Review

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Effects of biodiversity and its interactions on forest ecosystem multifunctionality

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Review

Effects of biodiversity and its interactions on forest ecosystem multifunctionality

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Abstract: Global change and human activities are altering biodiversity at an unprecedented rate worldwide, leading to sharp declines in global biodiversity and other ecological issues. Over the past 30 years, ecologists have increasingly focused on the question of whether and how the ongoing loss of biodiversity affects ecosystem functioning. This interest has led to the emergence of the field of biodiversity and ecosystem functioning (BEF) as a major research area in ecology. However, historically, researchers have predominantly focused on individual ecosystem functions, neglecting the capacity of ecosystems to provide multiple ecosystem functions simultaneously, known as ecosystem multifunctionality (EMF). This article reviews advances in EMF research, including the selection of functional indicators in EMF studies, different dimensions of biodiversity, the impacts of microbial diversity and biotic interactions on EMF, and drivers of EMF such as non-biological factors. By comprehensively analyzing the overall effects of aboveground biodiversity, belowground biodiversity, and non-biological factors on EMF, the study emphasizes the need to enhance research and application of ecosystem multiserviceability (EMS) approaches.

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The sharp decline in biodiversity caused by global change and human activities seriously impacts ecosystem function (EF) [1]. Since the 1990s, the relationship between biodiversity and ecosystem function (BEF) has become a hotspot in ecological research[2–6]. Initial studies mainly focused on the relationship between biodiversity and a single EF [5], but a single EF does not represent the overall impact of biodiversity on ecosystem functions [7–9]. Therefore, Sanderson et al. [10] proposed the term "ecosystem multifunctionality" (EMF). Hector and Bagchi [11] defined EMF as the ability of ecosystems to provide and maintain multiple functions and services simultaneously. Because there are trade–offs among EFs, managing ecosystems from the perspective of a single EF may weaken the provision or maintenance of other EFS [12]. Since then, EMF has been widely used. Manning et al. [4] divided multifunctionality into EF–multifunctionality and ES–multifunctionality for differentiation and calculation purposes. EMF provides a new and comprehensive perspective for ecosystem management. Researching forest EMF is of great significance for a comprehensive and systematic understanding of EF.

Human impacts on the earth's biological systems have led to a focus on how ecosystems continue to provide services and goods amidst miscellaneous global change scenarios [13]. As a result, tremendous efforts have been made to understand how biodiversity changes will affect ecosystem processes and ecosystem multifunctionality (EMF) [9]. Unlike individual ecosystem functions related to biomass production, resource use, and decomposition, EMF elucidates the ability of that ecosystem to simultaneously provide a multitude of ecosystem functions [14,15], which suggests that the analysis of a single ecosystem function has underestimated the effects of the loss of biodiversity on the provisioning of multiple ecosystem functions [16]. However, biodiversity is not the only factor in biological systems that can influence ecosystem functions and multifunctionality. Research suggests that various behavioral and physiological responses to global change drivers may have important implications for ecosystem functioning [17]. Losses from global change affect humans by simultaneously affecting soil microbial communities and plant diversity, thereby affecting multiple ecosystem functions and services [18].

1. Research Progress and Methods of Ecosystem Multifunctionality

Brockerhoff et al. [19] pointed out that EF and ES are defined respectively with a focus on "ecosystem" and "human". EF refers to the capacity of ecosystems to provide services directly or indirectly to humans. It involves biological, chemical, and physical mechanisms that support and maintain ecosystem integrity but do not necessarily translate into anticipated human benefits [20]. ES represents the contributions of ecosystems to humans, including products directly contributed by ecosystems that can be valued [21]. Forest managers and policymakers can predict the impact of biodiversity management on human well–being based on EF.

Forests provide various important EFs such as climate regulation, water supply and purification, pollination, and habitat provision for species [22]. EFs encompass biomass production, nutrient cycling, soil organic carbon storage, and litter decomposition[5]. In recent years, researchers have attempted to characterize overall ecosystem functioning with a single value [10–11], to clarify the ability and performance of ecosystems to simultaneously provide and maintain multiple ecosystem functions [4,11,23–24], thereby transitioning from focusing on single EF driving factors [14,23,25] to understanding multiple EF driving factors [26], promoting an important new stage in this research field. Studying EMF can elucidate how human factors such as biodiversity, environmental factors, and land use changes simultaneously impact multiple EFs.

