitations and needs in aquatic BEF assessments.

2. Methods

A literature review was conducted to identify key areas and bottlenecks in assessing aquatic BEF relationships. To this end, existing scientific and non-scientific literature related to BEF were reviewed and summarized. The literature search was conducted in two scientific libraries (Scopus and Web of Knowledge) using the keyword combination indicator*, biodiversity, ecosystem function*, meta-analys* and ecosystem service*. Various key papers were identified from this and both their reference lists as well as papers citing them were subsequently also appraised, following a snowball effect, i.e., increasing the number of relevant papers in the selected topic that were not captured by the selected key words. In addition, additional searches were conducted in the scientific libraries based on relevant keyword combinations noted in these papers such as aquat*, process*, BEF and function*. After evaluations of the abstract sections of the papers that were obtained from these literature searches, over 600 publications were selected to be thoroughly analysed in full. The information contained in approximately 130 of these publications was considered especially relevant through expert judgement, considering the scope of the present paper presented in the last paragraph of the Introduction section, and subsequently used for discussion (c.f. reference list). Considering that our aim was to assess the status of BEF research and identify research needs this review is purely descriptive not aiming for a formal and quantitative statistical evaluation.

3. Discussion of the selected publications

3.1. Mechanisms and shape of BEF relationships in aquatic realms

3.1.1. Underlying BEF mechanisms

Various different mechanisms have been indicated in existing literature to underpin the influence of biodiversity on ecosystem functioning, which include:

Complementary niche partitioning: occurs when several species that complement each other spatially and temporally in their resource use patterns coexist at a given site (Truchy et al., 2015). For example, Karlson et al. (2010) demonstrated that deposit-feeding marine macrofauna communities with greater diversity incorporated more N than the single-species treatment of the best-performing species, indicating transgressive overyielding through positive complementarity. More details on the transgressive overyielding concept have been detailed elsewhere (Schmid et al., 2008).

Facilitation: occurs when the activities of certain species enhance or facilitate the activities of at least one of these species and, consequently, improve ecosystem process rates. For example, facilitation is seen within the suite of processes sustaining water purification in freshwaters when diverse filter-feeder caddisfly assemblages capture more suspended material than they could do when in monoculture, due to "current shading", i.e. the deceleration of flow from upstream to downstream neighbours (Cardinale et al., 2002; Truchy et al., 2015). In addition, sediment retention by some invertebrates decreases near-bed shear stress in streams allows the installation of other organisms (Statzner et al., 2003).

Identity effects: occurs in situations where specific species have a disproportionate functional role and may in this way generate positive BEF relationships. This form of non-transgressive overyielding has also been termed sampling or selection effects (Strong et al., 2015). For instance, reduced nutrient recycling processes with declining fish diversity may be related to identity effects with relatively few fish species that dominate the nutrient recycling process (Allgeier et al., 2014; McIntyre et al., 2007).

BEF studies have explored various hypotheses for how organisms promote EFs, which include i) the diversity hypothesis: mechanisms including niche complementarity and insurance (compensatory dynamics through space and time); and ii) the mass ratio hypothesis: functional traits of dominant species chiefly promote EFs – identity effects (Duncan et al., 2015; Mokany et al., 2008; Vaughn, 2010).

Experimental BEF studies that focused on species richness have provided broad support for the diversity hypothesis, whereas trait-based studies demonstrated that many EFs are predominantly driven by mass ratio (Duncan et al., 2015; Mokany et al., 2008). Both hypotheses are ultimately due to trait expression and a combination of both species identity and richness may obviously play a significant role (Fu et al., 2014; Vaughn, 2010). This also indicates that the sole evaluation of taxonomic changes is insufficient when studying BEF relationships since species composition may change without concomitant functional changes (and vice versa), and ecosystem functioning may even change when species are unaffected, for example, through changes in the interactions or behaviours of the resident species (Truchy et al., 2015).

Evaluating species traits is also imperative since recent studies have demonstrated that global biodiversity loss preferentially affects species with bigger bodies, longer life spans, lower reproductive rates, more specialised resource uses, poorer dispersal capacities, among other traits that make them more prone to human pressures (Pinto et al., 2014). Oliver et al. (2015) noted that both response traits (attributes that influence the persistence of individuals of a species in the face of environmental changes) and effect traits (attributes of the individuals of a species that underlie its impacts on ecosystem functions and services) of species have a significant influence on ecosystem function resilience: "If the extent of species' population decline following an environmental perturbation (mediated by response traits) is positively correlated with the magnitude of species' effects on an ecosystem function (via effect traits), this will lead to less resistant ecosystem functions" [(see Oliver et al., 2015) for more details on species-, community- and landscape-level mechanisms underpinning resilient ecosystem functions]. Nevertheless, it has also been reported that trait-based BEF relationships tend to be highly variable and often are not a very good predictors of ecosystem functioning (Venail, 2017). From the above it may thus be concluded that BEF studies should include both taxonomic- and trait-based evaluations.

