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# Formation and effects of biodiversity: A brief history, underlying mechanisms, and future research directions

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## Abstract

Losses and gains in species diversity profoundly affect ecosystem functioning and its stability. Understanding the mechanisms underlying the formation and effects of biodiversity has long been a central scientific question in ecological research. While extensive studies have shown that biodiversity is governed by various ecological processes and is closely associated with ecosystem functioning and its stability, the mechanisms underlying diversity formation, as well as the explanatory mechanisms for the biodiversity–ecosystem functioning and biodiversity–ecosystem functional stability relationships, remain fragmented and lack a systematic integration. In this review, we explore recent advances in theoretical studies on the formation and effects of biodiversity along three aspects. First, we briefly introduce the history of research on biodiversity formation and effects. Second, we synthesize observed patterns in the relationships between biodiversity and ecosystem functioning, as well as between biodiversity and ecosystem functional stability. Third, we classify and discuss the mechanisms driving both biodiversity formation (community assembly and species coexistence) and its effects (biodiversity–ecosystem functioning and biodiversity–ecosystem functional stability). We then discuss future directions for research on the causes and consequences of biodiversity. Future research should integrate high-order interactions into species coexistence theory and quantitatively predict biodiversity responses to environmental changes. Meanwhile, it should consider a broader range of ecosystem functions beyond species biomass or abundance, and establish a multiscale theory of biodiversity effects based on long-term and large-scale spatial experiments. This review provides an integrated theoretical framework for the mechanisms driving diversity formation and its effects, which will deepen our understanding of the causes and consequences of biodiversity.

***Keywords:*** Biodiversity; Biodiversity–ecosystem functioning; Biodiversity–ecosystem functional stability; Formation; Effect

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## 1. Introduction

Biodiversity is critical to ecosystem functioning and its stability. Losses and gains in biodiversity not only affect ecosystem functioning,[1-3] but also affect the stability of ecosystem functioning.[4,5] As the global rate of species extinction has accelerated in recent years, there is an urgent need to understand the causes and consequences of biodiversity.[6-8] To identify the causes and consequences of biodiversity, researchers have carried out extensive studies focusing on three corresponding themes: (i) community assembly and species coexistence, (ii) biodiversity–ecosystem functioning (BEF), and (iii) biodiversity–ecosystem functional stability (BEFS). On the one hand, process-based community assembly and modern coexistence theory have deepened our understanding of biodiversity formation and maintenance. On the other hand, studies on BEF and BEFS have respectively explored the potential impacts of biodiversity changes on ecosystem functions such as biomass production and nutrient cycling,[9] and the capacity of biodiversity to maintain these functions in the face of disturbances.[4]

Understanding how biodiversity is formed and maintained remains one of the central issues in theoretical ecology. Community assembly plays a pivotal role in the formation and maintenance of biodiversity.[10] Community assembly theory suggests that community structure is controlled by deterministic processes (e.g., biological and environmental filtering) and stochastic processes (e.g., birth, death, speciation, extinction, and migration).[10] At the same time, traditional community ecology emphasizes that the attributes and species composition of coexisting species in a community depend on the species coexistence mechanisms; thus, the formation of biodiversity must also be affected by species coexistence mechanisms.

Modern coexistence theory suggests that species coexistence results from a trade-off between niche differences and fitness differences.[11,12] Extensive theoretical and experimental studies have been conducted to identify patterns in the BEF and BEFS relationships[13-16] and to elucidate the mechanisms driving these patterns.[17-19] Patterns of the relationship between biodiversity and ecosystem function and its stability can be broadly classified as positive, negative, and neutral.[13,14,20,21]

Based on the presence or absence of interspecific interactions, ecologists divide the mechanisms by which biodiversity affects the functional stability of ecosystems into interaction-independent and interaction-dependent mechanisms. However, there are still fierce debates regarding the mechanisms driving biodiversity formation and those underlying the effects of biodiversity on ecosystem functioning and its stability. In addition, research on the causes and consequences of biodiversity is fragmented and lacks mechanistic integration, making it difficult for those new to the field to grasp the conceptual framework.

In this review, we first explore the history of biodiversity formation and its effects on research. Secondly, we summarize the BEF relationship and the BEFS relationship. We then integrate the mechanisms underlying biodiversity formation and its effects. Finally, we discuss the future developments of the causes and effects of biodiversity. By establishing an integrated theoretical framework for the mechanisms underlying biodiversity formation and its effects, our review systematically clarifies the causes and ecological consequences of biodiversity. Such a framework provides a theoretical basis for maintaining ecosystem functions through biodiversity regulation, thereby contributing to addressing environmental problems, particularly in Asian regions under severe environmental stress.

## 2. History of research on biodiversity formation and its effects

### 2.1. Development history of biodiversity formation research

To understand the mechanisms underlying biodiversity formation and maintenance, researchers have conducted a series of theoretical studies on species coexistence and community assembly. Grinnell[22] first introduced the concept of the "niche," and the Russian biologist Gause[23] subsequently proposed the "competitive exclusion principle," which together laid the early foundation for species coexistence theory. The British ecologist Elton[24] expanded the niche concept and emphasized the role of interspecific interactions in species coexistence. Levins[25] quantified niche theory, promoting a shift from qualitative to quantitative research, and supplemented the explanation of species coexistence from a niche perspective. Grubb[26] put forward the concept of the "regeneration niche," which broadened the theoretical dimensions of species coexistence by integrating reproductive strategies with resource utilization. Tilman[27] proposed the "resource ratio hypothesis," arguing that species coexistence can be achieved when two competing species differ in their requirements for resource ratios. This hypothesis emphasizes the importance of the supply ratios of multiple limiting resources for species coexistence, thereby challenging the traditional view of "single resource limitation." Chesson[11] proposed modern coexistence theory to analyze the dual mechanisms of species coexistence: stabilizing mechanisms and equalizing mechanisms.

