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METHOD

Hill–Chao numbers allow decomposing gamma multifunctionality into alpha and beta components

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Abstract

Biodiversity–ecosystem functioning (BEF) research has provided strong evidence and mechanistic underpinnings to support positive effects of biodiversity on ecosystem functioning, from single to multiple functions. This research has provided knowledge gained mainly at the local alpha scale (i.e. within ecosystems), but the increasing homogenization of landscapes in the Anthropocene has raised the potential that declining biodiversity at the beta (across ecosystems) and gamma scales is likely to also impact ecosystem functioning. Drawing on biodiversity theory, we propose a new statistical framework based on Hill–Chao numbers. The framework allows decomposition of multifunctionality at gamma scales into alpha and beta components, a critical but hitherto missing tool in BEF research; it also allows weighting of individual ecosystem functions. Through the proposed decomposition, new BEF results for beta and gamma scales are discovered. Our novel approach is applicable across ecosystems and connects local- and landscape-scale BEF assessments from experiments to natural settings.

KEYWORDS

alpha multifunctionality, beta multifunctionality, BETA-FOR project, diversity decomposition, ecosystem functions, gamma multifunctionality, Hill numbers, species diversity

INTRODUCTION

Biodiversity–ecosystem functioning (BEF) research has provided strong evidence and mechanistic underpinnings to support positive effects of biodiversity on both single-ecosystem functions and multifunctionality (Gamfeldt et al., 2008; Hautier et al., 2020; Hector & Bagchi, 2007; Lefcheck et al., 2015; Meyer et al., 2018). Multifunctionality refers to the extent to which multiple-ecosystem functions are provided simultaneously (Byrnes et al., 2014; Manning et al., 2018). However, most of the reported positive BEF

relationships are the results of research at the alpha or within-ecosystem scale (Müller et al., 2023). Such a narrow focus ignores the effects of landscape homogenization in the Anthropocene due to increasing land-use intensity and the movement of species (Blowes et al., 2019; Dornelas et al., 2014; Gossner et al., 2016; Muthukrishnan & Larkin, 2020; Olden et al., 2004). Hence, there is an increasing demand for understanding what drives multifunctionality at larger, landscape scales (Manning et al., 2018; van der Plas et al., 2016). A key question is whether multifunctionality at these scales is driven mostly by high local

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multifunctionality due to high local biodiversity or by the spatial turnover in biodiversity and ecosystem functions that are provided by different localities within a larger spatial unit (Mori et al., 2016).

Biodiversity is a hierarchical multidimensional concept, which generally aims to quantify the variety, numbers and characteristics of living organisms present in a community. Despite a wide variety of biodiversity metrics, a consensus among ecologists seems to have emerged about the use of Hill numbers (Hill, 1973) for quantifying species diversity in ecological communities (Ellison, 2010 and papers that followed it). Hill numbers integrate species richness and species relative abundance into a continuum of measures, parameterized by a diversity order $q \geq 0$, a parameter that determines the measures' sensitivity to species relative abundance. Hill numbers of orders $q=0, 1$ and 2 unify three well-established indices of biodiversity: species richness ($q=0$), Shannon diversity ($q=1$, the exponential of Shannon entropy) and Simpson diversity ($q=2$, the inverse of the Gini–Simpson concentration index). Hill numbers have also been generalized to phylogenetic diversity and functional diversity, and the generalized framework is referred to as the attribute diversity or the Hill–Chao numbers (Chao et al., 2014, 2021). Because Hill numbers and their generalization form the fundamental basis of our methodology, we briefly review Hill and Hill–Chao numbers later.

Similar to the concept of biodiversity, the concept of multifunctionality also aims to encompass something that is inherently multidimensional: the overall functioning of an ecosystem (Manning et al., 2018). Multifunctionality includes a myriad of ecological processes that characterize and sustain ecosystems. Considering these processes simultaneously and deriving rigorous measures are therefore challenging. Since the foundational paper by Hector and Bagchi (2007), a number of multifunctionality measures have been proposed, discussed and debated. Previous measures include the overlap method (Hector & Bagchi, 2007), the averaging approach (Maestre et al., 2012), multivariate modelling (Dooley et al., 2015) and the threshold method (Byrnes et al., 2014; Gamfeldt et al., 2008; Meyer et al., 2018; Mori et al., 2023). Each of these different approaches has its strengths and limitations.

Some desired properties of an 'ideal' multifunctionality measure, as also discussed in Byrnes et al. (2014, 2023), should include (i) correcting for strong correlations between ecosystem functions to avoid redundancy; (ii) a flexible approach to quantify multifunctionality of different magnitudes based on low-, moderate- and high-performing functions; and (iii) the ability to quantify multifunctionality across spatial scales. An additional criterion is to provide weightings to functions to capture their priority or monetary service valuations depending on how we look at an ecosystem from an economical, societal or ecological perspective (Allan et al., 2015; Manning et al., 2018).

In biodiversity science, partitioning gamma diversity into alpha and beta components is well established; see Whittaker (1960, 1972) for pioneering decomposition work based on species richness, and Chao, Chiu, Wu, et al. (2019) for decomposition based on Hill numbers. These partitioning approaches have revealed that changes in beta diversity represent a strong signature of the Anthropocene (Beaumelle et al., 2020; Dornelas et al., 2014; Gamfeldt et al., 2013; Gossner et al., 2016; Magurran et al., 2018; McGill et al., 2015). However, it is still poorly known whether beta diversity is also important in driving the average levels or the spatial turnover of different ecosystem functions across localities, and hence larger-scale multifunctionality (Mori et al., 2018; van der Plas et al., 2023). Measuring the effect of beta diversity on multifunctionality is therefore critical for a more comprehensive understanding of the consequences of biodiversity change on ecosystem functioning (Eisenhauer et al., 2019; Gonzalez et al., 2020; Mori et al., 2018; Müller et al., 2023; van der Plas et al., 2016, 2019). A major reason why multifunctionality research has not been extended beyond the local scale is the lack of a statistical framework to decompose gamma multifunctionality into alpha and beta components (Mori et al., 2018).

Recently, Byrnes et al. (2023) made an important advance by introducing Hill numbers (Hill, 1973) to quantify multifunctionality, and to develop a class of multifunctionality measures that account for non-independence between functions using the method derived by Chao, Chiu, Villéger, et al. (2019). Byrnes et al. (2023) also suggested that decomposition and turnover in multifunctionality across space and time would be a worthwhile extension. In this paper, we show that a novel modification of their framework is needed to decompose multifunctionality across scales; see later text for more details.