3.1.2. Shape of BEF relationships

Early BEF research suggested that increased species biodiversity was positively related with improved ecosystem functioning, which lead to several hypotheses on this link in the 1980s and 1990s (see Naeem, 1998 for an overview). In the current millennium, this was followed by several meta-analysis of experimental data aimed at unravelling the shape and function of BEF relationships (e.g. Balvanera et al., 2014; Cardinale et al., 2011; Mora et al., 2014; Reich et al., 2012; Schmid et al., 2009; Stachowicz et al., 2007; Worm et al., 2006). After evaluating one hundred BEF studies, Srivastava and Vellend (2005) concluded that positive relationships between diversity and ecosystem function were mostly log-linear (53%), rather than linear (39%), with 8% showing other patterns. By fitting experimental data on how primary producer species richness influences the ecological processes in terrestrial, marine and freshwater ecosystems, using several mathematical functions (linear, exponential, log, power and Michaelis-Menten), Cardinale et al. (2011) concluded that the Michaelis-Menten function led to the best fit, although the difference of this function with the power model was not considerable (Cardinale et al., 2011). BEF relationship following this function can be described as $EF = EF_{max}(\frac{K}{S+K})$, where "EF" denotes the ecosystem function and "S" is a measure of diversity, "EF$_{max}$" is the maximum value for the EF and "K" is the value of S for which EF is half of the maximum value. Several shapes for BEF relationships have been reported and appear to depend on several factors like i) the taxonomic group considered (Delgado-Baquerizo et al., 2016a);

ii) the study type (laboratory or field) (Mora et al., 2014); iii) the nature of multi-trophic diversity interactions (Brose and Hillebrand, 2016) and especially iv) the type of the biodiversity indicators selected for the relationship (Fig. 1; Baldrighi et al., 2017; Thrush et al., 2017).

Mora et al. (2014) reported that BEF relationships in large-scale observational marine studies generally yield non-saturating (concave-up) patterns with slopes on log-log scale ranging between 1.1 and 8.4. In experimental marine studies, however, ecosystem functioning appears to rapidly saturate with increasing biodiversity in (concave-down) BEF functions with slopes on a log-log scale between 0.15 and 0.32 (Mora et al., 2014). This indicates that the Michaelis-Menten function is not adequate to be used in concave-up relationships, which is a serious limitation for comparing different relationship types, especially those types that emerge from observational marine studies (Mora et al., 2014). These authors subsequently discussed three hypotheses to explain this contrast between observational and experimental studies: i) the use of functional richness instead of species richness; ii) an increased production efficiency of species in producing biomass when more ecological interactions are present; and iii) the fact that communities are likely assembled in an ordered succession of species from low to high ecological efficiency (Mora et al., 2014).

Saturation response curves (concave-down) are usually associated with natural ecosystems in which a biodiversity increase leads to the occurrence of functionally-redundant groups of plants and animals, although microbial communities tend to be show exponential of linear relationships in natural ecosystems (Delgado-Baquerizo et al., 2016a). Several other authors have also discussed that differences in experimental designs will result in different BEF relationships (e.g. Byrnes and Stachowicz, 2009; Campbell et al., 2011; O'Connor and Bruno, 2009; Stachowicz et al., 2008). For example, Stachowicz et al. (2008) discussed that short-term experiments only detect a subset of possible mechanisms that may actually occur in the field in the long run since they lack sufficient environmental heterogeneity to allow expressing niche differences, and they are also of insufficient duration to allow capturing population-level responses such as recruitment. In line with this, spatial heterogeneity of the physical environment has been discussed to play a crucial role in mediating the effects of species diversity (Griffin et al., 2009). However, it should be noted that resource heterogeneity needs to be accompanied with a sufficiently broad trait diversity for resource partitioning to occur (Ericson et al., 2009; Weis et al., 2008).
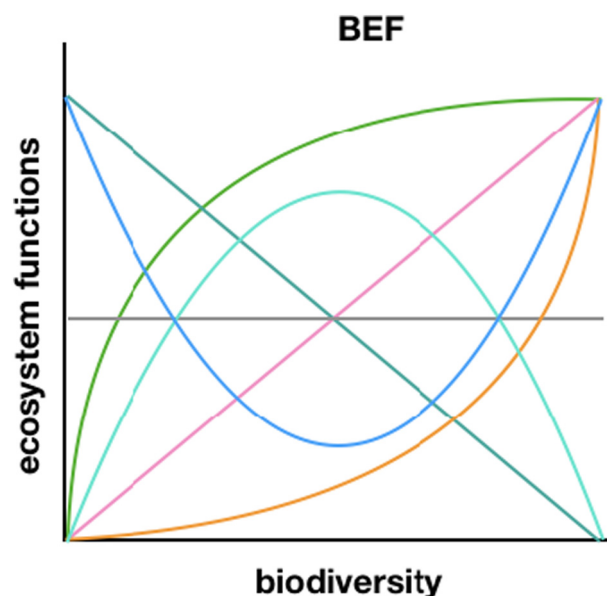

Fig. 1. Common shapes for nonlinear relationships between biodiversity and ecosystem functions (produced from shapes compiled by Thrush et al., 2017).

In contrast to the above, Godbold (2012) and Gamfeldt et al. (2014) only encountered small and mostly non-significant differences in marine BEF relationships when comparing experiments conducted in the laboratory, mesocosms or the field. Causal effects of phytoplankton diversity on functional properties in large-scale observational freshwater and brackish water studies have also been reported to be generally consistent with experimental and model ecosystem studies (Ptacnik et al., 2008; Zimmerman and Cardinale, 2013).

Regardless of the adopted experimental design, BEF relationships appear to be best approximated by a power function $EF = \alpha S^{\beta}$, where the constants "α" and "β" represent a scaling factor and a power index respectively (Gamfeldt et al., 2014; Isbell et al., 2015; Mora et al., 2014). The BEF curve shape changes with the value for the β constant where curves are increasingly saturating as β approaches 0 (zero), approximately linear when β equals 0.5, and increasingly linear as β approaches 1.0 (Isbell et al., 2015). Reported values for the constants "α" and "β" and hence the shape and strength of the BEF relationships are highly variable and appear to:

- at least partly depend on the environmental context and on which species are lost, e.g. the loss of initially rare species is likely to reduce ecosystem functioning less than the loss of initially abundant species;
- be stronger in experiments with long duration than in short-term experiments and also stronger in observational studies as compared to experimental studies (c.f. Discussion of the selected publications above);
- may have β-values >0.5 for some types of non-random biodiversity loss, and when considering the greater proportion of biodiversity that is required to maintain multiple ecosystem functions at multiple times and places (e.g. a large-scale observational study);
- show reduced slopes with increased disturbance level (Biswas and Mallik, 2011; Cardinale et al., 2000; Isbell et al., 2015; Mora et al., 2014).

