



# **Incorporating Effect Factors into the Relationship between Biodiversity and Ecosystem Functioning (BEF)**

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Abstract: Generally, the high levels of biodiversity found in natural ecosystems have positive effects on ecosystem functions (EFs), though the intensity and direction of such effects can vary. This is associated with the impacts of other EF-driving factors. In this study, the factors that affect biodiversity-ecosystem functioning (BEF) are reviewed and summarized, and current gaps in the research on the effects of these factors on BEF are discussed. Moreover, a new conceptual model, the generating-presentation model, accounting for links between effect factors and EFs, is built to provide a systematic means of understanding how different factors affect BEF. The model shows that the correlation between biodiversity and EFs can be described as involving a cascade process, while the separation of biodiversity and EFs from ecosystems without considering integrated features is not appropriate for BEF-related research. The generating-presentation model can comprehensively reflect the effects of different factors on EFs and thus has major theoretical and applied implications.

Keywords: community structures; conceptual model; multifunctionality; trophic level



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## 1. Introduction

Biodiversity decline over the past two decades has drawn more attention to the effects of biodiversity loss on ecosystem functions (EFs) [1,2]. This has led to the development of an ecological field examining the relationship between biodiversity and ecosystem functioning (BEF) [3]. Generally, high levels of biodiversity have positive effects on ecosystem functions. However, the intensity and direction of such effects can vary [4]. This is associated with the impacts of other EF-driving factors. For example, van der Plas [3] compared the effects of biodiversity, community composition, and abiotic conditions on EFs based on a review of BEF-related studies on terrestrial and aquatic ecosystems. The author's results show that the effects of biodiversity on EFs are dependent not only on community factors but also on the environment and the scale of the given community [3]. Therefore, to maintain a sustainable level of EF, the protection of abiotic conditions that maintain species and their functional traits and sustainable biodiversity is required. How can various factors of BEF be considered in a methodical way? Which effect factors should be considered in BEF research? These questions urgently need to be addressed.

The purpose of this study is to integrate the different factors that affect BEF and to propose a systematic way of understanding how different factors affect BEF. We first review recent BEF research, particularly that published over the past four years, and summarize the factors that affect BEF. Then, we describe current gaps in the research on the effects of these factors on BEF. Moreover, from conceptual models of links between effect factors and EFs provided in the literature, a new conceptual model is built to summarize the factors that affect BEF and to comprehensively describe ways of measuring the effects of different factors on EFs. This new conceptual model can clearly express the relationships between various effect factors and BEF, which has important theoretical and applied implications.

## 2. Community-Related Factors Affecting BEF

## 2.1. Community Structure

Community structures have a significant effect on BEF [5,6]. As variations in biodiversity characterize the dynamics of community composition, the integration of communityrelated factors (e.g., species abundance and distribution) into BEF research based on studies on biodiversity variation can further our understanding of the effects of community changes on EFs. For example, Cao et al. [7] quantified the species abundance and EFs of benthic invertebrates in Dian Lake (Yunnan, China) to evaluate the effects of the former on the latter. Their results indicate that the relative abundance of Annelida animals shows a significant linear correlation with ecosystem multifunctionality (MEF) [7]. Moreover, Huang et al. [8] performed a study on large-scale forest ecosystems and found high levels of tree species richness to be positively correlated with forest yields while this positive correlation is affected by tree growth rates. Bannar-Martin et al. [9] partitioned the relative contributions of species richness and community composition into EFs using the Pice equation. The study showed that considering biodiversity and community composition in temporal dynamics can predict EF variations more effectively than considering biodiversity alone [9]. However, species richness can be determined by the number of species in a community and the functional traits related to a given species. Therefore, the partitioning of the relative contributions of species richness and community compositions to EF can prove challenging [9]. This may account for the lack of case studies conducted in this area [10], which must be remedied in future BEF research.

