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Review

Towards mechanistic integration of the causes and consequences of biodiversity

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The global biodiversity crisis has stimulated decades of research on three themes: species coexistence, biodiversity–ecosystem functioning relationships (BEF), and biodiversity–ecosystem functional stability relationships (BEFS). However, studies on these themes are largely independent, creating barriers to an integrative understanding of the causes and consequences of biodiversity. Here we review recent progress towards mechanistic integration of coexistence, BEF, and BEFS. Mechanisms underlying the three themes can be linked in various ways, potentially creating either positive or negative relationships between them. That said, we generally expect positive associations between coexistence and BEF, and between BEF and BEFS. Our synthesis represents an initial step towards integrating causes and consequences of biodiversity; future developments should include more mechanistic approaches and broader ecological contexts.

Causes and consequences of biodiversity

The mystery of biodiversity in nature has motivated a long-standing quest for understanding the coexistence of species [1–3]. The accelerating rate of species extinction has made the need for a better understanding of the causes and consequences of biodiversity change even more urgent [4,5]. On the one hand, recent applications of **modern coexistence theory** (see Glossary) [2] have greatly deepened our insights into the **mechanisms** of maintenance of species diversity in nature [6–8] and how global change factors may drive biodiversity change [9–11]. On the other hand, numerous studies have examined the effects of biodiversity on **ecosystem functioning** and its **stability** [4,12–14], here referred to as BEF and BEFS, respectively. BEF and BEFS characterize, respectively, possible consequences of biodiversity change for specific functions of ecosystems (e.g., biomass production, nutrient cycling) and their ability to maintain these functions in the face of perturbations. While ecosystem functioning and stability are both multidimensional concepts [15,16], we focus mainly on the functioning represented by biomass production and its stability represented by temporal **invariability** of biomass production (i.e., the ratio of temporal mean to standard deviation), which have received most attention in the literature (see later).

Despite substantial progress on coexistence, BEF, and BEFS, these three themes are often studied independently of each other (Figure 1). For instance, separate studies based on the grassland biodiversity experiment at Cedar Creek, USA, have shown that functional trade-offs determine plant coexistence [17] and that plant diversity increases both biomass production [18] and ecosystem stability [19]. Similarly, in a tree diversity experiment in China (BEF-China), Germany *et al.* [20] explored the importance of Janzen–Connell effects in plant coexistence, and Huang *et al.* [21] and Schnabel *et al.* [22] revealed, respectively, positive effects of tree species diversity on ecosystem productivity and stability. Moreover, studies from the globally coordinated Nutrient Network have shown that eutrophication decreases species diversity [9], increases ecosystem productivity [23], and weakens the BEFS relationship [24]. While these studies give key insights for understanding

Highlights

Understanding the links between causes and consequences of biodiversity is key to achieving conservation of both biodiversity and its functions, yet previous studies have mostly studied them independently.

Ecologists have developed bipartite frameworks of high-level processes to understand mechanisms of species coexistence (niche and fitness differences) and biodiversity effects on ecosystem functioning (complementarity and selection effects) and stability (species stability and asynchrony).

These high-level processes represent combined effects of low-level processes, which mediate either positive or negative associations between coexistence and biodiversity effects on functioning or stability.

Our synthesis, based on high-level processes, provides a first step towards an integrative framework of biodiversity science. Future research needs to address low-level processes using more mechanistic approaches across broader contexts and scales.

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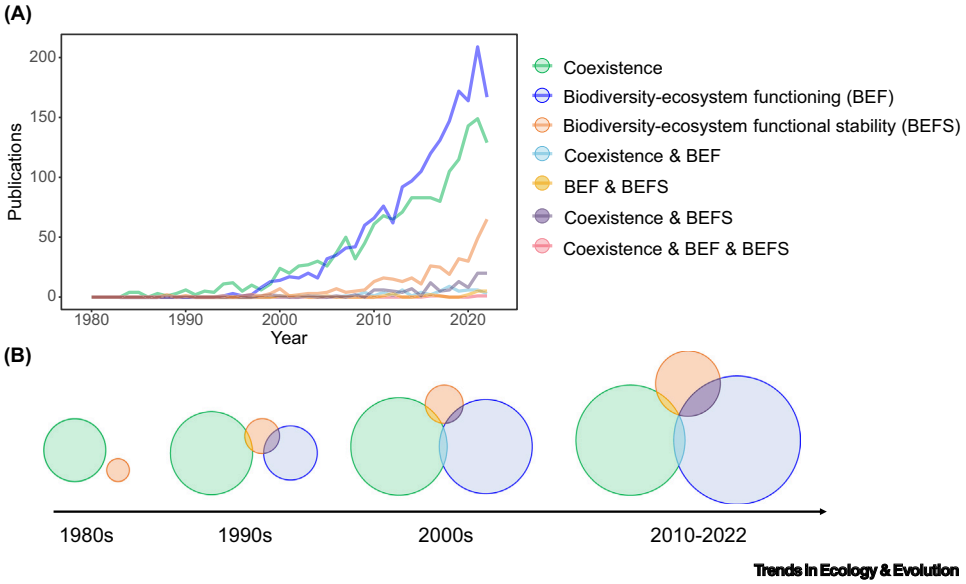

