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Predictability of Functional Diversity Depends on the Number of Traits

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Abstract: Analysis of functional diversity, based on plant traits and community structure, provides a promising approach for exploration of the adaptive strategies of plants and the relationship between plant traits and ecosystem functioning. However, it is unclear how the number of plant traits included influences functional diversity, and whether or not there are quantitatively dependent traits. This information is fundamental to the correct use of functional diversity metrics. Here, we measured 34 traits of 366 plant species in nine forests from the tropical to boreal zones in China. These traits were used to calculate seven functional diversity metrics: functional richness (functional attribute diversity (FAD), modified FAD (MFAD), convex hull hypervolume (FRic)), functional evenness (FEve), and functional divergence (functional divergence (FDiv), functional dispersion (FDis), quadratic entropy (RaoQ)). Functional richness metrics increased with an increase in trait number, whereas the relationships between the trait divergence indexes (FDiv and FDis) and trait number were inconsistent. Four of the seven functional diversity indexes (FAD, MFAD, FRic, and RaoQ) were comparable with those in previous studies, showing predictable trends with a change in trait number. We verified our hypothesis that the number of traits strongly influences functional diversity. The relationships between these predictable functional diversity metrics and the number of traits facilitated the development of a standard protocol to enhance comparability across different studies. These findings can support integration of functional diversity index data from different studies at the site to the regional scale, and they focus attention on the influence of quantitative selection of traits on functional diversity analysis.

Key words: trait; functional diversity; richness; evenness; divergence; stability; predictability

1 Introduction

Functional traits are core plant properties, and are closely related to the colonization, survival, growth, and mortality of plants (Cornelissen et al., 2003). In particular, these traits allow plants to optimize productivity (Craven et al., 2018; Xu et al., 2018b; Kordbacheh et al., 2019; Mahaut et al., 2020). Recently, scientists have demonstrated that community traits on per land area using community-weighted means (He et al., 2019a), scaled up from the organ or species level, could be used to interpret certain ecosystem processes and functions at larger spatial scales (He et al., 2019a). To date, trait-based approaches have been used to explore various ecological issues from the species or community level to the ecosystem level (Faucon et al., 2017; Greenwood et al., 2017; Ma et al., 2018).

There are trade-offs or synergies that exist among traits

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(Cornelissen et al., 2003; de Deyn et al., 2008; Reich, 2014; Li et al., 2015; He et al., 2019b), and studing multiple traits has hence become important. The classic leaf economic spectrum demonstrates the trade-off strategy of plant resources (Wright et al., 2004). The adaptation of a single trait to an environmental change may not be important as the adaptive evolution of the specific trait may lag behind environmental change, and the adaptation rather manifested as a coordinated adaptation of multiple traits. Plants adapt to the environment by adjusting multiple traits, with the complex relationships between these traits crucial for maintaining the ecosystem structure and function (Fontana et al., 2016). Furthermore, there is consensus that species diversity influences ecosystem functioning, as well as the diversity of functional traits within communities (Leps et al., 2006). The combination of functional diversity, community structure, and plant traits could help us explore how multiple traits determine ecosystem processes and functioning (Fontana et al., 2016).

Various indices have been proposed to measure plant functional diversity (Pérez-Harguindeguy et al., 2013). In general, functional diversity can be subdivided into functional richness, evenness, and divergence (Table 1). Functional richness indices can quantify the size of the niche space utilized by these measured traits per volume of multidimensional space. Functional evenness can describe the distribution of the trait space occupied by species traits. It refers to whether the distance between the traits of any two nearest species is equal in the trait space. The functional divergence describes the formation of species clusters in the character space, where higher dispersion indicates that the species clusters are distributed at the edge of the character space (Mason and Mouillot, 2005; Laliberte and Legendre, 2010; Schleuter et al., 2010) (The detailed formula is provided in the supplementary file). Through the research of functional diversity, certain diversity indexes have been developed, including functional attribute diversity (FAD) (Walker et al., 2005), convex hull hypervolume (FRic) (Laliberte and Legendre, 2010), functional evenness (FEve) (Laliberte and Legendre, 2010), functional divergence (FDiv) (Mason and Mouillot, 2005; Laliberte and Legendre, 2010; Schleuter et al., 2010), and quadratic entropy (RaoQ) (Botta-Dukát, 2005).

Functional diversity can be used to accurately assess and predict ecosystem functioning, because multiple traits collectively accomplish this (Kearney and Porter, 2006). Similarly, functional evenness and functional divergence are used to elucidate the variation in functional and adaptive mechanisms (Komac et al., 2015). Functional diversity has received extensive attention recently; and research on the relationships between functional diversity and ecosystem function has rapidly increased (Ross et al., 2017). However, dispute remains over how to scientifically calculate and use these metrics. In practice, researchers tend to select certain traits based on their own objectives or the availability of data, leading to inconsistent results across studies that make comparisons among studies difficult (Petchey and Gaston, 2002; Wright et al., 2006; Pasari et al., 2013). Knowledge about how to use a wide variety of plant traits is crucial because different traits will generate different results (Petchey and Gaston, 2006). Therefore, development of a uniform protocol is needed that could be used consistently, or that could enhance comparability across different studies. To accomplish this, it is necessary to identify how the number of selected traits influences functional diversity indexes from the site to the regional scale, and whether these influences are consistent across the different functional diversity metrics.

To explore these issues, we measured 34 traits of 366 plant species from nine forest communities along the North-South Transect of Eastern China (NSTEC), extending from the tropical to the boreal zones. Morphological, chlorophyll, stomatal, and anatomical leaf traits were measured, in addition to multiple element content, and other traits (Fig. 1). The main objectives of this study were to: 1) demonstrate the predictability of the functional diversity metrics by altering the numbers of selected traits, and 2) develop a uniform protocol for metrics that predict functional diversity consistently from the site to the regional scale for use in future studies.

The conceptual framework of functional diversity holds promise as a way to explore relationships in natural communities. Specifically, these functional diversity are predictable (invariably, regularly, or irregularly) under different scenarios of trait number, diversity in importance of different traits, and differences in species diversity. Development of a functional diversity protocol is needed to promote the applicability of these metrics.

2 Materials and methods

2.1 Study sites

Nine typical forest communities were selected for field sampling along the NSTEC (Fig. 2), which is the 15th standard transect of the International Geosphere-Biosphere Program (Zhang and Yang, 1995; Wang et al., 2016). To minimize the effects of human disturbance, we set up these sampling plots in national nature reserves. From south to north, the forests sampled were: tropical, south-subtropical evergreen broad-leaved, subtropical evergreen broad-leaved, and north-subtropical evergreen deciduous broad-leaved mixed forests. The study area covered almost all the main types of forest vegetation in the Northern Hemisphere (He et al., 2018). Across the study sites, the annual average temperature and precipitation ranged from –4.4 to 20.9 °C and 481.6 to 2449.0 mm, respectively, with the precipitation mainly concentrating in summer, from June to August (Xu et al., 2018a).