## 2.2. Trophic Level

Despite the significant effects of community trophic levels on BEF, few studies have been conducted in this area [11]. The complementarity effect is often employed to measure EF enhancement resulting from biodiversity [12]. In particular, the complementarity effect is related to numerous community-related features, including the niche difference of species within a community and interspecific competition [13]. However, trophic structures can affect the compensation effect by limiting interspecific competition, which is linked to the community compositions of trophic levels [14]. Hence, the effects of community trophic level structures on BEF are evident. However, research on the effects of EFs of biodiversity at different trophic levels and especially at high trophic levels remains limited [11,15]. Schuldt et al. [16] investigated the effects of biodiversity on MEF at multiple trophic levels for a forest ecosystem with rich levels of diversity in the sub-tropical zone. The study showed that the EF effects of species richness at high trophic levels can be transferred via the food web [16]. This indicates that biodiversity at high trophic levels can indirectly affect EFs via its effects on biodiversity at adjacent lower trophic levels. This cascade effect of biodiversity at high trophic levels on EFs highlights the importance of understanding the effects of biodiversity at multiple trophic levels on EFs. Moreover, Schuldt et al. [16] asserted that BEF-related studies focused on producers alone may underestimate the overall effect of biodiversity on EFs. Research on the effects of biodiversity or species composition at high trophic levels on EF may thus facilitate the development of theories and applications of ecology.

At high trophic levels, species are exposed to high levels of extinction risk, which may have severely negative impacts on EFs [17]. Therefore, research on the mechanisms dominating BEF under complex food web conditions is of great significance. Biodiversity at high trophic levels is not only key for MEF predictions but is also an important management objective [15]. The diversity of heterotrophic species is often regarded in studies as a component of MEF rather than as a factor driving EF [16]. However, these studies neglect the effects of biodiversity at high trophic levels on EFs, limiting a complete understanding of BEF [18,19]. The diversity of heterotrophic species cannot be replaced with plant diversity. However, relationships between MEF and biodiversity at high trophic levels have not yet been revealed. At the same time, for most ecosystems, biodiversity mechanisms at high trophic levels impacting MEF via the food web are not fully understood [20].

While few BEF studies have considered the food web, research on food chain energy fluxes is relatively mature [21]. The application of energy flux theories to biological chains can serve as a novel means of researching the formation of BEF in complex ecosystems [21]. For example, intraguild predation, which refers to predatory behavior between two species with the same prey, is often observed in food chain energy flows [17]. Intraguild predation can extend the vertical niche space and reduce energy flows from a low trophic level to a high trophic level, affecting biodiversity food web dynamics. Wang et al. [17] simulated a food web involving five species to show that the correlation between biodiversity and EFs is enhanced under intraguild predation. The study demonstrates that plant BEF model improvements based on studies considering multiple trophic levels are effective in clarifying the effects of biodiversity on EF [17]. Hence, future studies should focus more heavily on tests involving multiple trophic levels.

#### 2.3. Parasite-Host Relations

Species interactions have been widely investigated due to their significant effects on species functions, species diversity, and ecological processes [22]. However, the parasite-host relation, a key factor shaping species interactions, is rarely discussed in BEF studies. Few studies have explored the effects of parasite communities on EFs and ecosystem productivity [23]. Parasitic species impact the quantity and traits of hosts and can consequently further impact EFs. Thus, BEF-related studies must further consider parasite-host relations [23]. In particular, microbes, a key parasite species, rapidly respond to environmental changes. Based on this, the effects of the microbe community on plant community yields under global climate change and significant human disturbance must be better understood to maintain and optimize primary productivity.

Several studies have investigated the mechanisms underlying the effects of parasites on BEF. For example, Ferlian et al. [24] explored interactions between plants and mycorrhiza and demonstrated that the effects of plant diversity on EF tend to be more pronounced when intraspecific competition exceeds interspecific competition. Mycorrhiza can affect plant competition by providing water and nutrients to plants in exchange for photosynthetic products [25]. Moreover, mycorrhiza traits vary across plants [26]. Thus, mycorrhiza plays a key role in maintaining plant diversity and sustainable BEF. Laforest-Lapointe et al. [27] found a positive correlation between leaf bacteria diversity and ecosystem productivity. In particular, the authors demonstrate that both the functional characteristics of the host species and functional diversity have great impacts on the structure and diversity of leaf bacteria communities [27]. In other words, microbes can affect EFs through changes in the adaptability and phenotype of the host. Leaf bacteria diversity is proportional to the host yield, which can be attributed to the following three mechanisms. First, leaf bacteria can improve the host's resistance to viruses by increasing resource competitiveness, reducing the nutrient base and enhancing antibiotic production. Second, leaf bacteria can affect the production of plant hormones such as auxin and cytokinin. Third, nitrogen-fixing bacteria can facilitate the collection of nitrogen available to plants [27].