Drawing upon well-established approaches commonly employed in biodiversity research, we propose a general framework to quantify multifunctionality in such a way that all the above criteria are met, using a generalization of Hill numbers (Chao, Chiu, Villéger, et al., 2019; Hill, 1973). We first modify the approach of Byrnes et al. (2023) and consider function weights based on Hill–Chao numbers. For a single ecosystem, we propose a class of weighted multifunctionality measures for given function weights. Then, a class of measures that adjusts for correlations between functions is presented. One advantage of using Hill–Chao numbers instead of the original Hill numbers is that we can draw on biodiversity decomposition theory to obtain a meaningful decomposition of our proposed multifunctionality measure. Specifically, multifunctionality at larger spatial gamma scales can be decomposed into a within-ecosystem alpha component and an across-ecosystem beta component, and the correlations between functions can also be corrected for. Our suggested multifunctionality measure and decomposition approach are

applied to published data on tree species diversity and ecosystem functions collected in six European countries (Baeten et al., 2013). An R package ‘MF.beta4’ and online software are available to facilitate all computations and graphics (see Data Availability Statement).

A BRIEF REVIEW

Hill numbers (species diversity)

In the context of community ecology, assume that there are S species in a community, indexed by $i=1, 2, \dots, S$. Let z_i represent the raw abundance (number of individuals) of species i , or other metrics of species' dominance, such as biomass, coverage of corals or basal area of plants. The total abundance in the community is expressed as $z_+ = \sum_{i=1}^S z_i$. Here, $p_i = z_i/z_+$ denotes the relative abundance of the individuals of species i in the community, $\sum_{i=1}^S p_i = 1$.

Hill number or taxonomic diversity (TD) of order q is defined as the following function in terms of species richness and species relative abundances:

$${}^qTD = \left(\sum_{i=1}^S \left(\frac{z_i}{z_+} \right)^q \right)^{1/(1-q)} = \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)}, \quad q \geq 0, q \neq 1; \quad (1a)$$

$${}^1TD = \lim_{q \rightarrow 1} {}^qTD = \exp \left(- \sum_{i=1}^S \frac{z_i}{z_+} \log \frac{z_i}{z_+} \right), \quad q = 1, \quad (1b)$$

which is interpreted as the effective number of species. The parameter q (diversity order) determines the *sensitivity* of the measure to the relative abundance of species. As indicated in the introduction, the concept unifies different approaches, with Hill numbers of order $q=0, 1$ and 2 representing three well-established indices of biodiversity: (i) TD of $q=0$ reduces to species richness, which is sensitive to rare species; (ii) TD of $q=1$ reduces to Shannon diversity, which can be interpreted as the effective number of common or abundant species; and (iii) TD of $q=2$ reduces to Simpson diversity, which can be interpreted as the effective number of dominant or highly abundant species. By adjusting the diversity order q , we can shift the focus from rare species to dominant species and assess their respective impact on diversity changes.

Hill–Chao numbers (attribute diversity)

Chao et al. (2021) integrated the three dimensions of biodiversity: taxonomic diversity (TD), phylogenetic diversity (PD) and functional diversity (FD) into a unifying framework called attribute diversity or Hill–Chao

numbers. A *taxonomic attribute* means a species in TD, a *phylogenetic attribute* means a unit-length branch segment in a phylogenetic tree in PD and a *functional attribute* means a functional group in FD. In the unified framework, all measures can be formulated as Hill numbers of a *hypothetical* community which is decomposed into M subsets: the i -th subset consists of v_i attributes, and all attributes within the i -th subset have the same abundance a_i , $i=1, 2, \dots, M$. The total abundance among all attributes is denoted as $V = \sum_{i=1}^M v_i a_i$. Thus, the relative abundance of any attribute in the i -th subset is a_i/V . The *attribute diversity* (AD) or *Hill–Chao numbers* of order q is defined as the Hill number of order q for the hypothetical community:

$${}^qAD = \left(\sum_{i=1}^M v_i \left(\frac{a_i}{\sum_{j=1}^M v_j a_j} \right)^q \right)^{1/(1-q)} \quad (2a)$$

$$= \left(\sum_{i=1}^M v_i \left(\frac{a_i}{V} \right)^q \right)^{1/(1-q)}, \quad q \geq 0, q \neq 1;$$

$${}^1AD = \lim_{q \rightarrow 1} {}^qAD = \exp \left(- \sum_{i=1}^M v_i \frac{a_i}{V} \log \frac{a_i}{V} \right), \quad q = 1. \quad (2b)$$

For $q=0$, we have ${}^0AD = \sum_{i=1}^M v_i$, which represents the total number of attributes (i.e. attribute richness). For $q=1$ and $q=2$, AD can be interpreted as the effective number of abundant and dominant attributes respectively. See tab. 1 of Chao et al. (2021) for the formulas of TD, PD and FD and their corresponding values of M , v_i and abundance a_i ; $i=1, 2, \dots, M$, as special cases of Hill–Chao numbers.

The definition of ‘attribute’ in the formulation of Hill–Chao numbers in Equations (2a) and (2b) is generic and depends on the research questions and goals. For example, in the special case of TD, the research focus is to quantify richness/diversity of species; each species is then defined as a taxonomic attribute. Consider a hypothetical community in which there are S subsets and each subset consists of only one species. That is, letting $M=S$, $v_i=1$ and $a_i = z_i$ (raw abundance of species i) for $i=1, 2, \dots, S$, we have total abundance $V=z_+$ and $a_i/V = p_i$ (relative abundance of species i). Then, Equations (2a) and (2b) reduce to the ordinary Hill numbers in Equations (1a) and (1b). Similarly, an ‘attribute’ can also be a unit-length branch segment (for PD) to assess richness/diversity of lineages, or a functional group (for FD) to assess richness/diversity of functional groups. Here, we propose a novel extension by treating an ecosystem function as a multifunctionality attribute, so that biodiversity quantification can be applied to measure multifunctionality, as detailed in the next section. Under the mathematical frameworks of Hill numbers and Hill–Chao numbers, quantification of the diversity of species

(for TD), lineages (for PD), functional groups (for FD) and ecosystem functions are conceptually similar (Figure 1).

MULTIFUNCTIONALITY MEASURES IN A SINGLE ECOSYSTEM

Weighted multifunctionality measures (uncorrected for correlations)

Assume that there are L functions in an ecosystem and let f_i be the performance level of function i , $i=1, 2, \dots, L$. Here, f_i is a normalized function between 0 and 1. For positive functionality (i.e. high function value is desirable, such as productivity or carbon sequestration), ecosystems with the highest raw value in the data are transformed to the maximal value of 1, and those with the lowest raw value are transformed to the minimum value of 0; for negative functionality (i.e. low function value is desirable, such as nitrate leaching, herbivore damage or

greenhouse gas emission), the normalization is reversed. As indicated in the introduction, we can assign a weight w_i to function i , $i=1, 2, \dots, L$, to take into account the fact that there might be reasons for different functions to be assigned different importance values to align with policy priorities or economic valuation. Let a ‘multifunctionality attribute’ be an ecosystem function in the framework of Hill–Chao numbers in Equations (2a) and (2b). Consider a *hypothetical* ecosystem that is decomposed into L subsets: the i -th subset consists of $v_i = w_i f_i$ attributes (ecosystem functions), and the performance levels (analogous to abundance) for all attributes within the i -th subset are the same with level f_i , $i=1, 2, \dots, L$. That is, letting $M=L$, $v_i = w_i f_i$ and $a_i = f_i$ in Equations (2a) and (2b), we obtain the following proposed weighted multifunctionality measure (MF measure of order q):

$${}^q MF = \left(\sum_{i=1}^L w_i f_i \left(\frac{f_i}{\sum_{j=1}^L w_j f_j^2} \right)^q \right)^{\frac{1}{1-q}}, \quad q \geq 0, q \neq 1; \quad (3a)$$