From the early 1900s to the 1950s, it was generally accepted that niche differentiation was the basis for community assembly. Niche-based theories emphasized that community assembly was driven primarily by deterministic processes (i.e., environmental selection and interspecific interactions). In 2001, Hubbell[28] formally put forward the "neutral theory" for the first time in the *Neutral Theory of Biodiversity*. He emphasized that species in communities are functionally equivalent and that community assembly is mainly driven by stochastic processes, thus challenging the traditional view that "niche differentiation is the sole driver of community assembly." Since the early 21st century, researchers have moved away from debating whether deterministic or stochastic processes alone determine community assembly. Instead, there is a growing tendency to integrate neutral theory and niche theory, forming a theoretical framework that incorporates both stochastic and deterministic processes.[29-31]

### 2.2. Development history of biodiversity effect research

Research on biodiversity and ecosystem functioning dates back to Darwin's time. For instance, Sinclair[32] compared the effects of monoculture and mixture on plant productivity. After Goodman[33] published a review entitled *Diversity and Stability*, BEF research faded from view. In 1992, a new round of discussions on BEF was launched at the conference entitled "Biodiversity and Ecosystem Function" held in Germany as well as at the "United Nations World Conference on Environment and Development" held in Brazil, which reexamined the impact of biodiversity loss on ecosystem services and functions.

Schulze and Mooney's[34] monograph *Biodiversity and Ecosystem Function* laid the foundation for modern BEF research. Since 1993, numerous BEF experiments have been conducted, such as the Ecotron experiment,[35] the Cedar Creek field experiment,[36] and the Microcosm experiment.[37] However, there were many controversies regarding the validity of BEF experimental designs, the mechanisms by which diversity affects ecosystem function, and the correlation between the results of natural ecosystems and those of experimental ecosystems. For example, Tilman *et al.*[18] proposed the "sampling effect" and "complementarity effect"; Huston[38] questioned the correlation between diversity and stability; and Grime[39] proposed the mass ratio hypothesis. Over the past 20 years, ecologists have carried out extensive exploration and evaluation of this relationship. With the accumulation of experimental data and the development of theoretical models, a series of key findings have marked a milestone in the development of BEF research. Many historical debates have gradually subsided, and a general consensus has been reached on the relationship between biodiversity and ecosystem function.[40]

The term "biodiversity affects stability" was first used in Elton's[24] 1927 work. Then, in the 1950s, MacArthur[41] and Elton[42] proposed that ecosystems with high species diversity are more stable, and their work marked the beginning of research on biodiversity–stability relationships. In the 1970s, researchers began to use mathematical models to examine the relationship between biodiversity and stability and found that biodiversity reduced ecosystem stability, which was contrary to earlier views.[43,44] Over the next 20 years, ecologists found no clear link between biodiversity and stability. In the mid-1990s, ecologists conducted a series of experimental biodiversity studies to test the BEFS relationship. These biodiversity experiments focused primarily on plant communities and on plant community productivity stability.[36,37]

In recent years, ecologists have further advanced research on BEFS, which is mainly reflected in two aspects: experimental research and theoretical research. In terms of experimental research, ecologists have expanded diversity experiments from grassland ecosystems to forest, freshwater, and marine ecosystems,[40] which not only tests existing theories but also provides the experimental foundation for new theories.

In terms of theoretical research, many scholars have proposed a new framework of BEFS theory,[20,45,46] which has made significant contributions to deepening the understanding of biodiversity and ecosystem functional stability. For example, Liang *et al.*[47] extended the diversity–stability theory to a multi-spatial scale framework, revealing that biodiversity has consistent stabilization effects at different spatial scales, thereby highlighting the importance and necessity of large-scale biodiversity conservation. In 2025, Meng *et al.*[48] developed a BEFS theoretical framework, which decomposed the impact of biodiversity on ecosystem stability into two major mechanisms—interaction-independent mechanisms and interaction-dependent mechanisms—and highlighted that grassland ecosystem stability originates from species-specific dynamic responses rather than species interactions, thus challenging the traditional theoretical paradigm that the compensation effect governs stability.

## 3. Biodiversity–ecosystem functioning and biodiversity–ecosystem functional stability relationships

The BEF relationship is a concept used to describe the relationship between biodiversity and ecosystem function,

and it is one of the core issues in community ecology. Revealing the patterns of BEF relationships is the basis for interpreting the mechanisms by which biodiversity affects ecosystem functions. Generally, biodiversity has a positive, negative, or neutral effect, or no effect, on ecosystem functions.[49,50] Based on theoretical and experimental results, van der Plas[14] examined the relationship between biodiversity and ecosystem functions (individual function: biomass, decomposition, and soil carbon storage; multiple functions: multifunctionality) in different ecosystems (Table 1) and highlighted that in most cases, biodiversity increases biomass, while for decomposition rates and multifunctionality, biodiversity has more positive effects than negative effects, but neutral relationships are more common.

Finally, there is no significant relationship between biodiversity and soil carbon storage. In a meta-analysis of studies on microbial BEF relationships from 2000 to 2017, Saleem *et al.*[50] found that species richness was positively correlated with one or more ecosystem functions, such as abiotic and biotic stress resistance, nutrient cycling, and productivity, in approximately 80% of studies. In contrast, only 5% of studies reported that higher diversity impaired microbial community function.

Biodiversity not only affects ecosystem functions but also influences the sustainability of these functions. Ecosystem stability generally encompasses three dimensions: (i) temporal stability (changes in function over time), (ii) resistance (the ability of an ecosystem to resist disturbance), and (iii) resilience (the ability of an ecosystem to recover from disturbance).[20] Experiments and models have shown that biodiversity can have positive, negative, or no effects on individual components of stability, such as temporal stability, resistance, and resilience.[51]

The effects of biodiversity on these individual stability components differ. There is a strong correlation between biodiversity and the temporal stability of ecosystem functions. For example, plant diversity can enhance the temporal stability of plant biomass.[36] In another study, Isbell *et al.*[52] found that plant species richness increases biomass resistance but does not significantly affect resilience; in other words, biodiversity affects resistance to a far greater extent than resilience. Additionally, the effects of biodiversity on functional stability differ across different levels of biological organization (e.g., populations and communities).[53] For instance, Tilman *et al.*[54] demonstrated that biodiversity increases the temporal stability of productivity at the community level, while it decreases it at the population level.

