OPINION

Global Change Biology WILEY

Enhancing the structural diversity between forest patches—A concept and real-world experiment to study biodiversity, multifunctionality and forest resilience across spatial scales

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Abstract

Intensification of land use by humans has led to a homogenization of landscapes and decreasing resilience of ecosystems globally due to a loss of biodiversity, including the majority of forests. Biodiversity–ecosystem functioning (BEF) research has provided compelling evidence for a positive effect of biodiversity on ecosystem functions and services at the local (α-diversity) scale, but we largely lack empirical evidence on how the loss of between-patch β-diversity affects biodiversity and multifunctionality at the landscape scale (γ-diversity). Here, we present a novel concept and experimental framework for elucidating BEF patterns at α-, β-, and γ-scales in real landscapes at a forest management-relevant scale. We examine this framework using 22 temperate broadleaf production forests, dominated by *Fagus sylvatica*. In 11 of these forests, we manipulated the structure between forest patches by increasing variation in canopy cover and deadwood. We hypothesized that an increase in landscape heterogeneity would enhance the β-diversity of different trophic levels, as well as the β-functionality of various ecosystem functions. We will develop a new statistical framework for BEF studies extending across scales and incorporating biodiversity measures from taxonomic to functional to phylogenetic diversity using Hill numbers. We will further expand the Hill number concept to multifunctionality allowing the decomposition of γ-multifunctionality into α- and β-components. Combining this analytic framework with our experimental data will allow us to test how an increase in between patch heterogeneity affects biodiversity and multifunctionality across spatial scales and trophic levels to help inform and improve forest resilience under climate change. Such an integrative concept for biodiversity and functionality, including spatial scales and multiple aspects of diversity and multifunctionality as well as physical and environmental structure in forests, will go far beyond the current widely applied approach in forestry to increase resilience of future forests through the manipulation of tree species composition.

KEYWORDS
BETA-FOR, biodiversity, forest resilience, insurance hypothesis, multifunctionality, β-diversity

1 | INTRODUCTION

The complex relationships between biodiversity and ecosystem functions at various spatial scales are still insufficiently understood. In the context of global change, this is all the more critical for the development of effective strategies for sustainable management of the environment. Here, we present the background, the conceptual framework and an experimental design to study the effects of β-diversity on multifunctionality in temperate forests.

1.1 | Global landscape homogenization and its consequences for ecosystems

Habitat loss, overexploitation of biological resources, pollution, invasive species and climate change are the main causes of accelerated global decline in biodiversity and related ecosystem alterations

(Barnosky et al., 2011; Díaz et al., 2019; Maxwell et al., 2016; Sala et al., 2000). However, changes do not happen uniformly and vary across scales as the result of different drivers (e.g. local habitat destruction versus large-scale climate change) and with different consequences. Locally, taxonomic biodiversity decline is often dominated by the loss of species from communities through reductions in species richness or through changes in abundance and evenness (α-diversity) (Albrecht et al., 2021; Newbold et al., 2015). Species loss at the landscape scale (γ) can be brought about by a system-wide loss of species but, more frequently, it results from a decrease in dissimilarities between local communities (β-diversity), as landscapes become homogenized through human activities (Dornelas et al., 2014; Gossner et al., 2016; McGill et al., 2015). While landscape-scale homogenization through natural resource management can certainly increase the provisioning of targeted products like food or timber, the subsequent loss of biodiversity can have cascading negative effects on other ecosystem services and, thus, on society (Beaumelle

et al., 2020; Gamfeldt et al., 2013). Consequently, new management approaches are urgently needed to improve sustainability in land use and to promote and maintain ecosystem services to people in a changing world.

1.2 | Biodiversity–ecosystem functioning research beyond the α-scale

More than 25 years of biodiversity–ecosystem functioning (BEF) research has provided solid foundational knowledge about how α-diversity contributes to ecosystem functioning and stability at small scales, and how relationships at this scale ensure the delivery of ecosystem services, that is, the benefits people gain from nature (Cardinale et al., 2012; Isbell et al., 2017; Naeem et al., 2012; Weisser et al., 2017). For instance, past research has unravelled many mechanisms underpinning the relationship between biodiversity and productivity at the local scale, such as resource partitioning, abiotic facilitation and trophic interactions, based on observational, theoretical and experimental approaches (Duffy et al., 2017; Flombaum & Sala, 2008; Soliveres et al., 2016; Tilman et al., 1997). Similarly, increasing biodiversity at one trophic level, for example, plants, often increases associated biodiversity at other trophic levels so that 'diversity begets diversity' at the local scale (Dinnage et al., 2012; Eisenhauer et al., 2013; Scherber et al., 2010). Considering several trophic levels together has the potential to better explain ecosystem functioning (Hines et al., 2015; Lefcheck et al., 2015; Luo et al., 2022; Schuldt et al., 2018). Furthermore, the strength of the BEF relationships at the α-scale, measured via (standardized) slope, R^2 or regression coefficients, increases with the number of functions taken into account to quantify ecosystem multifunctionality (i.e. the extent to which multiple ecosystem functions are provided simultaneously) and is thus biased (Hector & Bagchi, 2007; Isbell et al., 2011; Meyer et al., 2018). This may also be true for the β-scale.