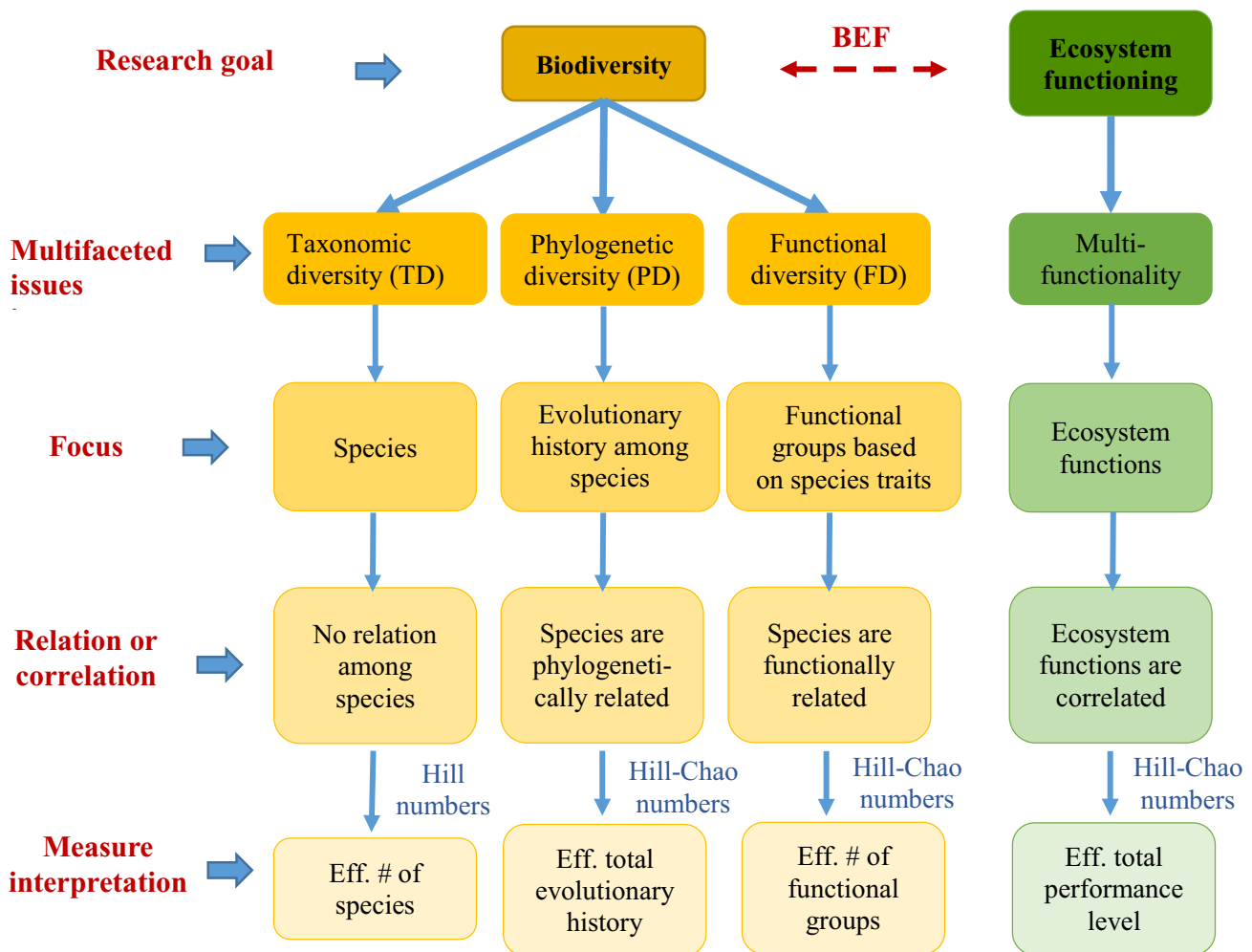


FIGURE 1 A schematic figure showing conceptual similarity between biodiversity research and ecosystem functioning research. In both research fields, the mathematical frameworks of Hill numbers and their generalization (Hill–Chao numbers) can be used to measure diversity and multifunctionality.

$${}^1MF = \exp\left(-\sum_{i=1}^L w_i f_i \frac{f_i}{\sum_{j=1}^L w_j f_j^2} \log \frac{f_i}{\sum_{j=1}^L w_j f_j^2}\right), \quad q=1. \quad (3b)$$

The measure qMF of order $q \geq 0$ quantifies the effective weighted sum of the (normalized) performance levels, where all functions perform at the same level. For the special case of $q=0$, the measure reduces to ${}^0MF = \sum_{i=1}^L w_i f_i$, which is the actual weighted sum of the (normalized) levels in the data. The measure qMF of $q=1$ can be interpreted as the effective weighted sum of levels based on moderate-performing functions; the measure qMF of $q=2$ can be interpreted as the effective weighted sum of levels based on high-performing functions.

Note that if all functions perform at the same level f , then ${}^qMF = f \sum_{i=1}^L w_i$ for all $q \geq 0$. Thus, if for an actual ecosystem, we obtain a numerical value ${}^qMF = x$, then the measure qMF of order q in the actual ecosystem is the same as a simple reference ecosystem with all L functions performing at the same level at $x / \sum_{i=1}^L w_i$. See Appendix S1 for a simple numerical example to illustrate the meaning of *effective* weighted sum of function levels. Because the measure qMF of all orders $q \geq 0$ are in the same units, we can depict a *multifunctionality profile* by plotting qMF as a continuous function of the parameter q . This profile conveys all the information in the function performance levels and thus completely characterizes multifunctionality in an ecosystem. The interpretation of the profile via numerical examples is provided in Appendix S1.

The unweighted case corresponds to the special case that all weights are the same. For example, (i) if all weights are the same with $w_i=1$, then ${}^0MF = \sum_{i=1}^L f_i$, which is the sum of all function levels. (ii) If all weights are $w_i = 1/L$, then ${}^0MF = (1/L) \sum_{i=1}^L f_i$, which is the simple average of all function levels. The latter has been used in the literature as the averaging method (Maestre et al., 2012).