Firstly, quantification methods for EMF need to be clearly defined. Current predominant quantification methods in research include Single–function approach, Turnover Approach, Averaging Approach, Single Threshold Approach, Multiple–threshold Approach, Multivariate Model Approach, and orthologous approach [3,11–12,16,24]. Each method has distinct advantages, limitations, and focuses. The Single–function approach analyzes the performance levels of multiple functions in a general linear model simultaneously but provides only qualitative descriptions without quantitative analysis of EMF. The Turnover Approach evaluates by quantifying the redundancy level of species maintaining the number of EMFs and contributions of each species to EMFs, but does not directly measure the weight of EMF and different functions. The Averaging Approach averages standardized values of each function [23–24], which is straightforward, intuitive, detects the relative importance of predictor variables [7,27], and is more suitable for linear model analysis of the relationship between biodiversity and ecosystem multifunctionality [8,23–24]. Threshold methods calculate the number of functions above a threshold (usually expressed as a percentage of the observed function value compared to the highest function value) or within a threshold range, but cannot reflect the importance of specific EFs. The orthologous approach refers to different species sharing similar functions from a common gene, particularly suitable for closely related microbial taxa. The Multivariate Model Approach evaluates the impact of various aspects of diversity (such as species composition, relative abundance, and evenness) on EMFs, losing less information in analysis, but is only applicable to studies with fewer functions (e.g., three functions). However, these methods for measuring EMFs do not consider the increased weight of EFs in certain aspects, leading to biases in multifunctionality metrics.

Different species' contributions to EFs result in trade–offs among EFs [28]. In forest management and operations, maximizing target EFs often involves diminishing other EFs [29]. Byrnes et al. [24] suggested addressing interactions among EFs using systematic modeling approaches such as Structural Equation Modeling (SEM) or dimensionality reduction methods like Principal Components Analysis (PCA). The trade–off relationships among EFs constrain the objective evaluation of EMF, thus Manning et al. [4] proposed a quantitative method that considers the issue of functional weighting. They first cluster EF variables involved, then quantify EMF based on a threshold approach assigning equal weights to each cluster [7,14,29].

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Once quantification methods are established, specific measurement indicators for EFs need to be selected. To date, there is no unified system of EF indicators, typically selected based on specific needs (Table 1).

Table 1. Selection of ecosystem function indicators in different studies.

Ecosystem types	Selecting target	References
Grassland ecosystem	Aboveground productivity, belowground productivity, aboveground vegetation carbon pool, plant biomass, root biomass, lignin and cellulose degradation rates, insect species diversity, plant nitrogen content, plant phosphorus content, soil carbon pool (soil organic carbon, total carbon), soil bulk density, soil inorganic nitrogen content, total nitrogen, hydrolyzable nitrogen, total phosphorus, available phosphorus, soil natural moisture content, capillary water holding capacity, pH, total porosity, PAR transmittance ratio, community resistance to invasion, capillary porosity, non–capillary porosity, aeration porosity, cation exchange capacity, soil clay, sand, silt, conductivity, C: N ratio, C:P ratio, N:P ratio	Hector & Bagchi, [11]; Zavaleta et al.[31]; Jing et al.[7]; Li et al.[32]
Forest ecosystem	Woody plant biomass, soil organic carbon content, soil hydrolyzable nitrogen, total nitrogen, plant nitrogen, total phosphorus, available phosphorus, plant phosphorus, nitrate (NO^{3-}), ammonium (NH^{4+}), amino acids, proteins, pentoses, hexoses, aromatics, phenolics, potential N transformation rate, two enzyme activities (β–1,9–glucosidase and phosphatase)	Soliveres et al.[33]; Huang et al. [29,33]

From Table 1, it can be seen that indicators such as plant biomass, soil organic carbon, soil total nitrogen, soil available phosphorus, soil total phosphorus, soil hydrolyzable nitrogen, plant nitrogen, and plant phosphorus are commonly used EF indicators in research [23]. They are related to soil accumulation of organic carbon, nutrient cycling and decomposition, nutritional reservoir of aboveground biomass, biomass accumulation, soil water retention, and water conservation functions, involving various aspects of soil water, fertilizer, air, heat, and multiple EFs [35]. Although these indicators are not exhaustive, they are commonly used in soil and vegetation surveys, providing comprehensive reflections of soil fertility conditions and are easy to investigate and measure [34].

2. Research Progress on the Relationship between Biodiversity and Ecosystem Multifunctionality (BEMF)

Research on Biodiversity–Ecosystem Functioning (BEF) has been ongoing for many years, with discussions on BEF increasing since the BEF conference held in Germany in 1992 [36]. Subsequent BEF experiments such as the Cedar Creek field experiment [37], European grassland BEF experiment [11], and BEF–China experiment [30] rapidly advanced BEF research and development [1,13]. Studies have found a positive correlation between EFs and biodiversity [14,28,37]. However, most BEF studies have focused only on the impact of biodiversity on individual EFs [11], even when multiple EFs are involved, each EF is independently analyzed [12].

