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Biodiversity and ecosystem functioning in naturally assembled communities

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ABSTRACT

Approximately 25 years ago, ecologists became increasingly interested in the question of whether ongoing biodiversity loss matters for the functioning of ecosystems. As such, a new ecological subfield on Biodiversity and Ecosystem Functioning (BEF) was born. This subfield was initially dominated by theoretical studies and by experiments in which biodiversity was manipulated, and responses of ecosystem functions such as biomass production, decomposition rates, carbon sequestration, trophic interactions and pollination were assessed. More recently, an increasing number of studies have investigated BEF relationships in non-manipulated ecosystems, but reviews synthesizing our knowledge on the importance of real-world biodiversity are still largely missing.

I performed a systematic review in order to assess how biodiversity drives ecosystem functioning in both terrestrial and aquatic, naturally assembled communities, and on how important biodiversity is compared to other factors, including other aspects of community composition and abiotic conditions. The outcomes of 258 published studies, which reported 726 BEF relationships, revealed that in many cases, biodiversity promotes average biomass production and its temporal stability, and pollination success. For decomposition rates and ecosystem multifunctionality, positive effects of biodiversity outnumbered negative effects, but neutral relationships were even more common. Similarly, negative effects of prey biodiversity on pathogen and herbivore damage outnumbered positive effects, but were less common than neutral relationships. Finally, there was no evidence that biodiversity is related to soil carbon storage.

Most BEF studies focused on the effects of taxonomic diversity, however, metrics of functional diversity were generally stronger predictors of ecosystem functioning. Furthermore, in most studies, abiotic factors and functional composition (e.g. the presence of a certain functional group) were stronger drivers of ecosystem functioning than biodiversity *per se*. While experiments suggest that positive biodiversity effects become stronger at larger spatial scales, in naturally assembled communities this idea is too poorly studied to draw general conclusions.

In summary, a high biodiversity in naturally assembled communities positively drives various ecosystem functions. At the same time, the strength and direction of these effects vary highly among studies, and factors other than biodiversity can be even more important in driving ecosystem functioning. Thus, to promote those ecosystem functions that underpin human well-being, conservation should not only promote biodiversity *per se*, but also the abiotic conditions favouring species with suitable trait combinations.

Key words: biodiversity, community composition, context dependence, ecosystem functioning, ecosystem multifunctionality, environment, global change, land use, spatial scale.

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I. INTRODUCTION

The 1992 Earth Summit in Rio de Janeiro increased interest in the question of how changes in biodiversity, and species loss in particular, affect the functioning of ecosystems (Schulze & Mooney, 1993). Soon after, some of the first publications experimentally linking biodiversity with ecosystem functioning emerged (Naeem *et al.,* 1994; Tilman, Wedin & Knops, 1996). These studies represented a major paradigm shift in ecological thinking. Until that time, biodiversity was mainly thought of as factor that responds to environmental change and ecosystem functions (Fig. 1A), but not as something that also drives ecosystem functioning (Fig. 1C) (Naeem, 2002; Hillebrand & Matthiessen, 2009; Tilman, Isbell & Cowles, 2014). Thus, a new scientific sub-discipline on 'Biodiversity and Ecosystem Functioning' (BEF) was born.

The BEF field was initially dominated by theoretical (e.g. Tilman, Lehman & Thomson, 1997; Loreau, 1998) and experimental studies (e.g. Tilman, Wedin & Knops, 1996; Hector *et al.,* 1999; Roscher *et al.,* 2003), where researchers typically simulated random biodiversity (e.g. species) loss [but see Naeem *et al.,* 1994 and Tilman & Downing, 1994, where biodiversity loss was non-random], and measured the responses of certain ecosystem functions, such as biomass production or litter decomposition. As such, BEF research initially focused on the causal effects of biodiversity on ecosystem functioning, in simplified systems where variation in other factors than biodiversity was minimal (Fig. 1B). The aim of these studies was to investigate whether biodiversity can drive ecosystem functioning, rather than to assess the strength of these effects in the real world. Various papers synthesizing this work have emerged, and based on these it is widely established that random biodiversity loss can reduce biomass production, carbon sequestration, litter decomposition rates and biomass stability, and increase disease prevalence (Loreau *et al.,* 2001; Hooper *et al.,* 2005; Balvanera *et al.,* 2006; Quijas, Schmid & Balvanera, 2010; Cardinale *et al.,* 2011, 2012; Lefcheck *et al.,* 2015).

What is less understood, as also highlighted by others (Loreau *et al.,* 2001; Hooper *et al.,* 2005; Cardinale *et al.,* 2011; Tilman, Isbell & Cowles, 2014; Isbell *et al.,* 2017) and the focus of this review, is how important biodiversity is in driving various ecosystem processes in non-manipulated, naturally assembled communities. In natural systems, variation in biodiversity is non-randomly distributed across space and time, and driven by various environmental factors, as well as by ecosystem functions such as plant biomass (Grime, 1973; Hautier, Niklaus & Hector, 2009) (Fig. 1C). There are various reasons why BEF relationships in naturally assembled communities might deviate from those in experimental communities. First, in most experiments, biodiversity loss is random, and variation in abiotic conditions is minimized. The question is whether the mechanisms that drive BEF relationships in such simplified systems are strong enough also to have a major impact in much more complex, real-world systems, where other community aspects not related to biodiversity *per se* (e.g. the presence of a keystone species) or abiotic conditions may outweigh any biodiversity effects (Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Díaz *et al.,* 2007). Second, in most BEF experiments, immigration of new species into communities is not allowed (and avoided by e.g. weeding). This contrasts with real-world situations, and both theoretical (e.g. Leibold, Chase & Ernest, 2017) and empirical studies (Petermann *et al.,* 2010; Veen, van der Putten & Bezemer, 2018) suggest that BEF relationships might be weaker in open communities, in part because species-poor communities tend to get invaded by species that increase their biomass production. Third, in naturally assembled communities, there can be feedbacks from ecosystem functions to biodiversity (Grace *et al.,* 2016). For example, in grasslands with high biomass production, various species can be forced to extinction due to competition for light (Grime, 1973; Hautier, Niklaus & Hector, 2009), and these feedbacks can therefore complicate BEF assessments in non-experimental systems. Some authors argued that due to these differences, biodiversity effects should be weaker in naturally assembled communities than in experiments (Grime, 1998; Wardle, 2016), while others argued the opposite (Turnbull *et al.,* 2016; Isbell *et al.,* 2017). Ultimately, however, only empirical investigations of BEF relationships in naturally assembled communities can completely resolve

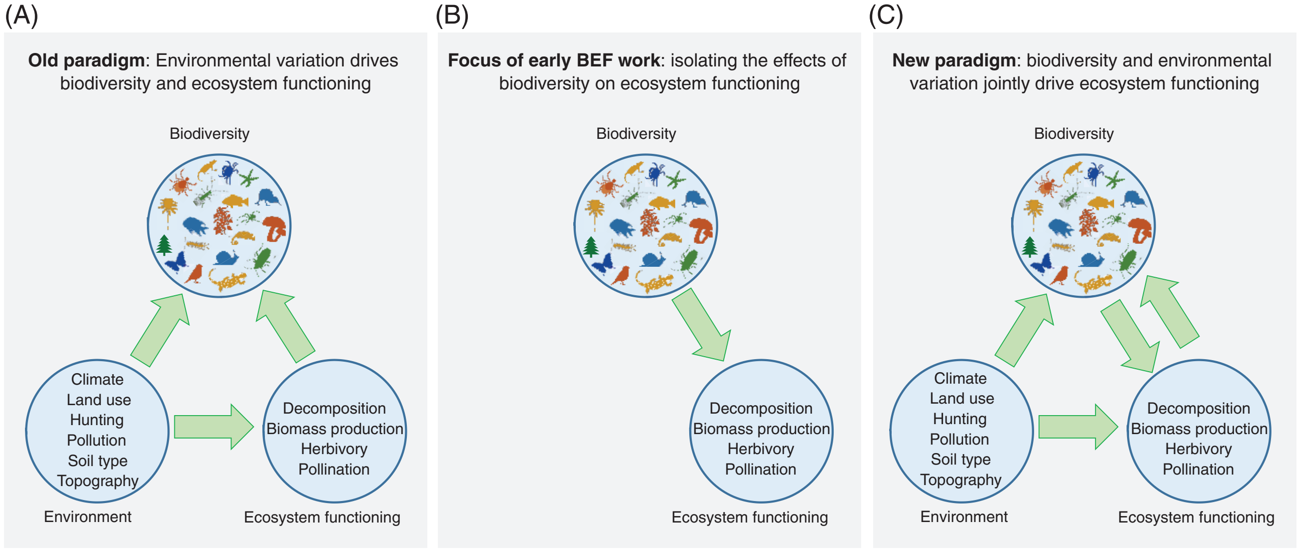

Fig. 1. In past decades, our view on the role of biodiversity in ecosystems, as well as approaches on how we study it, have changed. (A) Until the early nineties, the dominant paradigm was that biodiversity primarily responds to environmental and anthropogenic factors, but that it has only a minor role in driving ecosystem functions. (B) Most early biodiversity–ecosystem functioning (BEF) research focused on the causal effects of random variation in biodiversity on ecosystem functioning, while minimizing environmental variation and its effects. (C) It is currently recognized that biodiversity both responds to its environment and drives ecosystem functioning, although its importance compared to the effects of other drivers (e.g. abiotic drivers and functional composition) are still under debate.

this debate. Such studies should not only recognize, but also embrace the complexity of real-world ecosystems, by integrating insights on the drivers of biodiversity (Fig. 1A) and insights from BEF experiments (Fig. 1B).

Although some early examples do exist (e.g. McNaughton, 1977, 1985; Dodd *et al.*, 1994), non-experimental research on BEF relationships gained traction by the mid-2000s, following the publication of conceptual (Díaz & Cabido, 2001; Lavorel & Garnier, 2002) and empirical (e.g. Bai *et al.*, 2004; Cardinale *et al.*, 2005; Grace *et al.*, 2007; Vilà *et al.*, 2007) papers. The initiation of several collaborative, shared-platform projects (e.g. Fischer *et al.*, 2010; Maestre *et al.*, 2012; Baeten *et al.*, 2014; Borer *et al.*, 2014) further accelerated research into this topic. Several other studies have attempted to synthesize insights of non-experimental BEF studies, and have provided strong evidence that biodiversity in naturally assembled communities can increase average levels of biomass production (Mora *et al.*, 2011; Grace *et al.*, 2016; Liang *et al.*, 2016; Duffy, Godwin & Cardinale, 2017), as well as the temporal stability in biomass production (Houlahan *et al.*, 2018). However, these previous studies usually focused on a small number of ecosystem functions and taxa. This systematic review aims to go a step further than these previous works, by investigating the links of not only biomass production and biomass stability, but also other functions, to the biodiversity of a wide range of taxa in a variety of systems (although with an emphasis on terrestrial systems), and by also investigating how relatively important biodiversity is for these functions, compared to other drivers.