## 3. External Factors Affecting BEF

#### 3.1. Effects of Environmental Factors on BEF

Several studies have discussed the impacts of environmental changes on BEF, demonstrating the importance of environmental factors to BEF-related research [28–30]. For example, Nunes et al. [31] investigated environmental factors that affect beetles and revealed that community attributes and environmental variables can simultaneously affect EFs. In reference to grassland ecosystems, Zirbel et al. [32] demonstrated that multifunctionality variation shapes landscape compositions four times more than functional diversity. Moreover, the correlation between EF and environmental factors was found to be stronger than that between EF and biodiversity. Smeti et al. [33] investigated correlations between species diversity along the bottom muddy layers of rivers and several EFs (e.g., decomposition rate of organic substances) under environmental stresses of river basin pollutants. The study demonstrated that BEF is significantly affected by environmental stress [33]. Thus, BEF-related analyses must cover both community-related attributes and environmental factors.

Much attention has been paid to the effects of environmental changes on biodiversity, and mechanisms underlying environmental factors affecting biodiversity and EF are currently being explored at length [34]. These mechanisms can be grouped into four categories: resource availability efficiency, the spatial differentiation of resources, community habitat space, and the functional differences between species [35]. Due to differences in the methods and scales used, the reported mechanisms of environmental factors affecting EF under different experimental conditions show variations even for similar EFs [36]. For example, Spaak et al. [37] applied a theoretical analysis model to demonstrate that minor environmental impacts can lead to the collapse of EFs at a constant level of species richness. Moreover, the effects of environmental factors on EF can be expressed via community attributes such as population density and community composition rather than based on biodiversity [37]. For example, Liu et al. [38] investigated the effects of habitat fragmentation on EFs and revealed that non-biological environmental factors in fragmented landscapes can affect BEF under constant biodiversity levels. Habitat fragmentation can affect EF by shaping community composition (directly) or other environmental conditions (indirectly). The underlying mechanism associated with this process involves four factors [38]. First, habitat fragmentation can drive the nonrandom selection of species, while changes in community structure caused by the nonrandom selection of species may further influence EF. Second, habitat fragmentation results in the nonrandom decline of key functional traits, also affecting EF. Third, habitat fragmentation has a negative impact on species interactions and particularly on those of symbiotic species. This results in a reduced ecological complementarity effect, thus affecting EF [39]. Fourth, habitat fragmentation may affect species at different trophic levels (e.g., negative impacts on top predators), which consequently affects plant species via the top-down cascade effect [40]. Furthermore, the boundary effect induced by habitat fragmentation can affect environmental conditions such as temperature, humidity, wind, and light, subsequently affecting EF. The above works highlight the utility of considering various environmental factors in BEF-related research to investigate the direct and indirect effects of environmental factors on EF.

## 3.2. Effects of Climate Change on BEF

While the positive correlation between biodiversity and EFs is widely recognized, the majority of evidence of this relationship is based on small-scale observations [41]. As the effects of environmental factors (particularly of climate change) on BEF are still not fully understood, large-scale BEF-related studies face great challenges [35]. While both climate change and a decline in biodiversity will have a synergistic effect on ecosystems, the research on this topic remains limited [42]. On one hand, biodiversity may limit the effects of climate change on EF; on the other hand, climate change may alter the underlying mechanisms of BEF [43]. Thus, due to interactions between climate change and biodiversity loss, the effects of these two factors on EF cannot be separated.