## 4. Mechanistic synthesis of the formation and effects of biodiversity

Many mechanisms underlying the formation and effects of biodiversity have been proposed. These mechanisms, investigated from different scales and perspectives, are quite intricate and difficult to grasp for those new to the field. Here, we attempt to classify and introduce these major mechanisms, as illustrated in Figure 1.

### 4.1. Mechanisms of biodiversity formation

Based on differences in spatial scales, the mechanisms of biodiversity formation can be divided into local-scale and regional-scale mechanisms. Research on species coexistence mainly focuses on closed local communities (i.e., without dispersal or speciation processes). In contrast, community assembly primarily incorporates regional processes, aiming to understand patterns of species diversity within a multi-scale and dynamic framework.

#### *4.1.1. Species coexistence*

Coexistence theory provides a theoretical framework that greatly deepens our understanding of species coexistence. Modern coexistence theory is based on the invasion criterion, the central idea of which is that a species can persist if it exhibits a positive population growth rate (i.e., invasion growth rate) when rare in a steady-state subcommunity composed of all other species; if this condition is satisfied for every species, then coexistence is stable.[55]

Modern coexistence theory identifies two core mechanisms: stabilizing and equalizing mechanisms.[12] Stabilization mechanisms refer to the fact that because of niche differentiation among species in resource utilization and resistance to natural enemies, intraspecific competition is stronger than interspecific competition. Therefore, when a species becomes rare, it can grow rapidly and achieve a positive invasion rate; equalization mechanisms refer to different species having similar average fitness in the environment and thus similar invasion rates.[56] In other words, niche differences lead to stabilization, while reduced fitness differences lead to equalization.[11] Specifically, niche differences are used to measure the extent to which different species are constrained by different resources, natural enemies, or environmental factors.[12] In contrast, fitness differences reflect the competitive advantage of one species over others.[11] In the absence of niche differences, fitness differences impede species coexistence, leading to competitive exclusion.[4] Niche differences and fitness differences can be estimated by the invasive growth rate decomposition method, and species coexistence is assumed

if the niche differences exceed the fitness differences.[57] A recent meta-analysis based on 29 datasets reported that the occurrence of species coexistence is mainly driven by large niche differences rather than small fitness differences.[58]

Modern coexistence theory also provides a mechanistic explanation for why only certain species become invasive in new environments and how they impact biodiversity.[11,59,60] In ecology, when a species is introduced to a new environment, it may possess invasive potential if it maintains a positive invasion growth rate when it becomes rare,[55] but it is only considered an "invasive species" when it successfully establishes, spreads rapidly, and causes damage to the resident community.[61] The successful establishment of an invader depends on either a fitness advantage or niche difference from resident species, but only an overwhelming fitness advantage drives a species to expand and become dominant.[62] Invasive species drive biodiversity loss in resident communities by disrupting species coexistence.[63] In natural environments, resident species are expected to coexist if their niche differences are greater than fitness differences.[57] However, invasive species introduce overwhelming fitness differences that far exceed the niche differences of resident species.[62] This strong fitness advantage triggers the competitive exclusion of resident species, preventing coexistence, and ultimately causing biodiversity loss in resident communities.[59]

#### *4.1.2. Community assembly*

Niche theories emphasize that deterministic processes—such as biological interactions (e.g., competition, predation, reciprocity) and environmental filters (e.g., pH, temperature, salinity, and humidity)—play an important role in regulating microbial community structure.[11] However, neutral theory indicates that functional differences between species are not important, and community structure is mainly controlled by stochastic processes such as birth, death, speciation, extinction, and migration.[64] Vellend[30] classifies the factors that influence community assembly into four main processes: selection, dispersal, speciation, and drift.

(a) Selection

Selection refers to the niche-based deterministic processes that determine community structure due to fitness differences (e.g., survival, growth, and reproduction) among different species, including abiotic filtering (environmental conditions) and biotic filtering (e.g., competition, mutualism, and predation).[65] Based on environmental heterogeneity, selection can be divided into two categories: homogeneous selection and heterogeneous selection.[10] If environmental conditions (both abiotic and biotic) do not change drastically across space and time, community structure is expected to exhibit little variation, which is referred to as homogeneous selection.[31] Conversely, if environmental conditions fluctuate across space or time, high variation in community structure is expected, which is termed heterogeneous selection.[31]

(b) Dispersal

Dispersal refers to the movement and successful establishment of individuals or populations across space.[66] Dispersal limitation occurs when biological migration to new locations is impeded or its establishment is obstructed.[10] The influence of dispersal on community structure depends on its strength. Dispersal limitation usually results in an increase in community dissimilarity, whereas homogenizing dispersal (i.e., high dispersal rates) leads to the homogenization of community structure and low community turnover, that is, low community dissimilarity.[31]

Because dispersal depends on both deterministic and stochastic factors, it cannot be clearly classified as either deterministic or stochastic.[10] For example, dispersal is stochastic when dispersal rates depend on population size, as abundant species exhibit a higher probability of dispersal than rare species do.[10] In contrast, dispersal is deterministic if dispersal rates depend on species traits and active states, such as spores or dormancy.[10] Therefore, dispersal is theoretically considered deterministic, stochastic, or a combination of both. In recent years, microbial dispersal has been directly detected using microbial traps, fluorescent labeling, and live imaging-based approaches,[67,68] overcoming the previous limitation of inferring dispersal processes only from microbial distributions.

(c) Speciation

Speciation is an important process by which new species are generated. If speciation depends on genetic variation (e.g., gene mutation, expansion, or transfer), the speciation process is stochastic; if the speciation process depends on species traits, it is deterministic.[10] Thus, the influence of speciation on community structure is mainly driven by stochastic processes, although it may sometimes also be affected by deterministic processes. However, due to the large population sizes and diverse modes of genetic variation in microorganisms, microbial speciation rates are difficult to detect directly in natural environments.[69] Consequently, the contribution of microbial speciation to community assembly remains poorly understood.