One of the major drawbacks for the use of the Michaelis-Menten function in BEF is the fact that concave up effects result in negative "K" and only fit the data for biodiversity values above "K." When k is negative the Michaelis-Menten function is concave down for diversity values (S) below "K" (X-axis) and concave up for biodiversity values above "K", approaching $-\infty$ and $+\infty$ at values below and above "K", respectively (Fig. 2-A). Power functions with a negative β approach $+\infty$ asymptotically at diversity values (S) close to zero decreasing as the values for biodiversity (X-axis). The Michaelis-Menten function can be replaced with the power function (Fig. 2-B) even when the Michaelis-Menten functions provides a better fit, as the loss in statistical discrimination is negligible for positive "K" values and the latter is more flexible. Furthermore, a simple theoretical exercise demonstrates that power function provide a good fit to models using the Michaelis-Menten function (Fig. 2-C) with correlations between 0.95 and 1.

3.2. Analysis of whether BEF relations are interchangeable or ecosystem-specific

Various studies have concluded that there is a striking generality level in BEF relationships between freshwater, transitional/marine, and terrestrial, freshwater ecosystems, and also between organisms as divergent as predators and plants (Bruno et al., 2005; Cardinale et al., 2011; Gamfeldt et al., 2014; Handa et al., 2014; Hodapp et al., 2015; Lefcheck et al., 2015; Moore and Fairweather, 2006; Stachowicz et al., 2008). For example, Stachowicz et al. (Stachowicz et al., 2008) stipulated that, rather than the inherent differences between terrestrial and marine ecosystems, experimental design and approach determine contrasting BEF responses among systems.

Despite this apparent non-ecosystem specificity, Gamfeldt et al. (2014) discussed that the difference between terrestrial, and marine and terrestrial systems, in terms of their phylogenetic diversity at higher
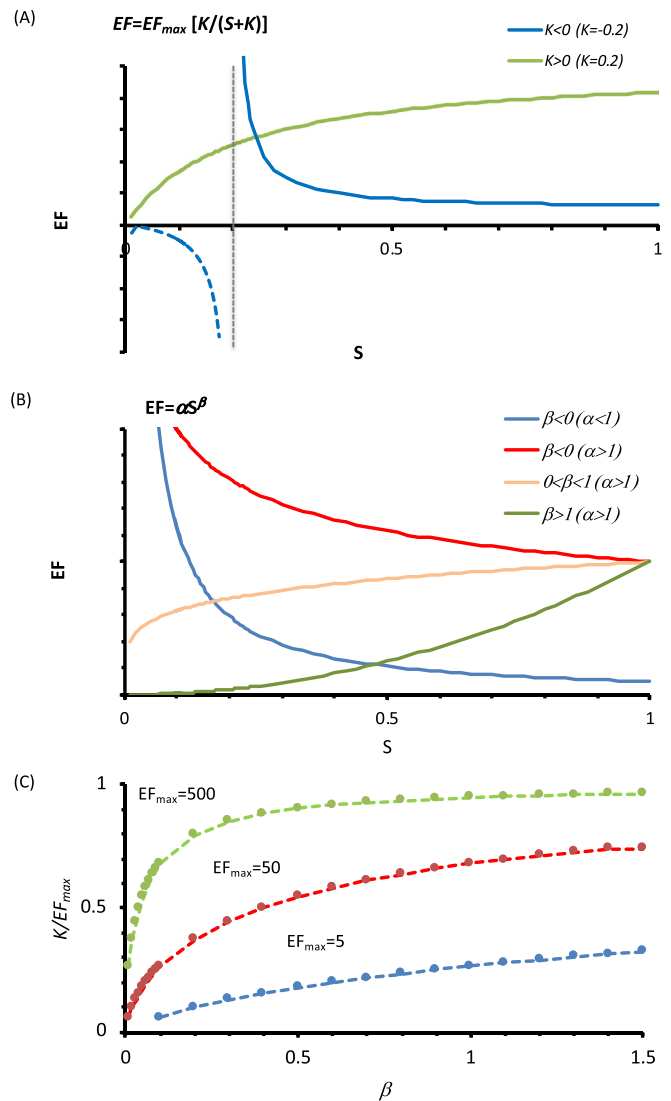
Fig. 2. Shapes of the Michaelis-Menten function (A), power function (B), and theoretical relationship between the slopes of the linearized forms of both functions for several values of EFmax (the Michaelis-Menten function was linearized with the Lineweaver–Burk transformation and the power function was linearized with a log-log transformation).

complexity levels should be considered. For example, whereas primary producers in the ocean belong to several kingdoms and fifteen phyla are endemic to marine environments, on land they mainly belong to the Plantae kingdom (Gamfeldt et al., 2014). Aquatic ecosystems are also characterised by more rapid biological processes, greater propagule and material exchange, often steeper physical and chemical gradients, and, in marine systems, higher metazoan phylogenetic diversity as compared to terrestrial ecosystems (Giller et al., 2004). The extrapolation of conclusions originating from terrestrial experiments to aquatic ecosystems is thus limited because of these inherent differences. Duncan et al. (2015) therefore concluded that a focus on within-ecosystem type studies is crucial, the more since the nature of BEF relationships highly depends on context parameters such as climatic and abiotic controls, management and disturbance.