BEF-related studies generally refer to climate change as the variation in precipitation and temperature. Numerous studies have used large-scale data platforms while others are based on controlled tests [44]. For example, Ratcliffe et al. [35] investigated the large-scale effects of potential driving factors on BEF based on the European Forest Data Centre platform. Their results suggest that the correlation between biodiversity and EF is strengthened under arid climates. In particular, due to the increasing levels of water stress induced by changes in climate, the importance of the effects of biodiversity on EFs in European forests may be enhanced [35]. Pires et al. [43] investigated the synergistic effects of precipitation variation and litter diversity on EF using controlled tests. Their results reveal that the effects of precipitation variation on scavenger communities are negatively related to litter diversity [43]. Thus, litter diversity can resist the effects of climate change. Variations in precipitation affect the underlying mechanisms that shape the effects of litter diversity on decomposition by hindering the complementarity effects of ecosystems while strengthening the selection effect. In reference to temperature variations, Wieczynski et al. [45] established a coupling relation for the trait-climate factors shaping forest ecosystems based on a global forest database. Functional diversity was found to decline with increases in latitude and altitude. Moreover, the study demonstrated that temperature and vapor pressure have strong impacts on the functional composition of the community and the ecological strategies of species [45]. Based on controlled tests, Garcia et al. [46] revealed a synergetic relation between global warming and biodiversity decline, which was in turn observed to have a negative impact on the functions of microbe communities. In terms of variations in the atmospheric composition, Eisenhauer et al. [47] investigated the effects of grassland plant diversity on MEF under four environmental conditions (natural ambient conditions,

and MEF that weakened with nitrogen enrichment [47]. According to the above studies, climate change has a significant impact on BEF. Therefore, the effects of climate change, as a natural disturbance, on EF can be adjusted by biodiversity [48]. Hisano et al. [49] reviewed BEF-related studies to reveal that biodiversity can mitigate (exacerbate) the negative (positive) impacts of climate change on EF. Similarly, numerous BEF-related studies have claimed that biodiversity can improve the productivity, stability, and ecological elasticity of an ecosystem, which consequently counteracts the impacts of climate change [50]. Hisano et al. [49] suggest that climate change can be regarded as a disturbance and hence can be incorporated into BEF research on disturbances. In particular, each form of climate change corresponds with different types of disturbances. For example, extreme and long-term climate events correspond to pulse and press disturbances, respectively. Biodiversity can promote the positive effects of disturbances on resource enrichment and productivity [48]. Furthermore, biodiversity can relieve the negative effects that disturbances may have on productivity, improving ecosystem stability [51]. For example, biodiversity can reduce the negative impacts of climate events on tree growth by regulating the demographic patterns, stability, and ecological elasticity of natural forest ecosystems.

increased  $CO_2$  concentrations, addition of nitrogen, and simultaneous increases in carbon dioxide and nitrogen). Their results showed a positive correlation between plant diversity

## 4. Spatial and Temporal Scale Effects on BEF

## 4.1. Spatial Scale Effects on BEF

BEF-related research conducted over different spatial scales and particularly of larger scales can facilitate a thorough and accurate understanding of BEF [52]. At present, biodiversity decline is widely observed with much research demonstrating that declines in the density of local plant species can damage both EF and ecosystem services [1]. However, most BEF-related studies focus on a specific region, and it thus remains unclear how biodiversity interactions across different spatial scales affect EF [53]. This limits our understanding of BEF variations as a function of spatial scale [54,55]. Recent studies have attempted to correlate the effects of biodiversity across different scales from metapopulation dynamics or new scale-up methods. For example, Bracken et al. [55] evaluated the scale dependence of the effects of species decline on the biomass of intertidal algae based on data from the coast of Maine in the USA. The study reveals weak (strong) effects of biodiversity on EF at small (large) scales. Hautier et al. [56] analyzed eight EFs over 65 globally distributed grassland ecosystems and found that plant diversity helps maintain the ecosystem services provided by grasslands at both regional and landscape scales. The study suggested that diversity at a single spatial scale can affect the EFs of other spatial scales [56]. Moreover, Lefcheck et al. [54] correlated the  $\beta$  diversity of tropical fish in Dominica with their herbivorous rate over varying spatial scales. Their results reveal that the herbivorous nature of fish is positively correlated with  $\beta$  diversity. This result is consistent with the spatial insurance hypothesis, i.e., due to spatial heterogeneity, biodiversity is particularly important at regional scales with different landscape units. However, research on local EFs that considers regional background information is lacking [54]. As natural resource

management is usually performed at regional scales, integration at this scale is of great significance. Moreover, an understanding of BEF across different spatial scales can help thoroughly and accurately reveal the underlying mechanisms of BEF and is thus of great significance to both theoretical studies and management practices used in the industry.