(d) Drift

Ecological drift refers to random fluctuations in the relative abundances of species within a community over time, driven by stochastic neutrality-based processes such as birth,

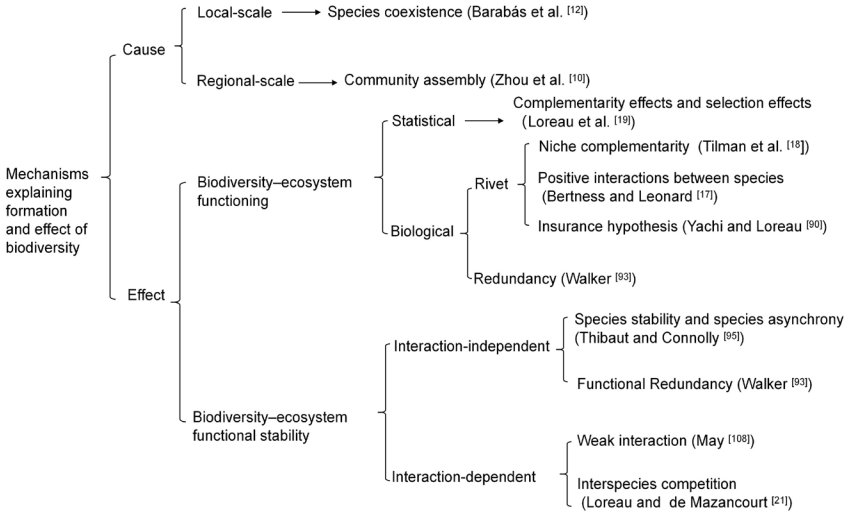


**Figure 1.** Classification of mechanisms underlying the causes and consequences of biodiversity

death, and reproduction.[70] The strength of ecological drift is strongly dependent on population size; its effects are more pronounced when population size is small.[71] Ecological drift plays a key role in shaping microbial community structure.[72] Microbial communities with large population sizes contain many rare taxa that are highly sensitive to ecological drift.[65] Furthermore, microbial communities often exhibit high functional redundancy, meaning that different populations share similar or the same function. Functional redundancy can enhance the neutrality, making populations with redundant functions more susceptible to drift.[10] However, because microorganisms have the ability to enter dormancy—which may allow them to avoid the effects of drift—directly detecting ecological drift in microbial communities remains challenging.

To quantify the relative contributions of deterministic and stochastic processes in community assembly, several ecological models have been developed, including the neutral community model, the β-nearest taxon index (βNTI), the framework of inferring community assembly mechanisms by phylogenetic bin-based null model analysis, and the normalized stochasticity ratio (NST).[10,29,31,73,74]

Neutral community model was used to estimate the effects of stochastic processes on community assembly by fitting the relationship between the species occurrence frequency and their relative abundance.[29,75] $R^2$ represents the goodness of fit of the model. An $R^2$ value close to 1 indicates that the community assembly is entirely governed by stochastic processes.[76] β mean nearest-taxon distance (βMNTD) measures the phylogenetic distance between each operational taxonomic unit in one community and its closest relative in another community.[77] βNTI reflects the magnitude of deviation between the observed βMNTD (βMNTDobs) and the null distribution of βMNTD (βMNTDnull).[10,77] When $|\beta NTI| > 2$, community turnover is dominated by deterministic selection ($\beta NTI < -2$ for homogeneous selection and $\beta NTI > +2$ for heterogeneous selection), whereas $|\beta NTI| < 2$ indicates that community assembly is mainly governed by stochastic processes (e.g., dispersal, diversification, and drift).[10]

Ning *et al.*[74] developed the framework of inferring community assembly mechanisms by phylogenetic bin-based null model analysis, which uses the β net relatedness index (βNRI) to identify the dominant ecological process within each bin and thereby infer the relative importance of individual processes at the whole community level. When $|\beta NRI| > 1.96$, community assembly is dominated by deterministic processes (homogeneous selection or heterogeneous selection),[31] whereas $|\beta NRI| \leq 1.96$ indicates dominance of stochastic processes (homogenizing dispersal, dispersal limitation, or drift). The NST is also used to quantify the relative importance of deterministic and stochastic processes in community assembly, where NST values > 50% or < 50% indicate more stochastic or more deterministic assembly, respectively.[73] These ecological models have been widely applied to investigate microbial community assembly in wetland, river, lake and reservoir ecosystems.

### 4.2. Mechanisms underlying the effects of biodiversity on ecosystem functioning

According to differences in explanatory perspectives, the mechanisms that elucidate the effects of biodiversity on ecosystem functions can be classified into two categories:

statistical and biological mechanisms.

#### 4.2.1. Statistical mechanisms

Complementarity effects and selection effects can be used to explain the positive effects of biodiversity on ecosystem functions.[19,78,79] Specifically, positive complementarity effects occur when species on average perform better when growing in mixtures than in monocultures, due to resource allocation, abiotic facilitation, or biotic feedback.[80] Conversely, positive selection effects occur when a more diverse community contains, and becomes dominated by, species with higher productivity in monoculture.[19] Complementarity effects and selection effects differ in the timescales at which ecosystem functions are expressed. Complementarity effects correspond to long-term effects,[81] while selection effects correspond to short-term effects.[82] Experimental studies have generally shown that complementarity effects are important processes driving positive relationships in the BEF relationship and that their effects increase with increasing functional differences between species.[83]

Loreau and Hector[84] decomposed the net biodiversity effect (i.e., the difference between the observed yield of mixtures and the expected yield in the absence of selection or complementarity effects) into two additive components representing complementarity effects and selection effects, respectively, using the additive partition method. The net biodiversity effect can be calculated using **Equation 1**:

$$\begin{aligned}\Delta Y = Y_O - Y_E &= \sum_i RY_{Oi}M_i - \sum_i RY_{Ei}M_i = \sum_i \Delta RY_i M_i \\ &= N\overline{\Delta RYM} + Ncov(\Delta RY, M)\end{aligned} \quad (1)$$

where:

(i) $N\overline{\Delta RYM}$ is the measure of the complementarity effect.
(ii) $Ncov(\Delta RY, M)$ is the measure of the selection effect.
(iii) $Y_o$ is the observed yield of species.
(iv) $Y_E$ is the total expected yield of the mixture.
(v) $RY_{Oi}$ is the observed relative yield of species $i$ in the mixture.
(vi) $RY_{Ei}$ is the expected relative yield of species $i$ in the mixture.
(vii) $M_i$ is yield of species $i$ in monoculture.
(viii) $\Delta RY_i$ is the deviation from expected relative yield of species $i$ in the mixture.
(ix) $N$ is the number of species in the mixture.

