

Variation in the methods leads to variation in the interpretation of biodiversity–ecosystem multifunctionality relationships

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Abstract

Aims Biodiversity is often positively related to the capacity of an ecosystem to provide multiple functions simultaneously (i.e. multifunctionality). However, there is some controversy over whether biodiversity–multifunctionality relationships depend on the number of functions considered. Particularly, investigators have documented contrasting findings that the effects of biodiversity on ecosystem multifunctionality do not change or increase with the number of ecosystem functions. Here, we provide some clarity on this issue by examining the statistical underpinnings of different multifunctionality metrics.

Methods We used simulations and data from a variety of empirical studies conducted across spatial scales (from local to global) and biomes (temperate and alpine grasslands, forests and drylands). We revisited three methods to quantify multifunctionality including the averaging approach, summing approach and threshold-based approach.

Important Findings Biodiversity–multifunctionality relationships either did not change or increased as more functions were considered. These results were best explained by the statistical underpinnings of the averaging and summing multifunctionality metrics. Specifically, by averaging the individual ecosystem functions, the biodiversity–multifunctionality relationships equal the population mean of biodiversity–single function relationships, and thus will not change with the number of functions. Likewise, by summing the individual ecosystem functions, the strength of biodiversity–multifunctionality relationships increases as the number of functions increased. We proposed a scaling standardization method by converting the averaging or summing metrics into a scaling metric, which would make comparisons among different biodiversity studies. In addition, we showed that the range-relevant standardization can be applied to the threshold-based approach by solving for the mathematical artefact of the approach (i.e. the effects of biodiversity may artificially increase with the number of functions considered). Our study highlights different approaches yield different results and that it is essential to develop an understanding of the statistical underpinnings of different approaches. The standardization methods provide a prospective way of comparing biodiversity–multifunctionality relationships across studies.

Keywords: averaging approach, biodiversity, ecosystem multifunctionality, multiple threshold approach, plant species richness, spatial scale

摘要: 生物多样性常常和生态系统多功能性(生态系统同时提供多个生态系统功能的能力)正相关。然而,生物多样性与生态系统多功能性的关系是否依赖于生态系统功能的数目有诸多争议。其中,生物多样性对生态系统多功能性的影响或许不随生态系统功能数目的变化而变化,或者随生态系统功能数目的增多而增强。我们期望通过研究不同生态系统多功能性指数的统计原理来解决这些争议。我们使用了模型模拟和一系列来自不同空间尺度(从局域到全球)和不同生物群系(温带和高寒草地、森林和干旱地)的经验数据。我们回顾了量化生态系统多功能性的三种方法,包括平均值法、加和法和阈值法。我们发现随着生态系统功能数目的增加,生物多样性与生态系统多功能性的关系要么不变,要么增强。这些结果可由平均和加和的多功能性指数的统计原理来解释。具体来讲,当利用生态系统功能的平均值计算多功能性指数时,由于多样性对多功能性的效应等于多样性对单个生态系统功能效应的平均值,所以不会随生态系统功能数目的变化而变化。同样的道理,当利用单个生态系统的加和值计算多功能性指数时,多样性的效应会随着生态系统功能数目的增加而增强。我们提出了一个改进的多功能性指数,将平均或加和多功能性指数转化为标准化的多功能性指数,以便于对不同研究的结果进行比较。此外,我们提出了基于变量数值范围的标准化方法来解决阈值法的数学假象问题(多样性效应随生态系统功能数目的增加而增强)。我们的研究表明,量化多功能性指数的方法不同,结果也不同。因此,有必要加深对不同方法数理基础的理解。而标准化的多功能性指数为比较不同研究中的生物多样性与生态系统多功能性的关系提供了有效的方法。

关键词: 平均值法,生物多样性,生态系统多功能性,多阈值法,植物物种丰富度,空间尺度

'The challenge remains to develop multifunctionality indices that appropriately account for the aggregate effects of contrasting individual functions when their responses depend on multiple drivers that vary in their effects either in space or time.'
(Bradford *et al.* 2014a)

INTRODUCTION

Over the past decade, a key question in ecology has been whether biodiversity increases the capacity of an ecosystem to provide multiple functions simultaneously (i.e. multifunctionality) (Gamfeldt *et al.* 2008; Hector and Bagchi 2007; Hines 2019; Manning *et al.* 2018). In general, as biodiversity increases, so does at least one ecosystem function—typically aboveground net primary productivity (ANPP), e.g. Hector *et al.* (1999), Hooper *et al.* (2012) and Tilman *et al.* (2014). However, an ecosystem performs a variety of functions in addition to ANPP, and indeed there is an emerging body of research that seeks to estimate multifunctionality and to understand how biodiversity influences multifunctionality (Byrnes *et al.* 2014a; Gotelli *et al.* 2011; Maestre *et al.* 2012; Manning *et al.* 2018; Zavaleta *et al.* 2010). While many biodiversity–multifunctionality studies provide evidence that increasing biodiversity leads to higher multifunctionality (Fanin *et al.* 2018; Hautier *et al.* 2018; Lefcheck *et al.* 2015), such biodiversity effects become increasingly complex in naturally assembled communities (Snelgrove *et al.* 2014; van der Plas 2019). This pattern likely emerges because the mechanisms underlying biodiversity–multifunctionality relationships are not well understood when the number of functions considered increases (Fanin *et al.* 2018; Gamfeldt and Roger 2017; van der Plas *et al.* 2016). For example, trade-offs among ecosystem functions could accumulate with the number of functions (Butterfield *et al.* 2016; Byrnes *et al.* 2014b; Dooley 2018; Lefcheck *et al.* 2015; Meyer *et al.* 2018), thereby offsetting the effects of biodiversity on multifunctionality (Byrnes *et al.* 2014a; Zavaleta *et al.* 2010). Alternatively, the rate of multifunctionality loss as biodiversity is lost may increase because the levels of redundancy across ecosystem functions become lower when more functions are considered (Delgado-Baquerizo *et al.* 2016a; Gamfeldt *et al.* 2008; Miki *et al.* 2014; Mori *et al.* 2016).

Currently, there are at least four ways to estimate multifunctionality (Byrnes *et al.* 2014a; Dooley *et al.* 2015; Hölting *et al.* 2019; Manning *et al.* 2018): the single functions approach, averaging approach, turnover approach and threshold-based approach (single vs. multiple thresholds) (see summaries by Byrnes *et al.* 2014a; Dooley *et al.* 2015). Investigators might use the single functions approach if they desire to evaluate whether high-diversity communities maintain more individual functions with higher values than do less diverse communities (Duffy *et al.* 2003). The averaging approach might be used if researchers want to compare the average effect of diversity on

multiple ecosystem functions (Hooper and Vitousek 1998; Maestre *et al.* 2012). The turnover approach might be used if the goal is to assess whether different species contribute different ecosystem functions or services (Hautier *et al.* 2018; Hector and Bagchi 2007; Isbell *et al.* 2011; Wagg *et al.* 2019). And finally, the threshold-based approach might be used if the aim is to compare whether a community can simultaneously achieve high levels of multifunctionality for a given threshold or multiple thresholds (Byrnes *et al.* 2014a; Gamfeldt *et al.* 2008; Zavaleta *et al.* 2010). Although these four approaches provide useful information about biodiversity–multifunctionality relationships, multifunctionality is not just a quantitative metric. Indeed, it is also applied to quantify the overall performance of ecosystem quality, i.e. the extent to which an ecosystem has desirable properties from the viewpoint of human society (Allan *et al.* 2015; Manning *et al.* 2018; Slade *et al.* 2017; Song *et al.* 2020). The problem with multiple metrics/valuations of multifunctionality is that it hinders synthesis across studies or comparing effects of particular sub-components of ecosystems (Byrnes *et al.* 2014a).