Our proposed multifunctionality measure (in Equation 3a) and Byrnes et al.'s (2023) measure are both based on the framework of Hill numbers. Nevertheless, there exists a theoretical difference between the two approaches. In biodiversity research, an important weak-monotonicity property for Hill numbers is that adding a very rare species to a community should increase Hill numbers of order $q > 0$. The corresponding property in multifunctionality is that adding an additional very low-performing function should increase the multifunctionality value. In Appendix S1, we prove that our measure does satisfy this weak monotonicity, whereas Byrnes et al.'s measure does not. For example, suppose we have four uncorrelated functions with performance levels (0.3, 0.5, 0.1 and 0.2) and all weights=1; by adding one additional low-performing function (say, 0.01), we then have five functions with levels (0.3, 0.5,

0.1, 0.2 and 0.01). For $q=1$, Byrnes et al.'s measure *decreases* from 0.951 (for four functions) to 0.799 (for five functions). Our measure increases from 1.0047 to 1.0059, signifying that the sum of performance levels slightly increases due to adding an additional function. For $q=2$, our measure increases from 0.9447 to 0.9452, whereas Byrnes et al.'s measure *decreases* from 0.853 to 0.701; see Appendix S1 for details.

Multifunctionality measures (corrected for correlations)

Byrnes et al. (2023) applied Chao, Chiu, Villéger, et al.'s (2019) method to propose a multifunctionality measure, which takes the non-independence of correlated functions into account. When two functions are correlated, they become 'redundant' in the sense that one can predict a function from the other one to some extent. To correct for redundancy, we also follow Chao, Chiu, Villéger, et al. (2019) to group functions into virtual 'clusters' (as independent functions) and then quantify multifunctionality based on the resulting clusters. Let the correlation between functions i and j be r_{ij} . We first transform r_{ij} to a distance d_{ij} in the interval $[0, 1]$. The choice of this transformation depends on contexts and objectives.

We adopt a simple transformation: $d_{ij} = \sqrt{1 - |r_{ij}|}$; see later text for a justification for our choice. The intuitive concept of Chao, Chiu, Villéger, et al. (2019) is the following: imagine that ecosystem functions are placed in a space with specified pairwise distances and are grouped into virtual clusters. As in most clustering algorithms, one must first determine a threshold level of distinctness, such that any two functions with distance greater than or equal to the specified threshold level are in different function clusters and vice versa. This approach requires a parameter τ (tau), which for the current context defines the threshold for distinctness between any two functions; τ can be chosen to be *any* positive value between 0 and 1.

Following Chao, Chiu, Villéger, et al. (2019), for any specified threshold level of distinctness τ , we define $d_{ij}(\tau) = \min(d_{ij}, \tau)$. Because of correlation between any two functions, the performance level of function i is increased from f_i to $a_i(\tau)$:

$$a_i(\tau) = f_i + \sum_{j \neq i} \left(1 - \frac{d_{ij}(\tau)}{\tau}\right) f_j = \sum_{j=1}^L \left(1 - \frac{d_{ij}(\tau)}{\tau}\right) f_j. \quad (4a)$$

The attribute contribution of function i becomes

$$v_i(\tau) = f_i \times \frac{f_i}{a_i(\tau)}. \quad (4b)$$

In Equation (2a), we let $M=L$, $v_i = w_i v_i(\tau)$ and $a_i = a_i(\tau)$ to obtain the following multifunctionality measure of order q when correlations are corrected for:

$${}^q MF^*(\tau) = \left(\sum_{i=1}^L w_i v_i(\tau) \left(\frac{a_i(\tau)}{\sum_{j=1}^L w_j v_j(\tau) a_j(\tau)} \right)^q \right)^{\frac{1}{1-q}}$$

$$= \left(\sum_{i=1}^L w_i \frac{f_i^2}{a_i(\tau)} \left(\frac{a_i(\tau)}{\sum_{j=1}^L w_j f_j^2} \right)^q \right)^{\frac{1}{1-q}}, \quad q \geq 0, q \neq 1. \quad (4c)$$

The measure ${}^q MF^*(\tau)$ quantifies the effective weighted sum of performance levels based on the resulting clusters of functions. When the threshold is set to be very low, we have $a_i(\tau) = f_i$, and each function forms a cluster; the measure ${}^q MF^*(\tau)$ reduces to Equation (3a) for any order q . In contrast, if we use a very high threshold, then nearly all functions are classified into a single cluster. Instead of using a single level of threshold, we consider all plausible thresholds in the interval $[0, 1]$ and depict the measure ${}^q MF^*(\tau)$ as a function of τ . In the analysis relying on real ecological data presented in the Application section, we compute the area under the τ -curve (AUC) in $[0, 1]$ to obtain an overall, integrated measure.

Regarding the transformation from correlation to distance for any pair of functions i and j , note that when all correlations are 0 (i.e. $r_{ij} = 0$ for all $i \neq j$), only under the condition $d_{ij} = 1$ can the formula ${}^q MF^*(\tau)$ reduce to ${}^q MF$ (for uncorrelated functions) for any specified threshold level. Thus, to ensure the coherence of the theory, a premise for a legitimate transformation between correlation and distance is that the pairwise distance for any two uncorrelated functions should attain the maximum distance of 1. Byrnes et al. (2023) transformed the correlation to a distance via $d_{ij} = (1 - r_{ij})/2$. When all functions are uncorrelated, $d_{ij} \equiv 1/2, i \neq j$; unless the threshold level is $\leq 1/2$, their formula cannot lead to the uncorrelated one.

There are many functions that satisfy the above premise. Consider an additional criterion: suppose an ecosystem function is measured in terms of a normalized value f_1 (e.g. percentage of foliage not damaged by insects or normalized volume of deadwood that was decomposed), the same function can also be measured by $1 - f_1$ (percentage of foliage damaged by insects or normalized volume of deadwood that was not decomposed). Because the correlation between f_1 and any other ecosystem function f_2 has the same magnitude of correlation (but different sign) as the correlation between $1 - f_1$ and f_2 , an additional criterion could be that a positive correlation and a negative correlation of the same magnitude lead to the same distance. We thus adopt the transformation $d_{ij} = \sqrt{1 - |r_{ij}|}$ to fulfil this additional criterion. In particular, the transformation leads to $d_{ij} = 0$ when $r_{ij} = 1$ or -1 . Under the above-specified premise, ecologists can choose any other transformation to adapt to different criteria, depending on research questions and goals. For example, if the additional criterion is to incorporate only

positive correlations and treat negative correlations as uncorrelated, then a proper transformation would be $d_{ij} = \sqrt{1 - \max(r_{ij}, 0)}$ or generally $d_{ij} = [1 - \max(r_{ij}, 0)]^k$ for any $k > 0$.