Figure 1. Trends of individual and joint studies on species coexistence, biodiversity–ecosystem functioning relationships (BEF), and biodiversity–ecosystem functional stability relationships (BEFS). (A) Number of peer-reviewed publications per year during 1980–2022, searched on Web of Science via search terms provided in Text S1 in the supplemental information online. Each theme or combination between them was searched separately. (B) Decadal trends for studies on coexistence, BEF, BEFS, and their combination. Note that these figures display temporal trends based on the number of publications directly from the search, though many studies may not address the respective theme(s) using mechanistic approaches (see main text).

the three themes individually, they nevertheless overlook the potential linkages between them. In particular, it remains unclear how mechanisms promoting species coexistence link to those underlying ecosystem functioning and stability, and whether mechanisms driving ecosystem functioning also regulate stability. These knowledge gaps create barriers not only for scientists pursuing an integrative understanding of biodiversity, but also for conservationists and managers aiming to maximize multiple benefits of ecological systems [25].

Recent efforts have attempted to link the causes (coexistence) and consequences (BEF and BEFS) of biodiversity (Figure 1). Theoretical models have been developed to study the interactions between coexistence, BEF, and BEFS, and to make predictions on their potential relationships [26–30]. Empirical studies have also emerged to explicitly test the potential linkages between the three themes. For example, recent experimental studies have shown that processes promoting species coexistence lead to positive effects of biodiversity on ecosystem productivity [31], and that processes underlying biodiversity effects on productivity also enhance ecosystem stability [32,33] (but see [34]). Here, we synthesize these advances towards integrating the causes and consequences of biodiversity change. We first review common approaches that have been developed for revealing mechanisms individually underpinning coexistence, BEF, and BEFS. We then summarize insights from theoretical and empirical studies to determine mechanisms that may jointly underpin the three themes. Finally, we identify key challenges for integrating these themes into a comprehensive theory of biodiversity and provide recommendations for future research.

Independent approaches to study coexistence, BEF, and BEFS

Researchers have investigated each of the three themes separately in a variety of ecological contexts, spanning a wide range of species interactions such as consumer–resource interactions, plant–soil feedbacks, food webs, etc. (Table 1). As a result, different studies emphasize different

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ecological processes, even though many may operate simultaneously in natural systems. To achieve more integrative perspectives, researchers have developed a bipartite framework for each theme that groups specific processes into two general types of mechanisms (Figure 2). Such bipartite frameworks allow comparison of broad mechanisms among different contexts and have thus been widely adopted in modern research on each theme.

Modern coexistence theory has defined two major mechanisms, namely stabilization arising from **niche differences** and equalization resulting from reduction in **fitness differences**, which together determine the outcome of species interactions and coexistence [2,35] (Figure 2). Specifically, niche differences quantify the degree to which different species are limited by different resources, natural enemies, or environmental factors, all of which may vary in space and time [35]. These niche differences result in stronger negative relationships between a species' density and its own population growth rate (intraspecific competition) than with the growth rates of other species (interspecific competition) [2]. By contrast, fitness differences characterize a species' competitive advantage over others (e.g., due to asymmetry in intrinsic population growth rates and sensitivity to competition) [2,36]. The fitness differences impair coexistence, causing competitive exclusion in the absence of niche differences. In practice, niche and fitness differences can be estimated through a decomposition of invasion growth rates, and species are assumed to coexist if their niche differences exceed fitness differences [37]. While the quantification of niche and fitness differences is often based on Lotka–Volterra competition models [2], recent studies have developed methods applicable to models that explicitly include resources and/or consumers [27,38] (Table 1). Empirical applications of this framework usually involve fitting a dynamical model using empirical data to estimate parameters representing species interactions, from which niche and fitness differences are then calculated [8,31,39]. A recent meta-analysis of 29 datasets showed that species coexistence is explained mainly by greater niche differences, rather than smaller fitness differences [40].