However, multifunctionality and biodiversity at the local scale differ from those at the landscape scale. While most BEF research has so far focused on local scales, we advocate for an increased focus on the landscape scale for a number of reasons. First, the landscape scale is the scale where many management decisions are actually made and applied, because each farm or forest enterprise manages many different plots, stands or fields. Second, it is the spatial scale that has the strongest influence on the distribution of populations of most species (Dornelas et al., 2014; Gossner et al., 2016; McGill et al., 2015). The biodiversity of a landscape is composed of a set of local communities of multiple interacting species, which are linked by dispersal, thus forming metacommunities. The scientific framework underpinning the metacommunity concept explicitly takes the separate and interactive roles of scale, dispersal and heterogeneity on biodiversity into account. As a result, it has developed various paradigms that explain the likelihood of species occurrence and coexistence, including patch dynamics, species sorting, mass effects and neutral models (Leibold et al., 2004; Logue et al., 2011). Thus, the metacommunity concept provides a theoretical framework to test for different mechanisms that may underlie observed patterns of species compositional and biodiversity variation in a landscape (Leibold et al., 2004). Similarly, multifunctionality at the landscape scale, which is most relevant for the provisioning of ecosystem services, differs from multifunctionality at the local scale. The between-habitat variation in contributions to multifunctionality at the landscape scale is expected to be low in homogeneous landscapes, because similar habitat types with similar species compositions and structures provide comparable ecosystem functions (Gamfeldt et al., 2013; Mori et al., 2016; van der Plas et al., 2016). In contrast, in landscapes with a high variety of habitats, different habitat types support different species and ecosystem functions, contributing to a high landscape-level multifunctionality (Hautier et al., 2020; Loreau et al., 2003). Furthermore, in abiotically heterogeneous landscapes, β-diversity can also provide performance-enhancing effects on single ecosystem functions, as different species with different habitat preferences are required in patches with different abiotic conditions (species sorting) to maximize biomass production (Isbell et al., 2018). Moreover, when compositions of species across habitat patches are more similar, representing a low β-diversity, they display more spatial and temporal synchrony in patch-scale ecosystem functioning than do those in heterogeneous landscapes, thereby reducing landscape-scale (i.e. γ-scale) ecosystem stability (Firkowski et al., 2022; Wilcox et al., 2017).

Despite strong theoretical arguments for why β-diversity should be important in driving ecosystem functioning at the landscape level, empirical tests confronting these theoretical expectations are still scarce, despite repeated calls for operationalizing BEF findings to management-relevant scales (Eisenhauer et al., 2019; Srivastava & Vellend, 2005; van der Plas et al., 2019). The few studies on biodiversity and ecosystem functioning at the between-patch scale can be divided into those on small and large scales. There are those using controlled experiments at small scales focusing mostly on micro- or mesocosm experiments or manipulating patches of a few square metres of grassland (Firkowski et al., 2022; Hammill et al., 2018; Hautier et al., 2020; van der Plas, 2021). Also, at the small scale, there are a number of observational studies, often on microorganisms or small invertebrates that use fine grain habitats (Ebeling et al., 2020; Hautier et al., 2018; Mori et al., 2016; Mori, Fujii, et al., 2015). At larger scales, notably in agriculture or forests, studies are almost exclusively observational (Albrecht et al., 2021; Dainese et al., 2019; Georgiev et al., 2022; Gossner et al., 2016; Grman et al., 2018; Ratcliffe et al., 2017; Schall, Schulze, et al., 2018; Sirami et al., 2019; van der Plas et al., 2016). Controlled experiments at these management-relevant scales are still rather focusing on early successional stages (Paquette et al., 2018).

Thus far, only two approaches exist to investigate the role of β-diversity for γ-diversity and γ-multifunctionality at larger scales. First, theoretical modelling approaches have used virtual landscapes to test for effects of biodiversity on multifunctionality using virtual species (Firkowski et al., 2022; Wang & Loreau, 2016). These studies have shown that increasing β-diversity stabilizes regional ecosystems via spatial asynchrony. Second, an increasing number

of studies assemble information gained from field observations of different local patches into new, virtual landscapes composed of different combinations of those patches (and hence use a 'hybrid approach' consisting of both empirical and modelling components), to infer their multifunctionality (Ebeling et al., 2020; Gossner et al., 2016; Schall, Schulze, et al., 2018; van der Plas et al., 2019). These applications focus on the additive effects of combining different local patches and their species compositions on biodiversity and multifunctionality at the γ-scale. However, these approaches are unable to consider potential interactions between patches or cross-boundary BEF effects (i.e. non-additive effects), caused by the movement of matter or organisms between them (Scherer-Lorenzen et al., 2022). Today, we have well-established metacommunity theory (Chase et al., 2020) and clear expectations that BEF relationships will change when scaling up BEF research (Gonzalez et al., 2020). However, we lack both the experimental data and the statistical frameworks for biodiversity and multifunctionality across scales, and experiments and empirical data at management-relevant scales (Eisenhauer et al., 2019).