Many studies have demonstrated that the positive contribution of species to multifunctionality increases with the number of functions (e.g. Hautier *et al.* 2018; Hector and Bagchi 2007; Isbell *et al.* 2011; Meyer *et al.* 2018). Recently, three studies have explored whether biodiversity–multifunctionality relationships are contingent on the number of functions considered. Using simulation models, Gamfeldt and Roger (2017) found that increasing the number of functions did not change biodiversity–multifunctionality relationships. That is, the effects of biodiversity on multifunctionality are approximately identical to the average effects of biodiversity on individual ecosystem functions. The results were supported by an empirical study examining biodiversity–multifunctionality relationships on Swedish islands (Fanin *et al.* 2018). However, a study conducted in a German grassland found different trends (Meyer *et al.* 2018). Specifically, as more functions were included in the estimate of multifunctionality, biodiversity–multifunctionality relationships became increasingly positive. These contrasting findings, obtained using different modelling and experimental approaches in different study ecosystems, highlight the need for additional and more detailed analyses of how the number of functions influences biodiversity–multifunctionality relationships.

Here, we use simulation models and empirical data to show that the statistical underpinnings of quantitative multifunctionality metrics are important for understanding whether increasing the number of functions will alter biodiversity–multifunctionality relationships. We first re-examine and expand the simulation models adopted by Gamfeldt and Roger (2017) by combining the averaging and summing multifunctionality metrics together. We then propose a way to convert the two metrics into a scaling one, which makes multifunctionality

comparable among studies. We also revisit the threshold-based approach to quantify multifunctionality (Byrnes *et al.* 2014a) and use the range-relevant standardization to deal with the mathematical artefact raised by Gamfeldt and Roger (2017). Finally, we compare biodiversity–multifunctionality relationships with the standardization methods using empirical studies from a number of ecosystems with an extensive range of climatic and edaphic conditions (Supplementary Fig. S1).

MATERIALS AND METHODS

A review of the averaging and summing approaches

Several quantitative approaches have been developed to examine biodiversity–multifunctionality relationships (Byrnes *et al.* 2014a; Dooley *et al.* 2015; Manning *et al.* 2018). Here, we reviewed two approaches. The averaging multifunctionality metric is one of the early and most commonly used approaches (Byrnes *et al.* 2014a; Hooper and Vitousek 1998; Maestre *et al.* 2012; Mouillot *et al.* 2011). A more recently developed approach is the summing multifunctionality metric (Meyer *et al.* 2018). Note that there are many versions of averaging indices that account for the standard deviation or geometric means of multiple single functions at the same time (see Supplementary Table S1 for more information). For simplicity, we identify the two methods as the averaging approach and the summing approach.

The averaging or summing metric usually regresses with biodiversity, and the regression slopes are referred to as the effects of biodiversity on multifunctionality (Gamfeldt and Roger 2017). One advantage of the averaging and summing approaches is that they are easy to calculate and interpret. Particularly, biodiversity–multifunctionality relationships can be analysed using general linear models (Byrnes *et al.* 2014a; Gamfeldt and Roger 2017; Maestre

et al. 2012). However, the averaging approach has been criticized for a variety of statistical and biological reasons (Byrnes *et al.* 2014b; Dooley 2018; Hines 2019). For instance, the averaging metric has the same value when two functions have an identical value or when one function makes a higher contribution and another one makes a lower contribution (e.g. the average of 5 and 5 is 5; the average of 1 and 9 is also 5) (Byrnes *et al.* 2014a; Dooley 2018). In addition, although this limitation is equally true for the summing metric, we acknowledge that only one study focuses on the summing approach as it applies to the study of biodiversity–multifunctionality relationships (Meyer *et al.* 2018). Simply put, this method has not been well explored, but we expect others will not adopt it without considering some of its limitations, such as weighting functions equally (but see Allan *et al.* 2015; Manning *et al.* 2018).

We explore the statistical underpinnings of the averaging and summing metrics using both simulation models and empirical data. We first note that the raw slope estimates (regression coefficients) do not help compare the strength of biodiversity effects when using these two multifunctionality metrics (Supplementary Note 1). In addition, we note that the averaging metric is mathematically equivalent to the summing metric if we standardize these two metrics to a common scale (e.g. centering and scaling the two metrics into the scaling multifunctionality metric) (Fig. 1; Supplementary Note 2). Most importantly, the values of the averaging and summing metrics are generally expressed in a relative scale. Therefore, we propose to use the scaling multifunctionality metric for data syntheses. Note that the scaling metric is not designed to solve the question of why biodiversity–multifunctionality relationships change with the number of functions considered. But this metric allows us to estimate the standardized slopes (or coefficients) of the general linear models between biodiversity and multifunctionality. As a result, the scaling approach could be used to compare results of different studies in a systematic way. Notably, there is