The mechanism behind BEF relationships also appear to differ between ecosystem types. For instance, positive BEF relationships reported in the marine environment for functions such as organic matter decomposition, primary and secondary production, and functions related with physical engineering (see Table 1 in the Supplementary material for a full list) are mostly driven by identity effects, whereas

complementarity appears to be prevalent in terrestrial ecosystems (e.g. Cardinale et al., 2007). In addition, terrestrial and aquatic ecosystems are known to be different in terms of the relative strength of bottom-up versus top-down effects (Srivastava et al., 2009).

Based on the above it may hence be concluded that BEF relations established in a certain ecosystem type may provide valuable indications for further study and/or additional evidence for their existence in other ecosystem types. However, BEF relationships cannot be fully extrapolated across ecosystem types.

3.3. Current research limitations and needs in aquatic BEF studies

Several factors are reviewed in the following subsections that have been discussed to either have a negative (−) or positive (+) effect on BEF relationships. These factors and their expected negative or positive effect are also visualized in Fig. 2.

3.3.1. Single versus multiple EF relationships
The influence of biodiversity on ecosystem function is known to be a consequence of a range of mechanisms (see Discussion of the selected publications above), which becomes increasingly important when considering an increasing number of ecosystem functions (Isbell et al., 2011; Mouillot et al., 2011). For example, in contrast to studies only evaluating a single ecosystem function and that only considered species richness as the biodiversity measure, Mouillot et al. (2011) noted a linear and non-saturating effect of the functional community structure on ecosystem multifunctionality. Since the functional traits and importance of complementarity may vary for different EFs, a greater level of biodiversity may thus be required to simultaneously support multiple EFs (Duncan et al., 2015). This hence implies that prior research may have underestimated the significance of biodiversity for ecosystem functioning since they mostly focussed on individual taxonomic groups and functions (Hector and Bagchi, 2007; Lefcheck et al., 2015).

On the other hand, limits to multifunctionality may arise from negative correlations among functions, and from functions that are not correlated with biodiversity (Meyer et al., 2017). Strong et al. (2015), for example, indicated that an increase in the functional output of a certain ecosystem function may change the availability of substrate or other resources for other ecosystem functions (the so-called "spill-over" effect). Subsequently, considering interactions between individual ecosystem functions may hamper determining the response of individual ecosystem functions to biodiversity (Strong et al., 2015). There is thus an eminent need for BEF research that considers multiple functions (e.g. Duncan et al., 2015; Gamfeldt et al., 2014; Strong et al., 2015). Few BEF studies have so far considered ecosystem multifunctionality (Nogueira et al., 2016) because of the complex issues related with multifunctionality analysis, the logistic means required to conduct experiments with many species richness levels, and the difficulty associated with the measurement of more than one or few ecosystem functions (Byrnes et al., 2014).

The complexity of considering multiple BEF relationships co-existing in natural ecosystems may be further illustrated with the fact that underlying diversity measures may also vary among these different BEF relationships. For example, Thompson et al. (2015) demonstrated that in natural pond zooplankton communities, biomass was best predicted by zooplankton trait-based functional richness, whereas phytoplankton abundance was best predicted by its phylogenetic diversity. Similarly, Hodapp et al. (2015) noted that different biodiversity aspects (evenness, richness) were significantly interrelated with different ecosystem functions (resource use efficiency, productivity).

Duncan et al. (2015) suggested to group EFs in accordance with their main contributing group (functional group or trophic level), biodiversity mechanisms and functional traits underpinning them. By deducting and considering the underlying species interactions structure, ecological networks could also aid in assessing relations between biodiversity and the multiple ecosystem functions underpinning them (Hines et al., 2015). For a more detailed discussion on the advances and challenges of the

multifunctionality concept in the field of BEF as well as land management research, the reader is referred to Manning et al. (2018).

3.3.2. Rare species and ecosystem connectivity
Common species are typically considered the main drivers of ecosystem processes (Moore, 2006; Vaughn, 2010). However, the high functional distinctiveness of rare species implies that they are also important in supporting vulnerable ecosystem functions, especially in species-rich ecosystems where high functional redundancy is likely to play an important role (Jain et al., 2014; Mouillot et al., 2013). Bracken and Low (2012), for example, demonstrated that realistic losses of rare species in a diverse assemblage of sessile invertebrates and seaweeds, collectively comprising <10% of the sessile biomass, resulted in a 42 to 47% decline in the consumer biomass. Interestingly, the removal of an equivalent biomass of the dominant sessile species had no effect on consumers (Bracken and Low, 2012). The above may also emphasize the importance of including ecosystem connectivity in study designs to allow for extrapolating BEF relationships to natural systems (Matthiessen et al., 2007). Communities that are connected via migration to a metacommunity are more stable and diverse than isolated communities so that corridors in interconnected metacommunities may mitigate (and even reverse) local extinctions and/or ecosystem process disruption (Downing et al., 2014; Loreau et al., 2003; Staddon et al., 2010). Habitat fragmentation, together with declining biodiversity, hence synergistically influence the predictability of ecosystem functioning (France and Duffy, 2006). For aquatic systems this is especially relevant, since dispersal barriers are typically weak and energy and material flow are relatively rapid between and within aquatic habitats (Giller et al., 2004; Hawkins, 2004).

3.3.3. Biological and trophic components
The scoring of the biological components indicates that large BEF evidence gaps align with several of the more functionally important trophic components (Strong et al., 2015).