DECOMPOSITION OF MULTIFUNCTIONALITY MEASURES

In biodiversity research, two major theoretical frameworks have been proposed and applied to quantify beta diversity: variance-based frameworks (e.g. Legendre & De Cáceres, 2013) and diversity decomposition (e.g. Whittaker, 1960, 1972). Chao and Chiu (2016) bridged the two frameworks by proving that they converge to the same classes of species compositional (dis)similarity measures. Thus, without losing generality, in this study, we focus only on the diversity decomposition scheme, which multiplicatively decomposes the gamma diversity into its within-assemblage component (alpha diversity) and across-assemblage component (beta diversity), and we develop an analogous framework to partition gamma multifunctionality into alpha and beta components.

Assume that there are N ecosystems: we first extend the one-ecosystem notation to multiple ecosystems. Let f_{ik} be the performance level for function i in ecosystem k , $i = 1, 2, \dots, L, k = 1, 2, \dots, N$. Our following decomposition is based on the weighted measure ${}^q MF$ (Equation 3a). For the unweighted case, we can simply substitute $w_i = 1$ or $1/L$ in the following formulas. For the gamma scale, the performance level of function i can be measured by the average

$$\bar{f}_i = (1/N) \sum_{k=1}^N f_{ik}.$$

Based on Equation (3a), gamma multifunctionality can be expressed as:

$${}^q MF_\gamma = \left(\sum_{i=1}^L w_i \bar{f}_i \left(\frac{\bar{f}_i}{\sum_{j=1}^L w_j \bar{f}_j^2} \right)^q \right)^{\frac{1}{1-q}} \quad (5a)$$

$$= \left(\sum_{i=1}^L w_i \bar{f}_i \left(\sum_{k=1}^N \frac{1}{N} \frac{f_{ik}}{\sum_{j=1}^L w_j \bar{f}_j^2} \right)^q \right)^{\frac{1}{1-q}}, \quad q \neq 1.$$

The gamma measure quantifies the effective weighted sum of performance levels in the pooled ecosystem or meta-ecosystem (Loreau et al., 2003). The corresponding alpha multifunctionality can be expressed as (Chao, Chiu, Villéger, et al., 2019):

$${}^q MF_\alpha = \frac{1}{N} \left(\sum_{i=1}^L \sum_{k=1}^N w_i \bar{f}_i \left(\frac{f_{ik}}{\sum_{j,m} w_j \bar{f}_j \bar{f}_m} \right)^q \right)^{\frac{1}{1-q}}$$

$$= \frac{1}{N} \left(\sum_{i=1}^L \sum_{k=1}^N w_i \bar{f}_i \left(\frac{f_{ik}}{N \sum_j w_j \bar{f}_j} \right) \right)^{\frac{1}{1-q}}, \quad q \neq 1. \quad (5b)$$

See Appendix S2 for the corresponding gamma and alpha formulas of $q=1$. The alpha multifunctionality can be interpreted as the effective weighted sum of performance levels per ecosystem. Then, beta multifunctionality is defined as the following ratio of gamma and alpha:

$${}^q MF_\beta = {}^q MF_\gamma / {}^q MF_\alpha. \quad (5c)$$

In Appendix S2, we proved that for all $q \geq 0$ gamma multifunctionality is always greater than or equal to alpha multifunctionality, and the gamma measure is always less than or equal to N times alpha measure for any $q \geq 0$. That is, the beta multifunctionality ranges between 1 and N . The beta measure attains the minimum value of 1 if all N ecosystems have identical performance levels for each function; that is, effectively, there is only one ecosystem. The beta measure attains the maximum value of N when there are no shared functions among the N ecosystems; that is, effectively, all N ecosystems are needed to provide all functions that are delivered at the gamma scale. Thus, beta multifunctionality can be interpreted as the effective number of multifunctional ecosystems.

The above decomposition is readily extended to the multifunctionality measures for correlated functions (in Equation 4c). Details are given in Appendix S2, where we derived gamma, alpha and beta multifunctionality measures to correct for correlations. All interpretations and properties that hold for the uncorrelated case are also valid for the correlated case.

AN APPLICATION

We applied our proposed new multifunctionality measure and its decomposition to a study on the effects of tree species diversity on ecosystem functioning, collected as part of the FunDivEUROPE project; see Baeten et al. (2013), van der Plas et al. (2016), Ratcliffe et al. (2017) and Scherer-Lorenzen et al. (2023) for data and detailed description. In the data, a total of 209 plots (each with 30 m \times 30 m) were established in mature forests in six countries, representing six major European forest types: boreal forest (Finland); hemiboreal (Poland); temperate deciduous (Germany); mountainous deciduous (Romania); thermophilous deciduous (Italy); and Mediterranean mixed (Spain). In each country, three to five common tree species were selected for the species pool; each of the 209 plots consisted of one to five tree species. The basal area of each

tree species within each plot was used as a proxy for species abundance to compute tree species diversity of orders $q > 0$. In our hierarchical framework, there are six countries. Within each country, there are 28–43 plots (see Table S3.1, Appendix S3), where each plot is designated as an ecosystem. In our following analysis, all functions are equally weighted (with weight = 1), although our approach can be used for any weight of functions.

Local within-plot BEF relationship (Figure 2)

In each plot, a total of 26 ecosystem functions or properties were measured; see Table S3.2 of Appendix S3 for a list of the 26 functions (with brief description) and their pairwise correlations. Because the six countries represent different ecosystems, all functions were normalized to the range of [0, 1] *within* a country. Figure 2 shows the scatter plots between tree species diversity of order q and a within-plot multifunctionality measure of the same order q for $q=0, 1$ and 2 when the correlations between any two functions are not incorporated (Equations 3a and 3b) or corrected for (Equation 4c). For the latter analysis, we adopted an overall, integrated measure by considering all plausible threshold levels in [0, 1]. We could also use different q values for species diversity and multifunctionality; see Appendix S3 (Figure S3.2) for the corresponding patterns with respect to tree species richness.

For each value of q , the relationship between tree species diversity and multifunctionality was modelled using a linear mixed-effects model with random slopes and random intercepts for each country. Figure 2 reveals the overall fixed-effect slopes (bold red lines) and each country's relationships (thin lines) estimated from the same linear mixed model. All the fitted results and the associated test of significance for the overall slopes were based on the output using the function 'lmer' in the R packages 'lme4' (Bates et al., 2015) and 'lmerTest' (Kuznetsova et al., 2017).

Regardless of whether correlations between functions are incorporated or not, the measure ${}^q MF$ based on the overall fits across the 209 plots exhibits a positive relationship with diversity for each fixed value of order q . The slopes are significant for $q=1$ and 2. The magnitude of the *slope* of the fitted linear trend increases with order q , signifying that the effect of species diversity on multifunctionality is stronger for high-performing functions than for low-performing functions.