BEF research has also clarified two sets of processes underlying the positive effects of biodiversity on ecosystem functioning, namely **complementarity effects** and **selection effects** [13,41] (Figure 2). Positive complementarity effects arise when species on average perform better when growing in mixtures than in monocultures, due to resource partitioning, abiotic facilitation, or biotic feedback [42]. By contrast, positive selection effects arise when a more diverse community includes, and becomes dominated by, species with higher productivity in monoculture [13]. An additive partitioning approach has been developed to quantify complementarity and selection effects using experimental data where initial species densities are typically equal [43]. This approach partitions the net biodiversity effect, measured by the difference in productivity between mixtures and monocultures, into two additive terms representing complementarity and selection effects. Experimental studies have generally shown that complementarity effects are the major process underlying positive BEF relationships, and that they increase with functional differences among species and strengthen over time [21,25,44].

BEFS research has also identified two processes underpinning ecosystem stability: namely **species asynchrony** and **species stability** [45] (Figure 2). Species asynchrony describes the incoherence of species dynamics through time, due to differential responses of species to environmental fluctuations, demographic stochasticity, or interspecific interactions [46,47]. Within a community, the overall species asynchrony increases as species richness and evenness increase, and it decreases as pairwise correlations among species increase [45,47]. By contrast, species stability captures the average population stability weighted by species abundance, which decreases with increasing environmental and demographic stochasticity and enhanced interspecific competition [46,47]. Mathematically, ecosystem stability can be expressed as the

Glossary

Complementarity effects: the diversity effect arising when species perform on average better when growing in mixtures than in monocultures, due to resource partitioning, abiotic facilitation, and/or biotic feedback.
Ecosystem functional stability: the ability of an ecosystem to maintain and/or return to the equilibrium state of its function in response to perturbations. Stability can be defined by multiple measures to depict different facets of ecosystem responses to perturbations.
Ecosystem functioning: the status of ecosystem properties or processes reflecting the sizes (e.g., biomass, carbon/nutrient stock) or flows of energy or materials (e.g., productivity, nutrient cycling).
Fitness differences: a species' competitive advantage over others due to asymmetry in intrinsic growth rates and sensitivity to competition, which prevents species coexistence.
High-level processes: the emergent processes resulting from combined and collective effects of low-level processes.
Invariability: the ratio of the mean to standard deviation of some ecosystem function over time, where a higher value indicates a more stable system.
Low-level processes: the basic ecological processes that describe interactions between species or between species and environments (e.g., competition, predation, facilitation, disturbance, etc.).
Mechanisms: processes that take place between biotic and/or abiotic components and produce observed ecological patterns. We distinguish high-level and low-level mechanisms according to the levels of biological processes specified.
Modern coexistence theory: a theoretical framework that interprets species coexistence from the balance between niche and fitness differences among species.
Niche differences: the strength of negative frequency dependence due to interspecific differentiation in resource use, natural enemy attack, space, and/or time, which stabilize species coexistence.
Selection effects: the diversity effect arising when a more diverse community includes and becomes dominated by species with a higher (positive selection)

product of species asynchrony and species stability [45]. Thus, biodiversity can enhance ecosystem stability via increasing species asynchrony, increasing species stability, or both [48]. This bipartite framework has been widely applied in theoretical and empirical analyses of ecosystem stability [24,48], which have shown that species asynchrony is the primary process underlying the stabilizing effects of biodiversity [33,48].

or lower (negative selection) function in monoculture.
Species asynchrony: the incoherence of species dynamics through time, due to species-specific responses to environmental fluctuations, demographic stochasticity, and/or negative interspecific interactions.
Species stability: the average population stability across species, often weighted by their abundance.

Integrating processes underlying coexistence, BEF, and BEFS

The bipartite frameworks introduced above provide approaches to study each of the three themes independently. They also provide a way to study them jointly [49]. Each bipartite framework includes one set of processes associated with the strength of interspecific relative to intraspecific interactions (i.e., niche differences, complementarity effects, and species asynchrony), and another set that reflects asymmetry in species performances (i.e., fitness differences, selection effects, and species stability). Therefore, links between coexistence, BEF, and BEFS may be studied by analyzing the relationships between processes within each of the two sets. This intuitive expectation has received some support from both theoretical and empirical studies [27,31–33]. However, processes within the two sets do not match perfectly, simply because coexistence, BEF, and BEFS reflect different, though interrelated, aspects of ecosystem processes and functions. Thus, we also expect associations between processes from different sets (e.g., niche differences in coexistence and selection effects in BEF), which complicates the integration of the three themes (Table 2). In the following, we summarize theoretical expectations as well as existing empirical evidence based on joint studies of different themes using the bipartite frameworks.