1.3 | Homogenization in production forests

Forests have an intricate three-dimensional structure and thus represent very complex habitats that provide many niches, allowing coexistence of numerous species (MacArthur & MacArthur, 1961; Vierling et al., 2008). This complexity scales from the tree level (Müller et al., 2014), over patches of successional stages (Heidrich et al., 2020; Hilmers et al., 2018), to landscapes containing a mosaic of different succession stages. A second axis of complexity is based on the amount and diversity of deadwood (Seibold, Bässler, et al., 2015). Forest management has shaped these structural components. A focus on timber production has shaped both α-diversity and β-diversity of forests for centuries (Aszalós et al., 2022). In the Middle Ages (500–1500 CE), multi-purpose forest management created a heterogeneous forest landscape of native tree species with coppicing, promoting early-successional stages and pastures, interspersed with veteran trees that harboured old-growth specialists (Miklín et al., 2018). In contrast, particularly in the Northern Hemisphere, modern forestry since the late 18th century, has focused increasingly on timber production (Rackham, 2008; Schelhaas et al., 2003) often at the expense of structural and biological diversity via planting even-aged conifer-dominated forests (Aszalós et al., 2022). In addition, since the early 19th century, forest management has systematically removed dying and dead trees as a precautionary measure against pest outbreaks, with the subsequent disappearance of forest specialists, including many birds, beetles, true bugs, lichens and fungi (Abrego et al., 2015; Seibold, Brandl, et al., 2015). Since the late 1950s, a shift to continuous cover forestry started in many countries in the global North (Pommerening & Murphy, 2004). This increased the vertical complexity of forests by avoiding larger gaps and promoting regeneration under the canopy of mature trees many years ahead of the final harvest. However, this created large-scale homogeneous two-layered forests with reduced horizontal complexity and biodiversity (Heidrich et al., 2020; Schall, Gossner, et al., 2018).

Two common features of natural forests are widely missing in these forests. First, early and late successional stages with their specific species compositions and microclimates are missing (De Frenne et al., 2019; Hilmers et al., 2018). Second, trees are typically harvested before their half-life, to avoid increasing damage by insects or fungi (Knoke, 2003; Larrieu et al., 2017). Consequently, resource availability is heavily reduced for many forest species, especially for species that depend on deadwood (Figure 1, Graf et al., 2022; Larrieu et al., 2017; Müller & Bütler, 2010). Experiments have shown that local diversity of deadwood is more critical for a high biodiversity than the amount, highlighting the important resource niche diversity over resource amount for deadwood-dependent species (Seibold et al., 2016). Moreover, deadwood in gaps supports a higher niche diversity via variation in microclimate compared to deadwood under a closed canopy (Lettenmaier et al., 2022). Today, production forests resemble one another structurally at the landscape scale, with little deadwood, the absence of old and very young forest stages, and low vertical complexity in middle-aged forests with few gaps. Several studies have shown that forest structural complexity affects diversity. For example, Heidrich et al. (2020) found horizontal heterogeneity in forests as most important for high diversity among different taxa and trophic levels. Similarly, Mori, Ota, et al. (2015) showed a substantial decrease in β-diversity of oribatid mites in homogeneous production forests compared to more natural forests with a higher habitat diversity.

Studies in disturbance ecology have found that the current observed increase in the severity and extent of various disturbance regimes such as drought, wildfires, windthrow and pest outbreaks in forests can be explained, not only by climate change, but also in large part by the anthropogenic homogenization of forests that has created highly susceptible forests over large areas (Biedermann et al., 2019; Seidl et al., 2014, 2016). This has refuelled interest in using forest structure as a tool for managing forest ecosystem functions and resilience. Hence, along with using the adaptive capacity of current tree species (Petrik et al., 2022) and supporting a diverse tree species composition (Messier et al., 2022), enhancing the variation in forest structure could also be a powerful and easily deployable approach to improve the resilience and multifunctionality of forests. Moreover, in the course of current natural disturbances, the previously scarce resource of deadwood is increasing in many places (Senf et al., 2019). This raises the question of how changes in structure and deadwood due to increasing disturbances along with intentional manipulations can be used to restore and support biodiversity and ecosystem functioning in homogenized production forests and to make them more resilient in a future climate. Here, we focus on management effects aiming at an increased heterogeneity on the landscape level. Heterogeneity is also driven by other factors such as forest ownerships, soil conditions and historical legacies, which also have important implications for ecosystem services (Simons et al., 2021). However, this large-scale heterogeneity is regularly not