Based on Figure 2, for a local within-plot scale, our analysis confirms a positive effect of biodiversity on multifunctionality in line with many previous theoretical and empirical studies (Lefcheck et al., 2015; Meyer et al., 2018). Our current data are not sufficient to model a causal relationship between biodiversity

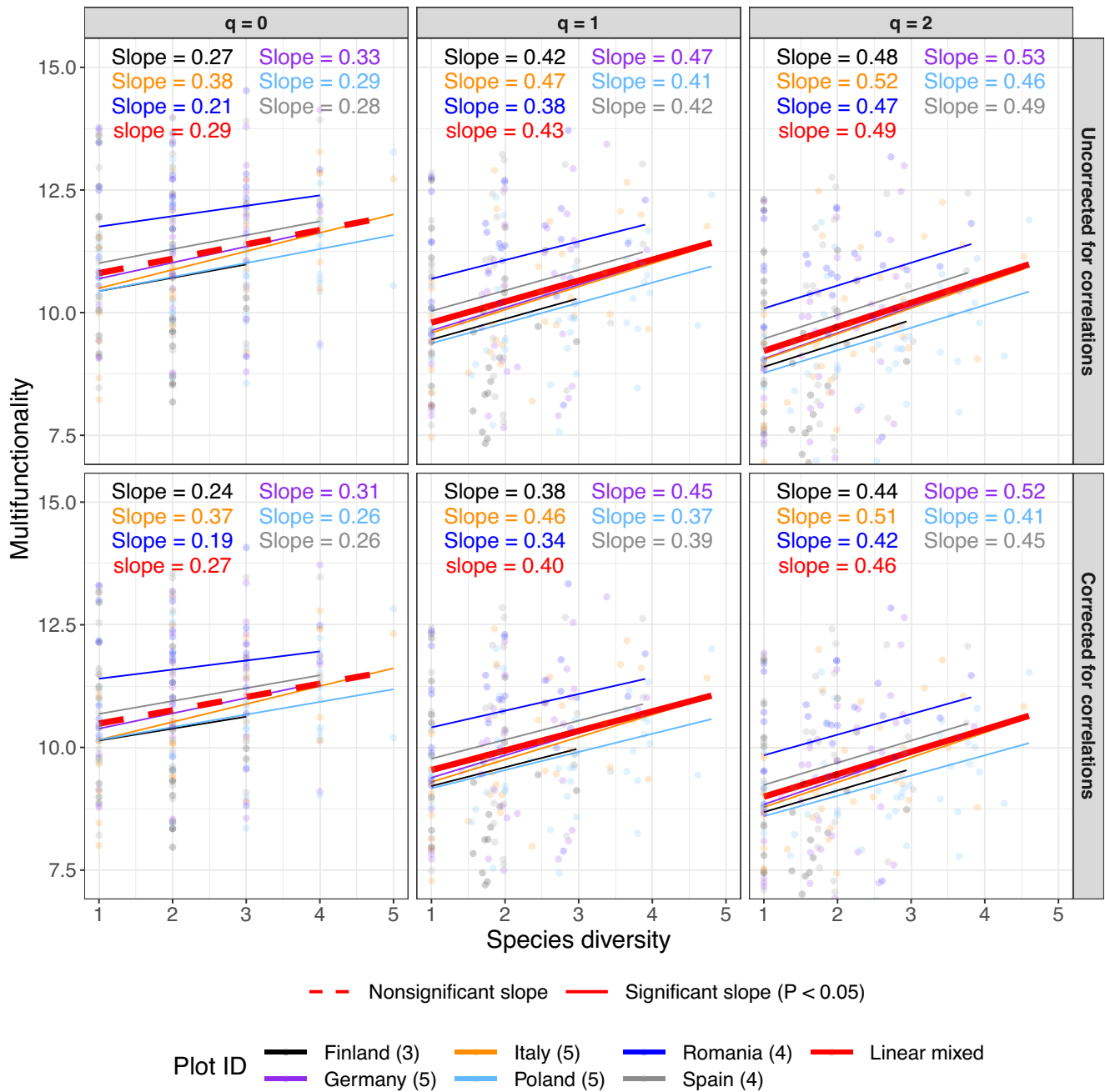


FIGURE 2 The patterns of within-plot multifunctionality measure of order $q=0$ (left panels), $q=1$ (middle panels) and $q=2$ (right panels) with respect to tree species diversity of the same order q based on 26 ecosystem functions collected in a total of 209 plots in six European countries, with species pool size in parenthesis after each country name in the legend, when all functions are assumed to be independent (upper panels, see Equations 3a and 3b), or when the correlation between any two functions is accounted for (lower panels, see Equation 4c but based on an integrated measure by considering all possible threshold levels). The relationship between tree species diversity of order q and within-plot multifunctionality values of the same order (data points in the background) was modelled using a linear mixed-effects model with random slopes and random intercepts for each country. This figure shows the overall fixed-effect slopes (bold red lines) and each country's relationships (thin lines) estimated from the same linear mixed model. A solid line in the overall fixed-effects fit is significant ($p < 5\%$) and a dashed line is not significant.

and multifunctionality (e.g. Dee et al., 2023); more data should be collected and further work on statistical modelling should be done to validate a potentially causal relationship.

When analysing the measures that account for correlations between functions, we again consistently

found positive relationships between tree species diversity and multifunctionality. As expected, due to correlation between functions, which induces redundancy among functions, the multifunctionality value (and slope with species diversity) based on our measure that accounts for correlations between functions is lower