Joint study of coexistence and BEF

The relationship between coexistence and BEF has been investigated in various theoretical models. Using a Lotka–Volterra model of two competitors, Loreau [26] showed that stable coexistence confers positive complementarity effects (or overyielding); however, this does not necessarily lead to positive net biodiversity effects on ecosystem functioning, which depend also on the sign and magnitude of selection effects [49]. Later studies developed consumer–resource models

Table 1. Summary of studies of coexistence, BEF, BEFS, and their linkages in various contexts

Context	Coexistence[a]	BEF[a]	BEFS[a]	Coexistence–BEF[b]	Coexistence–BEFS[b]	BEF–BEFS[b]
Competition						
Lotka–Volterra model	[2]	[26]	[47,55]	[26]	[30]	[30]
Resource competition	[27,87]	[41,50]	[88]	[27,28]	[29]	–[c]
Plant–soil feedbacks	[89]	[90]	[91]	–	–	–
Intransitive competition	[67]	[68]	–	–	–	–
Higher-order interactions	[66]	–	–	–	–	–
Fluctuation-dependent coexistence	[6,92]	–	–	[52]	[29]	–
Experimental tests	[7,79]	[18,21]	[12,19]	[31]	–	[32–34,58]
Trophic interactions						
Prey–predator interactions or food webs	[38,93]	[51,94]	[95]	–	–	–
Facilitation/mutualism	[53]	[96]	[97]	–	–	–
Larger scales						
Metacommunity process	[8]	[59]	[78,98]	[99]	–	–
Eco-evolutionary dynamics	[79,80]	[81]	[82,100]	–	–	–

[a]In the columns Coexistence, BEF, and BEFS, we selected one or two representative references as examples.
[b]In the columns about the linkages between coexistence, BEF, and BEFS, we include all relevant references found.
[c]No reference was found.

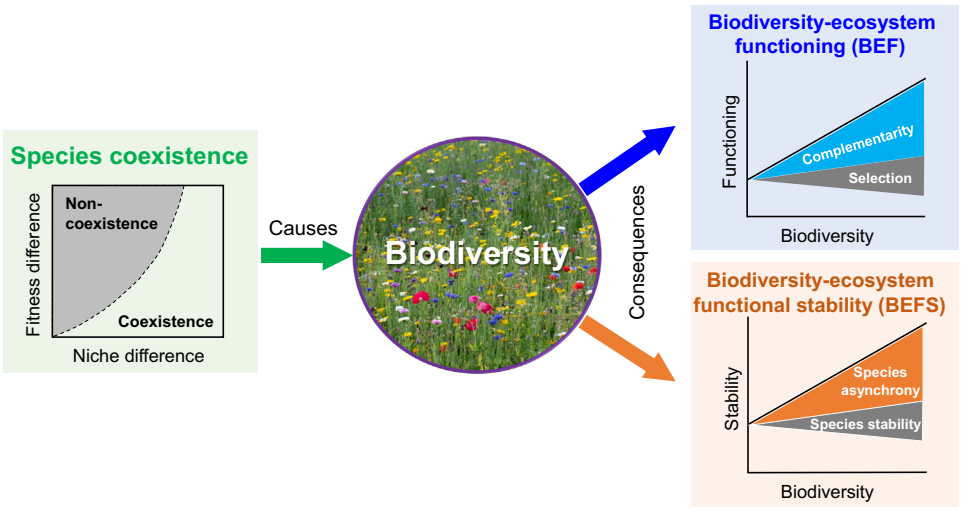

Figure 2. From causes (coexistence) to consequences (ecosystem functioning and functional stability) of biodiversity. Research on species coexistence, biodiversity–ecosystem functioning relationships (BEF), and biodiversity–ecosystem functional stability relationships (BEFS) has developed separate bipartite frameworks to understand the mechanisms of respective themes. Based on these frameworks, species can coexist if niche differences exceed fitness differences; biodiversity can increase ecosystem functioning through complementarity and/or selection effects; and biodiversity can increase ecosystem stability by influencing species asynchrony and/or species stability.

and used the bipartite framework to understand how coexistence mechanisms are linked to BEF [27,28,50]. These studies showed that niche differences and complementarity effects are positively related if they both arise from differentiation in resource uses [28,42], natural enemy susceptibility [51], temporal niches [52], or facilitation [53]. We note, however, that this association is not inevitable, because negative complementarity effects can arise even if niche differences are sufficient to ensure coexistence [26], and transient positive complementarity effects could persist over a considerable period even if niche differences were insufficient to maintain coexistence [28]. Fitness differences could be positively related to selection effects if the more productive species are also more competitive and dominate the community [41], or they could be negatively related if the less productive species tend to be more competitive and dominant [54]. Moreover, theoretical studies also showed that complementarity effects decrease with increasing fitness differences, due to dominance of the community by particular species, and selection effects decrease with increasing niche differences due to weakened species competition [27,28,30]. Overall, processes promoting coexistence (greater niche differences or smaller fitness differences) tend to enhance complementarity effects while weakening selection effects. Given that BEF is attributed mainly to complementarity effects in experimental systems [21,25,44], we expect that coexistence and BEF are often positively associated, although a negative association is theoretically possible [41,54].