#### 4.2.2. Biological mechanisms

The roles of different species in ecosystems vary significantly. The extinction of some species may trigger cascading losses of numerous other species in the community and even lead to the collapse of entire ecosystems. Such species, termed keystone species, play a critical role in maintaining ecosystem functioning.[85] In addition to keystone species, functionally redundant species have minimal impacts on ecosystem functioning due to their loss being compensated by other species contributing similarly to ecosystem functioning.[86] Based on whether redundant species are considered, the biological mechanisms by which biodiversity impacts ecosystem functioning can be further categorized into two groups: the rivet hypothesis—including niche complementarity, positive interactions between species, and the insurance hypothesis—and the redundancy hypothesis.

(a) Niche complementarity

The niche complementarity hypothesis postulates that coexisting diverse species, characterized by a variety of functional traits, exhibit distinct ecological niche requirements. Such divergence allows the community to utilize available resources more efficiently through niche differentiation and facilitation, thereby enhancing ecosystem functioning.[18,19] Moreover, greater niche differences strengthen the positive effect of species richness on ecosystem functioning.

Tilman *et al.*[18] demonstrated niche complementarity through modeling studies. Their model showed the relationship between total community biomass and community diversity as follows:

$$B_{(N)} = 1 - \left[1 - \frac{\pi}{ab + 2(a+b) + \pi}\right]^N \quad (2)$$

where $a$ and $b$ are the habitat heterogeneity indices for limiting factor 1 and limiting factor 2, respectively, $B$ represents total community biomass, and $N$ denotes number of species in a community.

(b) Positive interactions between species

Positive interspecific interactions, such as mutualism and commensalism, exist in ecosystems, where some species often benefit from others.[17] The positive interaction hypothesis posits that high species diversity increases the probability of positive interactions between species in the community, thereby promoting ecosystem functioning through increased positive feedbacks or improved resource-use efficiency.[87,88] Mulder *et al.*[89] conducted experiments to support this hypothesis, demonstrating that in favorable environments, bryophyte community biomass showed no significant correlation with species richness, whereas in arid environments, both community biomass and species survival rates increased as a result of intensified positive interactions driven by higher species richness.

(c) Insurance hypothesis

The insurance hypothesis suggests that greater biodiversity can prevent declines in overall ecosystem functioning caused by environmental variation, since different species respond to environmental change differently, leading to more predictable ecosystem functioning.[19,90] It was proposed to explain the relationship between biodiversity and ecosystem resistance to disturbances.[90,91] Yachi and Loreau[90] demonstrated the insurance effect of biodiversity through modeling studies, suggesting that increased diversity can reduce the temporal variability of productivity and enhance its overall level. This effect is attributed to the asynchrony of species' responses to environmental conditions, or temporal niche differentiation. When the external environment changes, niche differences among species enable them to achieve risk spreading.[92] Ecosystems with high species richness exhibit stronger resilience to changes in external conditions, whereas ecosystems with low species richness have a weaker ability to resist disturbances.

(d) Redundancy hypothesis

The redundancy hypothesis posits that a few key species play important roles in regulating ecosystem functioning, whereas other species that are functionally substitutable in ecosystems compensate for the functioning of rare species or abundant, functionally similar species that contribute little to a specific ecosystem function.[93] Evidence from biodiversity experiments in grassland ecosystems showed a saturating relationship between species diversity and ecosystem productivity,[94] indicating that many species within ecosystems may perform similar ecological roles and that changes in these species may have little effect on ecosystem functioning, thereby supporting the redundancy hypothesis. Functional redundancy may arise for two main reasons: first, different species may occupy similar ecological niches (i.e., niche overlap); second, some species may persist in ecosystems primarily through species immigration from outside the system.[92]

## 4.3. Mechanisms underlying the effects of biodiversity on ecosystem functional stability

Researchers have proposed numerous mechanisms to explain how biodiversity affects the stability of ecosystem functioning. Based on their dependence on interspecific interactions, these mechanisms can be categorized into two groups: interaction-independent and interaction-dependent mechanisms.[48] Interaction-independent mechanisms emphasize that species' inherent traits determine functional stability; these mechanisms primarily include species asynchrony, species stability, and functional redundancy. In contrast, interaction-dependent mechanisms explain how interspecific interactions influence the stability of ecosystem functioning, mainly including weak interactions and interspecific competition.

### *4.3.1. Interaction-independent mechanisms*

(a) Species asynchrony and species stability

Species asynchrony refers to the incoherence of species dynamics over time, which arises from the differential responses of species to environmental fluctuations, interspecific interactions, or demographic stochasticity.[95] Within a community, species asynchrony increases with higher species richness but decreases as the pairwise correlations among species increase.[95]

Species asynchrony manifests in two aspects. First, species respond to environmental fluctuations in opposite directions.[96] For instance, under specific environmental fluctuations, some species increase in abundance, while others decrease. Such opposite response directions weaken the variability in total community abundance, thereby enhancing functional stability. Second, there are differences in the response rates of species following environmental fluctuations.[21] For example, some species respond at time $t$ following a disturbance, while others respond at time $t$+1. This leads to temporal niche differentiation, which in turn moderates fluctuations in total community abundance and ultimately enhances the stability of ecosystem functioning. By contrast, species stability describes the average population stability weighted by species abundance, which decreases with increased environmental and demographic stochasticity and intensified interspecific competition.[97]

Species asynchrony and species stability can be calculated using the following equations[98]:

$$S_{pop} = \mu_{tot} / \sum_i \sigma_i = \sum_i \mu_i / \sum_i \sigma_i \quad (3)$$

$$\phi = \sum_i \sigma_i / \sigma_{tot} = \sum_i \sigma_i / \sqrt{v_{tot}} = \sum_i \sigma_i / \sqrt{\sum_{i,j} v_j} \quad (4)$$

where:

(i) $S_{pop}$ and $\Phi$ represent species stability and species asynchrony, respectively.
(ii) $\mu_i$ and $\sigma_i$ are the temporal mean and temporal standard deviation of the biomass of species $i$, respectively.
(iii) $v_{ij}$ is the covariance between the biomass dynamics of species $i$ and $j$.
(iv) $\mu_{tot}$, $\sigma_{tot}$, and $v_{tot}$ are the mean, standard deviation, and variance of total community biomass, respectively.