Relevant examples of evidence gaps for biological components are:

- Intraspecific variability - the key role of intraspecific variability for biodiversity sustenance in ecosystems challenged by environmental change has been the focus of discussion (De Laender et al., 2013).
- Bacterial diversity - although positive effects of microbial communities on ecosystem functioning have previously been demonstrated, namely they play a key role in maintaining multiple ecosystem functions and services simultaneously including nutrient cycling, primary production, litter decomposition and climate regulation (Delgado-Baquerizo et al., 2016b; Glöckner et al., 2012; Zeglin, 2015), BEF studies that consider microbial communities are relatively scarce (e.g. Dell'Anno et al., 2012; Venail and Vives, 2013). This is at least partly due to the fact that defining and measuring biodiversity in consistent and meaningful units for the microscopic biological components, such as the microbial assemblages, and at the genetic scale, pose significant challenges (Strong et al., 2015).
- Genetic diversity - significant effects of genetic diversity on ecological processes such as fluxes of energy and nutrients, primary productivity, community structure, interspecific competition, and population recovery from disturbance were revealed in a literature review by Hughes et al. (2008). It has also been shown in a marine habitat-forming species (the seagrass *Zostera marina*) that increasing genotypic diversity enhanced community resistance to disturbance by grazing geese (Hughes and Stachowicz (2004). Accordingly, genetic diversity might have important ecological consequences at different trophic levels (e.g., population, community and ecosystem) and in some cases the effects are comparable in magnitude to the effects of species diversity (Duffy, 2006; Hughes and Stachowicz, 2004; Latta et al., 2010; Massa et al., 2013; Roger et al., 2012).
- Phylogenetic diversity - given that many traits show a phylogenetic signal, the phylogenetic diversity of communities is also related with the functional trait space of a community, and thus with ecosystem

functioning (Best et al., 2012; Gravel et al., 2012; Griffin et al., 2013; Srivastava et al., 2012). In addition, phylogeny determines interactions among species, and so could help to predict how extinctions cascade through ecological networks and impact ecosystem functions (Srivastava et al., 2012).

Relevant examples of trophic components are:

- Taxonomic groups - primary producers have received particular attention on research on biodiversity decline and ecosystem function (Duncan et al., 2015; Lefcheck et al., 2015; e.g. Messmer et al., 2014). Also, predator diversity studies are particularly relevant to conservation because they focus on the trophic group that is most prone to extinction, (Byrnes et al., 2007) (Finke and Snyder, 2010). In addition, species at higher trophic levels nearly always measure diversity effects that span trough the trophic chain. However, the magnitude and direction of these effects are highly variable and are difficult to predict since these species exhibit many complex, indirect, non-additive, and behavioural interactions (Bruno and Cardinale, 2008; Bruno and O'Connor, 2005).
- Trophic composition – it has been shown that composition of the predator assemblage (strict predators; intraguild predators: predators that consume other predators with which they compete for shared prey resources; or a mixture of the two) can play an important role in determining the nature of the relationship between predator diversity and ecosystem function (Finke and Denno, 2005). Gamfeldt et al. (2014) reported that mixtures of species generally tend to enhance levels of ecosystem function relative to the average component species in monoculture, although they may have no effect or a negative effect on functioning relative to the 'highest-performing' species. Therefore, the structure of their interactions also needs to be accounted for to predict ecosystem productivity (Poisot et al., 2013).
- Trophic interactions (food-web) - in predator experiments, Griffin et al. (2013) reported that richness effects were stronger than those for primary producers and detritivores, suggesting that relationships between richness and function may increase with trophic height in food webs. Duffy et al. (2007) showed that the strength and sign of changes in predator diversity on plant biomass depends on the degree of omnivory and prey behaviour. It has also been shown that consumer diversity effects on prey and consumers strongly depend on species-specific growth and grazing rates, which may be at least equally important as consumer specialization in driving consumer diversity effects across trophic levels (Filip et al., 2014).

Subsequently, studies of single trophic levels are insufficient to understand the functional consequences of biodiversity decline (Gamfeldt et al., 2014; Hensel and Silliman, 2013; Jabiol et al., 2013; Lefcheck et al., 2015; Reynolds and Bruno, 2012; Thebault and Loreau, 2011; Vaughn, 2010). Community and food-web structure also influence species interactions and how species' traits are expressed, and both vertical (across trophic levels) and horizontal (within trophic levels) diversity are hence important (Duffy et al., 2007; Jabiol et al., 2013; Vaughn, 2010). For example, in marine macroalgae it has been shown that diversity directly increased consumer (benthos) diversity and that this increased consumer diversity in turn enhanced consumer stability via increased asynchrony among consumers (Ramus and Long (2016). In addition, multitrophic-level studies indicate that diverse assemblages of prey species, comparatively to depauperate ones, use their own resources more completely, are more resistant to top-down control, and increase consumer fitness (Stachowicz et al. (2007). In contrast, predator diversity can either increase or decrease the strength of top-down control because of omnivory and because interactions among predators can have positive and negative effects on herbivores (Stachowicz et al., 2007). Though, increased prey abundance may not pass up to higher levels of the food chain if such prey is largely tolerant to (or resistance of) predators at these higher trophic levels (Edwards et al., 2010; Graham et al., 2015). Likewise, in the

case of limited overlap between sensitivity and functionality, biodiversity modifications within one trophic level induced by non-random species loss (e.g. subsequent to exposure to pesticides) do not necessarily translate into changes in ecosystem functioning supported by other trophic levels or by the whole community (Radchuk et al., 2016). In brief, multitrophic interactions might depend on: i) trade-offs between competitive ability and resistance to predation; ii) the degree of dietary generalism among consumers; iii) intraguild predation; and iv) openness to migration (Duffy et al., 2007).