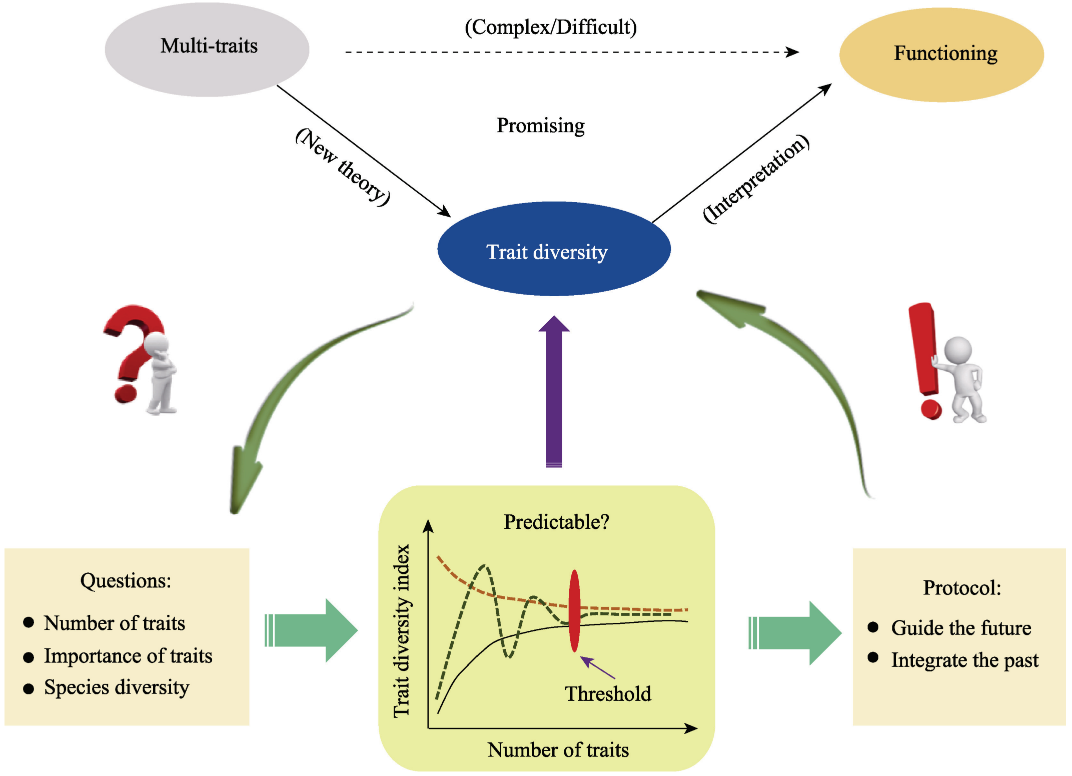
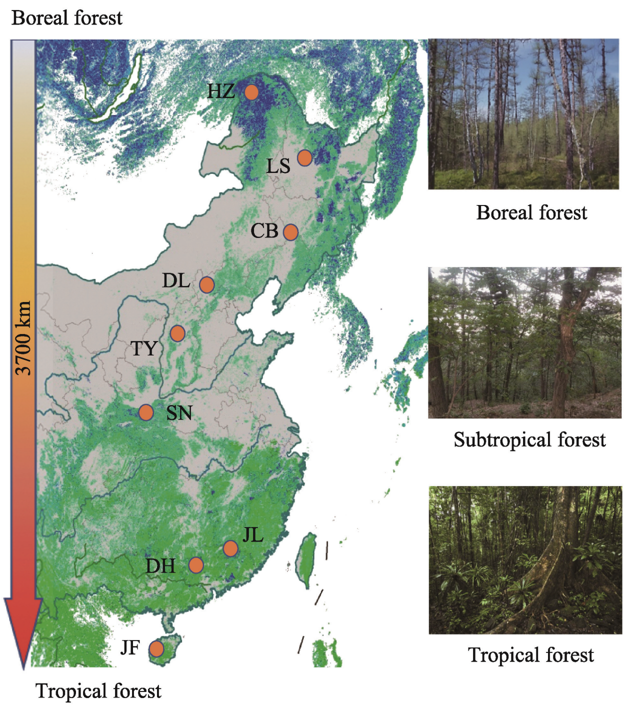


Fig. 1 The opportunities and challenges associated with functional diversity



Category	Traits
Morphological traits	Leaf area (LA)
	Leaf dry weight (LDW)
	Leaf water content (LWC)
	Specific leaf area (SLA)
	Leaf thickness (LT)
Stoichiometric	Leaf carbon content (C)
	Leaf nitrogen content (N)
	Ratio of C:N
	Leaf Ferrumcontent (Fe)
	Leaf Kaliumcontent (K)
	Leaf Magnesium content (Mg)
	Leaf Phosphorus content (P)
	The ratio C:P
Chlorophyll traits	Leaf Chlorophyll a content (*Chla*)
	Leaf Chlorophyll b content (*Chlb*)
	Total chlorophyll content (*Chl*)
	Ratio of *Chla*: *Chla*
Stomatal traits	Stomatal pore length (SPL)
	Stomatal pore width (SPW)
	Stomatal area (SA)
	Stomatal length (SL)
	Stomatal density (SD)
	Stomatal area fraction (P)
Anatomical traits	Upper epidermal cells width (UCW)
	Palisade tissue thickness (PT)
	Sponge tissue thickness (ST)
	Ratio of PT:ST
	lower epidermal cells width (LEW)
	vessels width (VW)
Other traits	Soluble sugar content (SSC)
	Starch content (SC)
	Non-structure carbohydrate (NSC)
	Ratio of SSC:SC
	Leaf calorific value (LCV)

366 species and 34 traits

Fig. 2 The spatial distribution of nine forest communities from the boreal to the tropical zone in China

Note: A total of 34 functional traits and 366 species were sampled across the nine forest sites (orange circles).

2.2 Field sampling and measurement of traits

Field sampling was carried out from the end of July to the beginning of August 2013. We set up four representative plots of 30 m × 40 m in each forest type to collect mature leaves of common tree species within and around the plots. The specific sampling method involved selection of healthy, disease-free, mature trees of different species. Thereafter, four branches at different levels and orientations, specifically from four different directions in the upper, southeast, and northwest of the canopy, were collected from each tree using high-pruning shears or artificial tree-climbing methods. A mixture of leaf samples was obtained from the cut branches, placed in plastic bags, and transported to a laboratory for processing. One tree in each plot represented one replicate; consequently, four trees were considered as replicates per site (Li et al., 2018).