In this review I first investigate the spread of studies on relationships between naturally assembled biodiversity and six categories of ecosystem functions (biomass stocks/production, litter decomposition, soil organic carbon storage, biomass stability, pathogen/herbivore damage and pollination) and ecosystem multifunctionality. I then investigate and discuss the balance of evidence regarding the direction of these BEF relationships, and I discuss their underlying mechanisms. I also discuss which components of biodiversity (e.g. taxonomic, functional or phylogenetic diversity) are most important in driving ecosystem functioning, and how strong the effects of biodiversity on ecosystem functioning are compared to the effects of functional composition and abiotic conditions, and I discuss at which spatial scales biodiversity matters most. Finally, I outline the main conclusions and research gaps, and I propose an agenda for future research directions that should advance our understanding of BEF relationships in complex, naturally assembled communities.

II. QUANTITATIVE RESPONSE OF ECOSYSTEM FUNCTIONING TO BIODIVERSITY IN NATURALLY ASSEMBLED COMMUNITIES

I performed a systematic literature search on empirical studies investigating the relationship between biodiversity and ecosystem functioning in naturally assembled communities, with the aims: (1) to investigate the coverage of existing studies in terms of the location, ecosystem type, functional groups and ecosystem-function types studied, as well as in their design, and to (2) investigate the balance of evidence for the existence of various types of BEF relationships in naturally assembled communities.

(1) Literature search

The literature search was performed using the Clarivate Analytics *Web of Science* database and focused on all studies published before 1 October 2018. I searched for studies including a combination of the terms 'ecosystem function(ing)' and either 'biodiversity' or 'species richness' or 'genetic diversity' or 'functional diversity' or 'phylogenetic diversity' or 'evolutionary diversity', and for studies combining the terms 'species richness' or 'biodiversity' with 'biomass production', 'productivity', 'soil organic carbon', 'decomposition', 'carbon storage', 'carbon stock', 'stability', 'herbivory', 'herbivore damage', 'pest damage', 'pathogen damage', 'pathogen infection', 'pollination' or 'ecosystem multifunctionality' in their title. This yielded a total of 8,619 published studies. I initially scanned the titles and/or abstracts of all of these, and read the complete papers when initial scans indicated the paper was potentially relevant. Cross-referencing of reviews yielded additional publications. Among these publications, I looked for studies that met all of the following criteria: (*i*) effects of biodiversity (with the most diverse communities containing >2 species) on ecosystem functioning (rather than *vice versa*) were statistically tested, in (*ii*) a field setting and in (*iii*) communities in which biodiversity or species composition were *not directly* manipulated (although in some studies factors indirectly driving biodiversity were manipulated, e.g. grazing or nutrient-addition experiments), and where (*iv*) at least one covariate related to abiotic variation (i.e. climate, soil type or topography) and/or functional community composition [e.g. the relative abundance of a species or functional type, principal component analysis (PCA) or non-metric multivariate dimension scaling (NMDS) axes of community data, community (abundance-weighted) means of trait value or a factor listing all present species] and/or other factors (e.g. total community biomass, successional stage, human population density, land use) was taken into consideration in the statistical analyses, to ensure a minimal effort to avoid the detection of spurious BEF relationships. Furthermore, studies that used a dilution gradient (Nadrowski, Wirth & Scherer-Lorenzen, 2010), i.e. where, by design, monocultures always contained the same species, were excluded, as in these it is extremely difficult to separate species-identity effects from real biodiversity effects. I focused on ecosystem functions that were relatively commonly studied, namely community-wide biomass production or stocks (in relation to the biodiversity of the same community), decomposition rates (i.e. leaf, root or standard litter biomass loss, in relation to plant or decomposer diversity), soil organic carbon storage (soil organic carbon or matter stocks, in relation to plant diversity), community biomass stability [measured as the (inverse of) temporal coefficient of variation in community-wide biomass stocks or production, in relation to the biodiversity of the same community], herbivore damage (in relationship to host, herbivore or predator diversity) or pathogen damage (in relation to host diversity), pollination (fruit or seed set, in relation to pollinator or plant diversity) or ecosystem multifunctionality (a metric quantifying the simultaneous performance of multiple ecosystem functions (Hector & Bagchi, 2007; Gamfeldt, Hillebrand & Jonsson, 2008), in relation to the diversity of any kind of taxonomic/functional group). While I reviewed studies performed in all ecosystem types, due to the focus on the above-mentioned ecosystem functions, of which some are most relevant in terrestrial ecosystems, studies based on aquatic systems are, although not excluded, less represented in this review. The communities in the selected studies were not directly manipulated, although most were not totally free of human influences, which include e.g. past logging or fishing activities, altered nitrogen deposition rates or livestock grazing. Hence, the term 'naturally assembled communities' is used throughout to indicate communities whose compositions were not directly manipulated, although they may have assembled semi-naturally rather than completely naturally.

(2) Spread of evidence

In total, I found 258 studies that met the criteria of my literature search (see online Supporting information, Appendix S1 for a complete list). Many of these reported multiple BEF relationships, because they studied: (*i*) multiple ecosystem functions (e.g. Ratcliffe *et al.,* 2017), (*ii*) multiple types of ecosystems/habitats (e.g. Vilà *et al.,* 2013), (*iii*) the diversity of multiple organism groups (e.g. Soliveres *et al.,* 2016*a*), (*iv*) multiple regions (with replicate plots/transects clustered within regions, e.g. Ratcliffe *et al.,* 2017), (*v*) multiple time periods (Mori *et al.,* 2017) and/or (*vi*) multiple spatial scales (e.g. Grace *et al.,* 2016). When multiple metrics of biodiversity (e.g. species richness, Shannon diversity, functional diversity and phylogenetic diversity) of the same functional group were simultaneously analysed as predictors of a certain ecosystem function (e.g. Hao *et al.,* 2018), I regarded these collectively as a single BEF relationship. Based on these criteria, I found 726 published BEF relationships in naturally assembled communities. The majority of studies were carried out in the Northern hemisphere, especially in North America (61 articles), Europe (72 articles) and Asia (56 articles) (Fig. 2A). Latin America was slightly less frequently studied, with 36 articles. Reported BEF relationships from Africa, Oceania and Antarctica were even scarcer (Fig. 2A). Twenty-four articles reported BEF relationships spanning cross-continental gradients. Until the mid-2000s, the number of publications per year was rather low, but by the late 2000s research output on this topic rapidly increased (Fig. 2C).

Given the dominance of studies carried out in the Northern hemisphere, it is no surprise that temperate grasslands (42 studies) and temperate/boreal forests (47 studies) were well represented. Tropical (or subtropical) forests and drylands/deserts were also frequently studied, in 40 and 25 publications, respectively. By contrast, only three studies reported relationships in tropical savannahs and grasslands,

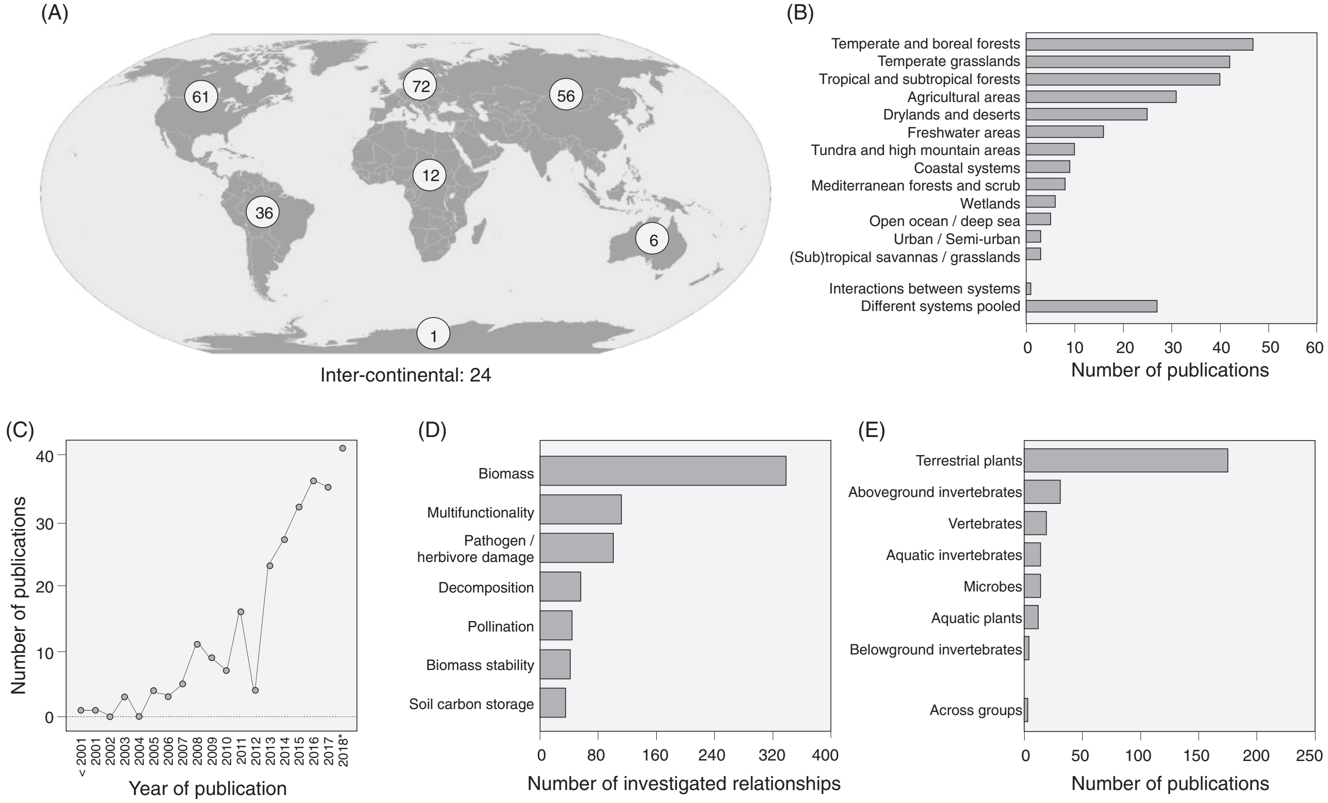

Fig. 2. Spread of evidence of studies on biodiversity–ecosystem functioning (BEF) relationships in naturally assembled communities. (A) Continental origin of publications. America is divided into North (USA and Canada) America and Latin America (Central and South America). (B) Broad ecosystem types in which the studies were carried out. (C) Years in which the studies were published. *Note that the number of studies published in 2018 represents only those added to the *Web of Science* Database before 1 October 2018. (D) Broad categories of ecosystem function types that were studied. (E) Broad categories of functional groups that were studied.

despite their large terrestrial distribution. Non-coastal (open ocean) marine systems were also understudied, with only 5 articles (Fig. 2B), partly due to the focus of this review on ecosystem functions which tend to be more relevant in terrestrial systems. Thirty-four studies focused on human-dominated systems, of which 31 were carried out in cultivated systems (e.g. croplands) and 3 in (sub-)urban settings. Twenty-nine studies were not confined to a single ecosystem type, but investigated BEF relationships across ecosystem types, or focused on functions delivered by mobile function providers (e.g. pollinators) from one ecosystem type (e.g forests) to another (e.g. croplands).