FIGURE 1 Concept of the BETA-FOR project and the underlying hypotheses. (a) Due to management history, forest districts have been reduced in their niche space ("Before") compared to natural forests, which is re-enhanced in our experiment (ESBC-After) using an Enhancement of Structural Beta Complexity. (b) This should translate into alterations of species coexistence, with (c) different response of biodiversity and (d) functionality of ecosystems in control and manipulated forest districts (Figure 2), creating a landscape with higher spatial variation in ecosystem functions (e). H1–H7 refer to the corresponding hypotheses (see main text).
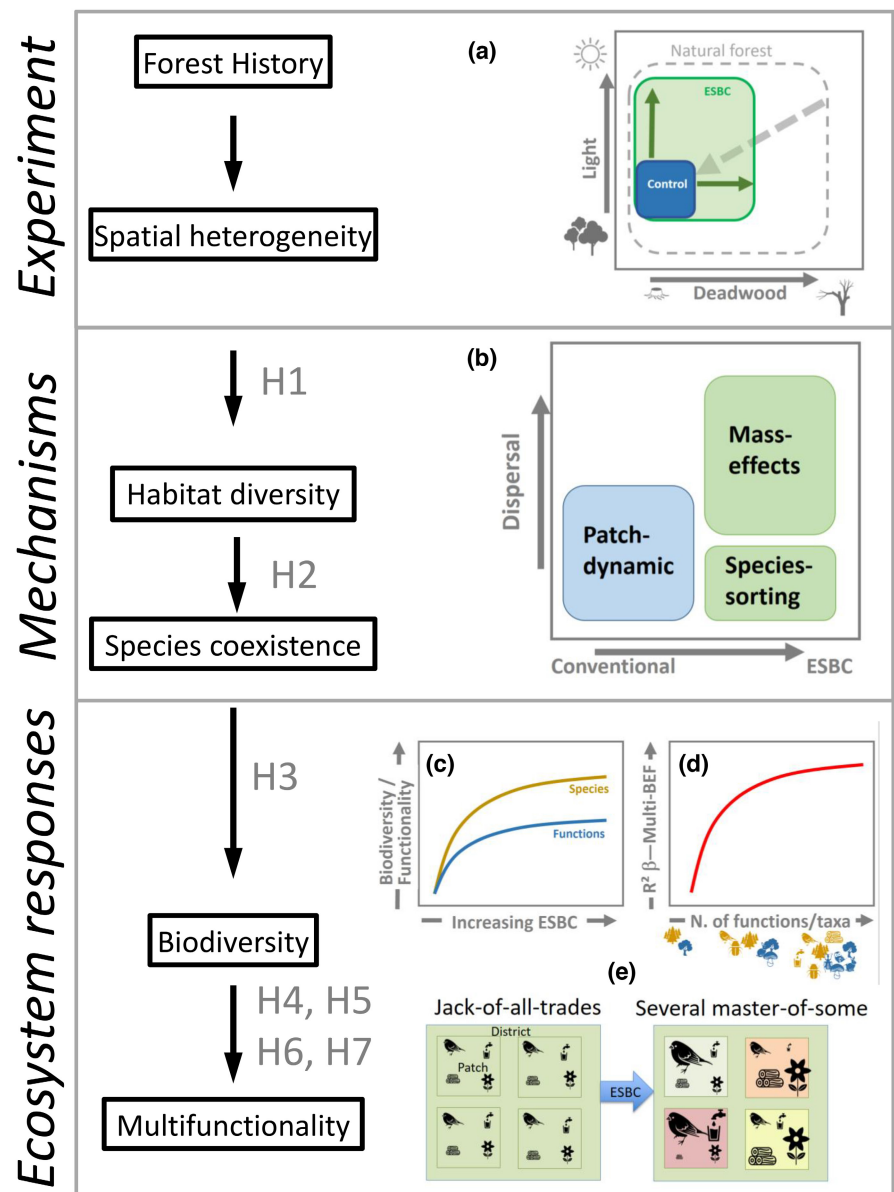
related to management decisions whose effects on heterogeneity and, consequently, on β-diversity and multifunctionality are our main research interest.

1.4 | Increasing heterogeneity in forests through novel management methods

Increasing awareness about the reduced complexity in many production forests compared to natural forests around the world has evoked a number of innovative approaches for managing forests, both for enhancing natural biodiversity and ecosystem services, and to increase resilience and adaptive capacity under global change. Most of them focus on the α-scale, but combining them offers excellent options to manipulate the β-scale. Based on the observation that even large-scale disturbances always leave parts of the forest unaffected (Donato et al., 2012), retention forestry aims to retain

groups of trees or deadwood after harvesting to maintain natural structure and function (Dörfler et al., 2018; Gustafsson et al., 2012; Lindenmayer et al., 2012; Thorn et al., 2020). Another approach is to create within-patch heterogeneity to induce premature senescence in younger forests. This can accelerate the ageing process to create a diversity of microhabitats and to support greater saproxylic species diversity (Cavalli & Mason, 2003; Sebek et al., 2013). A third option is to manage production forests for old-growth features, for example by prolonging the rotation cycle and by creating structural components that are typical for old-growth forests, such as large diameter deadwood or huge tree crowns (Bauhus et al., 2009; Larrieu et al., 2012; Moning & Müller, 2009). Here, canopy cover variation is a key factor in forming variation in habitat conditions (Entling et al., 2007; Heidrich et al., 2020; Mueller et al., 2016; Zellweger et al., 2017). Particularly for light-demanding tree species, open conditions are critical for recruitment. A number of these tree species are those expected to be suitable under warmer conditions in

the future (Messier et al., 2022). Moreover, variation in light and deadwood affects assembly processes (Bässler et al., 2016; Müller et al., 2022).