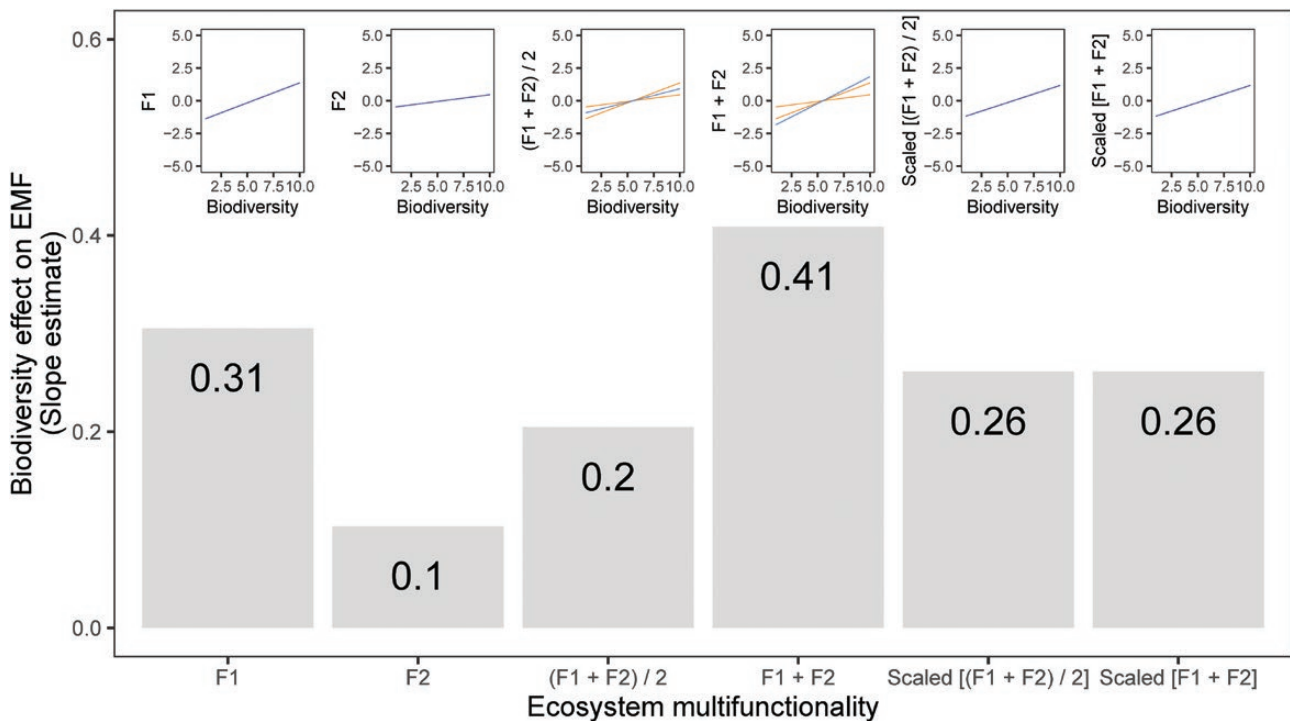


Figure 1: An example shows the effects of biodiversity on single functions and ecosystem multifunctionality (EMF). We simulate two ecosystem functions (F1 and F2), each with a standardized normal distribution. Numbers in the bars are slope estimates. The blue lines of the inset show the slopes of linear regression between biodiversity and ecosystem functions. The orange lines in the middle of the inset indicate the slopes obtained either from the averaging metric or from the summing metric. As illustrated in the figure, the Z-score-transformed averaging and summing metrics have the same slope estimate.

a long history of using standardized coefficients in multiple regressions and structural equation models (Grace and Bollen 2005; Grace *et al.* 2018). Some of the commonly used standardization methods include Z-score and range-relevant standardization (Grace and Bollen 2005; Grace *et al.* 2007, 2018; Schielzeth 2010). Here, we suggest a new approach—referred to as ‘scaling approach’—to convert the averaging or summing metrics into a single metric. In contrast to the traditional way, we use a Z-score transformation and then model the metric with the raw biodiversity data. Suppose that the estimated slope between the scaling metric and the raw biodiversity data is 0.2. We interpret this value to mean that, with each addition of one unit of biodiversity (i.e. an increase of one species), then multifunctionality increases by 0.2 standard deviations. Therefore, the semi-standardized slope estimate may provide an opportunity to make the multifunctionality metric comparable and interpretable across studies. Below we use simulation models to illustrate how different methods will affect our interpretation and comparison.

Simulation models for the averaging, summing and scaling approaches

To our knowledge, Gamfeldt and Roger (2017) were the first to quantitatively and explicitly address whether biodiversity–multifunctionality relationships depend on the number of functions. Here, in contrast with their methods, we used three metrics (averaging, summing and scaling) to quantify multifunctionality. Note the summing metric is not the same as the one proposed by Meyer *et al.* (2018). They calculated a metric by summing the axis scores of the principal component analysis (PCA). Their metric has the advantage that it corrects for the correlations among individual ecosystem functions by calculating the components of PCA which are, by definition, uncorrelated with each other. In this study, we calculated the summing metric directly by summing individual standardized ecosystem functions without correcting for the correlation structure of ecosystem functions. The summing metric thus enables us to make direct comparisons with the averaging metric. In addition, the scaling metric is a modified metric that can be calculated either from the averaging or summing metrics (Fig. 1). It is very similar but not exactly the same as Dooley’s scaled average multifunctionality (SAM) metric (Dooley 2018). However, the rationale for our metric is similar to SAM in that it converts the averaging or summing metric into a standardized one with a common scale (more information about the statistical rationales can be found in Supplementary Notes 1 and 2).

In brief, we simulated a species pool with 12 species, and each species performs nine ecosystem functions. Artificial communities were generated from the species pool. We simulated all possible combinations for the 12 species at each species richness level and generated a total of 4095 artificial communities at each step. We calculated ecosystem functions by averaging the function values that the species performed in the 4095 artificial communities. Meanwhile, we simulated a series of ecosystem functions subject to complementarity, which is one of the fundamental mechanisms to explain the observed positive effects of biodiversity on ecosystem functioning. We applied a saturating function for species richness and the complementarity factor (CF) to an ecosystem function in the following way:

$$CF = CF_{\max} \left(1 - e^{1-S^r} \left(1 - \frac{1}{CF_{\max}} \right) \right) \quad (1)$$

where CF is one when species richness is one, and the maximum CF (CF_{\max}) is three. S is species richness and r is the rate of CF reaching its maximum value (CF_{\max}). Each single function was standardized either with Z-score or its maximum value. In total, we simulated nine scenarios and generated various sets of functions that varied by the number of functions subject to complementarity. All possible combinations of the nine single ecosystem functions were used to

calculate the averaging, summing or scaling multifunctionality metrics in each scenario. We refer to Gamfeldt and Roger (2017) for more details of the simulations.

A review of the threshold-based approach

A second common approach to quantify multifunctionality is the threshold-based approach (Byrnes *et al.* 2014a; Gamfeldt *et al.* 2008; Zavaleta *et al.* 2010). Generally, it converts the matrix of ecosystem functions (n communities by m functions) into a binary matrix for a given threshold (or cut-off) and counts the number of functions that surpass a given threshold in a community. This process is very similar to the method used to calculate species richness in a community where species abundance is converted into a binary species table (presence and absence matrix) and the number of species in the community is counted. Next, the number of counted functions is fitted to a generalized linear model against biodiversity, and the slope of this linear model is referred as the effects of biodiversity on multifunctionality. The advantage of the threshold-based approach is that it can identify whether multiple functions reach to high levels of functionality at the same time. However, the biological interpretation for the threshold-based approach remains challenging (Gamfeldt and Roger 2017). In addition, the threshold-based approach is sensitive to the thresholds used to count the number of functions and the methods used to standardize single ecosystem function (Byrnes *et al.* 2014a; Gamfeldt and Roger 2017). Most importantly, Gamfeldt and Roger (2017) pointed out that both positive and negative effects of biodiversity on multifunctionality change with the number of functions, and that this pattern is likely due to a mathematical artefact (Supplementary Note 3). Therefore, the threshold-based approach may inhibit reliable comparisons across studies.

As we discuss above, the range-relevant standardization (Grace and Bollen 2005; Grace *et al.* 2018) may solve the mathematical issue and make the estimated slopes comparable across studies. Generally, the range of the number of functions surpassing a given threshold varies from zero to the total number of functions measured. Thus, if we standardize the number of functions surpassing a given threshold, we will obtain a series of standardized values ranging from zero to one. The slope estimates between the standardized number of functions and biodiversity should be comparable to a common scale.