From a mathematical perspective, ecosystem functional stability can be represented as the product of species asynchrony and species stability.[95] Hence, biodiversity

can enhance ecosystem stability by promoting species stability, increasing species asynchrony, or both.[98] For instance, Wilcox *et al.*[99] investigated the effects of stability and asynchrony across different biological levels of organization (e.g., species, population, and community) on the stability of ecosystem productivity. They found that higher asynchrony of species and community can buffer environmental fluctuations, thereby enhancing the stability of ecosystem productivity (Figure 2).

(b) Functional redundancy

In an ecosystem with high biodiversity, multiple species differ in taxonomic composition but are functionally substitutable—suggesting an ecological property referred to as functional redundancy.[100] We refer to species that have functional similarity and whose loss does not significantly affect ecosystem functions as "redundant species." The impact of functional redundancy on the stability of communities or ecosystems can be explained by the insurance effect.[101]

Species in an ecosystem can be classified into different functional groups.[93] If a functional group contains a large number of species, the loss of some redundant species within it will not affect the stability of ecosystem functions. This is because the loss of species in the same functional group can be compensated for by other species with similar functions that take over their roles, thereby maintaining ecosystem functions. However, when only one species remains in a functional group, the disappearance of such a species from the ecosystem will result in irreversible damage to the stability of ecosystem functions.[92] In summary, maintaining a certain level of functional redundancy is of great significance to ecosystem functional stability.

In ecological literature, the functional redundancy of a community is generally interpreted as the component of its taxonomic diversity that cannot be explained by its functional diversity.[102-104] Therefore, functional redundancy can be quantified by the difference between taxonomic diversity and functional diversity (**Equation 5**)[100]:

$$\begin{cases} FR_\alpha \equiv TD_\alpha - FD_\alpha \\ TD_\alpha \equiv GSI \equiv 1 - \sum_{i=1}^{N} p_i^2 = \sum_{i=1}^{N}\sum_{j\neq 1}^{N} p_i p_j \\ FD_\alpha \equiv \mathrm{Q} = \sum_{i=1}^{N}\sum_{j\neq 1}^{N} d_{ij} p_i p_j \\ d_{ij} = 1 - \dfrac{\sum_a \min(G_{ia}, G_{ja})}{\sum_a \max(G_{ia}, G_{ja})} \end{cases} \quad (5)$$

where:

(i) $FR_\alpha$ is the alpha functional redundancy.
(ii) $TD_\alpha$ is the alpha taxonomic diversity.
(iii) $FD_\alpha$ is the alpha functional diversity.
(iv) $d_{ij}$ is the functional distance between taxon-*i* and taxon-*j*, which can be calculated as the weighted Jaccard distance between the genomes of the two taxa.
(v) *GSI* indicates the Gini–Simpson index.
(vi) *Q* is the Rao's quadratic entropy.
(vii) $p_i$ and $p_j$ are the relative abundances of taxon-*i* and taxon-*j*, respectively.
(viii) *N* is the number of taxa in the local community.

#### *4.3.2. Interaction-dependent mechanisms*

Chamberlain *et al.*[105] clearly distinguished two dimensions of ecological interactions: interaction strength (strong to weak) and interaction sign (–, 0, +). Because the mechanisms by which competition and weak interactions affect ecosystem functional stability are fundamentally distinct, the interaction-dependent mechanisms explaining the effects of biodiversity on ecosystem functional stability can be classified into two categories: weak interactions and interspecific competition.

(a) Weak interaction

Weak interactions are defined as ecological interactions with relatively low strength between species,[106] which are characterized by low average degree (i.e., mean of all the node degrees) and low proportion of associations between taxa in co-occurrence networks.[107] Theoretical ecologist Robert May[108] proposed the classic complexity–stability theory (also known as stability constraints) in 1972, arguing that diverse communities tend to lose stability if they have strong interactions.

In essence, ecosystem stability depends on the relative strength of interspecific interactions against intraspecific interactions, as well as connectance.[108] According to May's[108] stability criterion, a large and complex random network remains stable when $\sigma(nC)^{-1/2} < 1$, where σ represents average interaction strength, *n* is the number of species, and *C* denotes connectance.[108,109] Under this framework, weak interspecific interactions imply that the species' growth rates are less sensitive to changes in the densities of other species, thereby enhancing ecosystem stability under external disturbances.[110,111] Conversely, strong interactions in highly complex ecosystems can make system stability highly susceptible to collapse because species' growth rates become highly sensitive to variations in other species' densities. Yonatan *et al.*[112] quantified the overall complexity of ecosystems using dissimilarity-overlap curve analysis (without network inference) and provided empirical support for this theory.