Keeton (2006) developed the concept of enhancing structural complexity (ESC) by increasing the variation in vertical and horizontal canopy density and by creating different types of deadwood within stands. In general, the ESC strategy appears promising for promoting biodiversity and presumably enhancing the diversity of ecosystem functions, but this concept lacks an explicit β-diversity component. More recently, the increase in natural disturbances in homogenized forests has also stimulated interest in alternative management systems, such as natural dynamics silviculture (Aszalós et al., 2022) that aim to emulate natural disturbance dynamics at stand- and landscape scales through silvicultural interventions. However, evidence for a causal chain from natural disturbances to BEF across scales is still limited, mainly because studies on natural disturbances often lack a properly replicated design, and simply do not often combine changes in β-diversity with variation in ecosystem functioning. So far, existing forest disturbance experiments have addressed only α-components of BEFs (e.g. Elek et al., 2018; Heikkala et al., 2016; Spence, 2001). To improve our understanding of BEF relationships at larger spatial scales, we need to complement these previous studies with new experiments manipulating spatially explicit β-components of forest biodiversity.

In summary, (i) heterogeneity of forests at the landscape scale has been reduced by modern forest management with focus on wood production, (ii) this heterogeneity is highly relevant for BEF, (iii) our understanding of how α- and β-diversity determine γ-diversity and γ-multifunctionality of temperate forests is limited, and (iv) climate change has already started to change forest heterogeneity, but the consequences for BEF at larger spatial scales remain unclear. This makes forests an ideal ecosystem for controlled BEF field experiments across scales with high management relevance (Mori et al., 2018). Which measures are taken to increase heterogeneity, and on which scale, depends on the forest habitat type.

2 | A RESEARCH AGENDA WITH APPLIED RELEVANCE

We made use of the fact that management-driven manipulations can easily be implemented in production forests of the temperate zone. We demonstrate how to use them in setting up a design suitable for BEF research under real-world conditions at a management-relevant scale. We expect that the results of such an experiment will be of high value for developing both BEF theory beyond the α-level and for adjusting forest management practices towards preserving biodiversity and various ecosystem functions. To address the above-mentioned research frontiers, we established the BETA-FOR project, an experiment in historically homogenized production forests (Figure 1a). We manipulated the within-patch (50×50m) heterogeneity using independent manipulations of deadwood amount and light conditions by gap felling (Figure 1a). We thus increased the

heterogeneity between patches in each of 11 treatment districts, each composed of a forest with similar history and species composition and of a similar size (about 10–20ha). According to metacommunity theory, the increase in heterogeneity in treatment districts should shift the mechanisms of community assembly from local patch dynamics to mass effects and species sorting modulated by dispersal rates of different groups (Logue et al., 2011). We expect that these manipulations will affect the mechanisms of community assembly and species coexistence, as well as forest multidiversity (taxonomic, phylogenetic and functional) and multifunctionality at the district level during the time span of a decade representing the typical window of silvicultural interventions in temperate forests. To study our main research question 'Does silvicultural Enhancement of Structural Beta Complexity (ESBC, see below) between forest patches increase biodiversity (taxonomic, phylogenetic and functional) and multifunctionality in forest landscapes and what are the main mechanisms driving this change?' we will test seven main hypotheses:

> **Hypothesis 1.** Increases in deadwood and light in ESC (Figure 1a) will lead to increased habitat diversity and biodiversity at the local scale (α-diversity) because of increases in habitat heterogeneity.

> **Hypothesis 2.** Compared to homogeneous Control districts, ESBC will shift assembly mechanisms of the meta-community in the landscape from patch dynamics to species sorting and mass effects, modulated by dispersal rates due to increased heterogeneity (Figure 1b).

> **Hypothesis 3.** ESBC increases β-diversity compared to conventionally managed forests because it increases structural heterogeneity (Figure 1).

> **Hypothesis 4.** With increasing patch heterogeneity, both biodiversity and ecosystem functionality increase, but biodiversity increases faster than ecosystem functionality because of partial functional redundancy of species (Figure 1c).

> **Hypothesis 5.** The increasing biodiversity in ESBC affects multifunctionality due to direct effects on trophic levels, and via propagating across the food web (Figure 3).

> **Hypothesis 6.** The strength (i.e. standardized slope) of the relationship between β-diversity and β-multifunctionality increases as a direct function of the number of taxa and ecosystem functions included (Figure 1d).

> **Hypothesis 7.** ESBC shifts a forest landscape from providing a few functions everywhere to a more heterogeneous landscape where many functions are provided because of the presence of diverse patches and the interactions that occur among them (Figure 1e).