Ecosystem functions related to biomass production or stocks were by far the most commonly studied (Fig. 2D). A large number of studies, especially recent ones, also analysed relationships between biodiversity and the simultaneous performance of multiple ecosystem functions [‘ecosystem multifunctionality’ (Hector & Bagchi, 2007)] (Fig. 2D).

Of the eight broad functional groups considered (Fig. 2E), terrestrial plants (especially vascular plants) were by far the most often studied (74% of studies). Among studies carried out in forests, much attention has been paid to the effects of tree diversity. Aboveground invertebrates (especially bees, dung beetles and ants) and vertebrates (especially birds and fishes) were also reasonably frequently studied, while much less attention has been paid to aquatic invertebrates or plants, microbes and belowground invertebrates (Fig. 2E). This may in part be due to the focus on a set of functions (Fig. 2D) which do not all strongly rely on aquatic plant or belowground invertebrates.

Separating the effects of biodiversity from those of other factors, including abiotic conditions and functional composition, is a major challenge when working with non-experimental data, and studies used different strategies regarding their design and statistical analysis to do so. In 32 studies (e.g. Ratcliffe *et al.*, 2017; Schuldt *et al.*, 2018), sampling locations were stratified by functional composition and/or biodiversity, in order to minimize covariation between biodiversity and the composition or dominance of certain species, and to maximize the variation in biodiversity compared to the variation of other potential drivers of ecosystem functioning. In other studies, plots were either stratified by factors other than biodiversity (e.g. soil type) or plots were designated at random locations or at regular intervals within the study area. This approach (used in e.g. Vilà *et al.*, 2013) is often suitable for studies comparing the relative importance of biodiversity *versus* those of other factors in driving ecosystem functioning, as the variation in neither of these factors is minimized. However, this can also make it challenging to separate their effects, if they covary. Regarding the statistical analysis, most studies used linear models [including generalized linear mixed models (GLMMs) and linear mixed models (LMMs)] to distinguish statistically between the effects of biodiversity and other factors on ecosystem functioning, (loosely) following the approach advocated by Díaz *et al.* (2007). Nevertheless, a surprisingly high number of studies (97, i.e. 41% of studies) (additionally) used Structural Equation Models (e.g. Grace *et al.,* 2007) to model the direct and indirect drivers of ecosystem functioning in an integrative way.

(3) Balance of evidence

Here, I provide the balance of evidence that biodiversity drives different types of ecosystem functions in real-world, non-experimental settings. I also discuss the extent to which findings are in line with experimental studies and ecological theory, and I discuss the potential mechanisms that may have caused the observed relationships. For the latter, I rely mostly on evidence from experimental studies, which are most suitable for gaining insights into mechanisms. However, whenever available, I also discuss studies that investigated BEF mechanisms in naturally assembled communities.

Due to the wide variety of spatial scales, designs, statistical methods and other aspects among the reviewed studies, it was not feasible to perform a meta-analysis to assess how biodiversity drives different ecosystem functions. Instead, I used a semi-quantitative approach, based on the direction of reported BEF relationships. To do this, I first categorized the 726 published relationships as positive, neutral or negative. Relationships were regarded as 'neutral' when either P values exceeded 0.05, or when statistical models without the biodiversity term were more parsimonous. When multiple components of biodiversity of the same functional group were analysed, significance was assessed based on the biodiversity metric with the strongest effect. In a few cases, different biodiversity indicators had significant, but opposing effects on the same ecosystem function. In these cases, when effect sizes (e.g. standardized regression coefficients) or r-values were not reported, I did not assign an overall effect. When standardized regression coefficients, standardized paths or r-coefficients were reported, and the positive and negative effect sizes differed by less than 0.1 units, the overall effect was treated as neutral. By contrast, the overall relationship was treated as 'positive' or 'negative' when the biodiversity metric with a positive effect had a standardized effect size that was at least 0.1 units higher or 0.1 units lower than the effect size of the biodiversity metric with the negative effect.

For each type of assessed BEF relationship (see Table 1 for an overview), I used χ^2-tests to investigate whether positive relationships were more or less common than negative relationships (thus ignoring non-significant relationships). If the outcome of the χ^2-test was significant ($P < 0.05$), I also assessed whether positive or negative relationships occurred in at least 50% of all cases (including neutral relationships), thus testing whether evidence for positive or negative BEF relationships is 'widespread' (>50% of cases in same, significant direction) or 'moderate' (<50% of cases in same, significant direction). If the outcome of the χ^2-test was non-significant, I regarded the assessed BEF relationship as 'inconsistent', when the number of investigated relationships exceeded 20, or as 'uncertain', when the scarcity of data (<20 investigated relationships) caused a high chance of type II errors.

(*a*) *Biomass*

Theory suggests that various mechanisms, including resource partitioning, competitive or facilitative interactions and negative soil feedbacks can drive positive relationships between the diversity of a certain trophic group and its biomass production (Tilman, Lehman & Thomson, 1997; Loreau, 1998). Meta-analyses based on hundreds of studies have shown that in experimentally manipulated communities, such positive relationships are indeed widespread (Cardinale *et al.,* 2011, 2012). Therefore, I expected to find similarly strong, positive relationships in naturally assembled communities. In total, my literature review yielded 338 reported relationships between biodiversity and biomass stocks or productivity in naturally assembled communities (Fig. 2D). The majority of these focused on plant diversity and primary biomass stocks or production, especially in forests, while the effects of animal diversity were studied less often.

In temperate forests, more than half of the studies reported positive relationships between tree diversity and tree biomass production, and slightly less than half of the reported relationships between tree diversity and tree biomass stocks were also positive (Table 1). By contrast, in tropical forests, positive relationships between tree diversity and tree biomass stocks or tree biomass production (the latter being less frequently studied) were approximately as common as negative relationships, and outnumbered by neutral ones (Table 1). Relationships between plant diversity and biomass production are often non-linear, and tend to flatten at higher diversity levels (Cardinale *et al.,* 2011). It is possible that the higher diversity in the tropics (where even the least-diverse stands typically contain dozens of tree species) precludes the detection of any relationship with biomass production. Four studies analysed productivity and standing stocks of tree biomass across both temperate and tropical forests, of which two were extremely well replicated (Chisholm *et al.,* 2013; Liang *et al.,* 2016), and observed overall positive relationships (Chisholm *et al.,* 2013; Guo & Ren, 2014; Liang *et al.,* 2016; Chen *et al.,* 2018).

While in experimental studies, positive tree diversity–productivity relationships are also predominant (Jactel *et al.,* 2018), a recent study found that these are less strong than in unmanipulated tree communities (Duffy, Godwin & Cardinale, 2017). Forests take dozens, if not hundreds of years to 'mature'. Therefore, the young age (usually less than 20 years) of current forest experiments (Verheyen *et al.,* 2016) might have precluded strong relationships between tree diversity and biomass

Table 1. Balance of evidence regarding different types of biodiversity–ecosystem functioning (BEF) relationships in naturally assembled communities. Focal group: the group of organisms whose biodiversity levels are related to the ecosystem function. Theory: expected direction of the relationship based on formal (i.e. mathematical) theoretical work. Observed relationships are shown for experiments, based on earlier meta-analyses, and for non-experimental studies, based on studies reviewed herein. For the latter, N refers to the number of investigated relationships. Both the frequency of positive (green), neutral (yellow) and negative (red) relationships are shown, as well as the overall patterns (arrows). Green arrows pointing upward depict either moderate (light) or widespread (dark) evidence for positive BEF relationships, while red arrows pointing downward depict moderate (light) or widespread (dark) evidence for negative BEF relationships. Horizontal arrows depict relationships that are either weak/inconsistent (yellow) or uncertain (white, when N < 20). The distinction between moderate and widespread BEF relationships was not made for theoretical expectations or experimental studies, hence the lack of light green/red arrows in these columns. Refer to Appendix S1 for a complete overview of the relationships upon which this table is based. Sources: a, Tilman, Lehman & Thomson (1997); b, Loreau (1998); c, Tilman (1999); d, Loreau (2001); e, Doak *et al.* (1998); f, Tilman, Lehman & Bristow (1998); g, Yachi & Loreau (1999); h, Schmidt & Ostfeld (2001); i, Hambäck *et al.* (2014); j, Thébault & Loreau (2003); k, Ives, Cardinale & Snyder (2005); l, Blüthgen & Klein (2011); m, Jactel *et al.* (2018); n, Cardinale *et al.* (2011); o, Cardinale *et al.* (2012) (this study showed mixed evidence regarding the plant diversity–herbivore damage relationship, hence two arrows are shown); p, Handa *et al.* (2014); q, Campbell, Murphy & Romanuk (2011); r, Cardinale *et al.* (2013); s, Lefcheck *et al.* (2015).

					Observed relationships			
Category of function	Ecosystem function	Ecosystem type	Focal group	Theory	Experiments	Non-experimental studies N		
Biomass	Tree biomass stock	Temperate forests	Trees	↗ a,b,c	↗ m	38		⇗
	Tree biomass production	Temperate forests	Trees	↗ a,b,c		61		↗
	Tree biomass stock	Tropical forests	Trees	↗ a,b,c	↗ m	44		➡
	Tree biomass production	Tropical forests	Trees	↗ a,b,c		17		⇨
	Plant biomass*	Grasslands	Plants	↗ a,b,c	↗ n	102		⇗
	Plant biomass*	Aquatic systems	Plants	↗ a,b,c	↗ n	21		↗
	Consumer biomass	All	Consumers	↗ a,b,c		24		↗
Decomposition	Decomposition	All	Plants	↘ d	↗ o	33		⇗
	Decomposition	All	Decomposers	↗ d	↗ p	20		➡
Soil carbon storage	Soil organic carbon stock	All	Plants		↗ o	35		➡
Biomass stability	Plant biomass stability	All	Plants	↗ e,f,g	↗ q,r	27		⇗
	Consumer biomass stability	All	Consumers	↗ e,f,g		13		↗
Pathogen / herbivore damage	Overall pathogen damage	All	Hosts		↘ o	17		⇨
	Damage by specialist pathogen	All	Hosts	↘ h		18		↘
	Herbivore damage	All	Plants	↘ h,i	➡↘ o	45		➡
	Herbivore damage	All	Herbivores	↗ j,k		10		⇨
	Herbivore damage	All	Predators	↘ k	➡ o	11		⇨
Pollination	Fruit or seed set	All	Plants			8		⇨
	Fruit or seed set	All	Pollinators	↗ l		36		↗
Ecosystem multi-functionality	Ecosystem multifunctionality	All	All		↗ s	111		⇗
	Ecosystem multifunctionality	Temperate forests**	All			16		↗
	Ecosystem multifunctionality	Tropical forests**	All			17		⇨
	Ecosystem multifunctionality	Grasslands**	All			55		➡

*In grasslands and aquatic systems, distinguishing between biomass stocks and production is challenging, hence I pooled biomass stock and production BEF relationships in grasslands.