(b) Interspecific competition

Interspecific competition—a loss–loss relationship—occurs if two microorganisms require the same limiting resource for their survival.[113] Competition often enhances ecosystem functional stability through two mechanisms:

(i) Increased species asynchrony: Ecologists have further explored the diversity–stability relationship using community dynamic models, demonstrating that interspecific competition amplifies population fluctuations, while strengthening temporal asynchrony among different species. This species asynchrony can buffer overall system fluctuations, thereby enhancing ecosystem functional stability.[21]
(ii) Reduced dependence between species: When interspecific interactions are competition-dominated, species exhibit lower interdependence. Under external disturbances, the decline of one species does not lead to the complete loss of a specific ecosystem function. Conversely, in cooperation-dominated systems where interdependence is high (e.g., mutualism), the disappearance of a single species may trigger a cascade effect, which ultimately leads to the collapse of ecosystem functional stability. In co-occurrence networks, the degree of competitive behaviours among community members can be quantified by negative cohesion.[114]

## 5. Conclusion and future directions

In the context of global biodiversity loss driven by human activities, it is essential to clarify the mechanisms underlying the formation and ecological effects of biodiversity. In this review, we systematically explored research progress on biodiversity formation (i.e., species coexistence and community assembly) and its effects (i.e., BEF and BEFS) from three key aspects: (i) a historical review of research on biodiversity formation and its effects; (ii) the BEF and BEFS relationships; and (iii) the mechanisms behind biodiversity formation and its effects. Our review established an integrated theoretical framework linking the causes and consequences of biodiversity, which is critical for conserving both biodiversity and ecosystem functions, thereby helping to address practical environmental issues such as water pollution, soil erosion, and global warming.

In the study of biodiversity formation, species coexistence and community assembly are the key mechanisms underlying biodiversity formation at local and regional scales, respectively.[10,12] The theoretical development of both theories is characterized by progressive refinement. Species coexistence theory has progressed through four stages: (i) the establishment of theoretical foundations; (ii) the development of niche theory; (iii) theoretical challenges and dimensional expansion; and (iv) the synthesis of modern coexistence theory. Community assembly theory has progressed through three stages: (i) the dominance of niche theory, (ii) the challenge of neutral theory to traditional paradigms, and (iii) the integration of deterministic and stochastic processes.

In the study of biodiversity effects, studies on BEF and BEFS mainly focused on "how biodiversity affects ecosystem functioning" and "how biodiversity affects ecosystem functional stability," respectively, with each having developed a clear trajectory. BEF research progressed through five stages: (i) early exploration; (ii) the establishment of modern research foundations; (iii) the outbreak of experimental studies and academic debates; (iv) the gradual formation of consensus; and (v) the deepening of research dimensions and systematic expansion. Most existing studies have confirmed that there is a significant positive correlation between species diversity and ecosystem functions (e.g., productivity, nutrient cycling).[50]

Statistical and biological mechanisms have been proposed to explain the relationship between biodiversity and ecosystem functioning.[92] Statistical mechanisms, including the complementarity effect and selection effect, tend to interpret empirical results from a statistical perspective. In contrast, biological mechanisms are based on the biological effects of biodiversity, including mechanisms such as niche complementarity, positive interactions between species, the insurance hypothesis, and the redundancy hypothesis. Research on BEFS has evolved through three stages: (i) the proposal of the "diversity–stability" relationship; (ii) experimental verification and the resolution of controversies; and (iii) the in-depth expansion of the research framework. Studies have revealed that biodiversity has significantly different effects on functional stability at distinct levels of biological organization (e.g., populations and communities)[53] and on various dimensions of ecosystem stability (e.g., temporal stability, resistance, and resilience).[36,52] The mechanisms by which biodiversity influences ecosystem functional stability fall into two categories: species-specific mechanisms (e.g., species asynchrony, species stability, and functional redundancy) and interspecific interaction mechanisms (e.g., interspecific competition and weak interactions).[48]

Despite the increasing number of studies that have investigated the causes and consequences of diversity, the current understanding of the underlying mechanisms remains limited. Based on current research progress, future studies may further explore the following directions:

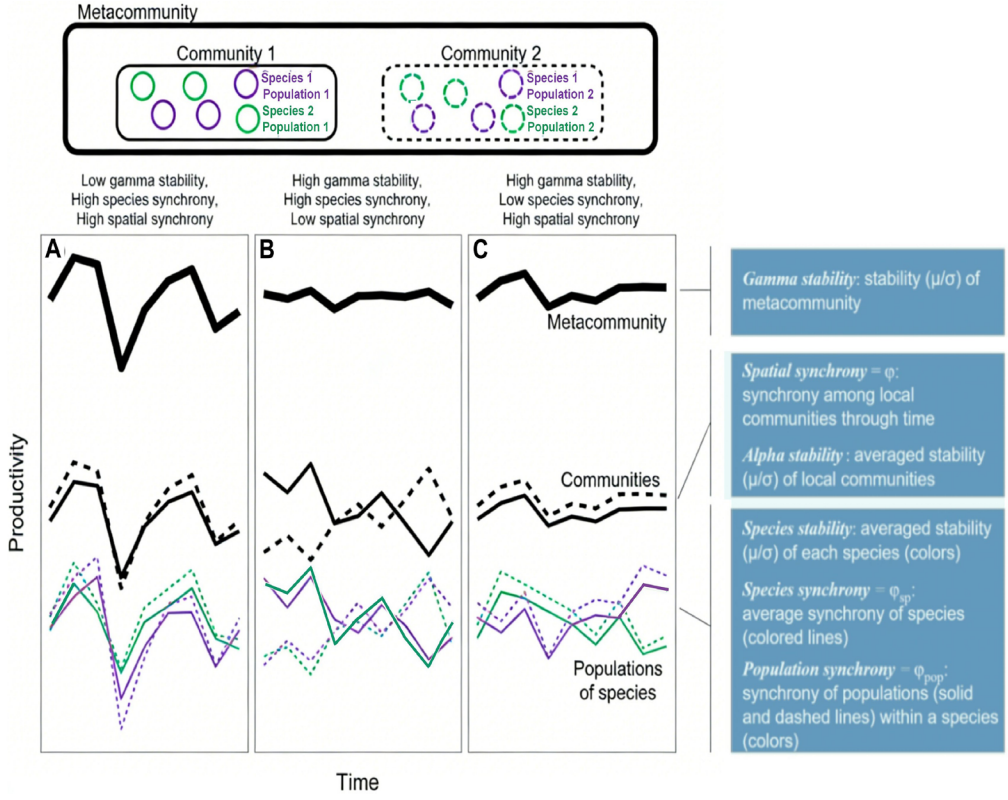


**Figure 2.** Conceptual framework illustrating how stability and synchrony across spatial scales within a metacommunity combine to determine ecosystem functional stability. (A) High synchrony at both species and community levels results in low metacommunity stability. (B) High species-level synchrony and low community-level synchrony result in high metacommunity stability. (C) Low species-level synchrony and high community-level synchrony result in high metacommunity stability. Adapted from Grime.[39]

(a) Biodiversity formation

Future studies should prioritize breakthroughs in two aspects. First, greater attention must be given to high-order interactions between species in research on species coexistence. Traditional species coexistence theories have largely relied on direct pairwise interactions between organisms,[115-119] often overlooking high-order interactions (Figure 3), where the strength of a direct interaction between two species is modified by the presence of a third species.[120-122] Such effects may be crucial for explaining coexistence in complex communities (e.g., multispecies systems). Second, research on biodiversity responses to environmental changes must be strengthened to develop quantitative predictive theories—for example, how environmental changes (e.g., climate warming and nitrogen deposition) affect species coexistence and species interactions.