As BEF research deepened, it became apparent that individual EFs cannot represent the impact of biodiversity on overall ecosystem functioning [7–9]. Therefore, there is widespread interest in quantifying the impact of biodiversity on EMF, and whether biodiversity's responses to individual EFs and EMF are consistent [24]. Hector and Bagchi [11] quantified for the first time the impact of biodiversity on multiple ecosystem processes and found that maintaining EMF requires a richer diversity of species. Consequently, research on Biodiversity and Ecosystem Multifunctionality (BEMF) gradually entered the spotlight. Gamfeldt et al. [12] and Zavaleta et al. [31] discussed the importance of biodiversity in maintaining higher functional levels of ecosystems. Since then, an increasing number of scholars have studied BEMF. In recent years, BEMF research has grown, focusing primarily on aspects such as temporal and spatial scales, experimental design, and measurement methods [22,24,33,39–41]. Maestre et al. [23] first studied the relationship between plant

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species richness and EMF in global dryland ecosystems and experimentally explored how changes in key attributes such as species richness, community composition, evenness, and spatial patterns simultaneously affect EMF. Pasari et al. [39] studied for the first time the impact of biodiversity on EMF across multiple scales. Byrnes et al. [24] used BIODEPTH experimental data and the multi–fund program, systematically addressed issues in BEMF research, and proposed the multiple–threshold approach for the first time. Wagg et al. [25] demonstrated the importance of soil microbial diversity and community composition in EMF in experiments on soil community diversity. Perkins et al. [40] first studied the relationship between changing environments and BEMF. Valencia et al. [41] first studied the relationship between functional diversity and EMF. Lefcheck et al. [14] systematically analyzed the role of biodiversity in EMF under different trophic levels, taxonomic groups, and habitat conditions. At the regional scale, forest EMF generally increases with increasing species richness [28,41]. Xu et al. [6] reviewed the research progress of BEMF and its future directions. In recent years, researchers have also explored whether biodiversity can promote EMF at landscape scales [22–41]. Despite the significant progress made in BEMF research [5,30], many questions remain unanswered. Moreno–Mateos et al. [42] found that biodiversity's impact becomes stronger when considering multiple functions, whereas Gamfeldt and Roger [8] found that changes in the number of functions do not alter the impact of BEMF. These inconsistent conclusions underscore the necessity of fully understanding environmental changes and trade–offs between EFs to elucidate the driving mechanisms of BEMF.

Furthermore, researchers have deepened their understanding of biodiversity attributes, proposing multiple attributes such as species richness reflecting species abundance and richness, functional diversity reflecting resource use strategies and life forms, and phylogenetic diversity reflecting different lineage evolution [9]. Research on how these multiple biodiversity attributes affect EFs and EMF is gaining increasing attention.

3. The Impact of Aboveground Biodiversity on Ecosystem Functioning

Early research on BEF relationships primarily focused on the species level [36]. Species richness is the most widely applied biodiversity metric in BEMF research [11,23,41]. Reduction in species is a primary cause of biodiversity loss. Different species contribute differently to EFs, and maintaining multiple functions in ecosystems requires higher levels of species diversity [30,38]. Gamfeldt and Roger [8] noted that species richness is widely used because it is the simplest and most operationally feasible metric. Increasingly, studies focus on the impact of species richness on EMF, with Gottschall et al. [43] finding a positive effect of species richness on EFs. Based on species abundance, the Shannon–Wiener index and Simpson's diversity index can concurrently consider rare and common species with different weights, providing a more realistic measure of species diversity [7]. Recent studies have found that although communities with high species diversity exhibit higher productivity, stronger nutrient cycling capabilities, and greater stability [44], not all forms of species diversity are positively correlated with EFs [5]. Thompson et al.[45] found that species diversity and EFs may exhibit negative correlations or even unimodal relationships.

In recent years, functional diversity and phylogenetic diversity have gained attention in BEMF research. Functional diversity extends from functional traits, mainly reflecting the composition and variation of physiological, morphological, or phenological traits of plants [46]. Functional traits are biological characteristics that influence species survival, growth, reproduction rates, and ultimate fitness [47]. They are closely related to individual growth, dispersal, and ecological strategies, playing a crucial role in BEMF research [48]. Functional traits relate to how species utilize resources, making them effective predictors of ecosystem functioning [49]. Phylogenetic diversity reflects the total sum of lineage distances among species in a community, relating to species richness and average phylogenetic relationships within the community [50]. It comprehensively reflects the assembly processes of communities. Often, it is impractical to measure all functional traits relevant to each ecosystem function. When phylogenetic diversity effectively includes unmeasured biological traits related to EFs, it becomes a key factor influencing EFs [51].