To support our speculation, we used soil microbial biomass from a pool of 82 ecosystem function indicators measured in an empirical study at the Jena biodiversity experiment (Meyer *et al.* 2018; Weisser *et al.* 2017). Similar to Gamfeldt and Roger (2017), we simulated a variety of scenarios by replicating soil microbial biomass many times (i.e. 5, 15, 25, 35 and 45 number of functions in total considered). Note that the simulations focussed on a single ecosystem function, but we treated the replications of microbial biomass as multiple ecosystem functions. Such scenarios are not ecologically relevant in a real study of biodiversity–multifunctionality relationships, but they illustrate the rationale and the cause of the mathematical artefact of the threshold-based approach. In addition, we used a hierarchical sampling approach, by which we randomly sampled a subset of the 82 functions from the Jena dataset (Supplementary Note 3). The hierarchical sampling approach enabled us to explore whether biodiversity–multifunctionality relationships changed when novel functions are included in estimate of multifunctionality.

Empirical data acquisition and description

We compiled five empirical datasets including two manipulative biodiversity experiments across nine grasslands and three observational studies spanning 300 sites around the world (Supplementary Fig. S1; Table S2). The two manipulative biodiversity studies include one grassland biodiversity experiment that measured 82 ecosystem

functions (Jena grassland) (Meyer *et al.* 2018; Weisser *et al.* 2017) and eight pan-European BIODEPTH grassland biodiversity experiments that measured six functions (Spehn *et al.* 2005). The three observational studies include 208 forest plots of the FunDivEUROPE platform with 26 measured functions in each single plot (Ratcliffe *et al.* 2017), 236 global drylands with 14 measured functions (Maestre *et al.* 2012; Ochoa-Hueso *et al.* 2018) and 60 Tibetan grasslands with eight measured functions (Jing *et al.* 2015). These five studies span local, regional and global spatial scales with diverse climates, vegetation and soil types. The ecosystem functions compiled from each study represent typically measured functions in terrestrial ecosystems (e.g. primary productivity, nitrogen and phosphorus pools in plants and soils, soil microbial biomass and enzymatic activities). All the surrogates of ecosystem functions used are either direct measures of ecosystem stocks (e.g. plant biomass and soil C stock), fluxes (e.g. productivity and decomposition) or indirect measures of ecosystem properties (e.g. light interception) (Meyer *et al.* 2018). We focussed on plant species richness because this was the only biodiversity metric common to all datasets.

Statistical analyses

To make our simulations comparable to Gamfeldt and Roger (2017) and to estimate biodiversity effects on multifunctionality, we used two data transformations—standardized to maximum value and Z-score—for the single ecosystem functions prior to the estimate of multifunctionality. For the observational studies and biodiversity experiments, we used general linear models without controlling for other abiotic variables (e.g. climate, land-use intensity and soil properties). Although these abiotic variables may affect the strength of biodiversity–multifunctionality relationships (Duffy *et al.* 2017), they will not affect our interpretation of the effects of biodiversity on multifunctionality.

To estimate the average effect of biodiversity on multifunctionality, we fitted linear regression models with all combinations of functions from one to the maximum number of functions considered within each simulation or empirical dataset; thus our method combined two multifunctionality approaches, the single functions approach (Byrnes *et al.* 2014a) and the multifunctionality metric approach.

For three datasets—Jena grassland, European forests and Global drylands (Maestre *et al.* 2012; Meyer *et al.* 2018; Ratcliffe *et al.* 2017)—if the ecosystem function combinations were greater than 500, we randomly sampled 500 combinations of functions and calculated multifunctionality for each combination of those single functions. We extracted the slopes and standard errors (s.e.) from linear models. We calculated the 95% confidence interval (CI = $1.96 \times \text{s.e.}$) for each slope estimate. If the lower 95% CI was higher than zero or the upper 95% CI was lower than zero, we categorized the slope estimates as positive or negative effects of biodiversity on multifunctionality, respectively.

Using the threshold-based approach we further compared the effects of biodiversity on multifunctionality using the five empirical datasets. Specifically, we followed the approach adopted by Byrnes *et al.* (2014a). We first standardized single functions to their maximum values by taking the mean of the six highest measures of each function as the maximum value. We counted the number of functions surpassing a given threshold ranging from 0.05 to 0.99. We conducted the threshold-based analysis by fitting the generalized linear models with the raw number of functions and the range standardized number of functions upon biodiversity.

All statistical analyses were conducted in R version 3.3.3 (R Development Core Team 2019). The threshold approach was conducted using the package ‘multifunc’ (Byrnes *et al.* 2014a).

RESULTS

Biodiversity–multifunctionality relationships vary with the averaging, summing and scaling approaches

Our simulation models revealed that the strength of biodiversity–multifunctionality relationships varied with the approaches used to estimate multifunctionality (Fig. 2). Generally, the averaging approach showed that the average estimated slopes relating biodiversity to multifunctionality did not change as the number of functions increased for a given number of functions subject to complementarity (e.g. three out of nine functions subject to complementarity). However, the strength of the average estimated slopes increased as the number of functions subject to complementarity increased (from zero to nine).

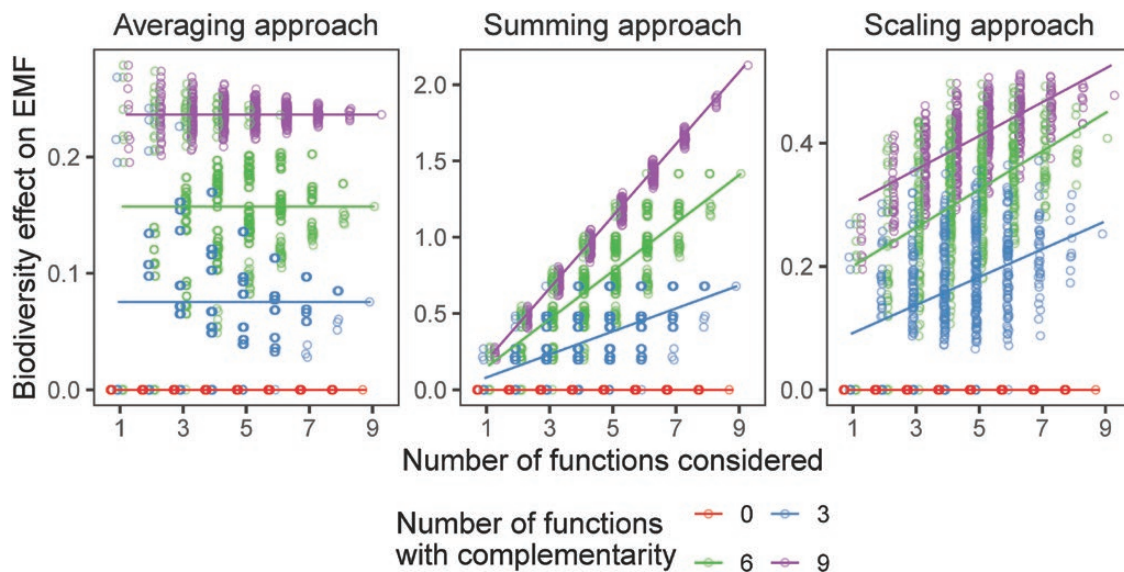


Figure 2: Summary of the simulations shows the effects of biodiversity on multifunctionality (EMF) in related to the number of functions included in the EMF estimate. The jittered points are the slope estimates showing the effects of biodiversity on EMF in each combination of the nine functions considered. Lines (average biodiversity effect on EMF) are the slopes of linear regression between the biodiversity–multifunctionality (all combinations of the nine functions) relationships and the number of ecosystem functions. Note that we use different ranges of y-axis to aid in visualization.