FIGURE 2 Study design of the BETA-FOR experiment consisting of forest districts with a size of 10–20 ha: (a) In the districts with treatment, we manipulate the local structural complexity by variation in light and deadwood (enhancing structural complexity), thereby Enhancing the Structural Beta Complexity (ESBC). (b) Treatments are distributed within the landscape via two different districts (control and ESBC). (c) District pairs (control and ESBC) form one site and are replicated 11 times throughout Germany.
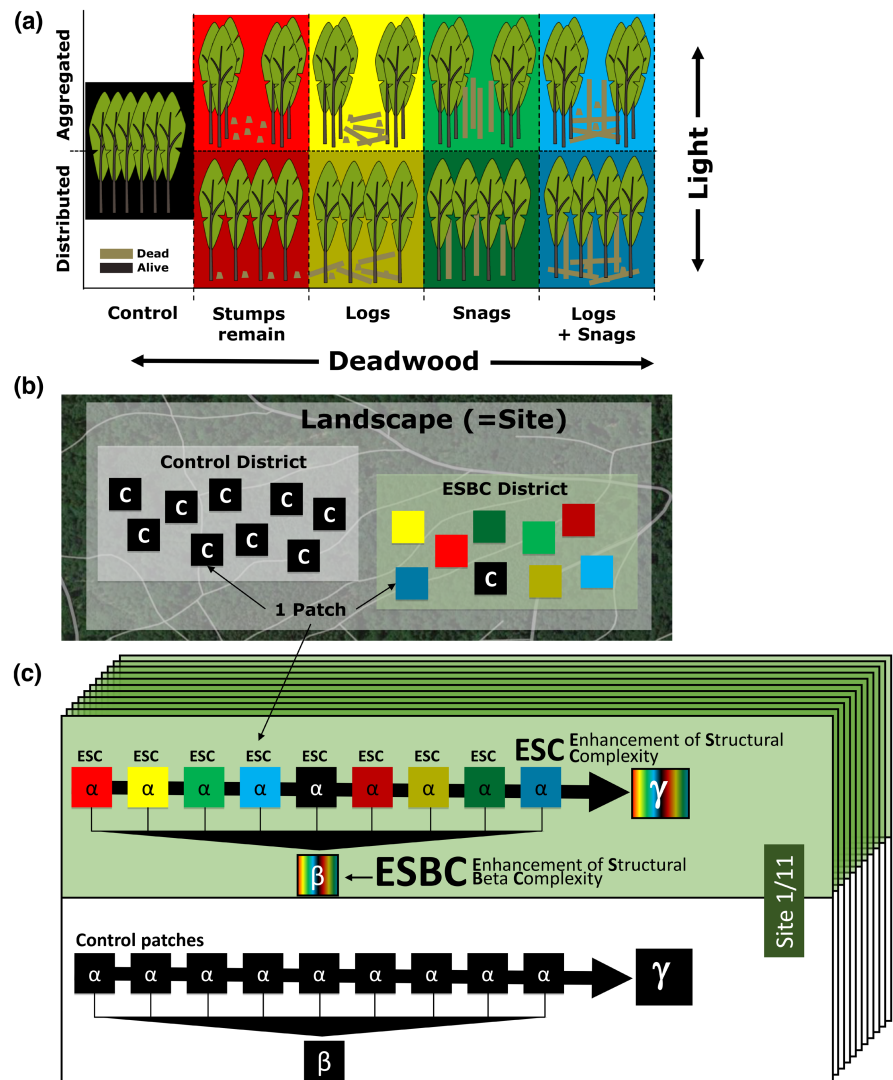
To test these hypotheses, we established 11 pairs of forest districts at 11 sites in Germany, with each district consisting of nine different patches (Figure 2). Within each pair of forest districts, one district was subjected to silvicultural interventions to manipulate the variation in canopy cover and deadwood features across patches, thereby mimicking the variation of successional stages in a natural forest. By killing ~30% of trees within the $50 \times 50\,m^2$ manipulation patches, leaving snags, logs, stumps or combinations in either aggregated or distributed spatial distribution, we aimed to increase within-district heterogeneity (Figure 2) and thus presumably biodiversity across trophic levels (Figure 3). The second district is a control stand. This is a comparable forest stand that undergoes uniform thinning approximately every 10 years, as is typical for production forests of this age. A comparable proportion of trees (~30%) as in the treatment stand is removed in the form of thinning. However, no deadwood from harvest residues remains on the site and no sustained openings in the canopy are produced. This design offers realistic comparisons between current production forests and ones designed to support wood production as well as biodiversity and ecosystem function. Furthermore, it allows controlling for effects of

the context. Results in BEF studies have been shown to be context dependent. With our experimental sites, we cover a broad range of the climatic conditions of temperate broadleaf forests in Europe.