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4. The Impact of Belowground Biodiversity on Ecosystem Functioning

Soil microbial communities are highly diverse, comprising a quarter of Earth's total biodiversity [25], and are among the most abundant and diverse organisms on the planet [52]. Soil plays a crucial role in biogeochemical cycles [53]. Soil microbial diversity also plays a key role in maintaining EMF, facilitating material cycling and energy flow between aboveground and belowground communities through processes such as litter decomposition and organic matter mineralization [54]. In agricultural ecosystems, soil microbial diversity shows a significant positive correlation with EMF [55]. Based on early experiments Bradford et al. [56] found that the functional complexity of soil communities enhances EMF indices derived from multiple methods. Wagg et al. [25] demonstrated that soil microbial community composition regulates and maintains EMF, with higher soil microbial diversity contributing to EMF enhancement. Research confirms that soil microbes are directly involved in complex physicochemical processes related to soil nutrients, thus influencing soil EF and EMF [15,27].

While aboveground biodiversity has received more attention in BEMF research, studies on the impact of belowground biodiversity on overall EMF have lagged [53,57]. Soil microbial diversity profoundly affects plant nutrient uptake and nutrient cycling between aboveground and belowground biological communities [58]. Therefore, understanding the impact of belowground biodiversity on EF and EMF is of paramount importance [53,56].

5. The Impact of Ecological Network Complexity on Ecosystem Functioning

In ecosystems, different species interact through material flow and exchange of energy and information, resulting in complex interactions such as competition, mutualism, predation, symbiosis, and parasitism, which are influenced by various biotic and abiotic factors [59]. Soil microorganisms do not exist in isolation, but form complex interspecies networks that, to a great extent, regulate the structure of an ecological community and consequently, the functions it provides to the ecosystem [60]. Co–occurrence network analysis is a useful tool for depicting and analyzing microbial relationships [61]. For example, through network analysis, He et al. [62] found that five years of switchgrass (*Panicum virgatum* L.) cultivation led to more complex microbial relationships than fallow soil, although there were no significant differences between the microbial community structures of switchgrass and fallow soil. Therefore, the complexity of microbial networks in forested soils might be affected by anthropogenic disturbances [63]. However, the responses of microbe networks to woodland use change remain unclear.

Soil biodiversity includes not only the abundance and number of species but also numerous complex interconnections. Ecological relationships are co–occurrence networks with their relationships as links and microbial taxa as nodes [64]. Networks are considered to compose the backbone of the effective flow of material, energy, and information throughout soil microbial systems and are thus imperative for achieving pivotal functional sides of ecosystems [25]. Although the coexisting soil microbial taxa in the soil supply raw material for related ecological interactions, the variation in the structure of the microbial community and its relationship to ecosystem function are not inevitably caused by univariate diversity or constituent indicators [65,66]. In addition, the interaction among taxa may alter over space, time, or environments. These results indicate that interaction between two species can supersede the influence of species identity and number, and the coexisting interactions between coexisting taxa may be the major driver of ecosystem processes [67]. In recent years, microbial network analysis has been widely accepted by microbial ecologists, and network connectivity is important for microbiome stability and EMF [25,68]. Nevertheless, studies on how the complexity of the soil microbiome responds to woodland use and seasonal change are ambiguous.

The drivers of EMF are also affected by other biotic and abiotic factors [23], which suggests that it will be a major challenge to separate the effects of biodiversity from these factors [5]. Forest management can directly affect aboveground biomass, and aboveground biomass can significantly influence the diversity and composition of soil microbial communities [69]. In addition, soil conditions are also the main drivers of EMF including soil pH [7], soil water content [70], and several other edaphic factors [71]. Climatic conditions also play a vital role in shaping the relationship

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between biodiversity and EMF, such as temperature and rainfall [7,29,54]. However, an increase in precipitation and soil temperature from the dry to rainy season may lead to compositional changes in soil microbial community composition [72]. Environmental changes could produce substantial and distinct influences on ecosystem functionality and multifunctionality (e.g., simultaneous performance of multiple ecosystem functions) by altering the biomass and diversity of ecological communities [33]. Crucially, although studies have found that climate at the regional scale could regulate the relationship between soil microbial or plant diversity and EMF [7], the degree of change in these relationships and whether their relative strength will change with woodland use intensity remain largely untested.

Therefore, while considering the direct and indirect impacts of environmental conditions on ecosystem functions (EF) and ecosystem multifunctionality (EMF), further research is needed on the interactions between aboveground and belowground biota, especially the effects of ecological networks on forest EMF.

In conclusion, we recommend that future research on BEMF relationships should progress by concurrently distinguishing between functions and services. Guidelines should be established for selecting indicators of functions or services for reference purposes. Future studies could focus on how typical forest BEMF relationships at different scales respond to global changes. This includes enhancing research on the comprehensive impacts of different dimensions of biodiversity, microbial diversity, and abiotic factors on EMFs, as well as studying the mechanisms of biological interactions' effects on EMFs. It is advisable to promptly apply newly proposed concepts (such as ecosystem multifunctionality) and developed methods (such as standardized methods based on variable numerical ranges) in relevant research.

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