#### 4.2. Effects of Temporal Scale on BEF

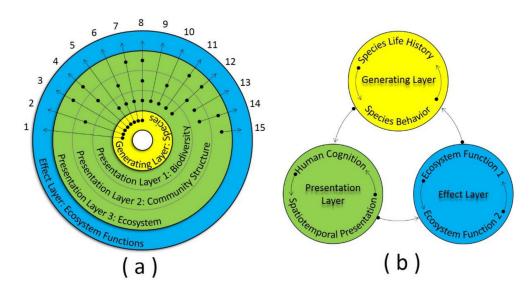
Understanding of the effects of biodiversity on EF as a function of time is essential to predict the effects of biodiversity change and management measures on EF and ecosystem services [57]. Research has indicated that the positive effects of biodiversity on EF can strengthen with time as a result of the enhancement of the interspecific complementarity effect with time [58]. For example, Guerrero-Ramírez et al. [59] used long-term biodiversity-controlled tests to demonstrate the positive correlation between biodiversity effects on EF for grasslands with time. This can be attributed to variations in species distribution patterns as a function of time. However, Guerrero-Ramírez et al. [59] did not observe any regular BEF trend as a function of time for forest ecosystems. To date, factors driving BEF trajectories with time have yet to be determined, and whether these factors are caused by changes in the environment must be clarified. It is also unclear whether these factors are consistent across environmental conditions. In particular, while soil characteristics may affect both transient BEF and its trend as a function of time, the exact mechanisms involved remain unclear [60]. For this reason, long-term BEF experiments in natural environments must be pursued.

Numerous controlled tests reported in the BEF-related literature do not consider temporal scales. In these tests, the natural reproduction and succession of species are usually terminated by the removal of non-sown species [61–63]. This not only enhances ecosystem selection and complementarity effects but may also reduce the effects of competition exclusion, resulting in indeterminate results [64]. For example, BEF studies conducted under non-weeding environmental conditions remain relatively limited compared to those of weeding environmental conditions [62]. The establishment of such non-weeding communities echoes the ecological restoration of abandoned farmland. Among these communities, the biodiversity of the initial community is controlled by a sowing event while the diversity and yield of subsequent communities is dependent on the development of the initial community. However, the effects of community development on BEF remain to be clarified. Veen et al. [65] observed that during the natural succession of a community, initial species (selected manually) affect the composition and biodiversity of the community at an early stage while biodiversity and EF are independently or negatively correlated during secondary community successions. The mechanisms behind these processes, however, require further investigation.

#### 5. Generating-Presentation Model

#### 5.1. Model Significance and Structure

The above review of the different effect factors discussed in BEF-related research shows that numerous research gaps on effect factors in BEF-related research remain and must be explored further. Thus, it is urgently necessary to construct a way to systematically consider factors that affect BEF and to provide suggestions for future research. We thus build a conceptual model with a circle-like structure called the generating-presentation model (Figure 1). The conceptual model summarizes the effect factors of BEF and comprehensively explores the effects of different factors on EFs. Because biodiversity can be regarded as a community-related factor that affects EF [9], a conceptual model accounting for the relationships among various effect factors and EFs can be used to express the links between effect factors and BEF.



**Figure 1.** The generating-presentation model. (a) The main section of the generating-presentation model includes three layers: the generating layer, presentation layer, and effect layer from the inner layer to the outer layer. The presentation layer includes three sublayers: presentation layers 1–3 from the inner layer to the outer layer. The focuses of each layer and sublayer are illustrated in the figure. "A•→B" denotes the effect of A on B. Ecosystem functions (EFs) can be affected according to 15 approaches. For example, approach 1 indicates that EF is directly affected by species life history or species behavior. Approach 2 states that EF can be affected by community structures and species life history or species behavior. (b) There is a feedback loop between the generating, presentation, and effect layers: variations in the presentation layer generated from variations in the generating layer. The generating layer shows an interaction effect between species life history and species behavior. The presentation layer illustrates interactions between human cognition and spatiotemporal scale. The effect layer reveals tradeoffs and synergies among different EFs.