**These analyses rely on a subset of the data (and are therefore not independent) of the analysis on ecosystem multifunctionality across all ecosystem types.

production, if these take longer to manifest. Indeed, meta-analyses based on mostly grassland experiments have shown that biodiversity effects become stronger with community maturation, due to increased species complementarity (Cardinale *et al.*, 2007, 2011). It is possible that processes such as species' complementarity in use of light (Jucker, Bouriaud & Coomes, 2015), are only strong enough in older forests to drive positive biodiversity effects.

In grasslands (broadly defined here as open systems without a closed tree canopy, thus including temperate grasslands and shrublands, drylands and tropical savannahs), 102 relationships were reported between plant diversity and biomass stocks or production. Positive relationships ($N = 39$; e.g. Grace *et al.*, 2016; Maestre *et al.*, 2016) outnumbered negative ones ($N = 9$; e.g. Xu *et al.*, 2018), although even more relationships ($N = 54$; e.g. Grace *et al.*, 2007; Díaz *et al.*, 2007) were neutral (Table 1). While thus only 38% of the relationships were positive, a review by Cardinale *et al.* (2009) on experimentally manipulated grassland communities showed a much higher fraction (85%) of significantly positive relationships. This suggests that the effect of plant diversity on grassland biomass production is weaker in complex, naturally assembled communities than in experiments. Alternatively, it might be that the observational studies have lower statistical power. Duffy, Godwin & Cardinale (2017) quantitatively compared the strength of grassland diversity–productivity relationships among experimental studies with a single, but well-replicated, observational study (Grace *et al.,* 2016), and found that in the latter, the relationship was much stronger. Given these contrasting findings, it is at this stage difficult to say in which setting the effects of plant biodiversity on herbaceous biomass production are most widespread and strongest, and future, formal meta-analyses based on a large number of both experimental and observational studies need to be performed before strong conclusions can be drawn.

In aquatic systems, I found only 21 reported relationships between the diversity of primary producers and primary productivity (Table 1). Out of these, 11 (e.g. Cardinale *et al.,* 2009) were positive, and only one was negative. These findings are largely in line with a meta-analysis that found positive effects of algal diversity on algal biomass in naturally assembled communities (Duffy, Godwin & Cardinale, 2017), and also with evidence from experimental studies, where generally positive relationships are also found (Cardinale *et al.,* 2011).

Twenty-four relationships were reported between the diversity of higher trophic levels (consumers) and their biomass production (Table 1). Of these, the majority (17, i.e. 71%) were significantly positive, with the remaining ones being neutral. Thus, despite relatively low research efforts, there is strong evidence that a high diversity of consumers leads to a higher consumer biomass. Most of this evidence comes from aquatic systems. For example, Mora *et al.* (2011) and Duffy *et al.* (2016), provide worldwide evidence for a positive relationship between reef fish diversity and biomass. These findings confirm experimental work assessed by Balvanera *et al.* (2006), who reported overall positive animal diversity–biomass relationships. Furthermore, a meta-analysis of marine biodiversity experiments revealed that secondary biomass production increases with herbivore diversity (Gamfeldt *et al.,* 2015).

Two broad, statistically defined categories of mechanisms that can underlie positive biodiversity–biomass production relationships have been intensively studied in (predominantly experimental) BEF studies: complementarity and selection effects (Loreau & Hector, 2001). Complementarity effects occur when the functioning of individual species is higher in mixed communities than in monocultures, e.g. due to increased resource partitioning, facilitative interactions, or due to a release of negative frequency dependency (caused by e.g. herbivores or pathogens) in mixtures. Selection effects occur when species that provide high function levels tend to dominate in diverse communities. Meta-analyses have shown that both complementarity and selection effects do, on average, promote biomass production in diverse, experimental plant communities (Cardinale *et al.,* 2009, 2011). In naturally assembled communities, complementarity and selection effects are more challenging to study, as they require species-specific measurements of biomass at different points in time. Nevertheless, there is some evidence that species complementarity in light capture and in water and nitrogen use may underlie positive biodiversity–productivity relationships in naturally assembled communities (e.g. Gaitán *et al.,* 2014; Kleinebecker *et al.,* 2014; Jucker et al., 2014*b*; Jucker, Bouriaud & Coomes, 2015). Furthermore, Kunstler *et al.* (2016) found that negative interactions are less strong in diverse communities than in species-poor ones, hinting at a role of resource partitioning and/or facilitation in underlying positive diversity–productivity relationships. Evidence that a release of negative effects of enemies in diverse communities (Janzen–Connell effects; Janzen, 1970; Connell, 1970) underlies positive biodiversity–productivity relationships also exists, as damage from specialist (but not generalist) arthropod herbivores is generally lower in diverse tree communities than in monocultures (Jactel & Brockerhoff, 2007). Nevertheless, investigating the mechanisms underlying relationships between biodiversity and biomass production is inherently difficult without experimental manipulations, so that we still poorly understand which of the different mechanisms driving biodiversity–productivity relationships in artificial communities are most important in complex, real-world systems.

(*b*) *Litter decomposition*

Litter decomposition (defined here as litter mass loss) is a key process enabling the recycling of carbon and nutrients (Swift, Heal & Anderson, 1979). Loreau (2001) developed a model study predicting a negative effect of plant litter diversity on litter decomposition, as a higher number of litter types should increase the probability that at least one of them will not be consumed by decomposers. However, the same study also predicted a positive effect of decomposer diversity on decomposition rates, due to resource partitioning between different decomposers. Hence, if plant diversity promotes the diversity of decomposing organisms, plant diversity might also have indirect, positive effects on litter decomposition rates (Hättenschwiler, Tiunov & Scheu, 2005), which may or may not overrule the direct, negative effects.

Meta-analyses on experimental studies have provided evidence that biodiversity of experimentally manipulated plant (Cardinale *et al.,* 2011, 2012) and decomposer communities (Handa *et al.,* 2014) generally have a positive effect on litter decomposition, in line with the idea that plant diversity might promote decomposition processes through driving changes in soil communities (Hättenschwiler, Tiunov & Scheu, 2005). Importantly, the average duration of decomposition experiments was relatively short (Cardinale *et al.,* 2011: 180 days; Handa *et al.,* 2014: 265 days), so that much less is known about later stages of decomposition. While studies based on naturally assembled communities similarly focused on the earlier stages of decomposition (with the duration of litter experiments ranging from 1 to 20 months, see Appendix S1), their overall results were rather mixed and not clearly driven by experimental duration. This might in part be because experimental duration *per se* is a poor proxy of the stage of litter decomposition, given that decomposition rates will likely vary greatly among studies because of different soil conditions. Positive ($N = 9$) plant diversity–decomposition relationships were more common than negative ones ($N = 1$, Table 1), but outnumbered by neutral relationships ($N = 23$, e.g. Díaz *et al.,* 2007; Carvalho *et al.,* 2014; Ratcliffe *et al.,* 2017). Most of these relationships ($N = 20$) focused on leaf litter decomposition, but also relationships based on standard litter types (tea bags, cellulose or wood, $N = 12$) or root decomposition ($N = 1$) were predominantly neutral. Furthermore, the effects of decomposer communities on decomposition rates are also very mixed, with positive biodiversity–decomposition rate relationships ($N = 5$; e.g. Fujii *et al.,* 2017) being hardly more common than negative relationships ($N = 2$; e.g. Tolkkinen *et al.,* 2013) and being outnumbered by neutral relationships ($N = 13$) (Table 1). Rare examples of positive plant diversity–decomposition relationships include a study performed in Mexican dry forests (Lohbeck *et al.,* 2015) and a study in Japanese temperate forests (Fujii *et al.,* 2017). Interestingly, in the latter, the positive relationship between tree functional diversity and litter decomposition was indirect, through an increase of fungal (decomposer) richness with tree diversity (Fujii *et al.,* 2017), as proposed by Hättenschwiler, Tiunov & Scheu (2005). Nevertheless, positive effects of plant or decomposer diversity on decomposition rates in naturally assembled communities are not widespread, suggesting that in complex natural systems, other drivers, such as abiotic conditions or the functional composition rather than diversity of litter types (Cornwell *et al.,* 2008), might be more important in explaining decomposition rates.

(*c*) *Soil organic carbon storage*

The storage of organic carbon in soils is, along with aboveground live carbon storage, an important process mitigating climate change (Fischlin *et al.,* 2007). Important factors driving variation in organic carbon storage include litter production and humidification (which increase carbon storage) and litter decomposition (which decreases it). Additionally, carbon can enter the soil through root exudation (Hinsinger *et al.,* 2009). Historically, the dominant view was that decomposition rates are primarily driven by the chemical composition of soil substrates, as some compounds (e.g. lignin) are inherently more resistant to microbial attack than other compounds (e.g. glucose) (Swift, Heal & Anderson, 1979). If true, one could imagine that the storage of organic soil carbon depends strongly on the identity of plant species (which vary in the chemical composition of their litter), as well as on their diversity. However, the current predominant view is that litter chemical composition may be less important for soil carbon storage, and that several (abiotic) soil conditions, such as soil aggregate stability, aeration and moisture content, have a major impact on the accessibility of soil carbon to active decomposer enzymes (Schmidt *et al.,* 2011). Thus, the question is whether, given the various other factors driving soil carbon storage, biodiversity also has a detectable effect.

Experimental studies have shown that in general, diverse plant communities have higher soil carbon stocks than less-diverse communities (Cardinale *et al.,* 2012). By contrast, studies investigating plant diversity–carbon stock relationships in naturally assembled communities did not find clear results (Table 1). Positive relationships between plant diversity and organic soil carbon stocks ($N = 10$, e.g. Gamfeldt *et al.,* 2013; Maestre *et al.,* 2016) were not significantly more common than negative ones ($N = 8$, e.g. Conti & Díaz, 2013) and outnumbered by non-significant relationships ($N = 17$, e.g. Butterfield & Suding, 2013). Most studies focused only on relatively shallow soil layers (Appendix S1), but the five reported biodiversity–soil carbon stock relationships from relatively deeper (>50 cm depth) soil layers showed similar, mostly neutral, overall relationships (e.g. Liu *et al.,* 2018). The fact that relationships between plant diversity and litter decomposition were often non-significant (see Section II.3*b*), and findings that some abiotic soil factors are among the most important controls of decomposition rates (Schmidt *et al.,* 2011; see Section III.1) may partially explain the similarly weak relationships between plant diversity and soil organic carbon stocks. Another possibility is that any positive effects of plant diversity on soil organic carbon storage are masked by negative feedbacks: in those systems where soils rich in organic carbon also have high soil fertility, the overabundance of resources may allow few plant species to coexist (Grace *et al.,* 2016). The development of a more formal theory, incorporating the effects of e.g. soil factors and (micro)climatic conditions would be highly useful for understanding under which conditions we can or cannot expect positive relationships between litter production, soil carbon stocks and the diversity of plants or other organisms.