Based on a biodiversity experiment using Mediterranean annual plants, Godoy *et al.* [31] quantified niche and fitness differences by parameterizing a model with experimental data, and explored how they are linked to complementarity and selection effects. Their results largely confirmed theoretical expectations that niche differences increase complementarity but decrease selection effects, whereas fitness differences increase selection but decrease complementarity effects. Furthermore, they showed that a larger excess of niche differences (relative to fitness differences) led to stronger complementarity effects and thus higher community productivity, which indicates a quantitative association between processes underlying coexistence and BEF.

Table 2. Scenarios for positive or negative associations between processes underlying coexistence (niche and fitness differences), BEF (complementarity and selection effects), and BEFS (species asynchrony and species stability) based on respective bipartite frameworks

Theme	Bipartitions	Scenarios for positive associations	Scenarios for negative associations
Coexistence ~ BEF	Niche differences ~ complementarity effects	Niche differentiations in resources, enemies, and/or abiotic requirement or facilitation lead to complementarity effects [27,28,38]	–[a]
	Niche differences ~ selection effects	–	Higher niche differences reduce species competition and thus weaken selection effects [31]
	Fitness differences ~ complementarity effects	–	Higher fitness differences lead to dominance by particular species and thus impair complementarity effects [27,31]
	Fitness differences ~ selection effects	Species with high productivity in monoculture have competitive advantages [41]	Species with low productivity in monoculture have competitive advantages [54]
Coexistence ~ BEFS	Niche differences ~ species asynchrony	In a strongly fluctuating environment, temporal niche differences increase species asynchrony due to differential responses to environmental fluctuations [29,46]	In a weakly fluctuating environment, greater niche differences weaken species competition and thereby reduce competition-driven compensatory dynamics [47]
	Niche differences ~ species stability	Niche differences increase species stability due to weakened competition-driven fluctuations [55] or increased population abundances by better buffering demographic stochasticity [56]	–
	Fitness differences ~ species asynchrony	–	Greater fitness differences cause the community to be dominated by particular species, which behave like highly synchronous aggregates of a population [45]
	Fitness differences ~ species stability	Species with competitive advantages exhibit higher stability [30]	–
BEF ~ BEFS	Complementarity effects ~ species asynchrony	Complementarity effects and species asynchrony both increase with greater niche differentiation and more even distributions of species abundance [32,58]	Strong interspecific competition weakens complementarity effects while increasing species asynchrony due to compensatory dynamics between species [46]
	Complementarity effects ~ species stability	Over-yielding effects (due to complementarity) can increase species abundance and buffer demographic stochasticity [56]	–
	Selection effects ~ species asynchrony	–	Selection effects lead to dominance by particular species and thereby weaken species asynchrony [45]
	Selection effects ~ species stability	Dominant species in the mixture have higher monoculture productivity and stability [30]	–

[a]No scenario could be found to create the respective relationship between the two variables.

Joint study of coexistence and BEFS

Coexistence and BEFS are also related via various processes [29,30]. As the discussion of relationships between coexistence and BEFS makes most sense in the presence of temporal environmental fluctuations, below we distinguish strong and weak environmental fluctuations depending on whether or not they could mediate species coexistence. In strongly fluctuating environments, temporal niche differences between species can simultaneously promote long-term coexistence via temporal storage effects [6] and enhance ecosystem stability by increasing species asynchrony [29], resulting in a positive association between niche differences and species asynchrony. However, under weak environmental fluctuations, niche differences could be negatively related to species asynchrony, because greater niche differences weaken interspecific competition and thereby reduce competition-driven compensatory dynamics between species [47]. Similarly, niche differences can increase species stability due to weakened competition-driven fluctuations [55] or increased population abundances that can better buffer demographic

stochasticity [56]. Fitness differences may also increase average species stability if species with competitive advantage are also more stable [30]. Finally, fitness differences could decrease species asynchrony by driving the community to be dominated by particular species and thus to behave like highly synchronous aggregates of a population [45]. Overall, processes promoting coexistence can have mixed impacts on both species asynchrony and species stability, resulting in either positive or negative associations between coexistence and BEFS. In spite of these theoretical expectations, we are unaware of any empirical study testing the links between processes underlying coexistence and BEFS.