2.2.1 Selection of metrics for plant traits

We measured 34 plant traits of 366 species in the nine forest communities, using a consistent method for recording specific traits across all forest types (cold-temperate to tropical) (He et al., 2020; Table S1 and Fig. S2).

2.2.2 Measurement of leaf morphological traits

Six to ten healthy, intact leaves were flattened out and scanned using a Cano Scan LiDE 110 (Japan), before determining their area using ImageJ software (Nanes, 2015). The leaves were dried to a constant weight in an oven and were weighed to calculate the specific leaf area based on the leaf area and dry weight (Wang et al., 2016).

2.2.3 Measurement of C and N content

An elemental analyzer method (vario MAX CN Elemental Analyzer, Elementar, Germany) was used to determine foliar N content. The leaves were first cleaned to remove soil and other impurities and then dried. The N content in 0.3–0.5 mg of the dried samples was determined (Zhao et al., 2014).

2.2.4 Measurement of chlorophyll traits

Fresh leaf samples (0.1 g) were cut into pieces and, together, with 10 mL of 95% ethanol, were homogenized in a mortar. An additional 5 mL of 95% ethanol was added to the homogenate, which was then filtered, and the filtrate diluted to 50 mL with ethanol. The chlorophyll-ethanol solution was injected into a cuvette with a light path of 1 cm. Pure ethanol was injected into another cuvette of the same specification to serve as a control. The chlorophyll content was calculated according to Lambert Beer's law (Li et al., 2018).

2.2.5 Measurement of stomatal traits

From the samples, five to ten leaves were cut into 1 cm x 0.5 cm sections along the main vein and fixed in FAA solution (75% alcohol : formalin : glacial acetic acid : glycerol = 90 : 5 : 5 : 5) (Field sampling was completed). These sections were dried, pasted to the sample stage, and observed using a scanning electron microscope (Hitachi s-3400 II, Hitachi, Japan). Three small blocks were randomly selected from the sample stage for observation. Two photographs were taken in each of the blocks, resulting in six replicate images for each species. The number of stomata in each image was counted and the area of each image was determined to calculate stomatal density. Five pores in each image were randomly selected to determine the average stomatal pore width, and length, and stomatal area (Liu et al., 2018).

2.2.6 Measurement of anatomical traits

Samples were removed from the FAA fixative and permanent cross-section slides were made using paraffin sectioning, with a total of three replicate sections per species. Anatomical data was acquired using scanning electron microscopy (Liu et al., 2019).

2.3 Selection of metrics for functional diversity

Functional diversity is used to reflect the overall difference or diversity of traits in plant communities. At the beginning of the formation of the functional diversity, the functional diversity index should generally meet the following criteria: 1) multiple traits must be processed simultaneously, 2) species traits and species richness influence the functional diversity of the community, and 3) increasing or decreasing the number of new species or traits affects functional diversity (Villéger et al., 2008). These criteria reinforce the fact that functional diversity requires consideration of both the number of species and traits. Although many types of functional diversity exist, we selected three kinds of diversity corresponding to the three components of functional diversity: functional richness, functional evenness, and functional divergence (Table 1).

Table 1 The protocol of the functional diversity index

Functional diversity	Specific indexes	Description	Predictable	Fitted equation
Functional richness	Functional Attribute Diversity (FAD)	The sum of the distances of species in trait space	Yes	$Y=513.356x^{0.5224}$†
	Modified FAD (MFAD)	Modified FAD, includes species diversity	Yes	$Y=12.4681x^{0.5224}$
	Convex hull hypervolume (FRic)	Convex hull hypervolume	Yes	$Y=0.6849x+5.3610$
Functional evenness	Functional Evenness (FEve)	Distribution rule of trait space occupied by traits	No	
Functional divergence	Functional Divergence (FDiv)	Dispersion of functional traits	No	
	Functional Dispersion (FDis)	Dispersion of functional traits	No	
	Rao's Quadratic entropy (RaoQ)	Both trait richness and trait dispersion	Yes	$Y=0.7969x–0.2641$

Note: † These prediction equations were reduced on all data of the nine forest communities from the tropical to the boreal zone. Detail information for each forest is presented in the supplementary files.

Functional richness is mainly used to quantify how much niche space is occupied by all species in the community (Laliberte and Legendre, 2010). Low trait richness indicates that the available niche in the community is occupied, meaning that some of the resources in the community are not utilized, resulting in lower productivity. In this study, we used the following functional richness indexes: functional attribute diversity (FAD), modified functional attribute diversity (MFAD) (Schmera et al., 2009), and convex hull hypervolume (FRic) (Villéger et al., 2008).

The evenness of traits (FEve) is the distribution law of the mean value of species traits in the trait space. This index quantifies the degree of trait uniformity. Low trait evenness indicates that some resources are over-utilized, whereas other resources are rarely utilized or have not yet been utilized.

Trait dispersion can be used to describe the degree of convergence of traits in the functional space. High functional dispersion indicates that the species group is distributed at the edge of the trait space. This metrics can be used to indicate the degree to which community resources differ as well as the degree of competition. We selected the following three trait dispersion indexes for used in our study: functional divergence (FDiv), functional dispersion (FDis), and Rao's Quadratic entropy (RaoQ).

2.4 Statistical analysis

The seven functional diversity metrics mentioned above (specific index in Table 1) were calculated using R language and FDiversiry software (Casanoves et al., 2011). Based on the well-matched trait and species data collected, we developed a calculation scheme to explore our objectives. The importance of different traits was attenuated by random selection and repeated simulation. At the same time, the multi-site simulated sampling ensured consistency of species diversity. In this way, we could focus more on the effect of trait number on functional diversity. In practice, the procedure was as follows: 1) according to the calculated metric of functional diversity, corresponding data were consistently compiled; 2) different sampling scenarios were simulated and specific trait indicators were extracted from the data table; 3) R language was used to randomly select trait indicators according to a specific number, and these metrics were calculated; and 4) the selected number of plant traits was increased one at a time from 3 to 34, with these traits being randomly selected 100 times, and the average was calculated as the result of each cycle.