We will use various sampling techniques to collect data on forest structure including conventional field measurements of trees and deadwood, terrestrial laser scanning, and airborne remote sensing techniques using drones and satellites with information on airborne lidar, radar and optical data. Biodiversity data of various taxa will be collected belowground and aboveground, and in the canopy (Figure 3). Taxa are selected across kingdoms and trophic levels, as suggested for multitrophic studies (Seibold et al., 2018). These taxa have different mobility, ecological constraints, and body size and act at different scales ranging from micrometres to hectares, providing opportunities for analyses incorporating different dispersal rates and abilities. Similarly, to cover the major ecosystem functions in temperate forests (Schuldt et al., 2018), we will assess key processes, capturing those related to carbon (soil respiration, different aspects of productivity, carbon sequestration in soil and biomass) and nutrient cycling (microbial processes, organic matter decomposition), as well as to micro-climate regulation. Furthermore, biotic
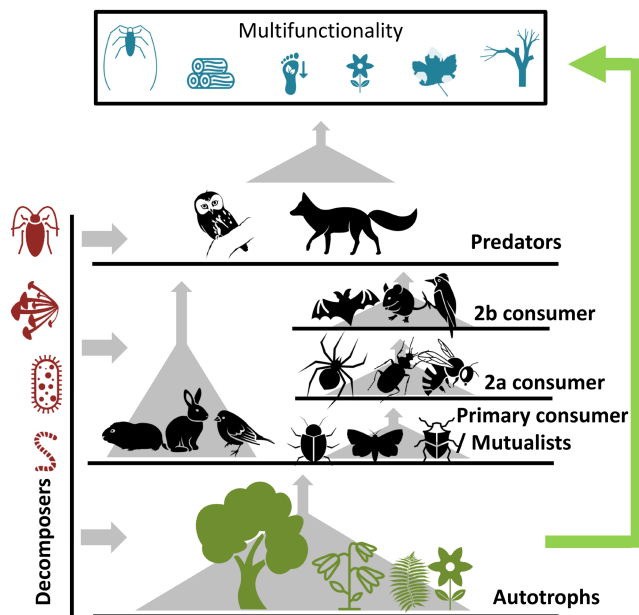
FIGURE 3 Representation of different trophic levels among the 18 taxonomic groups sampled in all patches. Grey arrows show propagating biodiversity effects through the trophic levels (H7). The green arrow is an example of direct effects of a taxonomic group of a trophic level on multifunctionality.

processes will be quantified, including tree regeneration and mortality, pollination, seed dispersal, resistance to herbivory, predation and parasitism (Schuldt et al., 2018). Several of these processes directly or indirectly underpin important ecosystem services, such as timber production or climate regulation. This comprehensive assessment of biodiversity and ecosystem functions will be important to assess how different organisms respond and interact and how this affects ecosystem functions at different scales. In addition, it makes it possible to assess whether biodiversity affects ecosystem functions directly or via the propagation of biodiversity effects through higher trophic levels. (Figure 3).

3 | A BRIEF DESCRIPTION OF THE PROPOSED ANALYSIS FRAMEWORK

In BEF studies, species richness is the most frequently used biodiversity measure. However, richness only uses information on species presence/absence and disregards species abundance/evenness. To incorporate species abundance/evenness into biodiversity measures, a consensus among ecologists in biodiversity research has emerged that Hill (1973) numbers (effective number of species) should be used to quantify species or taxonomic diversity (TD; see Ecology forum Ellison, 2010 and subsequent papers).

Hill numbers, parameterized by a diversity order $q \geq 0$, represent a continuum of TD measures which include the three most widely used species diversity measures: (i) the Hill number of order $q = 0$ reduces to species richness that treats species equally and thus is sensitive to individuals of rare species; (ii) the Hill number of

order $q = 1$ reduces to the exponential of Shannon diversity, which treats individuals of each species equally and thus is sensitive to abundant/common species; and (iii) the Hill number of order $q = 2$ reduces to the inverse of the Simpson concentration index and is sensitive to very abundant or dominant species. Therefore, the role of rare, common and dominant species can be assessed using this framework. For example, Wang and Loreau (2016) applied the Hill number of $q = 2$ to assess the relationship between diversity and temporal variability across scales. By being able to continuously shift the focus from rare species to dominant species, Hill numbers are particularly attractive for BEF studies, where relationships between diversity and functions can be based on rare or dominant species, or both. Their application in our approach will be a novel contribution to BEF research.

One advantage of using Hill numbers is that the framework provides a unified approach to include species differences with respect to species' evolutionary history (i.e. phylogenetic diversity [PD]) or species traits (functional diversity [FD]; see Chao & Colwell, 2022 for a review). TD quantifies the effective number of equally abundant species, PD quantifies the effective number of equally divergent lineages, and FD quantifies the effective number of equally distinct virtual functional groups. Thus, the framework permits the use of the same units for TD, PD and FD and can be implemented to disentangle biodiversity changes across the three dimensions of diversity in the BEF relationship, which is also novel for BEF studies.

Biodiversity is inherently a hierarchical concept covering different structural, ecological integration levels ranging from genes to ecosystems (Gaggiotti et al., 2018). In our hierarchical framework, there are 11 sites (landscapes). Within each site, there are two districts (Control and ESBC); in each district, there are nine patches (Figure 2). α-, β- and γ-biodiversity can be defined 'relatively' at each level. There have been many definitions, concepts and measures of β-diversity. Chao and Chiu (2016) bridged two major approaches (the variance framework and diversity decomposition) by showing that the two approaches lead to the same Jaccard- and Sørensen-type (dis)similarity measures. Thus, in our analysis, we will focus on the multiplicative decomposition, that is, we apply Whittaker's (1960, 1972) original multiplicative definition of β-diversity but use Hill numbers for any diversity order $q \geq 0$.