The summing and scaling approaches demonstrated that the average estimated slopes increased with the number of functions. Furthermore, we found that the averaging and summing approaches were sensitive to the methods used to standardize single function (standardized to maximum value vs. Z-score). That is, the strength of biodiversity–multifunctionality relationships estimated by the Z-score for single function was ~10 times higher than the maximum standardization (Fig. 2; Supplementary Fig. S2). In contrast, we obtained the same biodiversity–multifunctionality relationships using the scaling approach whichever the standardization methods used (Fig. 2; Supplementary Fig. S2). Finally, when we grouped biodiversity–multifunctionality relationships into two categories (significantly positive and neutral), we found that, when functions were subject to complementarity, the positive effects of biodiversity on multifunctionality were most commonly observed when the number of functions included increased (Supplementary Note 4; Fig. S3).

We found qualitatively similar results when we examined the empirical datasets. The average effects of biodiversity on multifunctionality did not change with the number of functions included in the averaging multifunctionality metric, but it increased with the summing and scaling multifunctionality metrics (Fig. 3). Results of biodiversity experiments such as the Jena grassland and European grasslands were similar with those of observational studies such as European forests, Tibetan grasslands and global drylands. Among all the studies, the European forests had the largest variability in the effects of biodiversity on single ecosystem functions (Fig. 4a) and scaling multifunctionality (Fig. 4b). Biodiversity–multifunctionality relationships in temperate grasslands were as strong as they were in global drylands (Fig. 4b). Furthermore, the probability of biodiversity having positive, neutral or negative effects on multifunctionality changed with the number of functions included (Supplementary Note 4; Fig. S4). Positive biodiversity effects on multifunctionality were more common as the number of functions included increased in the

Jena grassland, European grasslands, Tibetan grasslands and global drylands. In contrast, neutral biodiversity effects on multifunctionality were more common as the number of functions included increased in the European forests.

Biodiversity–multifunctionality relationships vary with the standardization methods of the threshold-based approach

For the simulations using soil microbial biomass data from Jena grassland, we found that the effects of biodiversity on multifunctionality (raw slope estimates) increased as the number of functions increased (see Supplementary Note 3 for details). However, the effects of biodiversity on multifunctionality were identical at a given threshold when the standardized slopes were estimated. When exploring the other 82 functions measured in the Jena experiment, we found similar results to what we found with soil microbial biomass (data not shown). In addition, using the hierarchical sampling simulations, we found that increasing the number of functions increased the strength of biodiversity–multifunctionality relationships when we used the raw number of functions that surpassed a given threshold (Supplementary Note 3). In contrast, we found that the average effect of biodiversity on multifunctionality did not change with the number of functions in total considered when we standardized the number of function surpassing a given threshold. Introducing novel functions for the estimate of multifunctionality decreased the range of 95% CIs.

For the empirical datasets, we compared the results using the raw number of functions and the range-relevant standardized number of functions. The trends using the raw number of functions were similar with those using the range-relevant standardized number of functions, but they were different in the strength of biodiversity effects (Fig. 5). That is, the effects of biodiversity on multifunctionality increased with the number of functions included using the raw number of functions. Using the range-relevant standardized number of functions, our results showed that biodiversity in the European forests had the largest effects

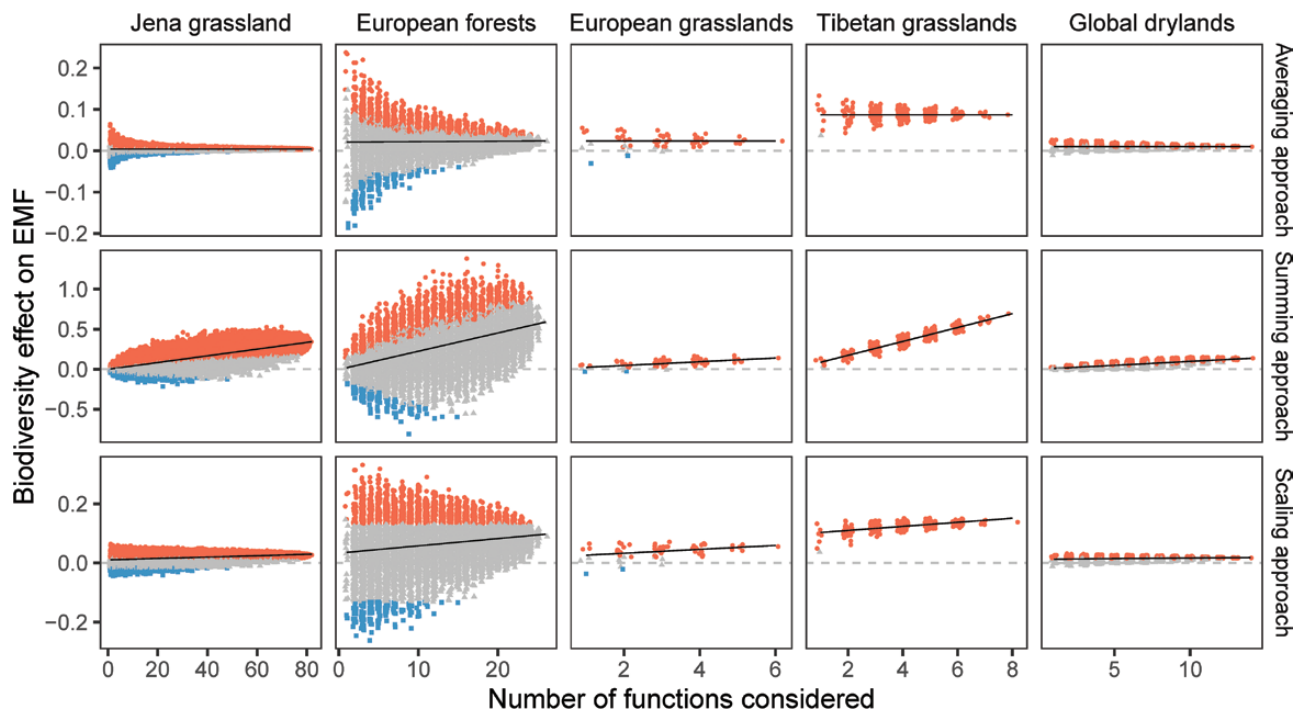


Figure 3: Relationships between the number of functions included in the estimate of multifunctionality (EMF) and the effects of biodiversity on EMF in five empirical datasets. Black lines (average biodiversity effect on EMF) are the slopes of linear regression between the number of functions and the biodiversity–EMF relationships. Red points indicate significantly positive effects of biodiversity on EMF, grey points indicate neutral effects, and blue points indicate significantly negative effects of biodiversity.