3 Results and discussion

Altering the number of traits had different effects on the metrics of functional diversity. The specific indexes FAD, MFAD, FRic, and RaoQ were predictable using the equations indicated in Fig. 3 and Table 1. Theoretically, the niche space of functional richness quantification depends on the traits of species (Fig. 3). The more functional traits included, the larger the niche space that can be quantified (Mason et al., 2005). Therefore, the trait richness metrics could be measured and used to predict the total resource or niche space of different communities (de la Riva et al., 2018; Solefack et al., 2018)(Figs. S1–S4). Using a different number of traits to calculate functional diversity should yield

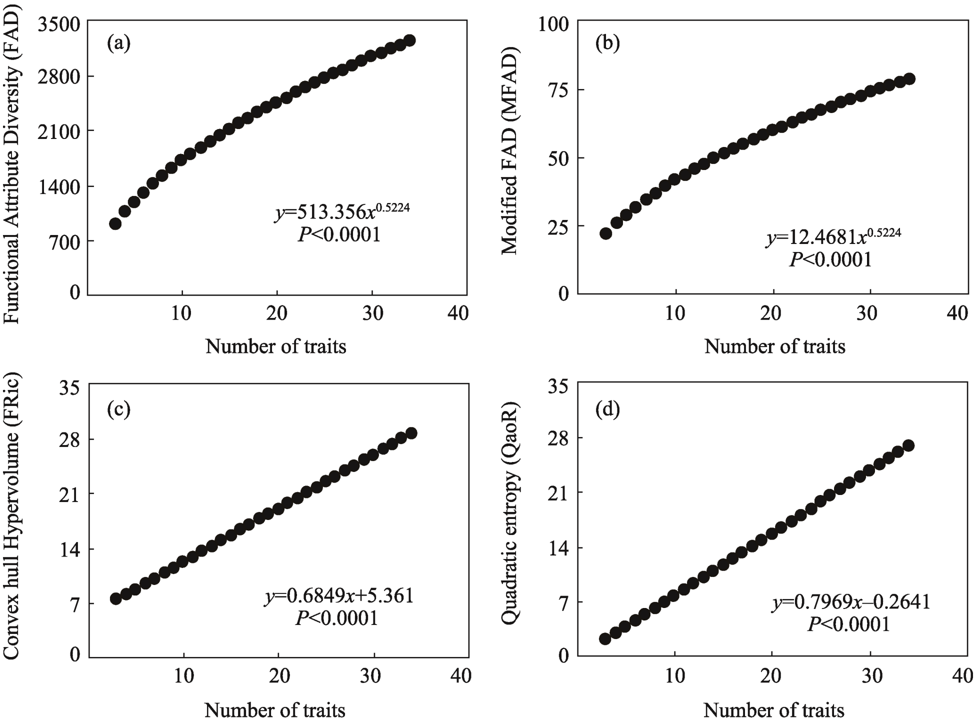


Fig. 3 Relationship between functional diversity metrics and trait number

different results.

Four of the seven functional diversity metrics included in this study were predictable, namely functional attribute diversity (FAD), modified FAD (MFAD), convex hull hypervolume (FRic), and Rao's quadratic entropy (RaoQ). When the number of traits increased from 3 to 34, 100 random combinations were calculated on average (The supplementary files provide these equations for the different regions).

The three metrics of trait richness and RaoQ increased with the number of selected traits. Specifically, FRic showed a linear increasing trend, and FAD and MFAD were well fitted as power functions (Table 1 and Fig. 3). Furthermore, RaoQ was linearly correlated with the number of selected traits, similar to FRic. A plausible explanation for these results is that the calculated equation (Eqs.1–16) contained information on both functional richness and trait dispersion; however functional richness was dominant. Furthermore, the general equations used to determine FAD, MFAD, FRic, and RaoQ were similar across the forest communities sampled (from the tropical to the boreal zone); however, some data sets differed among these functional richness metrics (Tables S2–S5).

Some of the functional diversity metrics could not be predicted, including FEve, FDiv, and FDis. The R^2 of FEve fitting curve is not predictable and ranged from 0.033 to 0.808. The metrics FDiv and FDis were similar, with R^2 values ranging from 0.3792 to 0.9546. Laliberté and Legendre (2010) improved FDiv to achieve FDis. The similarity of the FDis and FDiv results in this study may be due to the fact that the distribution of the center of gravity was offset through calculating the mean value of FDis and FDiv multiple times, therefore making the difference between them smaller. Altering the number of traits resulted in irregularly or even consistent change in these metrics, making it difficult to identify any clear trends (Figs. S5–S7). The indexes FEve, FDiv, and FDis have been commonly used as indicators for quantifying the range of traits and the degree of distribution rules (Kraft and Ackerly, 2010). Our results indicated that the three functional diversity range and distribution metrics were more variable than the functional richness metrics. Consequently, we suggest that the three range and distribution indexes should be used cautiously, especially avoiding reliance on experience or extrapolation of the unknown from the known, because the number of traits had an unpredictable effect on them. Therefore, our findings show that the selection of traits or number of traits is very important when using these metrics.

Determination of functional diversity provides a promising approach for explaining variation in community or ecosystem function, including productivity, nutrient acquisition, flexibility, and resilience (Cornwell et al., 2006; Sonkoly et al., 2019), and can also reflect the adaptation of the community to anthropic disturbances (Biswas et al., 2019). Consequently, the metrics of functional diversity have been widely used across multiple fields of ecology (Petchey et al., 2004). However, our results showed that only one component of functional diversity (mainly functional richness) was predictable, indicating the necessity to further consider the theoretical basis for applying functional diversity. In practice, scientists generally cannot evaluate the repeatability or comparability of different studies, due to differences in the number of selected traits. Theoretically, it is speculated that the basis of calculated functional diversity is similar to species diversity (Petchey and Gaston, 2002), and the theoretical basis of the latter is the theory of niche complementarity. The differentiation of different species is actually the differentiation of traits. The basis of functional diversity is a variety of plant traits and their adaptation and response to environmental changes. Plant traits more directly reflect the resource acquisition of species and the complementation of a niche (Mason et al., 2005; Poos et al., 2009). Therefore, using functional diversity to directly measure all aspects of the spatial distribution of traits in a niche could be used to test these theoretical mechanisms. However, the methods used to calculate functional diversity cannot be overlooked, because of the difference in the relative importance of specific traits. For example, Fig. 3 shows that, as used in this study, the three metrics of trait richness (FAD, MFAD, and FRic) and RaoQ were predictable and similar in different regions. Consequently, these functions should be used as a protocol for guiding future studies or should be incorporated into different studies.