Joint study of BEF and BEFS

The positive effects of biodiversity on both the mean (BEF) and stability (BEFS) of ecosystem functions have been widely documented [14,57]; however, these two effects do not necessarily coincide with each other [30,34]. Even though a higher mean biomass tends to promote stability, processes underlying BEF and BEFS could be linked in various ways [32]. First, complementarity effects can be positively related with species asynchrony, as they both tend to increase with greater niche differentiation and more even distributions of species abundance [32,33,58]. However, competition may mediate a negative correlation between them by weakening complementarity effects while increasing species asynchrony by driving compensatory dynamics between species [46]. Second, complementarity effects can be positively related to species stability, because over-yielding due to complementarity effects can increase species abundance and buffer demographic stochasticity [56]. Third, species selection effects (as opposed to temporal selection effects [59]) tend to reduce species asynchrony due to continued dominance by certain species [45]. Fourth, selection effects and species stability can be positively related when the community is dominated by species with high monoculture productivity that can better buffer demographic stochasticity and are thus more stable [30]. Combined, complementarity effects tend to increase ecosystem stability by promoting asynchronous responses to environmental fluctuations or via over-yielding effects [56], whereas selection effects impair these stabilizing effects [30]. Again, since BEF is mainly attributed to complementarity effects [21,25,44], we expect biodiversity effects on functioning and stability (i.e., strengths of BEF and BEFS) to be positively associated, although negative associations are also possible.

Several empirical studies have tested the relationships between biodiversity effects on functioning and stability. A meta-analysis of 34 experiments showed that biodiversity can enhance both productivity and stability, yet the two effects are independent of each other [34]. But this analysis did not quantify the processes underlying biodiversity effects. Another study using grassland experimental data showed that ecosystem stability increased with complementarity effects but decreased with selection effects [58]. Based on 24 agricultural biodiversity experiments across Europe and Canada, Yan *et al.* [32] used bipartite frameworks to disentangle processes underlying both BEF and BEFS and showed that complementarity effects (averaged across years) were positively related to species asynchrony, resulting in a positive association between productivity and stability. More recently, analyses of a long-term grassland experiment showed that complementarity effects increased and their relationship with species asynchrony strengthened over time, leading to even stronger associations between BEF and BEFS at later stages of the experiment [33].

Challenges and future research

Challenge I: deriving high-level biodiversity mechanisms from low-level processes

The bipartite frameworks allow us to address links between processes underlying the causes (coexistence) and consequences (BEF and BEFS) of biodiversity in a general context (Table 2). This provides an important and tractable first step to integrating the three fields of

research, which can be accomplished with existing theoretical tools, and which can be widely applied across systems and contexts. However, there are also challenges in linking the bipartite frameworks. The components from these frameworks do not map onto specific biological processes [42]; instead, they typically describe **high-level processes** emerging from a variety of **low-level processes**, which are in turn determined by the biology and environment of resident species and their interactions [60] (Figure 3). This causes correlations between the two components within each bipartite framework [35,47,55,61,62], and may explain why links between different bipartite frameworks do not only occur among components capturing either interspecific interactions or asymmetry (Table 2 and Figure 3). In other words, linkages between different components are higher-level correspondences that arise from shared constraints caused by lower-level ecological processes. Thus, although bipartite frameworks have proved useful to link the causes and consequences of biodiversity, interpretations should be treated with caution since the fundamental ecological processes are not explicitly resolved.

To overcome this challenge, future research could use more mechanistic approaches based on low-level processes to integrate the causes and consequences of biodiversity change (climbing down the ladder in Figure 3). As we are still far from a complete mechanistic understanding of all ecological processes driving coexistence or biodiversity effects on functioning and stability, a tractable next step may be to examine detailed processes relating to certain types of interactions (e.g., resource competition, or plant–soil interactions) (Table 1). For instance, if we understand mechanistically how species coexist through their use of resources, the efficiency in which they convert resources into biomass, and how other species modify resource availability, we should be able to interpret the associations between coexistence, BEF, and BEFS directly from these