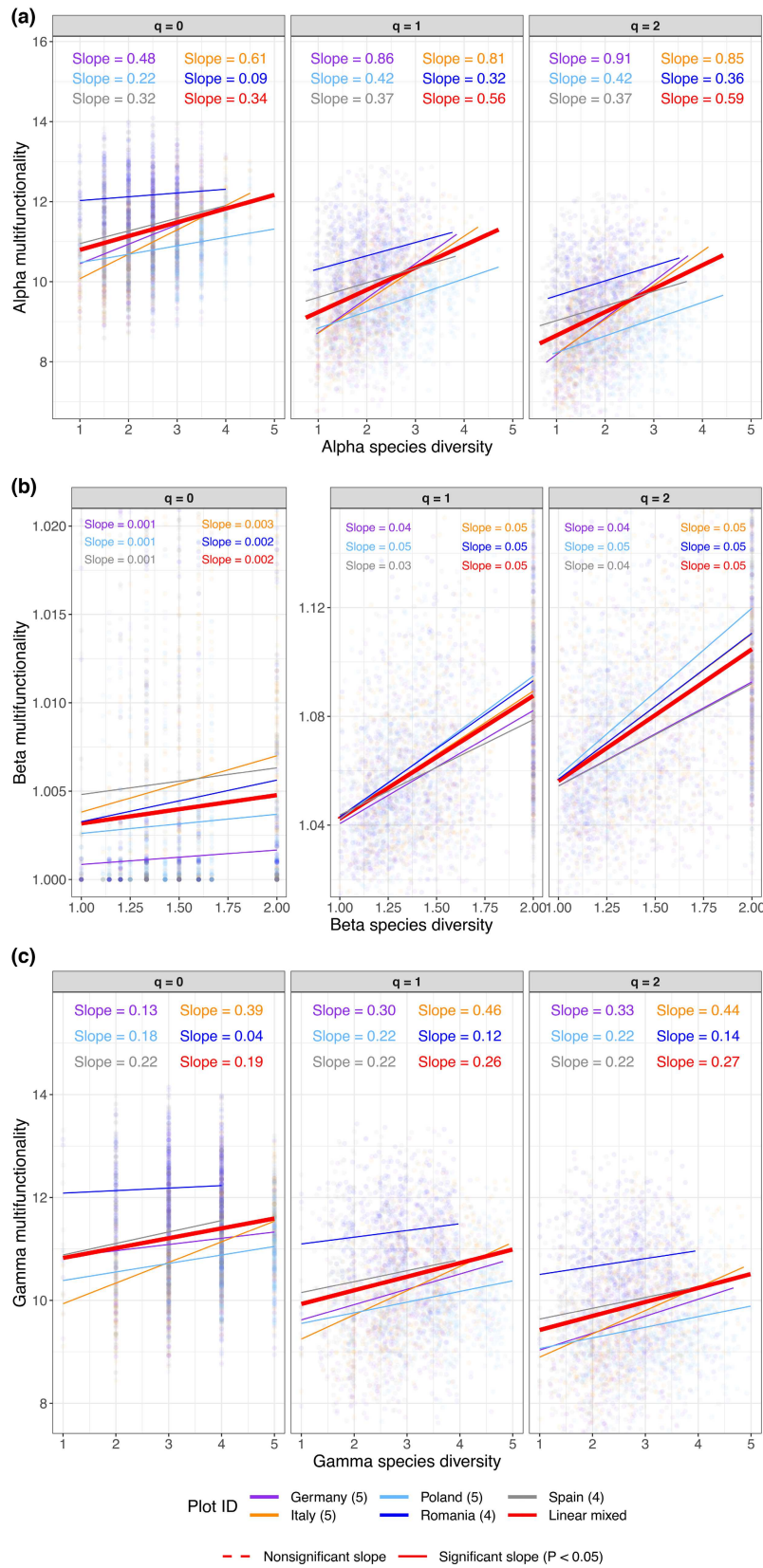


FIGURE 3 Biodiversity–multifunctionality relationships across spatial scales when the correlation between any two functions is not incorporated (see Equations 5a–5c). The patterns of (a) alpha multifunctionality versus alpha species diversity, (b) beta multifunctionality versus beta species diversity, and (c) gamma multifunctionality versus gamma species diversity, of order $q=0$ (left panels), $q=1$ (middle panels) and $q=2$ (right panels), based on any two chosen plots within each of the five European countries (Finland was not included). For each scale, the relationship between alpha/beta/gamma multifunctionality values of order q (data points in the background for all possible pairs of plots) and diversity of the same order was modelled using a linear mixed-effects model with random slopes and random intercepts for each country. This figure shows the overall fixed-effect slopes (bold red lines) and each country's relationships (thin lines) estimated from the same linear mixed model. A solid line in the overall fit is significant ($p < 5\%$) and a dashed line is not significant. All linear fits for overall fixed-effects slopes are significant.

than the corresponding value when functions are assumed to be independent. Nevertheless, the multifunctionality value and slope in the two cases (uncorrected and corrected for correlations) differ to a limited extent due to generally weak correlations among functions; see Appendix S3 for the magnitudes of all the pairwise correlations.

BEF relationships across spatial scales (Figures 3 and 4)

Because our gamma and alpha formulas can be applied to any hierarchical structure, we demonstrate the decomposition of our measure qMF based on all pairs of plots separately *within each country*. Due to sparse data in Finland, with richness levels of only one or two species in 90% of the 28 plots, our following analysis is based on the five other countries. For each pair of plots, we computed alpha, beta and gamma for tree species diversity as well as the corresponding alpha, beta and gamma multifunctionality values for $q=0, 1$ and 2 . Here, alpha scale refers to individual plots, whereas the gamma scale refers to the two collective plots.

The empirical BEF relationships for alpha, beta and gamma scales are presented in Figure 3 (uncorrected for correlations between functions) and Figure 4 (corrected for correlations). To examine the effect of alpha/beta/gamma species diversity on the corresponding alpha/beta/gamma multifunctionality value, as we did in the within-ecosystem analysis, the BEF relationship for each scale was modelled using a linear mixed model with random slopes and random intercepts for each country. Based on the overall (fixed-effect) slopes (bold red lines in Figures 3 and 4) and each country's relationship (thin lines in each figure), our results showed positive relationships between tree species diversity and multifunctionality, irrespective of the scale (alpha, beta or gamma) at which tree species diversity and multifunctionality are quantified, and irrespective of whether correlation between functions is incorporated or not. In other words, for any fixed diversity order q , alpha multifunctionality is positively related to alpha species diversity; beta multifunctionality (i.e. the turnover in ecosystem functions and performance level across plots) is positively related to beta

diversity (i.e. the turnover in species composition and abundance across plots), which is consistent with van der Plas et al. (2016); gamma multifunctionality is positively related to gamma diversity. Multifunctionality can be enhanced at the gamma scale by increasing alpha tree species diversity and beta diversity because both scales jointly contribute to higher gamma diversity and gamma multifunctionality. Such conclusions are valid not only for species diversity but also for species richness; see Figures S3.3 and S3.4 in Appendix S3. However, more data are needed and further modelling should be done to validate a potentially causal relationship (Dee et al., 2023).

The patterns in Figures 3 and 4 are generally similar, except that gamma and alpha multifunctionality values (and slopes with species diversity) for incorporating correlations in Figure 4 are slightly lower than the corresponding values in Figure 3. In contrast, beta multifunctionality values (and slopes) are similar in the two figures. Analogous to the findings in Figure 2, Figures 3 and 4 also reveal that the slope is generally stronger with higher values q , that is, the effect at each scale (alpha, beta and gamma) is stronger when common/abundant species and ecosystem functions provided at high levels are considered, than the effect when rare species and low-performing functions are considered. This conclusion is valid not only for the overall fits but also for the fits in each country.

For both gamma and alpha scales, Figures 3 and 4 reveal for each country's fit that positive BEF relationships for all orders $q=0, 1$ and 2 are weaker (i.e. the magnitude of the slope in each panel is relatively lower than any of the other countries) for the data from mountainous deciduous forest in Romania than any of other countries. The weaker relationship in Romania is in line with an earlier study on the data, which did not detect a positive biodiversity–productivity relationship in Romania (Jucker et al., 2016 Suppl.). Furthermore, Ratcliffe et al. (2017) found that relationships between tree diversity and ecosystem functioning and multifunctionality are weaker in countries with relatively small functional diversity in their tree species pool, like Romania. However, for the BEF relationship between beta multifunctionality versus beta species diversity, the fitted results in Romania exhibit comparable positive slopes as the other four countries.