The number of traits is a non-negligible factor for the study functional diversity; however, there is no implementation standard that can be referenced at present. Consequently, small numbers of traits (three or four) have been used to calculate functional diversity in previous studies (Mensah et al., 2016; Staples et al., 2019). Researchers should design experimental protocols for their own experimental purposes more rigorously and scientifically. Some researchers may consider functional redundancy and abandon the use of larger number of functional traits in their analyses (Correia et al., 2018; Lozanovska et al., 2018; Kearsley et al., 2019). Thus, it is important to determine which functional traits perform the more important roles in the community, along with identifying the importance of the traits (Garcia et al., 2015). In natural communities, functional redundancy must exist, and could facilitate the stability and anti-interference ability of the community (Pillar et al., 2013). In this study, the predictive equations of the three trait richness metrics (FAD, MFAD, and FRic) and RaoQ increased non-linearly with the number of traits. This may be related to functional redundancy between traits, and requires further study. Furthermore, researchers are encouraged to select more traits to explore ecosystem processes and functions, to reduce potential errors, and facilitate comparisons across studies in the future.

Using a database of consistently measured traits of plant species found in a range of forest types, we explored the predictability of functional diversity with respect to trait richness, trait evenness, and trait divergence. Our results demonstrated that only the three trait richness metrics and RaoQ were predictable, in relation to the influence of the number of traits on functional diversity. The relationship between each of the three functional richness metrics and number of traits, as well as the relationship between entropy and trait number, are expected to provide standard protocols to enable incorporation of different studies from the site to the regional scale in future. However, at present, uniform standards on what number of traits influences other functional diversity indexes do not exist, nor is there information about how this is achieved. More research is required to improve both the theory of, and methodology used to calculate functional diversity, even though the conceptual framework of functional diversity is promising.

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功能多样性的预测准度受所选择的植物性状数量制约

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摘　要：植物功能多样性（Functional diversity）是将植物功能性状与群落结构相结合而推导的整合参数，为人们揭示植物适应策略、植物性状间关系以及植物性状与功能间关系等提供了一种可选择的新技术手段。然而，至今人们还不清楚功能多样性参数与所选取性状数量的关系，即它是否存在性状数量的依赖性？这些信息对正确使用功能多样性参数至关重要。本文利用中国东部森林样带 9 个典型森林生态系统的规范化测定的 366 个乔木物种和 34 种功能性状，对 7 个广泛使用的功能多样性参数的数量依赖性进行了检验，它们分别是功能丰富度参数（functional attribute diversity, FAD; modified FAD, MFAD; convex hull hypervolume, FRic）、功能均匀度参数（functional evenness, FEve）、功能离散度参数（functional divergence, FDiv; functional dispersion, FDis; quadratic entropy, RaoQ）。分析结果表明：功能丰富度参数均随着所选择性状数量增加而增加，但功能离散度的各个参数对性状数量变化表现出不一致趋势。整体而言，虽然 FAD、MFAD、FRic、RaoQ 随着性状数量变化而变化，但它们是可预测的，可比较的。实验结果证明所选择的性状数量强烈地影响功能多样性参数，大部分参数随着性状数量变化是可预测的，证实了功能性状参数是具有重要潜力的技术手段（特定地点研究和不同研究间的比较），因此在使用过程中需要高度重视性状数量选择的影响。

关键词：性状；功能多样性；丰富度；均匀度；离散度；稳定性；可预测性

Appendix Ⅰ

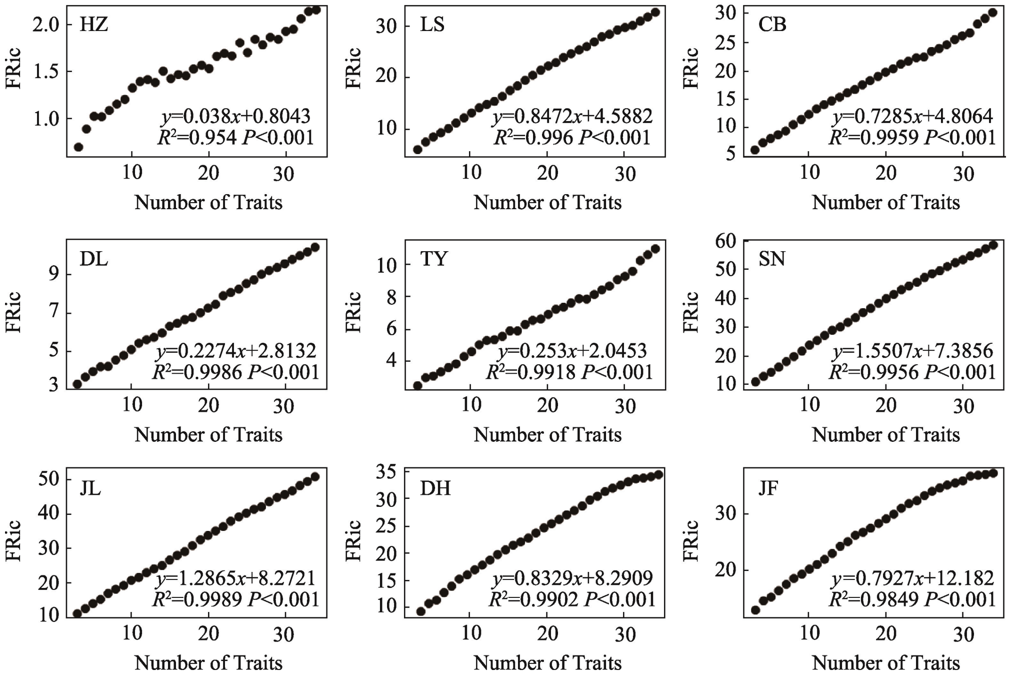

Fig. S1 The relationship between convex hull hypervolume (FRic) and the selected number of traits in different typical forests

Note: HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DongLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