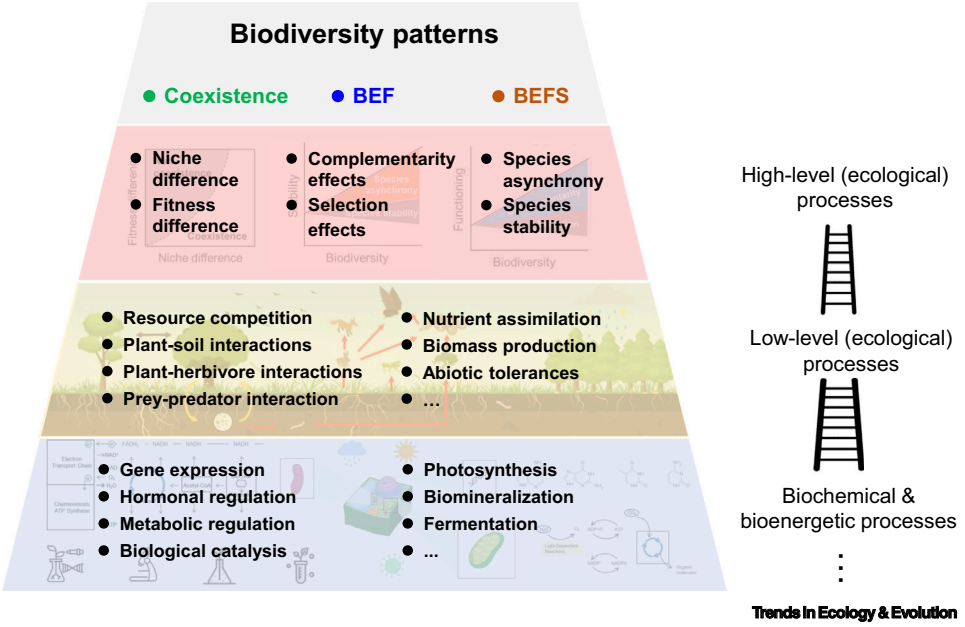

Figure 3. Mechanisms underlying species coexistence, biodiversity–ecosystem functioning relationships (BEF), and biodiversity–ecosystem functional stability relationships (BEFS) at different hierarchical levels. Components from bipartite frameworks represent high-level ecological processes, which emerge from combined effects of low-level ecological processes (e.g., resource competition, nutrient assimilation, etc.). Different bipartite frameworks combine low-level ecological processes in different ways, resulting in either positive or negative associations between high-level processes from different frameworks. Similarly, low-level ecological processes emerge from combined effects of biochemical and bioenergetic processes, which are in turn regulated by fundamental physical and chemical laws (represented by the ellipsis).

low-level processes [50]. Such efforts will also shed light on the interdependence between high-level processes within and between bipartite frameworks [27,61]. However, approaches based on low-level processes cannot be easily generalized across types of interactions or ecosystems. Given this trade-off between generality and precision [60,63], an integrated framework of coexistence, BEF, and BEFS may require multilevel approaches combining high- and low-level processes (i.e., climbing up and down the ladder in Figure 3).

Challenge II: integrating causes and consequences of biodiversity change in broader contexts

Given the still limited efforts to address links between coexistence, BEF, and BEFS (Figure 1 and Table 1), our synthesis is largely built upon insights from Lokta–Volterra competition and consumer–resource models. It remains an open question whether, and under what conditions, such insights (summarized in Table 2) apply to more complex systems (e.g., food webs and multispecies communities). In particular, modern coexistence theory has relied largely on two-species systems [36], which are much less diverse than those studied in BEF and BEFS research [14]. Recent theoretical efforts have proposed new definitions of niche and fitness differences for multispecies systems [36,64]; however, these have not yet been linked to BEF or BEFS, although doing so empirically would be feasible as BEF effects are already calculated in multispecies communities. However, one challenge in doing so is that novel coexistence mechanisms can emerge in multispecies systems (e.g., higher-order interactions or indirect interactions such as intransitive competition) [65–67]. Theoretical frameworks for linking higher-order or indirect interactions to BEF or BEFS are still largely missing (but see [68]). In addition, processes underlying BEF and BEFS may feedback to influence coexistence, for example, by reducing the temporal variability of species and thus their persistence [69]; again, a general framework to disentangle these feedbacks is currently lacking.