(*d*) *Biomass stability*

Long before the first biodiversity experiments, ecologists already wondered about the relationships between biodiversity and biomass stability. While different researchers have focused on different measures of stability (Donohue *et al.,* 2016), my focus here is on biomass stability at the community level, measured as the invariability (inverse of coefficient of variation) of biomass production. In the 1950s, MacArthur (1955) and Elton (1958) argued that a higher diversity and trophic complexity in food webs should be related to a higher population and ecosystem stability. By contrast, using food-web models, May (1973) concluded that biodiversity should negatively affect population-level biomass stability. One of the first empirical studies carried out showed a positive relationship between plant diversity and community-level biomass stability (Tilman & Downing, 1994). While this finding is seemingly in contrast with May's (1973) work, Tilman (1999) showed that increased community-level but decreased population-level biomass stability are in fact in line with May's (1973) theory. Various mechanisms, many of which are not mutually exclusive, have been hypothesized to explain positive relationships between the diversity of a taxonomic/functional group and its community-wide biomass stability. These include, but are not restricted to, (*i*) demographic stochasticity causing averaging effects ('portfolio effects') (Doak *et al.,* 1998; Tilman, Lehman & Bristow, 1998), (*ii*) interspecific interactions causing compensatory changes in the abundances of conspecific species (Tilman, Lehman & Bristow, 1998), (*iii*) species' differences in their response to environmental fluctuations, causing an increase in average biomass and asynchrony ('insurance hypothesis') (Yachi & Loreau, 1999; de Mazancourt *et al.,* 2013), and (*iv*) differences in the speed at which different species respond to disturbances (Loreau & de Mazancourt, 2013). Experimental evidence confirms that positive relationships between plant diversity and plant community biomass stability are indeed widespread (Jiang & Pu, 2009; Campbell, Murphy & Romanuk, 2011; Cardinale *et al.,* 2013; Isbell *et al.,* 2015). However, much less is understood about the mechanisms underlying these relationships. Some studies partitioned biodiversity–stability relationships into the biodiversity effects on average biomass (the numerator part of the stability metric) and the effects on the temporal standard deviation of biomass (the denominator of the stability metric), or on biodiversity effects on metrics of synchrony in species' population sizes. These studies found that all effects are important, in line with (although not conclusive evidence for) the ideas that asynchronous responses caused by environmental fluctuations (Craven *et al.,* 2018) and/or interspecific interactions (Gross *et al.,* 2014) drive relationships between biodiversity and stability.

Research carried out in naturally assembled communities is largely in line with experimental findings, in that positive relationships between plant diversity and community-wide biomass stability ($N = 13$, e.g. Chalcraft, 2013) outnumber negative relationships ($N = 0$). Nevertheless, non-significant relationships are also common ($N = 14$, e.g. Zhang *et al.,* 2016) (Table 1). Similar patterns are found for animals and microbes, with positive diversity–biomass stability relationships ($N = 11$, e.g. Blüthgen *et al.,* 2016; Wagg *et al.,* 2018) outnumbering non-significant ($N = 2$, Blüthgen *et al.,* 2016) and negative ($N = 0$) relationships. These findings are in line with another recent meta-analysis, which showed that both animal and plant richness in natural communities are often (in approximately 30% of cases) significantly positively related to community biomass stability (Houlahan *et al.,* 2018), although this study did not investigate whether patterns were driven by covariation in abiotic conditions or functional composition. Various authors showed that increased community stability in diverse communities is associated with asynchronous population fluctuations (Hautier *et al.,* 2014; Jucker *et al.,* 2014*a*; Blüthgen *et al.,* 2016; Ma *et al.,* 2017), although such relationships are statistically almost inevitable (Loreau & de Mazancourt, 2013). Thus, the more interesting question is through which ecological mechanism biodiversity can promote asynchrony. Some studies found that asynchrony is linked with species' responses to environmental conditions, but not with species interactions (Thibaut, Connolly & Sweatman, 2012; Tredennick *et al.,* 2017), hinting at the importance of environmental fluctuations in diversity–biomass relationships in natural communities.

(*e*) *Pathogen and herbivore damage*

Humans, plants and animals all face damage by other organisms, such as pathogens or consumers, and a large body of BEF studies have investigated how biodiversity may affect pathogen load, herbivory or predation rates. Theoretical work suggests that the direction of biodiversity effects on pathogen and herbivore damage depends strongly on which trophic group is under consideration. A high biodiversity of host species is expected to reduce pathogen or herbivore damage if these pathogens/herbivores specialize on one or a few host species. This is because a high diversity is usually associated with low relative abundances of suitable host species, causing a 'dilution effect' hampering pathogen/herbivore transmission (Schmidt & Ostfeld, 2001; Hambäck *et al.,* 2014). Importantly, the dilution effect is only expected to drive the damage by specialist pathogen and herbivore species, so that negative relationships between host diversity and overall pathogen/herbivore damage (including the damage caused by generalist species) are not necessarily expected. In contrast to host diversity, a high diversity of herbivores is expected to increase damage levels, due to resource partitioning (Thébault & Loreau, 2003; Ives, Cardinale & Snyder, 2005). Following the same principle, a high diversity of 'natural enemies' (e.g. predators or parasitoids feeding on plant herbivores) is expected to reduce herbivore damage (Ives, Cardinale & Snyder, 2005; Greenopp *et al.,* 2018), although intraguild predation might weaken such relationships (Letourneau *et al.,* 2009). Through dilution effects and resource partitioning, biodiversity can thus have important consequences for the strength of trophic interactions, including herbivory and pathogen load, and when specialist herbivore or pathogen species are involved, this can have consequences for ecosystem services such as human or livestock disease mitigation, or crop damage.

However, the empirical evidence for these predictions is rather mixed. Experimental studies do show general support for a negative relationship between host diversity and pathogen damage or infection, but evidence that host diversity or predator diversity also reduce herbivore damage is mixed at best (Cardinale *et al.,* 2012). Non-experimental studies are largely in line with this (Table 1). Negative relationships between host diversity and damage or infection by specific (and often specialist) pathogen species ($N = 11$, e.g. Johnson *et al.,* 2013) outnumber both positive and neutral ones ($N = 0$ and $N = 7$, respectively). By contrast, but in line with theory, negative relationships between host diversity and overall damage by (both specialist and non-specialist) pathogens ($N = 5$, e.g. Tylianakis, Tscharntke & Klein, 2006) are not much more common than positive relationships ($N = 3$) and outnumbered by neutral relationships ($N = 9$, e.g. most relationships in Ratcliffe *et al.,* 2017). Most studies on herbivore damage focused on overall herbivory levels, rather than on damage by specific species. This may explain why negative relationships between plant diversity and herbivory damage ($N = 9$, e.g. Yguel *et al.,* 2011) were hardly more common than positive relationships ($N = 2$, e.g. Schuldt *et al.,* 2018) and greatly outnumbered by neutral relationships ($N = 34$, e.g. Ratcliffe *et al.,* 2017). Out of the 45 investigated relationships on plant diversity and herbivory damage, only two focused on damage by a specialist herbivore, of which one (Fierke, Kelley & Stephen, 2007) demonstrated the theoretically expected negative relationship. These results are largely in line with a meta-analysis based on both experimental and observational studies, which showed that tree diversity strongly reduces damage by specific herbivore species, but has no consistent effects on damage by more generalist species (Jactel & Brockerhoff, 2007). The fact that many herbivores are rather generalist (Novotny *et al.,* 2010) may thus hamper strong relationships between plant diversity and herbivory rates. There was no clear evidence that herbivore or predator diversity are related to herbivory damage, although it should be emphasized that the effects of herbivore or predator diversity are not sufficiently well studied (10 and 11 published relationships, respectively) to draw general conclusions.

(*f*) *Pollination*

Conceptual models suggest that a high diversity of pollinating animals should increase pollination success (fruit or seed set), due to functional complementarity among pollinator species (Blüthgen & Klein, 2011). Similarly, one could hypothesize that a high plant diversity should lead to pollination success, as plants belonging to different species might compete less strongly for pollinators. Alternatively, if pollinators are specific regarding the species they pollinate, a high plant diversity may result in less-efficient pollination, as pollinators have to move more to find suitable flowers. Only a few experimental studies investigated effects of pollinator diversity on fruit and seed set, with most (Albrecht *et al.,* 2012; Fründ *et al.,* 2013), but not all (Fontaine *et al.,* 2006), showing positive relationships. Observational studies on links between pollinator diversity and pollination success are much more common. In those, positive relationships ($N = 18$, e.g. Klein, Steffan-Dewenter & Tscharntke, 2003*a*; Garibaldi *et al.,* 2013) outnumber both negative ($N = 1$, Brittain *et al.,* 2010) and neutral relationships ($N = 17$; e.g. Bartomeus *et al.,* 2014) (Table 1). Observational studies linking plant diversity with pollination success are much rarer, with only 8 (e.g. Klein, Steffan-Dewenter & Tscharntke, 2003*b*; Carvalheiro *et al.,* 2011) investigated relationships. Nevertheless, the fact that all are neutral suggests that plant diversity is less important than pollinator diversity for pollination success.

(*g*) *Ecosystem multifunctionality*

Ecosystem multifunctionality is defined as the simultaneous performance of multiple ecosystem functions (Hector & Bagchi, 2007; Gamfeldt, Hillebrand & Jonsson, 2008), and is usually measured as an average of standardized ecosystem function values within a site, or as the number of functions with levels exceeding a minimal threshold (Byrnes *et al.,* 2013; Manning *et al.,* 2018). Given that various individual ecosystem functions are theoretically expected to increase with biodiversity (Table 1), one might also expect positive responses of ecosystem multifunctionality. Initially, various studies (e.g. Hector & Bagchi, 2007; Gamfeldt, Hillebrand & Jonsson, 2008; Isbell *et al.,* 2011) argued that ecosystem multifunctionality should increase more strongly with biodiversity than individual ecosystem functions, although new theory indicates that this is not inevitable (Gamfeldt & Roger, 2017). Regardless, there is widespread evidence that among experimental studies, ecosystem multifunctionality generally increases with biodiversity (Lefcheck *et al.,* 2015). In naturally assembled communities, the picture is more mixed (Table 1). While positive relationships ($N = 34$, e.g. Maestre *et al.,* 2012; Jing *et al.,* 2015; Ratcliffe *et al.,* 2017) between biodiversity and ecosystem multifunctionality outnumber negative ones ($N = 13$, e.g. some of the relationships in Allan *et al.,* 2015), the majority of investigated relationships are neutral ($N = 64$, e.g. many of the relationships in Soliveres *et al.,* 2016*a*). Positive effects of biodiversity on ecosystem multifunctionality were most frequent in temperate forests, while positive effects were not more common than negative effects, and outnumbered by neutral effects, in tropical forests and temperate grasslands (Table 1). However, due to the paucity of studies and the variation among them in e.g. sampling design and functions measured, it is too early to say whether biodiversity–multifunctionality relationships differ among major ecosystem types. The finding that biodiversity–multifunctionality relationships in observational studies were generally weaker than in experiments, might be partly due to the fact that analyses in many observational studies (e.g. Soliveres *et al.,* 2016*a*; Schuldt *et al.,* 2018) are explorative rather than strongly hypothesis driven, so that some of the investigated relationships were unlikely to be strong. Thus, while some biodiversity components of naturally assembled communities can increase ecosystem multifunctionality, certainly not all aspects do, and effects depend strongly on the individual ecosystem functions included in multifunctionality metrics (see e.g. Allan *et al.,* 2015).