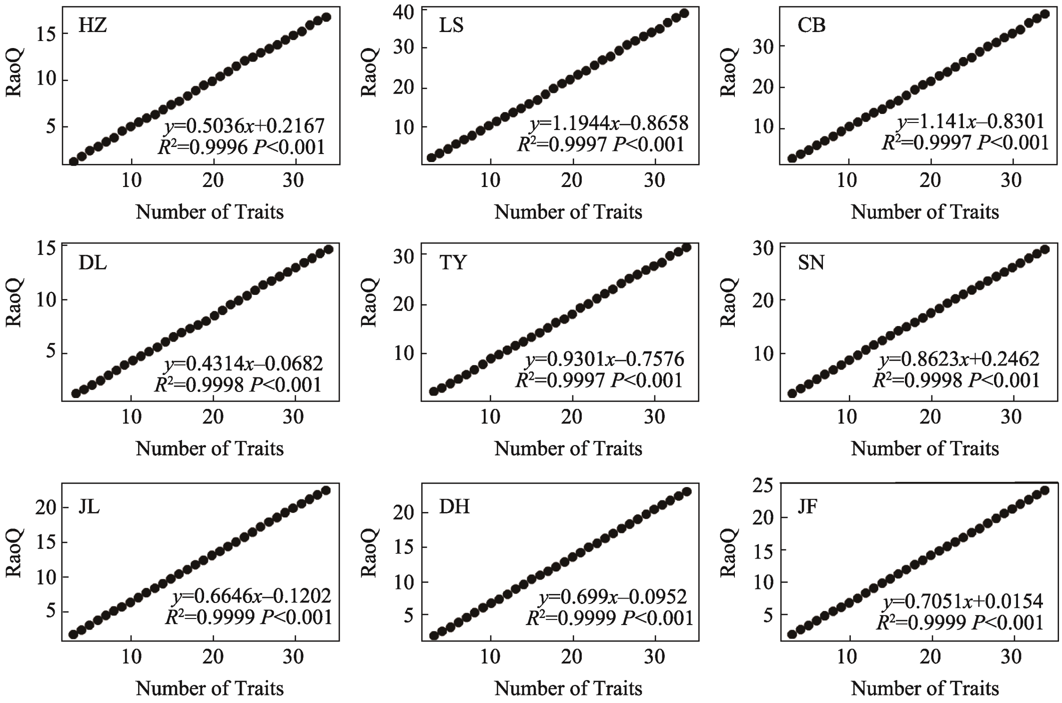

Fig. S2 The relationship between quadratic entropy (RaoQ) and the number of traits in different typical forests

Note: HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DongLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

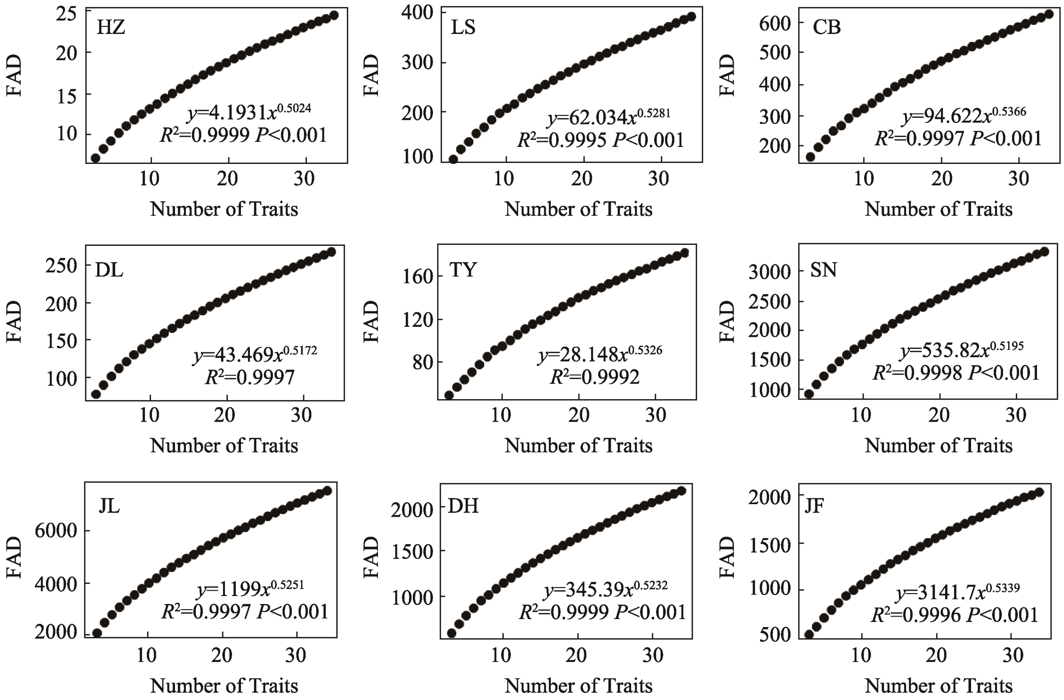

Fig. S3 The relationships between functional Attribute Diversity (FAD)and the number of traits in different typical forests

Note: HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DongLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

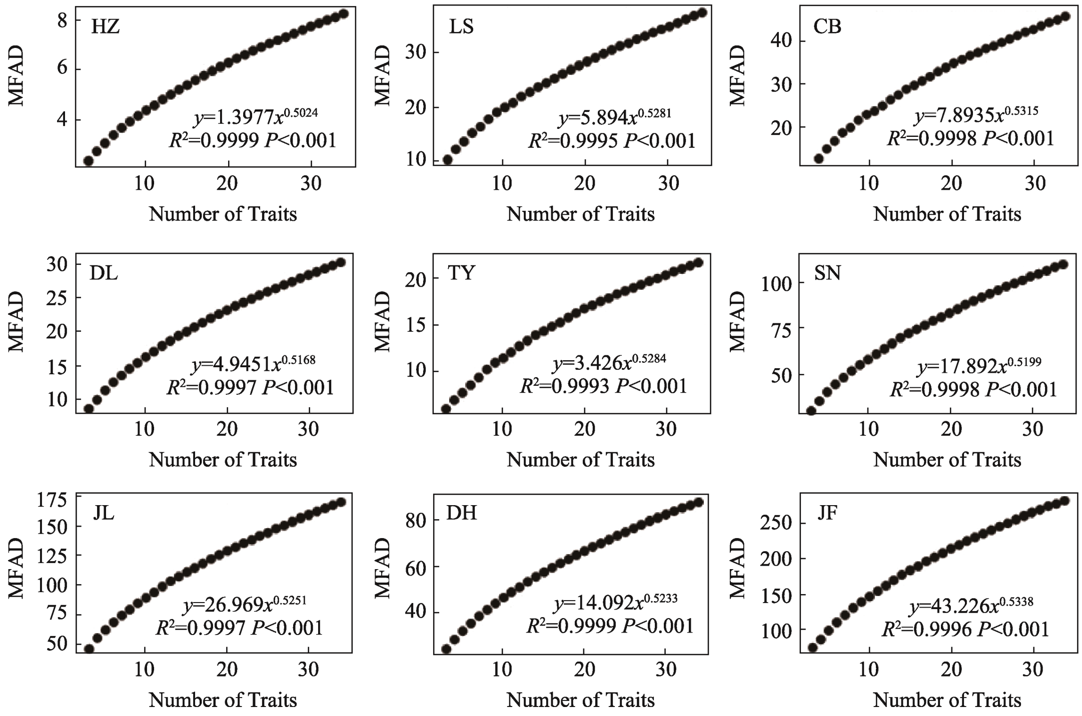

Fig. S4 The relationships between modified Functional Attribute Diversity (MFAD) and the number of traits in different typical forests

Note: HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DongLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