Future research should also integrate causes and consequences of biodiversity in the context of multifunctionality and multiple spatiotemporal scales (Table 1). While our synthesis focused on the mean and stability of ecosystem productivity, various metrics have been proposed to characterize different facets of ecosystem functioning [70] and stability [16]. Mechanisms underlying biodiversity effects on different facets of functioning and stability may differ or even exhibit trade-offs [71,72], and hence relate to coexistence mechanisms differently. In particular, coexistence mechanisms might link strongly with biodiversity effects on productivity and its stability because species biomass production is a measure of performance and is therefore a direct outcome of species interactions as well as a function itself (e.g., [41,50]). By comparison, coexistence mechanisms might link less strongly with other functions (e.g., decomposition or nutrient cycling), which could be directly driven by other trophic levels or abiotic factors [73,74]. However, linking coexistence mechanisms to these functions may allow a better understanding of the feedback between coexistence and BEF or BEFS. For instance, functions related to nutrient cycling can influence the dynamics of species competing for nutrients and hence coexistence among them [75,76]. At larger spatial scales, metacommunity processes could contribute new mechanisms for coexistence, BEF, and BEFS, respectively, via spatial storage [2], spatial selection effects [59,77], and spatial insurance effects [78]. Over long timescales, eco-evolutionary dynamics have been shown to modulate mechanisms of coexistence [79,80], BEF [81], and BEFS [82], potentially mediating associations between them. Understanding the relationships between storage effects, selection, and insurance across space and time will be an important step forward for achieving an integrative biodiversity theory for management and conservation in the face of global environmental changes.

Challenge III: combining theoretical and empirical efforts

Our analysis shows that experimental studies are still limited in testing linkages between coexistence, BEF, and BEFS (Table 1). Two issues play a role. First, understanding coexistence and BEF/BEFS requires different experimental contexts. For instance, global change experiments

have been implemented to explore the causes of biodiversity change, where biodiversity is the dependent variable (e.g., [9]). Meanwhile, biodiversity experiments are employed to understand the consequences of biodiversity change (BEF and BEFS), where biodiversity is the independent variable (e.g., [12,18]); because species richness is held constant and no species are allowed to invade, these experiments deliberately decouple processes of species assembly and coexistence from BEF and BEFS processes. For instance, selection effects arising from competitive dominance increase community production while impairing coexistence, blurring the relationship between the realized diversity and production [41,83]. In addition, in experiments with unequal initial species abundances (e.g., [32]), selection effects should be used cautiously when deriving implications for coexistence. Second, empirical quantification of coexistence mechanisms is difficult to do with direct analysis of experimental data, and instead typically requires first fitting a model to empirical data and then analyzing the fitted model [39]. By comparison, mechanisms of BEF and BEFS are relatively easy to quantify using experimental data; however, many biodiversity experiments do not run long enough to study BEFS; thus, empirical tests on linkages between BEF and BEFS mechanisms are still limited (but see [32–34]).

More empirical efforts are needed to explore linkages between causes and consequences of biodiversity in realistic systems, so as to distinguish the alternative outcomes predicted by theoretical models (Table 2 and Figure 3). As many theoretical predictions summarized herein are derived from simple models, empirical patterns may be weaker due to the complexity of ecological interactions in realistic systems, undetected confounding covariables, demographic stochasticity, or observational errors [56,83]. For this purpose, long-term biodiversity experiments provide an opportunity to estimate species interactions for assessing coexistence [84] as well as quantify mechanisms of BEF and BEFS (e.g., [33,56]). Moreover, factorial experiments of biodiversity and environmental change can provide further insights into how mechanisms of coexistence, BEF, and BEFS, as well as their relationships, respond to environmental changes. For instance, Hong *et al.* [85] showed that positive BEF relationships hold consistently under environmental changes, but their strengths vary with environmental conditions. Godoy *et al.* [31] showed that the positive correlation between niche differences and complementarity effects strengthens under drought conditions, highlighting interactions between the environment and biodiversity.

Concluding remarks

Our society is increasingly concerned with the biodiversity crisis and its ecological impacts. Recently, new global targets were set under the post-2020 Global Biodiversity Framework [86]. To support implementation of these targets, an advanced biodiversity science is urgently needed to link the causes and consequences of biodiversity in an integrative framework. Such a framework is key to achieving conservation of both biodiversity and its ecological functions. By summarizing current knowledge and future challenges on the linkages between the causes and consequences of biodiversity change, our synthesis clarifies where we stand and identifies where we should go. This provides a first step rather than a final solution to achieve an integrative framework. Future research is needed to clarify the functional implications of biodiversity maintenance using more mechanistic approaches and across broader contexts and scales (see Outstanding questions). To achieve this goal, we advocate close collaborations among scientists focusing on different research themes, ecological contexts, and methodologies.

Outstanding questions

How do mechanisms of multispecies coexistence (e.g., intransitive competition and higher-order interactions) influence BEF and BEFS relationships?

To what extent do mechanisms underlying causes and consequences of biodiversity change in local communities extend to large spatial scales?

How do eco-evolutionary dynamics regulate coexistence, BEF, and BEFS, and does evolution of enhanced coexistence lead to evolution of more positive BEF and BEFS?

Will global change factors modulate the mechanisms of coexistence, BEF, and BEFS, as well as relationships between them?

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Declaration of interests

No interests are declared.

Supplemental information

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