(4) Effects of sampling design

In 32 studies (e.g. Ratcliffe *et al.,* 2017; Schuldt *et al.,* 2018), sampling locations were stratified by functional composition and/or biodiversity, in order to minimize covariation between biodiversity and species composition, and to maximize the variation in biodiversity compared to other potential drivers of ecosystem functioning. These studies reported 155 BEF relationships. In theory, a stratified sampling design should be most powerful for detecting effects of biodiversity on ecosystem functioning. To investigate whether this was indeed the case, I compared the proportion of positive, neutral and negative BEF relationships among studies with and without a stratified plot design, and I used

Chi-squared tests to investigate whether these proportions differed significantly (Fig. 3). Contrary to expectations, for most types of ecosystem functions, qualitative outcomes did not differ much between studies with *versus* without a stratified plot design (although for some functions, e.g. pollination, replication was low). For functions related to biomass production and pathogen/herbivore damage, neutral relationships were even slightly more common in studies using a stratified plot design, whereas positive and negative relationships were slightly less common. Normally, maximizing variation in a predictor value of interest (here: biodiversity), through e.g. a stratified sampling design, should increase the power to detect its effects on the response variable (e.g. McClelland, 2000). However, if biodiversity covaries with another factor (e.g. soil fertility) that strongly drives ecosystem functioning, then effects of this other factor could be misattributed to those of biodiversity when sampling locations are not stratified. Furthermore, the much larger sample sizes in forest inventory studies (e.g. Paquette & Messier, 2011; Vilà *et al.,* 2013; Ruiz-Benito *et al.,* 2014), which are typically not stratified by biodiversity, might have led to more significant results in these types of studies.

III. RELATIVE IMPORTANCE OF BIODIVERSITY

In addition to biodiversity, various other factors, including climatic variation, soil type, (anthropogenic) disturbances, land use and functional composition can drive ecosystem functioning. This leaves the question of how important biodiversity is, compared to other factors, in driving ecosystem functioning. Furthermore, biodiversity is composed of different factors (e.g. taxonomic, functional and phylogenetic diversity) and its effects can be studied across a range of spatial scales, so a major question is which components of biodiversity are most important in driving ecosystem functioning, and at which spatial scales?

(1) Effects of biodiversity *versus* those of functional composition and abiotic factors

While biodiversity, in the narrow sense, describes the genetic, taxonomic, functional or phylogenetic diversity among individuals or species co-occurring within a certain locality, other properties of communities can also drive ecosystem functioning (Grime, 1998; Wardle *et al.,* 2000; Lavorel & Garnier, 2002). These components include the presence or relative abundance of a certain species (e.g. a top predator) or functional group (e.g. legumes), a combination of species, or the mean of a functional trait value (e.g. animal body size or leaf nitrogen content), and are hereafter jointly termed '(variation in) functional composition'. Similarly, ecosystem functioning can be driven by abiotic factors. While abiotic conditions comprise a very large number of factors, including certain land-use components or anthropogenic disturbances, the focus here is on the effects of climatic variation, topography and soil conditions. Earlier comparisons based on experimental studies found that biomass production and decomposition rates vary as strongly or even more strongly across gradients of sown biodiversity levels than across climatic gradients or gradients in nutrient additions (Hooper *et al.,* 2012; Tilman, Reich & Isbell, 2012). However, these studies were criticized as their biodiversity gradients might not be representative of more natural systems (Wardle, 2016), so that the relative importance of biodiversity *versus* those of other global-change drivers is still under debate (Wardle *et al.,* 2000; Srivastava & Vellend, 2005; Turnbull *et al.,* 2016; Duffy, Godwin & Cardinale, 2017).

I investigated whether effects of biodiversity were stronger than those of (*i*) functional composition and (*ii*) abiotic factors. This was done by comparing, *within* those non-experimental BEF papers collated in Section II that simultaneously quantified the effects of at least one biodiversity indicator and at least one functional composition or abiotic factor variable, the strength of these different types of predictors. Thus, the idea of this comparison was to investigate whether, within a given context (e.g. the grassland communities in which a study was performed), the *natural variation* in biodiversity was more or less important for ecosystem functioning than the *natural variation* in functional composition and/or abiotic conditions. These comparisons were based on the available summary statistics, e.g. (total) standardized effect sizes, variance partitioning, partial R^2 values, standardized path coefficients, parsimony or significance levels. A few studies (e.g. Delgado-Baquerizo *et al.,* 2016) reported the total standardized effects of the different categories of predictors, e.g. using variance partitioning. However, most studies only reported the effects of each predictor variable separately. In those cases I compared the effects of the strongest biodiversity indicator with the effects of the strongest indicator of functional composition and/or abiotic factors. Thus, when multiple biodiversity indicators were analysed, only the one with the strongest effects was considered, and similarly, when multiple indicators of functional composition or abiotic factors were analysed, I only considered those with the strongest effect and ignored the rest. Each comparison could have only two outcomes: either the biodiversity indicator had the strongest effect [because its standardized regression coefficients, path coefficient or partial r value was highest, or because its P or Akaike information criterion (AIC) value was lowest], or the indicator of functional composition/abiotic variation had the strongest effect. In some cases, such comparisons were impossible, e.g. because exact P values or other summary statistics were not reported. I used χ^2 tests to assess whether the proportion of cases in which biodiversity had stronger or weaker effects on ecosystem functioning than functional composition or abiotic factors significantly deviated from 50%.

In 333 (i.e. 46%) of the 726 investigated BEF relationships, variables related to functional composition were included as covariates. Some of these allowed for the comparison of effects of biodiversity *per se* with those of functional composition (Fig. 4A). This showed that in most cases, compositional effects were stronger than biodiversity effects

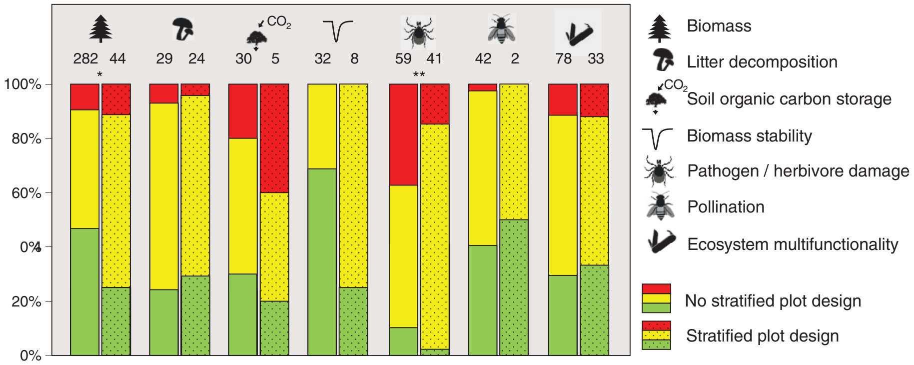

Fig. 3. The proportion of positive (green), neutral (yellow) and negative (red) biodiversity–ecosystem functioning (BEF) relationships among studies without and with (dotted) a sampling design stratified by biodiversity and/or functional composition, for different types of ecosystem functions. Numbers above the bar indicate the number of assessed BEF relationships, and asterisks indicate whether the proportion of cases with positive, neutral and negative BEF relationships differed depending on sampling design (χ^2 test).

[145 out of 209 (69%) cases ($\chi^2 = 31.39$; $P < 0.0001$)]. However, the relative importance of biodiversity *versus* functional composition depended strongly on the type of ecosystem function. For example, compositional effects were especially important in explaining variation of biomass stocks or production (in 89% of the 119 cases compositional effects were strongest, see e.g. Lavorel *et al.,* 2011; Ruiz-Benito *et al.,* 2014; Poorter *et al.,* 2017) or soil carbon stocks or storage (where compositional effects were strongest in 84% of the 19 cases, e.g. Díaz *et al.,* 2007; Lavorel *et al.,* 2011; Ratcliffe *et al.,* 2017). Thus, dominant species or traits are more important than their diversity in driving variation in dead or live biomass. I also compared the relative importance of functional composition *versus* biodiversity *per se* in driving primary biomass stocks or production for four broad categories of habitat types [temperate and boreal forests, (sub)tropical forests, grasslands and aquatic systems] separately. This showed that effects of functional composition were generally strongest in temperate forests and grasslands, whereas in tropical forests, biodiversity *per se* and functional composition were approximately equally important (Fig. 4C). In contrast to individual ecosystem functions, ecosystem multifunctionality was approximately as often best predicted by biodiversity ($N = 16$; e.g. Allgeier *et al.,* 2015; Ratcliffe *et al.,* 2017; Gross *et al.,* 2017) as by species composition ($N = 13$; e.g. Soliveres *et al.,* 2014). A possible explanation for this is that while individual species often differ in their effects on individual ecosystem functions, there are often trade-offs among species' traits promoting different functions, so that 'super-species' maximizing all ecosystem functions do not exist (e.g. Gamfeldt *et al.,* 2013; van der Plas *et al.,* 2016*a*). This makes the overall effects of dominant species or functional types on ecosystem multifunctionality rather moderate.