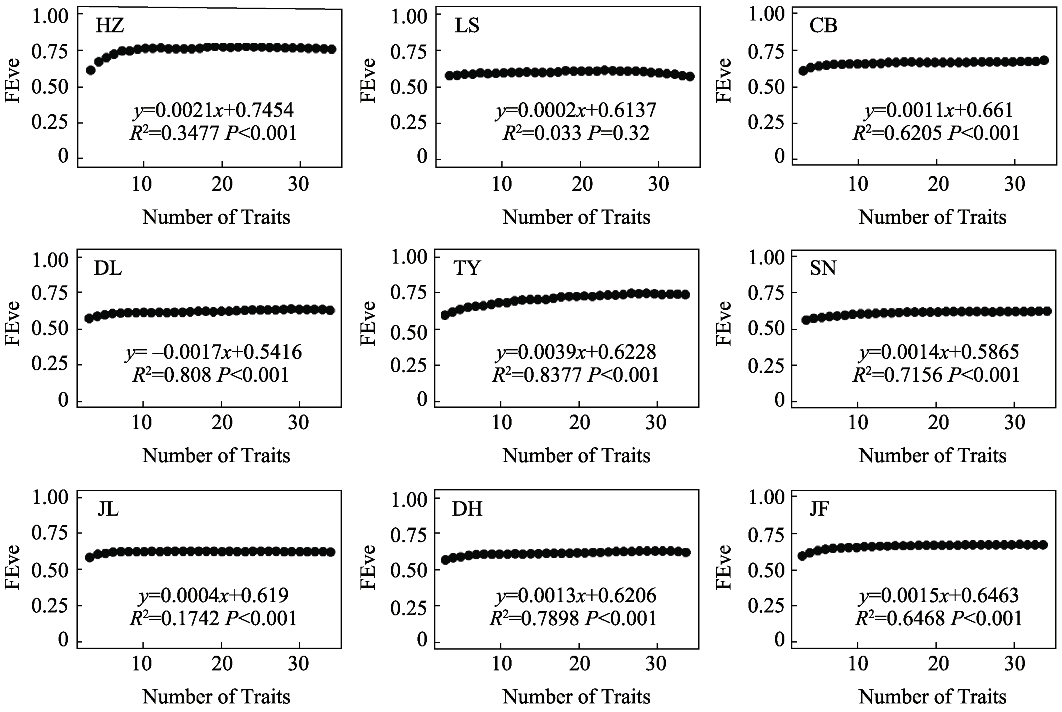

Fig. S5 The relationships between functional evenness (FEve) and the number of traits in different typical forests

Note: HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DongLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

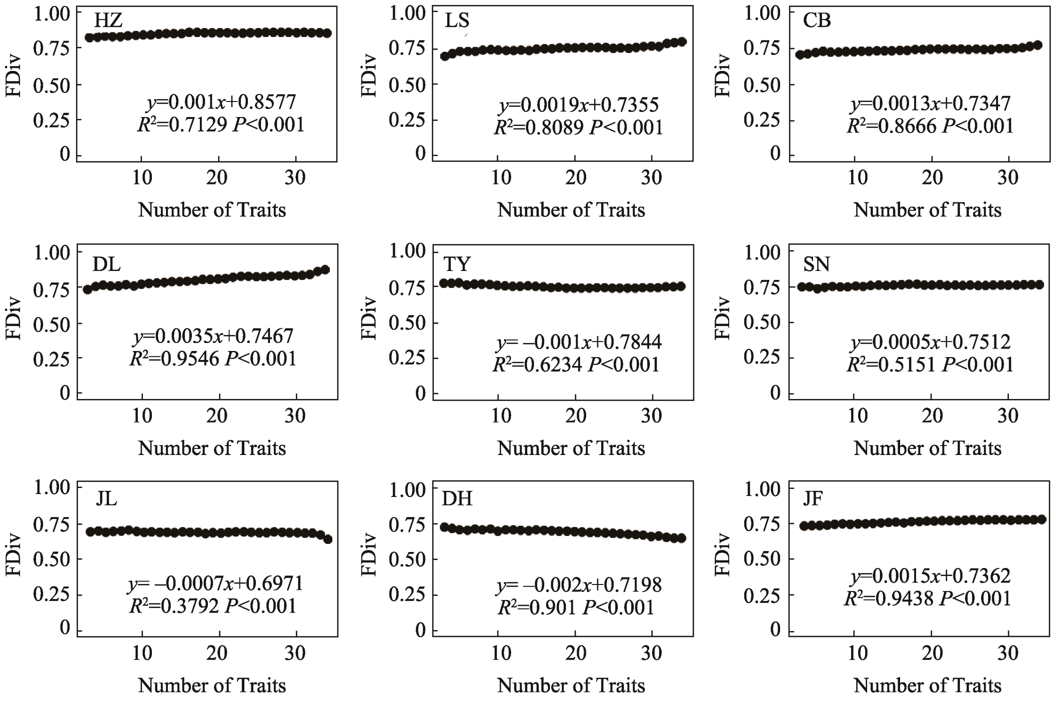

Fig. S6 The relationship between functional divergence (FDiv) and the number of traits in different typical forests

Note: HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DongLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

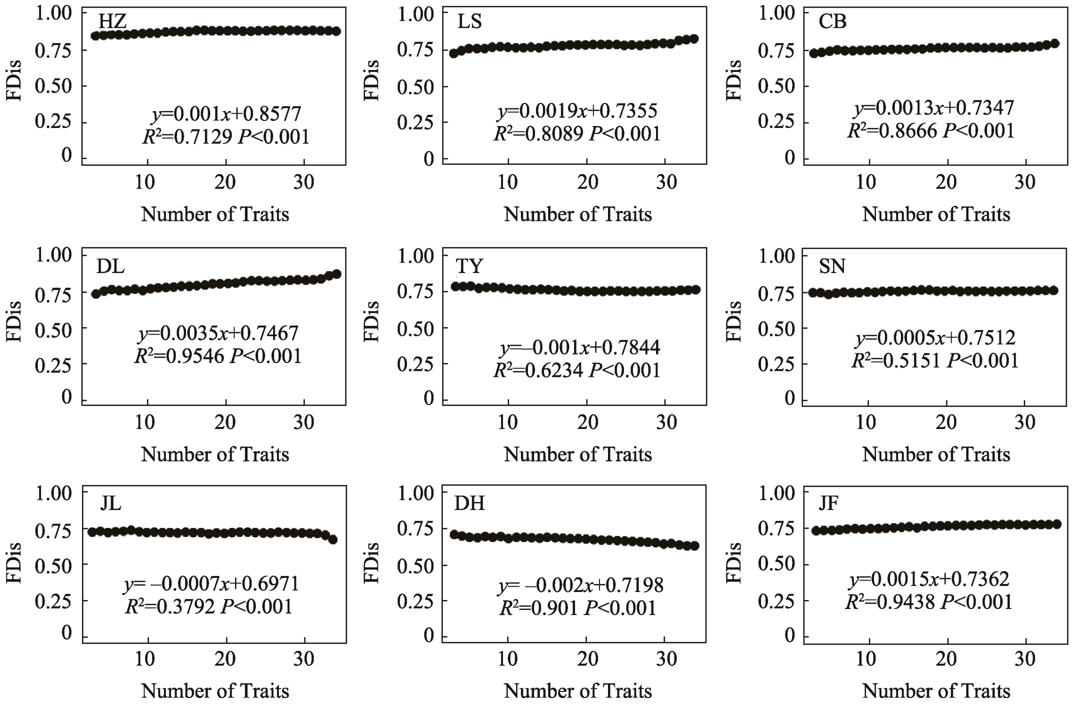

Fig. S7 The relationship between functional dispersion (FDis) and the number of traits in different typical forests