3.3.4. Random versus realistic species losses

While most studies of the relationship between biodiversity and ecosystem functioning have examined randomized diversity losses, several recent experiments have employed nested, realistic designs and found that realistic species losses may have larger consequences than random losses for ecosystem functioning (e.g. Bracken and Williams, 2013; Larsen et al., 2005; Naeem et al., 2012; Walker and Thompson, 2010; Wolf and Zavaleta, 2015). The difference in functional consequences of random and ordered extinctions depends on the underlying BEF mechanism (Gross and Cardinale, 2005).

Experiments with controlled (non-random) removal of species hence appear to be a good way forward to increasing our understanding of realistic species losses, although such experiments are fraught with practical obstacles and difficulties over interpretation of results (Raffaelli, 2004). In such experiments, the realistic order in which species are to be lost is determined by their susceptibilities to different types of disturbances (Raffaelli, 2006; Solan et al., 2004). Disturbance, in turn, can moderate relationships between biodiversity and ecosystem functioning by increasing the chance that diversity generates unique system properties (i.e. "emergent" properties), or suppressing the probability of ecological processes being controlled by a single taxon (i.e., the "selection-probability" effect) (Cardinale and Palmer, 2002). This becomes even more complex when multiple disturbances or pressures are considered. For example, Byrnes et al. (2007) discussed that most extinctions (~70%) occur at high trophic levels (top predators and other carnivores), while most invasions are by species from lower trophic levels (70% macroplanktivores, deposit feeders, and detritivores). These opposing changes thus alter the shape of marine food webs from a trophic pyramid capped by a diverse array of predators and consumers to a shorter, squatter configuration dominated by filter feeders and scavengers (Byrnes et al., 2007). Changes in the food web with successive extinctions make it difficult to predict which species will show compensation in the future (Ives and Cardinale, 2004). This unpredictability argues for 'whole-ecosystem' approaches to biodiversity conservation, as seemingly insignificant species may become important after other species go extinct (Ives and Cardinale, 2004).

3.3.5. Environmental conditions

The effects of biodiversity losses on ecosystem functions depend on the abiotic and biotic environmental conditions (e.g. Boyer et al., 2009; Capps et al., 2015; Vaughn, 2010). Changes in water chemistry parameters (such as pH, temperature, alkalinity and water hardness) and physical conditions (e.g. water current), for example, may affect species life-history parameters and hence also directly or indirectly influence BEF relationships (Jesus et al., 2014; Schweiger and Beierkuhnlein, 2014). In line with this, Boyer et al. (2009) noted that species richness increased algal biomass production only at two of the four field sites that differed naturally in environmental conditions.

The main abiotic drivers of ecosystem functioning relevant for aquatic realms discussed by Truchy et al. (2015) include: temperature, as a basic driver of metabolic processes; light and nutrient availability, particularly important for primary producers (and nutrients also for decomposers); substrate composition; sediment loading, which can decrease light availability and hence limit primary production; hydrological regimes, which are fundamental organisers of temporal patterns in biotic structure and ecosystem process rates; and interactions

between these various abiotic drivers. Under rapid global change, simultaneous alterations to compositional diversity and environmental conditions could have important interactive consequences for ecosystem function (Mokany et al., 2016). Despite this clear importance of abiotic condition on BEF relationships, many previously conducted BEF studies did not include testing of abiotic factors, which hampers interpretation of such study findings (Strong et al., 2015). There is hence a need for experimental studies that explicitly manipulate species richness and environmental factors concurrently to determine their relative impacts on key ecosystem processes such as plant litter decomposition (Boyero et al., 2014).

3.3.6. Spatial-temporal scale

The spatial-temporal scale of BEF evaluations has also often been indicated to influence study findings (e.g. Hodapp et al., 2015; Isbell et al., 2011; McBride et al., 2014; Thompson et al., 2015; Vaughn, 2010; Venail et al., 2010). For example, strong species-identity effects at local scales can become species-richness effects at larger scales, as different species traits are favoured in different habitats (Vaughn, 2010). After evaluating 17 grassland biodiversity experiments, Isbell et al. (2011) reported that different species promoted ecosystem functioning during different years, at different places, for different functions and under different environmental change scenarios. The species needed to provide one function during multiple years were also not the same as those needed to provide multiple functions within one year (Isbell et al., 2011) and may also vary between seasons (Frainer et al., 2013). After studying nutrient recycling by freshwater mussels, Vaughn (2010) also concluded that this relationship was dynamic because both environmental conditions and mussel communities changed over the 15-year study period. Both the net effect of diversity and the probability of polycultures being more productive than their most productive species increases through time, because the magnitude of complementarity increases as experiments are run longer (Cardinale et al., 2007; Reich et al., 2012; Stachowicz et al., 2008). Similarly, species richness explained an increasing proportion of data variation as ecosystem processes complexity (EPC) increased, and complementarity may be stronger as EPC increases (Caliman et al., 2013).