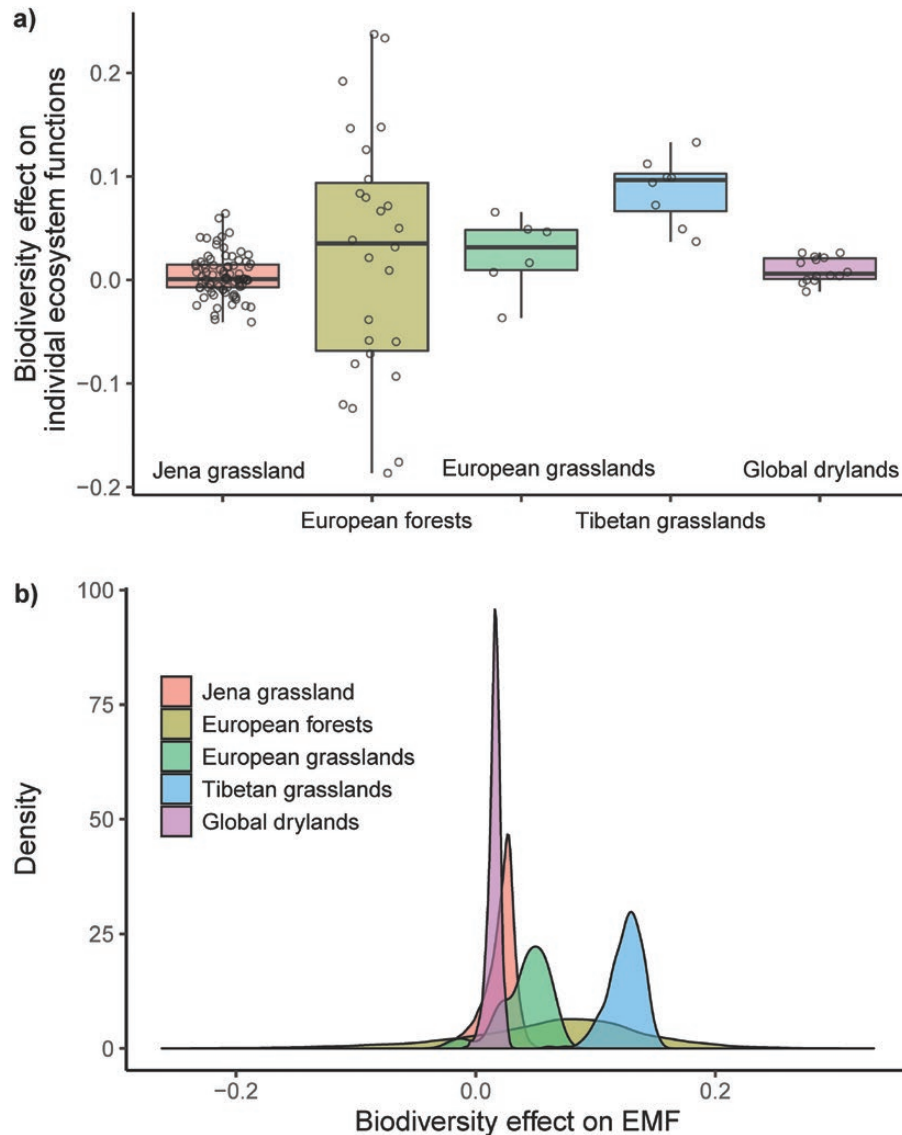


Figure 4: Effects of biodiversity on single ecosystem functions and multifunctionality (EMF) across five empirical datasets. (a) Each boxplot shows the effects of biodiversity on single ecosystem functions; each jittered point represents the slope estimate of the relationship between biodiversity and the single ecosystem functions; the lines in the box denote median, the middle 50% of the data are represented by the interquartile range box and the bottom 25% and the top 25% of the data are represented by the whiskers. (b) The density plot shows the effects of biodiversity on EMF (the scaling metric is reported here).

and highest variability on multifunctionality, and that biodiversity in the Tibetan grasslands also had larger effects than did biodiversity in the Jena grassland, European grasslands and global drylands (Fig. 5). Most importantly, the results of the threshold-based approach using the range standardized number of functions (Fig. 5) were generally in line with the results of the scaling approach (Fig. 4).

DISCUSSION

In this study, we demonstrated that the effects of biodiversity on multifunctionality varied across simulations and empirical datasets. Most interestingly, using the same dataset but different multifunctionality metrics, the effects of biodiversity on multifunctionality either increased or did not change with the number of functions. Although some previous studies found similar results when applying the averaging and summing multifunctionality metrics and the threshold-based approach (Fanin *et al.* 2018; Gamfeldt and

Roger 2017; Meyer *et al.* 2018), we note that these results depended primarily on the underlying statistics of these metrics rather than 'real' effects of biodiversity on multifunctionality. That is, the result arises because of math, not ecology. Below, we firstly provide our statistical explanations for whether biodiversity–multifunctionality relationships change with the number of functions. Then we discuss how the standardization methods can be used to improve our understanding of biodiversity–multifunctionality relationships across studies.

First, for the averaging approach, biodiversity–multifunctionality relationships are obtained from the relationship between biodiversity and single ecosystem function as follows (see proof of the equation in Supplementary Note 2):

$$\beta_{\text{EMFav}} = \frac{1}{n} \sum_{i=1}^n \beta_i \quad (2)$$

where β_{EMFav} is the slope estimate between biodiversity and multifunctionality. It can be expressed as the expected average effect of biodiversity on multifunctionality. β_i is the slope estimate of any