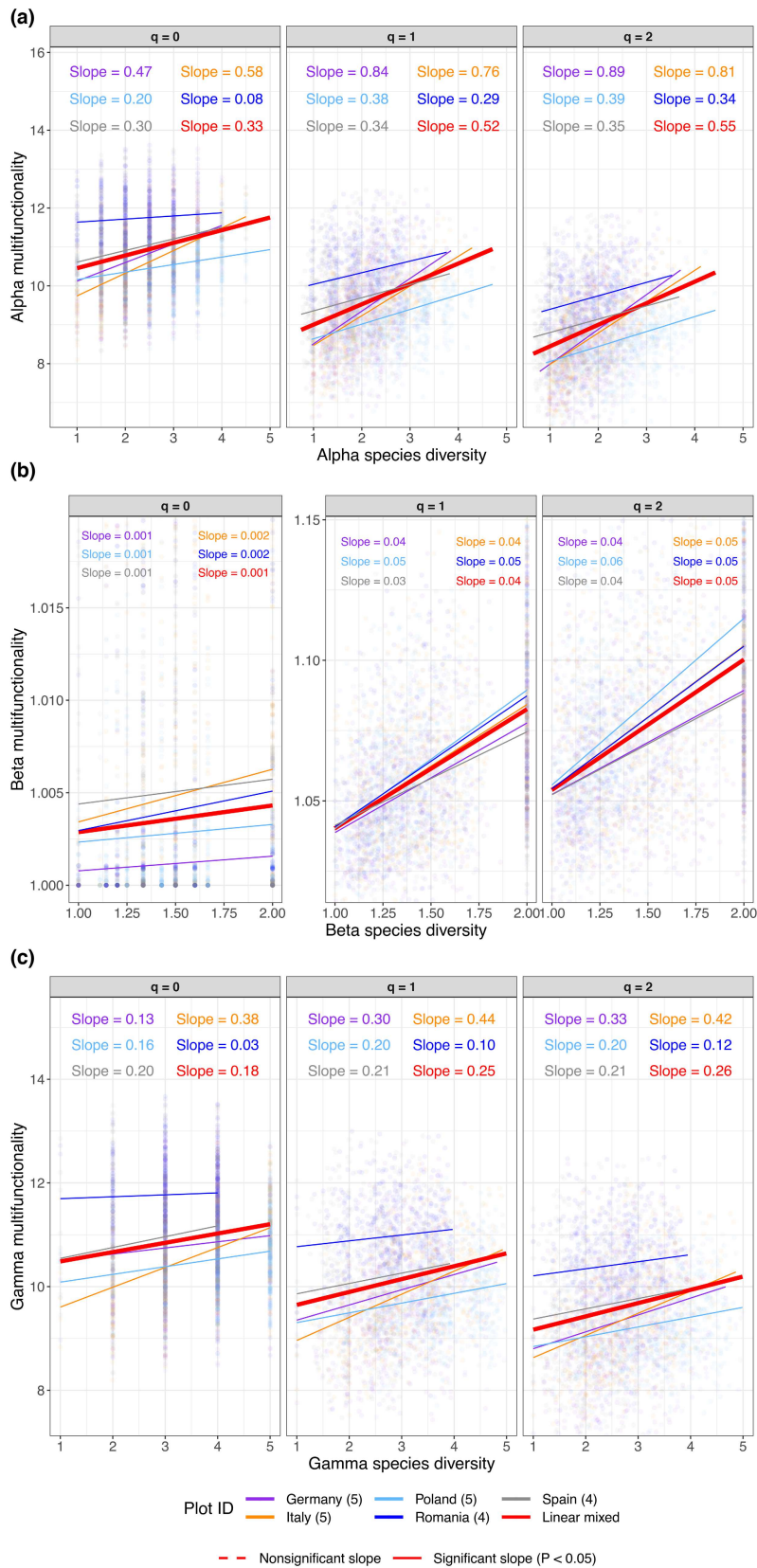


FIGURE 4 Biodiversity–multifunctionality relationships across spatial scales when the correlation between any two functions is incorporated; see Equations (S2.3)–(S2.5) in Appendix S2. (a) Alpha multifunctionality versus alpha species diversity, (b) beta multifunctionality versus beta species diversity, and (c) gamma multifunctionality versus gamma species diversity. Other legend is the same as in Figure 3, except that the pairwise correlation between any two functions is incorporated, and alpha/beta/gamma multifunctionality for correlated functions is based on an integrated measure by considering all possible threshold levels.

CONCLUSIONS

Since at least Mori et al. (2018), the BEF science community has recognized the urgent need for a rigorous theoretical framework and the collection of more large-scale empirical evidence to expand research on the effects of biodiversity on ecosystem multifunctionality beyond the local alpha scale. This research development is essential to address pressing questions about the consequences of biodiversity change in the Anthropocene and is of great fundamental as well as applied importance. Our study proposes a generalized framework based on Hill–Chao numbers which allows decomposition of multifunctionality at gamma scales into alpha and beta components. The framework can be adapted to the specific needs of users by adjusting the sensitivity of the measure from rare to dominant functions, and by weighting individual functions from an economical, societal or ecological perspective. Figure 1 shows that our framework opens novel avenues for comprehensive analyses of biodiversity in three dimensions (taxonomic, functional and phylogenetic), as well as multifunctionality across scales. Although this paper only considers two levels of biodiversity (alpha and gamma), our approach potentially can be extended to accommodate more complex hierarchical structures.

AUTHOR CONTRIBUTIONS

Jörg Müller motivated the project. Anne Chao and Chun-Huo Chiu conceived the statistical ideas and developed the methodology. Fons van der Plas and Michael Scherer-Lorenzen contributed the principal data. Anne Chao, Chun-Huo Chiu and Kai-Hsiang Hu analysed the data and developed the software/graphics; Jörg Müller, Fons van der Plas, Marc W. Cadotte, Oliver Mitesser, Simon Thorn, Akira S. Mori, Michael Scherer-Lorenzen, Nico Eisenhauer, Claus Bässler, Benjamin M. Delory, Heike Feldhaar, Andreas Fichtner, Torsten Hothorn, Marcell K. Peters, Kerstin Pierick and Goddert von Oheimb provided additional perspectives and contributed to the interpretation of the results. Anne Chao and Jörg Müller led the writing, and all authors edited critically the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14336>.

DATA AVAILABILITY STATEMENT

The ecosystem function variables and biodiversity data that support the findings of this paper are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.9ghx3ffpz> (Scherer-Lorenzen et al., 2023); an R package ‘MF.beta4’ used in statistical analyses is available on CRAN and Github https://github.com/AnneChao/ELE_MF.beta4. For readers without an R background, the online software ‘MF.beta4’ is available from https://chao.shinyapps.io/MF_beta4/ to facilitate all computation and graphics.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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