What is now sorely needed is a new generation of experiments that target how spatial scale and heterogeneity, realistic local extinction scenarios, functional and phylogenetic composition, and other aspects of environmental change (especially temperature, ocean acidification and pollution) influence the relationship between different dimensions of aquatic biodiversity and ecosystem functioning, and under natural conditions across spatial and temporal scales (e.g. Gamfeldt et al., 2014; Hensel and Silliman, 2013; Kominoski et al., 2009; Narwani et al., 2015). Observational (i.e. correlational) field studies would provide one way forward because they do not require logistically-challenging manipulations, allowing the description of diversity-function relationships of entire sites and regions (Gamfeldt et al., 2014). Additionally, such studies would allow for evaluating BEF curves likely to occur in the actual field and may hence also aid in validating the way data and curves from experimental data may be used to predict these real-world BEF relationships (Figs. 1 and 3). BEF relationships have been demonstrated to be potentially different on local and regional scales (e.g. Bond and Chase, 2002). Consequently, successfully predicting linkages between biodiversity and ecosystem function requires using multiple empirical approaches across scales. Larger and consequently more complex approaches are ecologically more realistic than smaller systems (Liu et al., 2018; Thompson et al., 2018; Vaughn, 2010). On the other hand, smaller-scale (experimental) approaches are easier to replicate and manipulate and they have therefor been proven to be more useful in elucidating the chain of events or evaluating a specific correlation between e.g. a certain (group of) species on a given ecosystem function (Fig. 4).

Most of the studies on BEF relationships have put emphasis mainly into species richness while assuming randomization of community composition which is unrealistic. To overcome this limitation recent studies tested the importance of community assemblages to drive ecosystem functions (Bannar-Martin et al., 2018).

Furthermore, based on lessons learnt from previous experimental and theoretical work, Giller et al. (2004) suggested four experimental designs to address largely unresolved questions about biodiversity-ecosystem functioning relationships:

- investigating the effects of non-random species loss through the manipulation of the order and magnitude of such loss using dilution experiments;
- combining factorial manipulation of diversity in interconnected habitat patches to test the additivity of ecosystem functioning between habitats;
- disentangling the impact of local processes from the effect of ecosystem openness via factorial manipulation of the rate of recruitment and biodiversity within patches and within an available propagule pool; and
- addressing how non-random species extinction following sequential exposure to different stressors may affect ecosystem functioning.

3.3.7. Trait-based evaluations

Strong et al. (e.g. Strong et al., 2015) evaluated the need for traits-based analysis in relation to the underlying BEF mechanism. They noted that BEF relationships underpinned by identity effects are often irregular when maintained in structural biodiversity units and that taxonomic units may hence benefit from translation into functional diversity using traits-based analysis. For BEF relationships emerging from
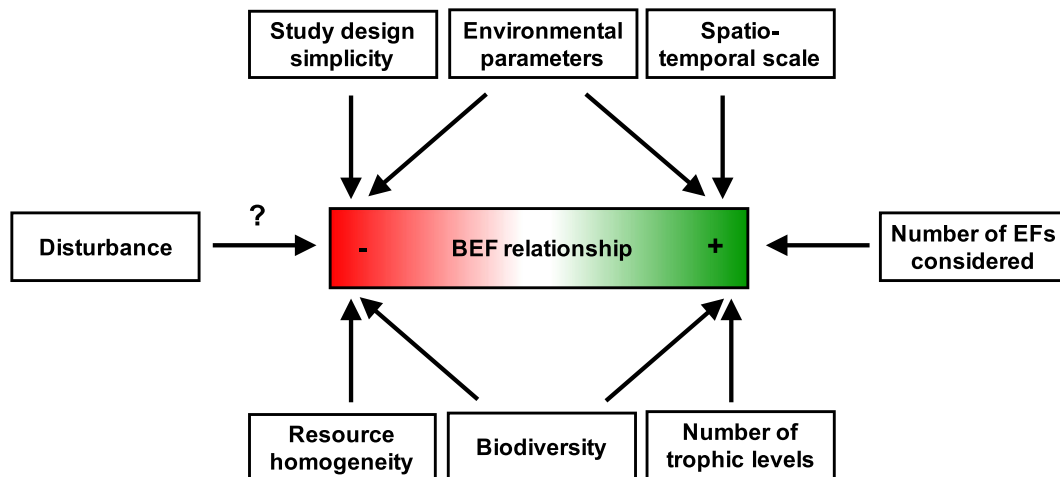

Fig. 3. Factors discussed in the present paper to have either a positive (+) or negative (−) effect on biodiversity-ecosystem functioning relationships.

Laboratory   **Model ecosystems**   **Field studies**

Control of environmental parameters
Reproducibility
Rate of study performance
Precision

Complexity
Spatial-temporal scale
Ability to track energy and materials between compartments
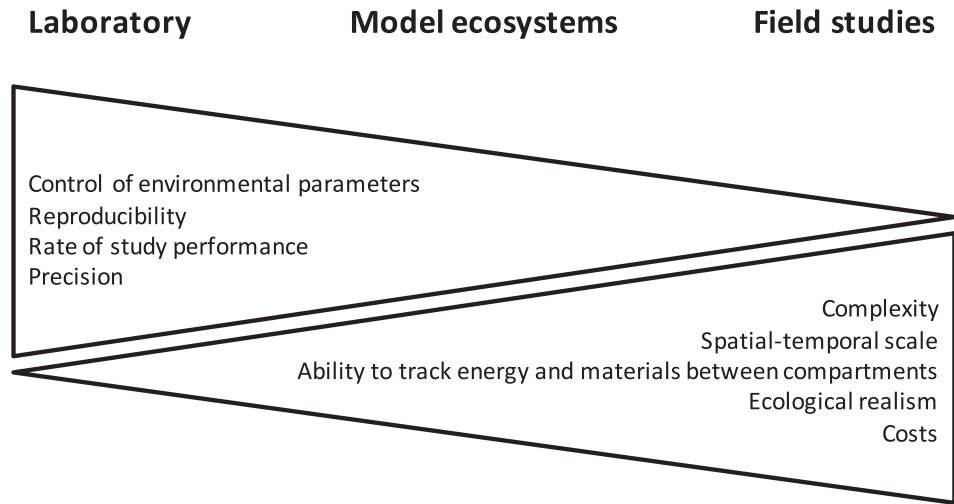Ecological realism
Costs