The main section of the generating-presentation model is composed of three layers: a generating layer, presentation layer, and effect layer from the inner layer to the outer layer. The presentation layer includes three sublayers: presentation layers 1–3 from the inner layer to the outer layer. Each layer and sublayer has its own structure and implications. The outer layer or sublayer includes an inner layer or sublayer except for the effect layer.

#### 5.2. Generating Layer

The generating layer represents the effect factors related to a species' life history and behavior. Due to biodiversity, community structures and biological parts of ecosystems can be considered as the existential state of species at a higher scale, and this layer can then be defined as the generating layer. Variations in biodiversity, community structures or biological parts of ecosystem can result from variations in the generating layer similar to how bodily variations can result from gene variations. The generating layer covers two features: species life history (e.g., the birth, senility, illness, and death of a species) and species behavior (e.g., competitiveness, mutualism, predation, etc.). There is an interaction effect between these two sections. For example, Maynard [22] quantified the links among a competitive network structure, biodiversity, and community functioning, and found that a competitive network can determine the direction of BEF relationships.

#### 5.3. Presentation Layer

The presentation layer represents the effect factors related to biodiversity, community structures, and ecosystems. The layer represents the existential state of species and is thus regarded as a presentation layer because variations in the generating layer can be represented by this layer. The presentation layer includes three sublayers. The first sublayer (presentation layer one) is related to biodiversity and can be considered part of the community structure. Biodiversity often refers to functional diversity, phylogenetic diversity, species classification diversity, and so on. However, according to Oehri et al. [52], landscape diversity is also positively linked to EFs. The second sublayer (presentation layer two) represents the community structure and can be viewed as a part of an ecosystem. According to the works reviewed above, many effect factors of community structure are related to different aspects of community structure aside from biodiversity, including species' spatial patterns and trophic level structures. However, Delgado-Baquerizo et al. [66] found that the BEF relationship can also be affected by the biodiversity and multifunctionality can be affected by soil biodiversity. The last sublayer (presentation layer three) is related to ecosystems and covers not only biological features but also abiotic environments. Due to the strong effects of environmental factors such as temperature and geology on EFs [67–69], presentation layer three reflects abiotic factors in most cases.

Moreover, the presentation layer reflects the interactions between human cognition and spatiotemporal scales. First, the presentation of species in this layer depends on levels of human cognition. The development of human cognition can enhance the form of presentation used. For example, according to human cognitive development, numerous biodiversity indexes with different ecological implications have been built to reflect certain aspects of biodiversity [53,70]. According to cognitive development, different methods for expressing community structures such as pattern indexes have also been proposed [71]. Second, as it is meaningless to study biodiversity, communities, and ecosystems without considering a spatiotemporal scale, human cognition about biodiversity, communities, and ecosystems is limited by the spatiotemporal scale. Moreover, the development of human cognition can also improve our understanding of scale effects and can further enhance the accuracy of species presentation in the presentation layer. Over the last three decades, numerous studies have focused on BEF at fine scales and over short time periods [72]. Such studies reveal the mechanisms of BEF at small scales but do not test the mechanisms involved at larger scales. Further understanding the role of scale in BEF research can help guide policies on BEF management [53].

#### 5.4. Effect Layer

The effect layer focuses on EFs and forms the outermost layer of the generatingpresentation model. Because EF is related to the effects of ecosystems, the layer is termed the effect layer. Within this layer, there are tradeoffs and synergies among different EFs. In addition, variations in the presentation layer generated from variations in the generating layer can influence the effect layer. The effect layer can also have feedback effects on the generating layer. A feedback loop thus exists between these three layers.

#### 6. Discussion

#### 6.1. Measuring Factors Affecting EFs

From the generating-presentation model we can conclude that EFs can be affected by different factors corresponding to different layers or sublayers through 15 approaches. For example, according to approach 1, EFs are directly affected by species life history or species behavior. According to approach 2, EFs can be affected by community structures and species life history or species behavior. Among the 15 approaches, 8 (approaches 5–12) are related to biodiversity. Based on the factors identified to affect BEF in recent research, various effect factors are incorporated into the generating-presentation model (Table 1). It should be noted that the generating-presentation model can incorporate not only factors affecting BEF but also those affecting EFs. In other words, biodiversity is identified as a common factor that affects EFs in the model.