In 476 (i.e. 65%) of the in total 726 investigated BEF relationships, variables related to abiotic conditions were included as covariates, and in 294 cases their effects could be compared with those of biodiversity. In 195 cases [i.e. 66% of the cases ($\chi^2 = 31.35$; $P < 0.0001$)] the effects of abiotic conditions were most important (Fig. 4B). However, the relative importance of biodiversity depended strongly on the ecosystem function type. For soil carbon storage, 75% of the 24 studies reported stronger effects of abiotic conditions than effects of biodiversity (e.g. Gamfeldt *et al.,* 2013), and a similar, although non-significant, trend was found for decomposition rates. Also for biomass stocks or production, in the majority of cases (71% of 156), abiotic factors were more important than biodiversity (e.g. Díaz *et al.,* 2007; Ruiz-Benito *et al.,* 2014). This finding was rather ubiquitous, and observed in both temperate forests, tropical forests and grasslands (Fig. 4C). However, these findings differ from the synthesizing work of Duffy, Godwin & Cardinale (2017), who found that effects of biodiversity on biomass production were approximately as strong as the effects of abiotic factors. Their synthesis was based on a smaller number of studies than reviewed here (e.g. not including the many studies published in 2017 or 2018), and it is possible that the inclusion of some forest-inventory studies in the present review, spanning large abiotic gradients (e.g. Ruiz-Benito *et al.,* 2014), or some recently published studies from tropical forests (e.g. Poorter *et al.,* 2017; Sullivan *et al.,* 2017; van der Sande *et al.,* 2017*a*), where biodiversity effects tend to be weak, at least partly explains this discrepancy. For pathogen/herbivore damage, cases where abiotic factors were more important ($N = 11$, e.g. Mitchell, Bennett & Gonzalez, 2014) were approximately as common as cases where biodiversity was more important ($N = 13$, e.g. Yguel *et al.,* 2011). For most other types of ecosystem functions, the number of reported relationships was too low to draw final conclusions (Fig. 4B). Ecosystem multifunctionality was in 20 cases most strongly associated with biodiversity (e.g. Allan *et al.,* 2015), but in slightly more cases ($N = 36$) most strongly with abiotic factors (e.g. Delgado-Baquerizo *et al.,* 2016). Importantly, biodiversity and abiotic factors, such as climate, can also interact in driving levels of ecosystem functioning, which complicates comparisons of their relative

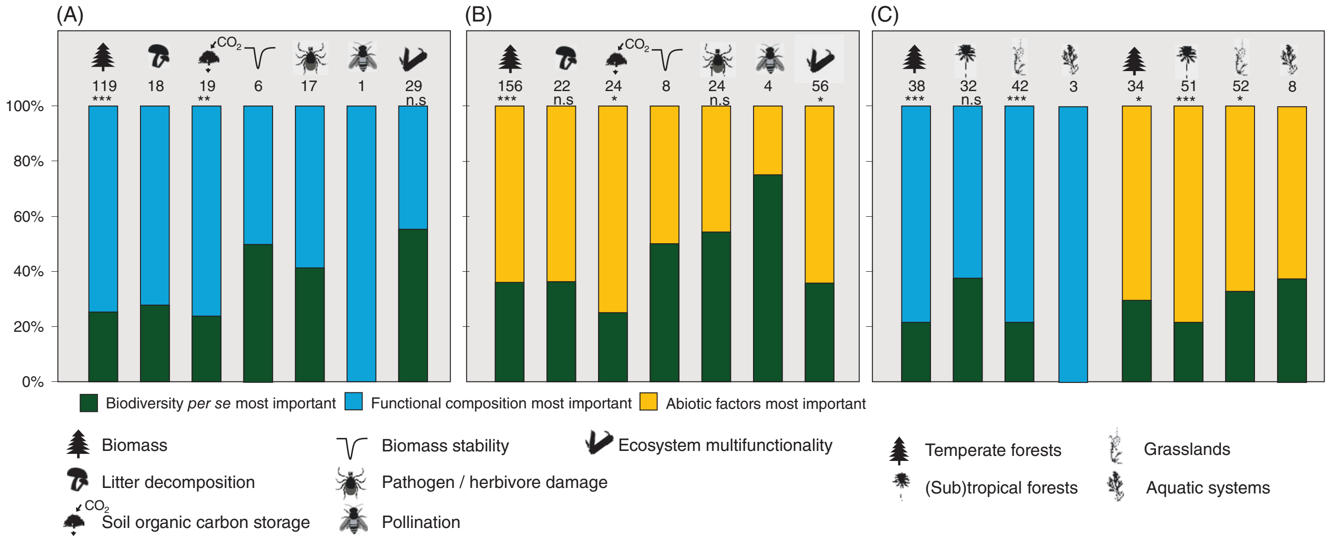

Fig. 4. The relative importance of biodiversity *versus* other factors in driving ecosystem functioning. (A) Proportion of incidences in which biodiversity *per se* (green) or functional composition (blue) was more important for explaining variation in ecosystem functioning. (B) Proportion of incidences in which biodiversity *per se* (green) or abiotic factors (yellow) were more important for explaining variation in ecosystem functioning. (C) Proportion of incidences in which biodiversity *per se* (green) *versus* functional composition (blue) or abiotic factors (yellow) was more important for explaining variation in plant biomass production, in temperate forests, tropical forests, grasslands and aquatic systems. Numbers above the bars indicate the number of reported relationships, and asterisks show whether the number of cases where biodiversity had the strongest effects differ significantly (χ^2 test) from the number of cases where functional composition or abiotic factors had the strongest effects: n.s,. $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. For groups of functions that were studied infrequently ($N < 20$), no indication of significance is given.

importance. For example, as discussed in Section II.3*a*, effects of tree diversity on forest biomass production are generally more positive in temperate regions than in the tropics. Also other studies have reported that positive biodiversity effects can become weaker in less-productive (colder and/or drier climates, or poorer soil conditions) areas (e.g. Paquette & Messier, 2011; Bowker, Maestre & Mau, 2013; Wu *et al.*, 2015; Ratcliffe *et al.*, 2017). However, a more comprehensive assessment is needed to understand the full complexity of context-dependent biodiversity effects.

Given that both abiotic conditions and the functional composition of communities can strongly drive ecosystem functioning, the question is: how does accounting for all these possible drivers of ecosystem functioning – or failing to do so – affect the conclusions of BEF studies? Some studies analysed BEF relationships both with *and* without the inclusion of covariates related to either (*i*) functional composition *only*, (*ii*) abiotic factors *only*, or (*iii*) community composition and abiotic factors *simultaneously*. I investigated how accounting for these separate and combined groups of covariates affects the qualitative conclusions of BEF studies, by comparing the qualitative outcomes (either positive, neutral or negative) of BEF relationships before and after accounting for covariates. I classified 'true' BEF relationships (i.e. those based on analyses accounting for covariates) as either more positive (true relationship is positive, *versus* neutral or negative relationships when not accounting for covariates, or true relationship is neutral, *versus* a negative relationship when not accounting for covariates), more negative (when the opposite happened), or the same as the 'raw' (i.e. when not accounting for covariates) relationship. Among the 26 cases for which I could assess the effects of functional composition-related factors on BEF relationships, I found that accounting for functional composition qualitatively affected 15 (i.e. 58%) of the outcomes, in some ($N = 9$) cases leading to more-positive BEF relationships, and in a similar ($N = 6$) number of cases to more-negative BEF relationships (Fig. 5). In many more (143) cases I could assess the consequences of accounting for abiotic factors on BEF relationships. These qualitatively affected 29 (i.e. 20%) of the outcomes, in most (19) of these leading to more-negative BEF relationships, and in a smaller (10) number of cases to more positive BEF relationships (Fig. 5). Surprisingly, this result differs from findings by Duffy, Godwin & Cardinale (2017), who found, based on a smaller set of studies, that accounting for abiotic factors made biodiversity–biomass production relationships on average more positive. This may at least partly be explained by the inclusion of new studies herein, in which biodiversity is strongly driven by management-related soil factors (e.g. Soliveres *et al.*, 2016*a*), and in which not accounting for these factors strongly inflates BEF relationships. In 147 (i.e. 20%) of the total 726 investigated BEF relationships, both variables related to functional composition *and* abiotic factors were included as covariates. For 48 BEF relationships, I could assess the joint effects of these factors on BEF relationships, and in 17 (35%) of those, relations were qualitatively affected. In 10 cases, simultaneously accounting for both types of variables

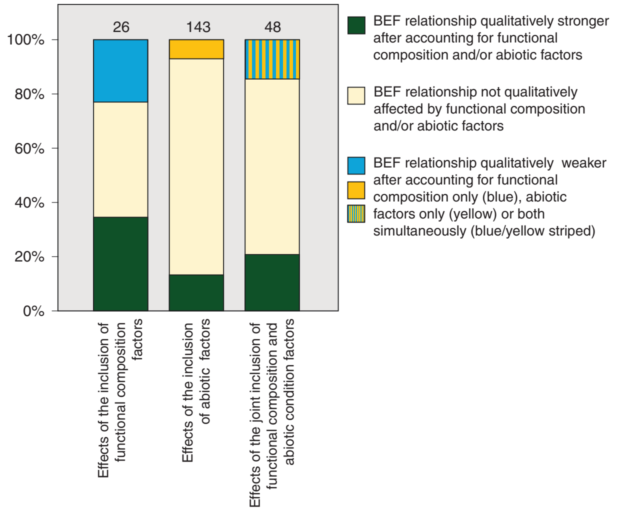

Fig. 5. Proportion of cases in which the qualitative conclusions regarding biodiversity–ecosystem functioning (BEF) relationships are altered by the inclusion of covariates related to functional composition and/or abiotic factors in statistical models.

made BEF relationships more positive, and in the remaining seven cases, relationships became more negative (Fig. 5). In summary, while there is no clear overall direction (either positive or negative) in the response of BEF relationships to the inclusion of factors related to functional composition and/or abiotic conditions as covariates in statistical models, including these covariates is nevertheless important in order to make statistical models as reflective of reality as possible. Not doing so leads to qualitatively different conclusions in approximately 20–58% of the cases. Importantly, this 20–58% may be an underestimate, as it is likely that not all studies reviewed here included all important drivers of ecosystem functioning in their analyses. Various studies included only a single covariate in their analyses, and only 20% of the assessed BEF relationships included both abiotic factors and variables related to functional composition in their analyses, even though both types of factors can strongly drive ecosystem functioning.

Studies simultaneously investigating the effects of biodiversity on ecosystem functions, and the feedbacks of ecosystem functioning on biodiversity, are even scarcer. Various studies have investigated how ecosystem functions, especially plant biomass, can influence (plant) diversity, through e.g. effects on light competition (e.g. Grime, 1973; Waide *et al.,* 1999; Hautier, Niklaus & Hector, 2009). Even though there is no consensus on whether a general plant biomass (predictor)–biodiversity (response) relationship exists [e.g. compare Pierce, 2013 with Adler *et al.,* 2011 and Grace *et al.,* 2014], it is clear that these factors are often related. Therefore, studies should ideally simultaneously study the effects of biodiversity on ecosystem functioning and the feedbacks of ecosystem functions on biodiversity, but most studies focus on either the one or the other relationship. A notable exception is the study by Grace *et al.* (2016), who used a worldwide network of grassland plots to unravel some of the highly complex interrelationships between plant diversity and biomass production. They found that while plant diversity can promote plant biomass production, there are also important feedbacks whereby plant biomass decreases plant diversity through a reduction in light availability. However, it is not yet known whether taking this full complexity of nature into account will alter the conclusions regarding BEF relationships in other contexts, and future studies should account for this complexity to gain a better understanding of the interrelationships between biodiversity and ecosystem functioning.