Fig. 4. Advantages and disadvantages of different experimental approaches (adapted from Brock et al. (2000) and Vaughn (2010)).

complementarity, direct (taxonomic) measures of biodiversity, such as species richness, may be sufficient to express the influence of biodiversity on ecosystem functioning (Strong et al., 2015). Given that BEF relationships in the marine environment appear to be mostly driven by identity effects (c.f. the section "Can BEF relationships be extrapolated over ecosystem types?" above), trait-based analysis may be a promising way forward for these ecosystem types, although several constraints with such analysis have been reported, which include:

- Most studies of how biodiversity influences ecosystem function have examined single traits (e.g., the ability to break down leaves, rates of primary production), which is an oversimplification of species' roles, and very likely has led to underestimates of the impacts of species losses (Vaughn, 2010);
- The rate, efficiency or influence of a particular role on ecosystem functioning is not coded within biological trait analysis, and this is understandable considering how the performance of any species can change depending on numerous factors including age/life stage, season, abundance, habitat, community composition and environmental conditions (Frainer et al., 2013; Queirós et al., 2011; Reiss et al., 2009; Strong et al., 2015; Truchy et al., 2015; Vaughn, 2010);
- Efficient ways are needed to extrapolate information about key functional traits of known species to estimate the traits of poorly known species, which number in the millions, especially microbial species (Naeem et al., 2012).
- Some species may be difficult to allocate to any, broadly defined, functional group, because they possess a high number of unique traits (Mouillot et al., 2013; Truchy et al., 2015).
- Related with this, (freshwater) species are often placed into functional categories on the basis of shared autecological traits (i.e., trophic mode, behaviour, habitat, life history, morphology) that may not translate into shared ecological function (Poff et al., 2006; Usseglio-Polatera et al., 2000; Vaughn, 2010). As discussed above ("Mechanisms and shape of BEF relationships in aquatic realms - Underlying BEF mechanisms"), a distinction between response (traits to cope with abiotic filtering and biotic interactions) and effect traits (those with a direct link with ecosystem function) has been therefore been suggested (e.g. Oliver et al., 2015; Suding et al., 2008). In addition, the degree of redundancy among species assigned to many of such functional groups or guilds is unknown (Vaughn, 2010).

3.3.8. Ecological modelling of BEF relationships

Early BEF syntheses were based on expert opinions or qualitative summaries and interpretation of data, which resulted in inconsistent conclusions, forcing researchers to confront their hypotheses with more quantitative forms of analyses (Cardinale et al., 2011; Naeem et al., 2012). In the past decade, several meta-analyses on data obtained from manipulative experimental BEF experiments have been conducted to attain evidence for BEF relationships (e.g. Balvanera et al., 2014; Cardinale et al., 2011; Mora et al., 2014; Reich et al., 2012; Schmid et al., 2009; Stachowicz et al., 2007; Worm et al., 2006). Since BEF evidence is hence mainly based on experimental studies, it has been debated in recent years as to whether these results are transferable to natural ecosystems, the more since BEF relationships may be different under both conditions (c.f. Fig. 1). To date, only a few studies have addressed the challenge of validating experimentally derived theories with data from natural aquatic ecosystems (e.g. Duffy, 2009; Hodapp et al., 2015; Thompson et al., 2015). Recently an attempt has been made to discuss the use of integrated models for this purpose (Mokany et al., 2016). Furthermore, it has been shown that these must be able to simulate and project simultaneous changes in biodiversity composition, and ecosystem function, over space and time for large regions, incorporating interactions between composition and function. The development and application of integrated models of composition and function in natural ecosystems face a number of important challenges, including biological data limitations, system knowledge and computational constraints (Mokany et al., 2016). For example, due to the multivariate nature of most ecological data, the methodology applied to assess fundamental mechanisms must accommodate the multivariate nature of these dependencies, as well as direct and indirect influences, e.g. by using structural equation models (SEMs) (Cardinale et al., 2009; Hodapp et al., 2015).

Integrated models could highlight priorities for the collection of new empirical data, identify gaps in our existing theories of how ecosystems work, help develop new concepts for how biodiversity composition and ecosystem function interact, and allow predicting BEF relations and its drivers at larger scales (Balvanera et al., 2014; Fung et al., 2015; Mokany et al., 2016; Queirós et al., 2015; Strong et al., 2015). Such models could also form components within larger 'integrated assessment models', improving consideration of feedbacks between natural and socioeconomic systems (Mokany et al., 2016), ultimately aimed at better informing management as is seen in the framework underlying the IPBES (Diaz et al., 2015).

4. Conclusions

Considering the aims of this paper as outlined in the Introduction section, it can be concluded that:

1. Mechanisms and shape of aquatic BEF relationships are highly context-dependant, but that they appear to be best approximated by a power function in most situations;
2. BEF relationships are commonly the result of multiple interactions of environmental variables involving confounding factors;
3. Although a striking level of generality in diversity effects across terrestrial, freshwater, and marine ecosystems have been reported, BEF relationships cannot be directly extrapolated across ecosystem types due to intrinsic system-specific characteristics;
4. Despite considerable research efforts and progress into BEF relations in the past decades, several research limitations and gaps still exist;
5. Depending on the specific research question that is tackled, both observational and experimental studies may increase our understanding of BEF relationships;
6. Meta-analysis and validation of modelling approaches based on existing data, provided that they carefully consider the aspects discussed in the present paper (spatial-temporal scale, number of EFs considered in the studies used, etc.; see Fig. 3) appear to be a good way forward to operationalize BEF research.

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