Approach	Meaning
1	EF is affected by species life history or species behavior directly.
2	EF is affected by the community structure, and species life history or species behavior.
3	EF is affected by the ecosystem, and species life history or species behavior.
4	EF is affected by the ecosystem, community structure, and species life history or species behavior.
5	EF is affected by biodiversity, and species life history or species behavior. Examples can be found in studies [23,24,57,65].
6	EF is affected by the community structure, biodiversity, and species life history or species behavior. Examples can be found in studies [14].
7	EF is affected by the ecosystem, biodiversity, and species life history or species behavior. Examples can be found in studies [43].
8	EF is affected by the ecosystem, community structure, biodiversity, and species life history or behavior. Examples can be found in studies [29,34,37,45].
9	EF is affected by biodiversity directly. Examples can be found in studies [53,55,66].
10	EF is affected by the community structure and biodiversity. Examples can be found in studies [11,16,21].
11	EF is affected by the ecosystem and biodiversity. Examples can be found in studies [32,35,49,54,59].
12	EF is affected by the ecosystem, community structure, and biodiversity. Examples can be found in studies [7,28,31,33,38,47].
13	EF is affected by the community structure directly.
14	EF is affected by the ecosystem and community structure.
15	EF is affected by the ecosystem directly.

**Table 1.** The approaches to express the effects of factors on ecosystem functions (EFs) in generating-presentation model.

The generating-presentation model provides a useful reference system for EFs or ecosystem services research. In future BEF research, the approaches of effects of biodiversity on EFs or ecosystem services can be clearly presented by this model. For instance, some recent BEF studies cited in this article can be grouped in approaches 5–12 (Table 1).

#### 6.2. Integrating Factors Affecting BEF with the Generating-Presentation Model

In general, the ultimate goal of BEF research is to evaluate the state of EF. In some cases, the correlation between biodiversity and EF has been described as involving a cascade process [72]. On one hand, as expressed by the approaches illustrated in the generating-presentation model, this cascade process indicates that biodiversity, which is affected by species, can influence the community structures and compositions of ecosystems. On the other hand, as Isbell et al. [72] showed in their research, because of cascade processes, the impacts of human activities on BEF may increase at larger spatial and longer temporal scales. Furthermore, community structures and compositions can affect ecosystem processes, which can in turn further lead to a variety of EFs. However, as a dynamic and open system, the natural ecosystem has a typical dissipative structure whose factors have complex sources. As a result, the separation of biodiversity and EFs from the ecosystem without considering integrated features is not appropriate for BEF-related research.

Biodiversity decline has drawn attention to the effects of biodiversity loss on EFs [2,73]. However, biodiversity is only a factor that affects EFs. Thus, when the research object is to evaluate the state of EF, not only biodiversity but other factors must be studied—especially when the main effect factors do not include biodiversity (approaches 1–4 and 13–15 of the generating-presentation model). However, when the research objective is to evaluate the state of biodiversity, factors related to biodiversity, such as land-use change, may be considered [74]. These two research objectives are relatively independent of each other, though relationships between biodiversity and EFs have been found in numerous studies. Therefore, research on BEF may not be relevant in reference to certain areas, as relationships between biodiversity and EFs are not always significant in certain regions.

## 7. Conclusions

As a new avenue for research in ecology, BEF research generally focuses on the effects of biodiversity loss on EF. However, other factors, with the exception of biodiversity, also affect EF and play an important role in BEF-related studies. In this work, the different factors that affect BEF have been reviewed and summarized, and a new conceptual model, the generating-presentation model, accounting for the links between effect factors and EF has been built to provide a systematic means of understanding how different factors affect BEF. The model shows that correlations between biodiversity and EF can be described as involving a cascade process and that the separation of biodiversity and EFs from the ecosystem without considering integrated features is not appropriate for BEF-related research. The generating-presentation model thus comprehensively reveals the effects of different factors on EFs and thus has key theoretical and applied implications. It is suggested that the integration of effect factors in BEF could allow us to greatly advance our knowledge of BEF.

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