(2) Relative roles of taxonomic, functional and phylogenetic diversity

The earliest BEF studies (e.g. Naeem *et al.,* 1994; Tilman & Downing, 1994) focused primarily on the effects of taxonomic diversity, especially species richness, on ecosystem functioning. However, theoretical studies (Tilman *et al.,* 1997; Loreau, 1998; Tilman, 1999) suggested that functional differences among species should underlie relationships between biodiversity and ecosystem functioning, which led to experimental studies linking within-community diversity in functional traits (‘functional diversity’; Díaz & Cabido, 2001; Petchey & Gaston, 2006) to ecosystem functioning. These found that functional diversity indeed drives ecosystem functioning, and sometimes more strongly so than taxonomic diversity (Tilman *et al.,* 1997; Hooper & Vitousek, 1998). As organisms are characterized by an infinite number of traits, and it is impossible to measure all of these, some have argued that phylogenetic diversity, measuring the diversity in evolutionary origin of co-occurring species (Faith, 1992), might actually be better than functional-diversity metrics in explaining variation in ecosystem functioning (Cadotte, Cardinale & Oakley, 2008). However, a more recent meta-analysis on experimentally manipulated communities does not support this idea (Venail *et al.,* 2015). Regardless, naturally assembled communities are in many ways different from experimentally manipulated communities, and hence a main question is which component of biodiversity – taxonomic, functional or phylogenetic – is most important in driving ecosystem functioning. Separating these effects can be challenging, due to shared variance between these biodiversity components, although they typically also have independent effects (Craven *et al.,* 2018).

To assess which type of biodiversity indicator most strongly drives ecosystem functioning within studies, I categorized biodiversity indicators as measures of either taxonomic diversity (which only consider information regarding the presence/abundance and identity of species), functional diversity (which also considers information regarding the functional traits or functional type of species/individuals) or phylogenetic diversity (which also considers information regarding the evolutionary relationships among species). I compared the strength of the effects of taxonomic, functional and phylogenetic diversity on ecosystem functioning based on the available summary statistics, e.g. standardized effect sizes, partial R^2 values, standardized path coefficients or significance levels. When multiple metrics were available, I always compared the effects of the strongest taxonomic diversity indicator with the effects of the strongest indicator of functional and/or phylogenetic diversity. Each comparison between a taxonomic biodiversity indicator and an indicator of functional diversity could have only two outcomes: either the taxonomic diversity indicator had the strongest effect (because its standardized regression coefficients, path coefficient or partial r value was highest, or its P or AIC value was lowest), or the indicator of functional diversity had the strongest effect. In some cases, such comparisons were impossible, because the necessary statistics were not reported. Comparisons between taxonomic and phylogenetic diversity, and between functional and phylogenetic diversity, were carried out in the same way. I used χ^2 tests to assess whether the proportion of cases in which taxonomic, functional or phylogenetic diversity had stronger or weaker effects on ecosystem functioning deviated from 50%.

In the 78 cases where effects of functional and taxonomic diversity were jointly studied, most [$N = 53$, i.e. 68% of the cases ($\chi^2 = 10.05$; $P = 0.0015$), e.g. Paquette & Messier, 2011; Gross *et al.,* 2017] found that the effects of functional diversity were more important, *versus* 25 cases where taxonomic diversity was more important (e.g. Vilà *et al.,* 2007), thus supporting theory (Tilman, Lehman & Thomson, 1997; Loreau, 1998; Tilman, 1999). Cases where taxonomic and phylogenetic-diversity effects could be compared were much scarcer ($N = 18$). While in a small (but non-significant) majority ($N = 10$, e.g. Yguel *et al.,* 2011) of these, phylogenetic diversity effects were stronger than those of taxonomic diversity (which had strongest effects in 8 cases, e.g. Lasky *et al.,* 2014), given this small difference and the low number of studies, it is too early to draw general conclusions. Similarly, only 15 cases allowed for a comparison of the effects of functional diversity with phylogenetic diversity. Nevertheless, cases in which effects of functional diversity were strongest ($N = 12$, e.g. Paquette & Messier, 2011; Hao *et al.,* 2018) strongly outnumbered cases where phylogenetic diversity was more important ($N = 3$, e.g. Hao *et al.,* 2018) ($\chi^2 = 5.40$; $P = 0.0201$). Thus, in most cases, functional diversity is more important in explaining ecosystem functioning than taxonomic diversity or phylogenetic diversity.

(3) The relative importance of biodiversity across spatial scales

The vast majority of both experimental and non-experimental studies on biodiversity and ecosystem functioning were carried out at relatively small spatial scales. To illustrate, Cardinale *et al.* (2011) reported that the median plot size of plant-diversity experiments is 3 m^2. A major question is whether BEF relationships as observed at local scales, and their underlying mechanisms, are also present at the much larger spatial scales at which ecosystem functions are most relevant for service provisioning (Geijzendorffer & Roche, 2014; Isbell *et al.,* 2017). This question is logistically extremely challenging to answer with experiments, but in recent years researchers have started to investigate BEF relationships at larger scales using observational approaches.

Various theoretical studies have predicted that positive effects of biodiversity on ecosystem functioning (primary productivity in most cases) should also be present at larger spatial scales (Loreau & Gonzalez, 2003; Cardinale, Ives & Inchausti, 2004; Thompson & Gonzalez, 2016; Delsol, Loreau & Haegeman, 2018), although different underlying mechanisms (such as dispersal and species-sorting processes) become important at these larger spatial scales. What is less understood, is whether BEF relationships will become stronger or weaker at large spatial scales. A meta-analysis has shown that plant-diversity experiments using large plot sizes usually have stronger biodiversity–productivity relationships than those with smaller plots (Cardinale *et al.,* 2011), although the assessed experiments differed in more components (e.g. species pool size, abiotic conditions) than in spatial scale alone. In naturally assembled communities, only five studies looked at BEF relationships across spatial scales, while accounting for abiotic variation and/or functional composition. Some of these provided evidence that biodiversity is more strongly related to biomass production at large than at small scales (Chalcraft, 2013; Grace *et al.,* 2016; Hao *et al.,* 2018), while others found the opposite (Chalcraft, 2013; Chisholm *et al.,* 2013; Piñeiro-Guerra *et al.,* 2014; Hao *et al.,* 2018). Other studies investigated a related question, namely whether spatial turnover in community composition (β-diversity; Whittaker, 1960) can promote individual ecosystem functions, or ecosystem multifunctionality. A high β-diversity is usually associated with high heterogeneity in habitats, climatic conditions or topography, and can decrease due to (anthropogenically driven) homogenization of these factors (McGill *et al.,* 2015), making it highly relevant to understand its effects on ecosystem functioning. Nevertheless, only very few studies (also reviewed in Mori, Isbell & Seidl, 2018) so far have investigated this question. By combining local-scale, plot-based field measurements with simulation models, van der Plas *et al.* (2016*b*) showed that forest landscapes with a high β-diversity should have higher landscape-scale ecosystem multifunctionality, due to the spatial turnover in ecosystem functions that are provided in forests with different species. Similarly, Mori *et al.* (2016) also found that different fungal communities provided different functions, suggesting that β-diversity should promote landscape-scale multifunctionality. Only three studies investigated β-diversity in actual landscapes. Hautier *et al.* (2018) found that in grasslands, β-diversity increased landscape-scale multifunctionality, because different species provided different functions at high levels, in different environments. In another grassland study, Grman *et al.* (2018) found similar results, and they suggested that higher abundances of service-providing organisms of higher trophic levels, or ecosystem function trade-offs within patches, might have been responsible for these patterns. By contrast, across different terrestrial vegetation types of Australia, Burley *et al.* (2016) found that neither α- nor β-diversity had meaningful effects on primary productivity, although the very large scale of this study might have obscured the detection of processes important for BEF relationships. In summary, the few studies published so far indicate that biodiversity may not only be important at local scales, but also at larger scales, for ecosystem functioning. At the same time, this is an emerging area in BEF research, with major research gaps. For example, major questions that merit further study include whether α- or β-diversity is most important for ecosystem functioning, and which mechanisms drive BEF relationships and ecosystem services at larger scales. Answering these questions requires a joint effort of theoreticians, meta-community experiments and large-scale field assessments.

IV. FUTURE DIRECTIONS

While non-experimental BEF studies have yielded various insights into how biodiversity is related to ecosystem functioning in naturally assembled communities, there also remain important knowledge gaps, of which some of the most important ones are:

(1) Most non-experimental BEF studies have been carried out in temperate forests or grasslands, in cultivated areas, drylands or in tropical forests, and focused on plant diversity, rather than on the diversity of higher trophic levels. Therefore, we do not yet understand whether the conclusions above also hold in rarely studied biomes such as oceanic systems or tropical savannahs, and whether animal diversity is as important as plant diversity for ecosystem functioning.

(2) While studies increasingly account for variation in abiotic conditions and functional composition when analysing BEF relationships, these efforts are often quite moderate. It is largely unknown to what extent more integrative studies, accounting for all relevant abiotic and compositional factors as well as feedbacks from ecosystem functions to biodiversity, will alter our understanding of BEF relationships.

(3) It is largely unknown whether phylogenetic diversity is more or less important for ecosystem functioning than taxonomic diversity.

(4) It is unclear whether the effects of biodiversity become stronger over larger spatial scales. This is largely due to a paucity of studies, so future work should assess the scales at which biodiversity matters most.

Future studies could attempt to fill these knowledge gaps, by studying BEF relationships in a wider range of ecosystem types than has been done so far, by studying the effects of biodiversity across multiple trophic groups and by studying BEF relationships over larger spatial scales. In so doing, increasingly refined insights into the relationship between biodiversity and the functioning of ecosystems can be developed. As yet, the value of BEF studies for applications in nature conservation and policy has been limited (Srivastava & Vellend, 2005; Balvanera *et al.*, 2013, but see Peh & Lewis, 2012). Filling the identified research gaps will make BEF findings increasingly useful for policy in the future. Importantly, biodiversity is only one of the many factors driving ecosystem functions and the ecosystem services these underpin. Thus, taking the full complexity of natural systems into account, including the identification of abiotic conditions that benefit species combinations with suitable traits, is crucial in developing strategies to maximize both biodiversity and ecosystem functioning.

V. CONCLUSIONS

(1) This study forms the most comprehensive review so far on biodiversity–ecosystem functioning studies in non-experimental systems. In non-experimental systems, biodiversity change is non-random, and biodiversity is only one of multiple factors that drive the functioning of ecosystems.

(2) In some ecosystem types, plant or animal diversity in natural, non-manipulated communities promotes both primary and secondary biomass production in the majority ($>50\%$) of cases, although the effects of plant diversity are more mixed in grasslands and tropical forests. Furthermore, there is also strong evidence (support in $>50\%$ of the studies) that a high animal diversity increases the stability of secondary biomass stocks and that pollinator diversity increases pollination success.

(3) Biodiversity more often has positive than negative effects on the stability of plant biomass stocks, decomposition rates and ecosystem multifunctionality, and plant or host diversity more often has negative than positive effects on pathogen or herbivory damage, but most reported BEF relations regarding these functions are neutral. There is no clear evidence that plant biodiversity affects soil carbon storage.

(4) While most BEF studies in natural systems have focused on the effects of taxonomic biodiversity, in most cases, the effects of functional trait diversity are stronger.

(5) While biodiversity affects many types of ecosystem functions positively in various contexts, in most cases, its effects are less strong than those of abiotic factors. Furthermore, the effects of biodiversity *per se* are generally less strong than changes in functional composition (e.g. the replacement of one species by another).

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.
Appendix S1. Details of all case studies included in the systematic review.

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