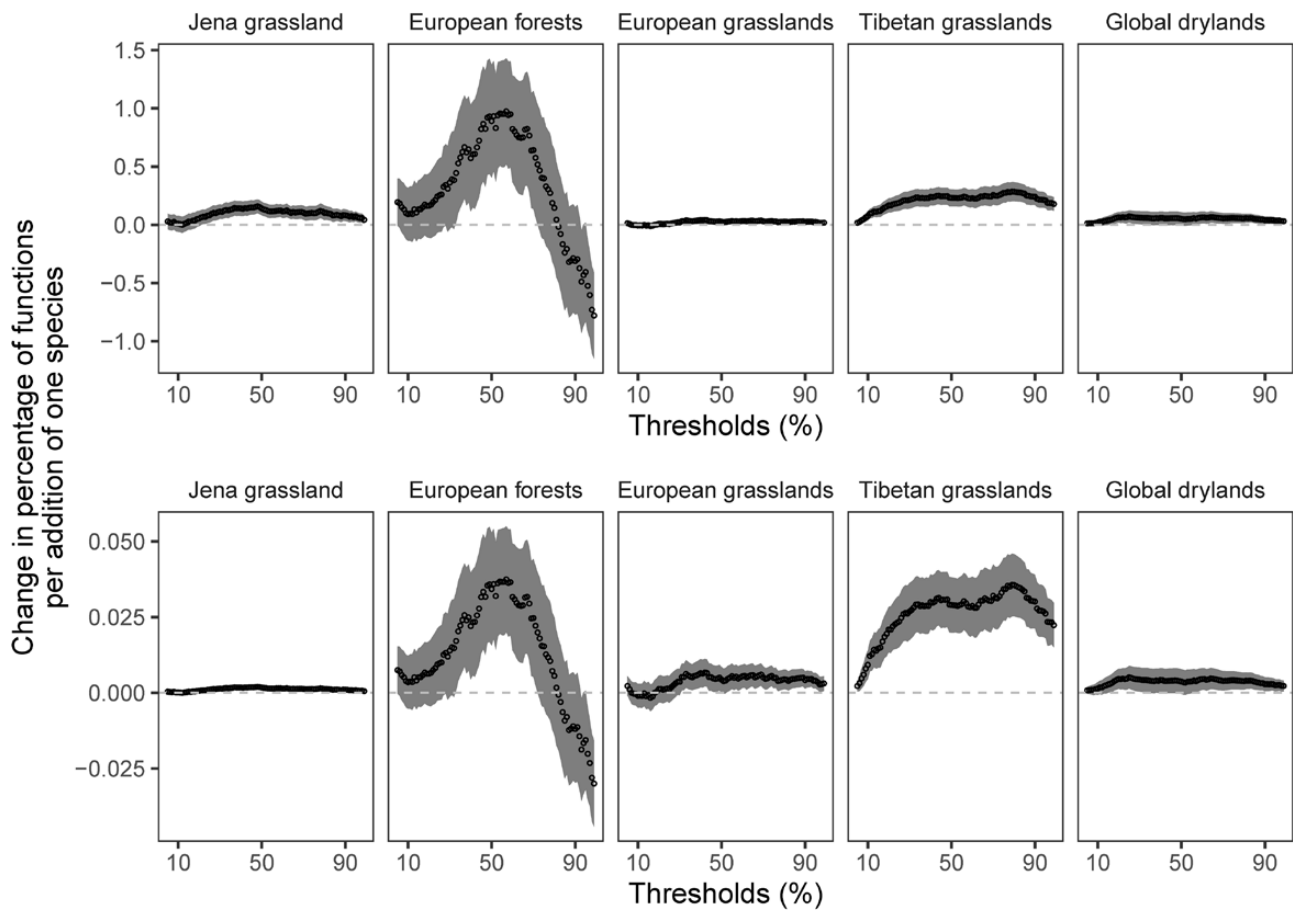


Figure 5: Effects of biodiversity on multifunctionality using the threshold-based approach across five empirical datasets. The upper panels summarize the results using unstandardized number of functions surpassing a given threshold. The lower panels summarize the results using standardized number of functions, which puts the effect size (change in number of functions per addition of one species) on a common and comparable scale across different studies.

one of the regression slopes ranging from one to n single ecosystem functions. In an extreme case in which these single functions have identical slope estimates for the relationships between biodiversity and single ecosystem functions, all the n single functions would have the same regression slopes $\beta_1 = \beta_2 = \dots = \beta_n$, then we would obtain the following regression slopes for the averaging approach:

$$\beta_{EMFav} = \frac{1}{n} \sum_{i=1}^n \beta_i = \frac{1}{n} (n \times \beta_i) = \beta_i \quad (3)$$

The effects of biodiversity on multifunctionality ultimately equal the average slope estimates between biodiversity and single ecosystem functions, and thus biodiversity–multifunctionality relationships would not change as the number of functions increased. Furthermore, the population mean may become higher when there are more ecosystem functions subject to complementarity because of higher slope coefficients obtained. Therefore, we can explain why the strength of the average biodiversity effect on multifunctionality increases with the number of functions subject to complementarity (Gamfeldt and Roger 2017). In addition, since the population mean increases with the number of functions subject to complementarity, the fraction of biodiversity having a positive effect on multifunctionality increases with the number of functions subject to complementarity in the same way (Supplementary Figs S3 and S4).

Second, for the summing approach, biodiversity–multifunctionality relationships can be obtained from the relationship between biodiversity and single ecosystem functions as follows:

$$\beta_{EMFsum} = \sum_{i=1}^n \beta_i \quad (4)$$

In an extreme case the same as the averaging approach in which these single functions have identical slope estimates, we would obtain the following regression slopes for the summing approach:

$$\beta_{EMFsum} = \sum_{i=1}^n \beta_i = n \times \beta_i \quad (5)$$

The expected effects of biodiversity on the summing multifunctionality tend to approach the sum of the slope estimates between biodiversity and single ecosystem functions. Thus, the biodiversity–multifunctionality relationships would increase with the number of ecosystem functions. In comparison to the averaging approach, our results showed that the summing approach gave different weights to the importance of single ecosystem functions (Hörling *et al.* 2019). Consider the hypothetical example that we have three ecosystem functions and the effects of biodiversity on each single ecosystem functions are 0.2, 0.4 and 0.6, respectively. The averaging approach would give a weight of 1/3 to each function while the summing approach would give a weight of 1. Therefore, we would derive the effects of biodiversity on multifunctionality to be 0.5 for the averaging approach and 1.2 for the summing approach. Therefore, the underlying assumptions are that for the averaging approach biodiversity affects the level of multifunctionality via averaging effects of single functions, while

for the summing approach biodiversity affects multifunctionality via simple additive effects of single functions.

Third, for both the averaging and summing approaches, the methods used to standardize single function influenced the strength of biodiversity–multifunctionality relationships (Fig. 1). However, the scaling multifunctionality metric was not sensitive to the methods used for standardizing single ecosystem functions (Fig. 2; Supplementary Fig. S2). The scaling metric thus puts the slope estimates into a common scale and aides in comparisons among different empirical studies. Traditionally, the standardized coefficients (or slope estimates) can be obtained in two ways (Grace *et al.* 2018). The first is to standardize the response variables and predictors using Z-score or range-relevant standardization before fitting the models. The second is to obtain the raw slope estimates in advance and then standardize the slope estimates by the ratios of the standard deviations of predictors and response variables. In this study, we used the former way to derive the standardized slope coefficients. One of the advantages of standardized coefficients is to provide a common scale to compare the relative importance of predictors (e.g. biodiversity, climate and soil physicochemical properties) on response variables for between-study comparisons (Schielzeth 2010). The idea to use the scaling metric was consistent with the methods often used in the study of biodiversity–multifunctionality relationships, in particular estimating the standardized coefficients by using either structural equation models (Delgado-Baquerizo *et al.* 2016b; Jing *et al.* 2015; Lefcheck and Duffy 2015; Wang *et al.* 2019) or bivariate and multivariate linear models (Le Bagousse-Pinguet *et al.* 2019; Soliveres *et al.* 2016a, 2016b). Therefore, we argue that this approach, which could provide a standard way to compare results among studies, should become the standard approach for synthetic studies or for studies that compare the influence of biodiversity on multifunctionality. However, we caution that the influence of increasing biodiversity on the scaling multifunctionality metric ($\beta_{\text{EMF}_{\text{SCA}}}$) with the number of functions does not imply a biological mechanism that drives biodiversity–multifunctionality relationships (Supplementary Note 2). The increase in $\beta_{\text{EMF}_{\text{SCA}}}$ could arise from the decline in the variation in the level of multifunctionality and the average pairwise correlations among single functions with increasing number of functions considered (Supplementary Note 2).