(b) Biodiversity effects

With regard to research objects, current BEF and BEFS studies are mainly conducted in terrestrial ecosystems such as grasslands and forests, and thus future research should focus on the underlying mechanisms of biodiversity effects in aquatic ecosystems (e.g., freshwater and marine systems). In addition, as existing studies largely concentrate on the effects of biodiversity on productivity (biomass and plant cover), future research should place greater emphasis on other ecosystem functions, particularly the cycling of key elements (carbon, nitrogen, and phosphorus), including processes such as the decomposition of organic matter, $CO_2$ fixation, and organic carbon export.

In terms of research scales, future BEF and BEFS experiments should be conducted at different temporal, spatial, and biological organization scales. In doing so, we can better: (i) determine the types of BEF and BEFS relationships at different temporal and spatial scales; (ii) investigate how the mechanisms underlying these biodiversity effects (e.g., selection effects and complementarity effects) change across temporal and spatial scales; and (iii) comprehensively quantify the effects of different biological organization scales (e.g., individuals, assemblages, meta-assemblages, and macro-systems) on ecosystem functioning and its stability.

**Table 1. Types of biodiversity–ecosystem functioning relationships across ecosystem types**

| Number of ecosystem functions | Classification of function | Ecosystem function | Ecosystem type | Target group | Theoretical relationship | Observed relationships | |
|---|---|---|---|---|---|---|---|
| | | | | | | Experimental studies | Non-experimental studies (*n*) |
| Individual ecosystem function | Biomass | Biomass stock | Temperate forests | Trees | +[18,46,123] | +[125] | + (38) |
| | | Biomass production | Temperate forests | Trees | +[18,46,123] | NA | + (61) |
| | | Biomass stock | Tropical forests | Trees | +[18,46,123] | +[125] | Neutral (44) |
| | | Biomass production | Tropical forests | Trees | +[18,46,123] | NA | Neutral (17) |
| | | Biomass | Grasslands | Plants | +[18,46,123] | +[126] | + (102) |
| | | Biomass | Aquatic systems | Plants | +[18,46,123] | +[126] | + (21) |
| | | Biomass | Terrestrial and aquatic systems | Consumers | +[18,46,123] | NA | + (24) |
| | Decomposition | Decomposition | Terrestrial and aquatic systems | Plants | –[124] | +[40] | + (33) |
| | | Decomposition | Terrestrial and aquatic systems | Consumers | +[124] | +[127] | Neutral (20) |
| | Soil carbon storage | Soil organic carbon stock | Terrestrial and aquatic systems | Plants | NA | +[40] | Neutral (35) |
| Multiple ecosystem functions | Ecosystem multifunctionality | Ecosystem multifunctionality | All | All | NA | +[128] | + (111) |
| | | | Temperate forests | All | NA | NA | + (16) |
| | | | Tropical forests | All | NA | NA | Uncertain (17) |
| | | | Grasslands | All | NA | NA | Neutral (55) |

Notes: Observed relationships are shown for experimental studies (based on meta-analyses) and non-experimental studies (based on literature reviews). "+" and "–" indicate positive and negative biodiversity–ecosystem functioning relationships, respectively. "NA" indicates data not available. "*n*" denotes the number of investigated relationships. The table is adapted from van der Plas *et al.*[14]

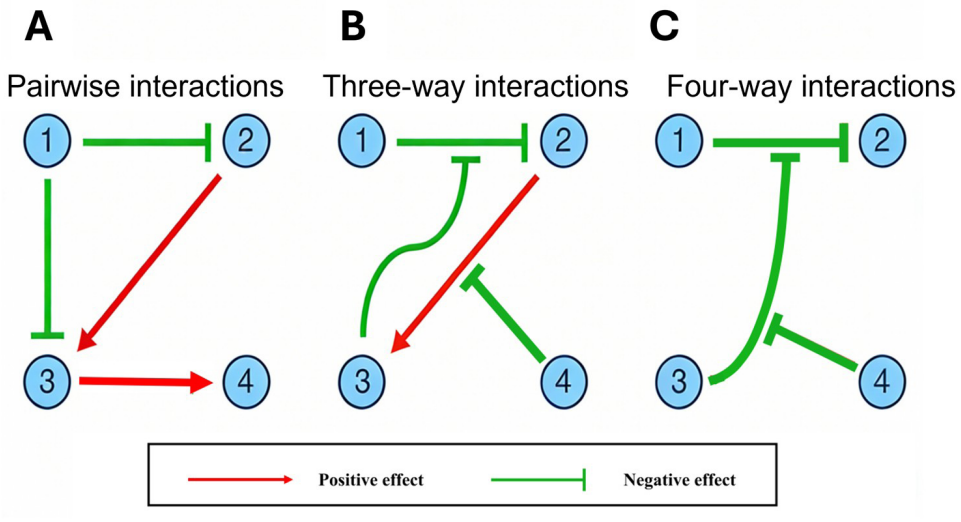


**Figure 3.** Higher-order interactions between species. Adapted from Bairey *et al.*[120]

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## Conflict of interest

The authors declare that they have no competing interests.

## Author contributions

*Conceptualization:* Fang Luo
*Methodology:* Liuqing Zhang
*Writing–original drift:* Fang Luo
*Writing–review & editing:* Huan Hu

## Availability of data

Not applicable.

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