We are predominantly interested in assessing the extent of differentiation between patches in a specific district. Thus, α-diversity refers to within-patch diversity, which can be interpreted as the average effective number of species per patch. γ-diversity refers to the diversity of a district (consisting of nine patches) and can be interpreted as the effective number of species in a district. β-diversity is defined as γ-diversity divided by α-diversity, and measures the degree of species compositional differentiation among patches. β-diversity attains a minimum value of 1, if all nine patches are identical in terms of species identity and abundance, and it attains a maximum value of 9, when no species are shared among communities. Thus, β-diversity is expressed in units of 'patch equivalents' or effective number of patches; it can be further transformed to Jaccard- and Sørensen-type (dis)similarity measures in a fixed range

of [0, 1]. Similar interpretation and transformations can be extended to PD and FD in a parallel way.

In many BEF analyses, biodiversity, in most cases the number of species, was experimentally manipulated, for example, by sowing or planting different numbers of plant species (Paquette et al., 2018; Weisser et al., 2017), thus obviating issues of undersampling and statistical estimation of biodiversity. As such, most BEF analyses are conducted conditional on species richness and assume that there are no undetected species/diversity. Although this precondition simplifies the quantification of diversity and its change, the resulting BEF relationship should not be used for inference or prediction in real-world systems due to the lack of adequate statistical models and proper estimates of sampling errors/uncertainties. The assumption of diversity being known and predetermined might be true only in fully controlled manipulative experiments generally restricted to plants with sessile life cycles. In most empirical studies, particularly including higher trophic levels and mobile organisms, this assumption is violated regularly. For our real-world and multi-trophic BEF framework, we therefore aim to use statistical sampling models and assess sampling errors/uncertainties of variables subsequently fed into inferential models revealing causal relationships.

Estimates of diversity, including species richness at any hierarchical level or scale, depends on an adequate sampling/effort. To control for sampling effects, we can statistically quantify sampling completeness and propose standardization techniques (rarefaction/extrapolation) for α-, β- and γ-diversity with confidence intervals (Chao & Jost, 2012). In addition, if data are sufficient, undetected species/diversity in samples can be inferred. The methods tackling the problem of unseen species can also be applied to multivariate analyses with community matrices (Gotelli & Chao, 2013) and tests of meta-community paradigms in empirical approaches (Logue et al., 2011). Rigorously incorporating sampling models in multi-trophic BEF studies and combining them with pertinent generalized linear mixed models to assess the effect of potential covariates or environmental variables, also in confirmatory path analyses to test for indirect effects across trophic levels, is a novel aspect in our approach.

For the analysis of multifunctionality, a number of methods have been proposed (see Byrnes et al., 2014; Meyer et al., 2018). However, we plan to expand the Hill numbers in a way that multifunctionality can be quantified conceptually in the same way as biodiversity described above. This incorporation of Hill numbers in multifunctionality will then allow us to decompose γ-multifuntionality into α- and β-components, allowing the development of a consistent framework for use in BEF research in real world landscapes across scales.

4 | CONCLUSION

In times of global change with increasing disturbances and decreasing global biodiversity, it is crucial to test real-world applications of BEF theory across different biomes and realms to increase the effectiveness of management strategies with the aim to halt biodiversity loss and to increase ecosystem resilience. At the α-scale, it has been shown that results of BEF experiments are realistic (Duffy et al., 2017; Jochum et al., 2020) and that the underlying theory is applicable (e.g. Civitello et al., 2015; Eisenhauer et al., 2016). However, for β-diversity, we need new approaches to move from modelling and virtual landscapes to working with real-world conditions. This is an important research frontier because β-diversity may be particularly sensitive to global environmental change (Dornelas et al., 2014) as well as a key determinant for the functioning and stability of ecosystems (Catano et al., 2020; Grman et al., 2018; Hammill et al., 2018; Hautier et al., 2018, 2020; Loreau et al., 2021; Wang et al., 2021). We consider our concept to be highly innovative, both from the analytical perspective and the experimental approach. Our experiment, with replicated manipulations at landscape scales with high management relevance, and including control landscapes, is currently unique for temperate forests. In addition, the consideration of all trophic levels and a broad set of ecosystem functions make our approach novel. Our statistical framework will unify different aspects of biodiversity along Hill numbers when decomposing γ into α and β and will take into account unobserved species. This will provide an important step forward in BEF studies conducted under real-world conditions. Expanding the Hill numbers to multifunctionality will also allow us to present a new unifying BEF analysis framework based on the same mathematical principles for biodiversity and multifunctionality.

Despite the intense social debate and huge monetary investment to improve land-use strategies throughout Europe, particularly in agriculture and forestry, approaches focused on these ecosystems lack similar concepts and experimental approaches (e.g. European Green Deal, EU Biodiversity Strategy for 2030). Our approach may serve as a blueprint for introducing environmental heterogeneity in BEF research with applications to foster biodiversity and ecosystem multifunctionality across spatial scales in various environments, and to guide sustainable land use under changing environmental conditions.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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