Finally, for the threshold-based approach, when increasing the raw number of functions, a mathematical artefact emerged as increased the effects of biodiversity on multifunctionality. Gamfeldt and Roger (2017) also found that when the number of functions in total considered varies, the threshold-based approach might be not suitable for comparing the effects of biodiversity on multifunctionality among studies. The mathematical artefact appeared to contradict the original idea of the threshold-based approach (Byrnes *et al.* 2014a; Lefcheck *et al.* 2015). However, we demonstrated that this mathematical artefact was due to the upper limits of the number of functions per addition of one species increasing with the number of functions in total considered (Supplementary Note 3). When we used the range-relevant standardization, we found that the standardized slope estimates between biodiversity and the number of functions surpassing a given threshold were identical for soil microbial biomass in the Jena biodiversity experiment. This finding was in line with a recent analysis of the Global drylands dataset (Le Bagousse-Pinguet *et al.* 2019), which the biodiversity effects on multifunctionality were comparable when the standardized regression coefficients were used to quantify the effects of biodiversity on multifunctionality.

Over the past decade, we have moved toward a better understanding of how biodiversity is related to multiple ecosystem functions simultaneously. However, in this study, we showed that the interpretation of biodiversity–multifunctionality relationships varies with the method considered, and that the standardization methods

provide a valuable opportunity to improve our understanding of the statistical mechanisms underlying multifunctionality. The choice of standardization methods is thus critical and has a significant impact on the outcomes of a study (Gamfeldt and Roger 2017; Schmid *et al.* 2017). However, to date, there has not been a unified or best method for estimating ecosystem multifunctionality (Byrnes *et al.* 2014a; Hölting *et al.* 2019; Manning *et al.* 2018), and different approaches for quantifying biodiversity–multifunctionality relationships yield different results (Gamfeldt and Roger 2017; Meyer *et al.* 2018); this is an obvious and dispiriting set of circumstances if the goal of a research is to advance our understanding of how biodiversity affects ecosystem multifunctionality.

The standardized multifunctionality metrics we propose here are desirable and have several advantages when examining spatial or temporal variation in biodiversity–multifunctionality relationships. First, they enable the interpretation of biodiversity effects easily. Second, they facilitate between-study comparisons by estimating a standardized effect size for quantitative reviews and meta-analyses. We therefore suggest the use of standardized multifunctionality metrics (e.g. scaling or range-relevant metrics), especially when the studies use different numbers of ecosystem functions or measure different ecosystem functions. There are, however, three important caveats. First, standardized multifunctionality metrics cannot overcome the limitations of the averaging approach, threshold-based approach or the other commonly used approaches (Byrnes *et al.* 2014a; Dooley *et al.* 2015). Second, different ecosystem properties (and hence multifunctionality metrics) might be valued in different ecological contexts, so some researchers may prefer other multifunctionality metrics (Hölting *et al.* 2019). For example, when researchers quantify multifunctionality, the idea is not necessarily to make a metric i.e. comparable across studies, instead they might be interested in optimizing overall ecosystem functioning by exploring different scenarios of stakeholder priorities given to single ecosystem functions (Allan *et al.* 2015; Manning *et al.* 2018; Slade *et al.* 2017). Finally, when individual functions are driven by different factors (Bradford *et al.* 2014b), it would be interesting to explore the effects of biodiversity by using single functions approach and multiple indices of overall ecosystem functioning (Byrnes *et al.* 2014a; Ratcliffe *et al.* 2017).

In this study, we have focussed on plant species richness as the measure of biodiversity in part because this is easier than trying to estimate abundance, and in part because most early experimental studies focussed on biodiversity as the number of species and controlled the number of species in plots. However, in natural communities or in hyper-diverse communities, it is challenging to detect all of the species present (Chao *et al.* 2017). It would be interesting to use abundance-based diversity indices in future studies such as the exponential of Shannon entropy and the inverse of Simpson index. Those indices are the effective numbers of species and estimate the true diversity by giving different weights to rare vs. common species (Jost 2006). In addition, our simulations and statistical analyses focussed on multifunctionality metrics with Gaussian distributions. We did not evaluate whether other data distributions (e.g. binary, log-normal and skewed) influenced the metric performance (Schoolmaster *et al.* 2012). When there is a combination of distributions in the data, the convergence of statistical models may disappear because of deviations in normality and linearity. The range-relevant standardization (Grace *et al.* 2018) might be more appropriate in this situation. Future studies should also focus on deepening our understanding of how ecosystem functions interact with each other (e.g. trade-offs and synergies) (Dooley *et al.* 2015; Meyer *et al.* 2018; Slade *et al.* 2019) and the underlying statistical underpinnings of different multifunctionality metrics (Hölting *et al.* 2019). This would improve the interpretation and comparison of biodiversity–multifunctionality relationships.

CONCLUSIONS

The most interesting result from our work is that we can now compare, on a level playing field, how biodiversity is related to multifunctionality across studies that differ in scale and system. Similarly with van der Plas (2019), we found that biodiversity is key driver of multifunctionality in naturally and randomly assembled communities. The scaling and range-relevant approaches allow us to do this because they put biodiversity–multifunctionality relationships on a common scale. Our approach would allow comparisons among systems that differ in land-use history, climate, soil properties or other factors. In fact, it will increase the likelihood that we understand how those factors might alter the relationship between biodiversity and multifunctionality in a changing world. Taken together, our findings suggest that standardization methods are a useful way of comparing biodiversity–multifunctionality relationships among studies.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.
 Note 1: Schematic representation of the biodiversity effect on single functions and ecosystem multifunctionality.
 Note 2: Mathematical background/underpinnings of the averaging, summing and scaling multifunctionality metrics.
 Note 3: A review of the mathematical artefact for the threshold-based approach.
 Note 4: Summary of the methods on the fraction of positive, neutral, or negative biodiversity effects on multifunctionality.
 Table S1: Summary of the averaging multifunctionality metrics.
 Table S2: Summary of the five empirical data sets used in the study.
 Figure S1: Distribution of the experimental and observational studies used in this study.
 Figure S2: Summary of the simulations showing the effect of biodiversity on ecosystem multifunctionality (EMF) in relation to the number of functions included in the EMF estimate.
 Figure S3: Fraction of biodiversity having positive and neutral effects on ecosystem multifunctionality (EMF).
 Figure S4: Results from empirical datasets showing changes in the fraction of biodiversity having positive, neutral and negative effects on ecosystem multifunctionality (EMF) as the number of functions increases.

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Conflict of interest statement. The authors declare no competing financial interests.

Code and Data Availability

R scripts are deposited to Github (<https://github.com/XJingPKU/BEMFmetric>). Part of the empirical datasets from the Tibetan grasslands are deposited to Zenodo (<https://zenodo.org/record/2650366#.XMCxZDBKjbo>). The other datasets can be found within each of the published papers (Maestre *et al.* 2012; Meyer *et al.* 2018; Ochoa-Hueso *et al.* 2018; Ratcliffe *et al.* 2017; Spehn *et al.* 2005).

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