Note: HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DongLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

Appendix Ⅱ

Table S1 The list of these selected traits and their abbreviations

Category	Traits	Unit	Abbreviation	Category	Traits	Unit	Abbreviation
Morphological traits	Leaf area	cm^2	LA	Stomatal traits	Stomatal pore length	μm	PL
	Leaf dry weight	g	LDW		Stomatal pore width	μm	PW
	Leaf water content	%	LWC		Stomatal area	mm^2	SA
	Specific leaf area	mm^2 mg^{-1}	SLA		Stomatal length	μm	SL
	Leaf thickness	mm	LT		Stomatal density	pores per mm^2	SD
Stoichiometric	Leaf carbon content	%	LCC		Stomatal area fraction	%	P
	Leaf nitrogen content	%	N	Anatomical traits	upper epidermal cells width	μm	UEW
	Ratio of C:N	NA	C/N		Palisade tissue thickness (PT)	μm	PT
	Leaf Ferrum content	mg g^{-1}	Fe		Sponge tissue thickness (ST)	μm	ST
	Leaf Kalium content	mg g^{-1}	K		Ratio of PT:ST	NA	PT/ST
	Leaf Magnesium content	mg g^{-1}	Mg		lower epidermal cells width	μm	LEW
	Leaf Phosphorus content	mg g^{-1}	P		vessels width	μm	VW
	Ratio of C:P	NA	C/P	Other traits	Soluble sugar content (SSC)	mg g^{-1}	SSC
Chlorophyll traits	Leaf Chlorophyll a content	mg g^{-1}	*Chl a*		Starch content (SC)	mg g^{-1}	SC
	Leaf Chlorophyll b content	mg g^{-1}	*Chl b*		Non–structure carbohydrate	mg g^{-1}	NSC
	Total chlorophyll content	mg g^{-1}	*Chl*		Ratio of SSC:SC	NA	SSC/SC
	Ratio of *Chla*: *Chlb*	NA	*Chl a/b*		Leaf calorific value	kJ cm^{-2}	LCV

Table S2 The predictive equations of trait richness index (FRic) prediction equations at different sites (mean ±SE)

Area	Site[†]	Fitted equation ($y = kx + \mathrm{b}$)	k	R^2
Temperate zone	HZ	$y = 0.038x + 0.8043$	0.038±0 a‡	0.954
	LS	$y = 0.8472x + 4.5882$	0.8472±0.0587 b	0.996
	CB	$y = 0.7285x + 4.8064$	0.7285±0.2366 b	0.9959
Subtropics	DL	$y = 0.2274x + 2.8132$	0.2274±0.0925 a	0.9986
	TY	$y = 0.253x + 2.0453$	0.253±0.0956 a	0.9918
	SN	$y = 1.5507x + 7.3856$	1.5507±0.1718 c	0.9956
Tropic	JL	$y = 1.2865x + 8.2721$	1.2865±0.2096 c	0.9989
	DH	$y = 0.8329x + 8.2909$	0.8329±0.5388 b	0.9902
	JF	$y = 0.7927x + 12.1820$	0.7927±0.1592 b	0.9849

Note: [†] HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DangLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

[‡] There is no significant difference between data with the same alphabet in each column ($P < 0.01$).

Table S3 The predictive equations of quadratic entropy (RaoQ) at different sites (mean ±SE)

Area	Site[†]	Fitted equation ($y = kx + b$)	k	R^2
Temperate zone	HZ	$y = 0.5036x + 0.2167$	0.5036±0 ab[‡]	0.9996
	LS	$y = 1.1944x - 0.8658$	1.1944±0.1098 f	0.9997
	CB	$y = 1.141x - 0.8301$	1.141±0.2149 f	0.9997
Subtropics	DL	$y = 0.4314x - 0.0682$	0.4314±0.0366 a	0.9998
	TY	$y = 0.9301x - 0.7576$	0.9301±0.0862 e	0.9997
	SN	$y = 0.8623x + 0.2462$	0.8623±0.1035 de	0.9998
Tropic	JL	$y = 0.6646x - 0.1202$	0.6646±0.1134 bc	0.9999
	DH	$y = 0.699x - 0.0952$	0.699±0.0609 cd	0.9999
	JF	$y = 0.7051x + 0.0154$	0.7051±0.0433 cd	0.9999

Note: [†] HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DangLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

[‡] There is no significant difference between data with the same alphabet in each column ($P < 0.01$).

Table S4 The predictive equations of functional attribute diversity (FAD) at different sites (mean ± SE).

Area	Site[†]	Fitted equation ($y = Ax^k$)	k	R^2
Temperate zone	HZ	$y = 4.1931x^{0.5024}$	0.5024±0 a[‡]	0.9999
	LS	$y = 62.034x^{0.5281}$	0.5281±0.0075 bc	0.9995
	CB	$y = 94.622x^{0.5366}$	0.5366±0.0063 c	0.9997
Subtropics	DL	$y = 43.469x^{0.5172}$	0.5172±0.0023 b	0.9997
	TY	$y = 28.148x^{0.5326}$	0.5326±0.0163 b	0.9992
	SN	$y = 535.82x^{0.5195}$	0.5195±0.0050 b	0.9998
Tropic	JL	$y = 1199x^{0.5251}$	0.5251±0.0020 bc	0.9997
	DH	$y = 345.39x^{0.5232}$	0.5232±0.0018 bc	0.9999
	JF	$y = 3141.7x^{0.5339}$	0.5339±0.0015 c	0.9996

Note: [†] HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DangLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

[‡] There is no significant difference between data with the same alphabet in each column ($P < 0.01$).

Table S5 The predictive equations of modified functional attribute diversity (MFAD) at different sites (mean ±SE)

Area	Site[†]	Fitted equation ($y = Ax^k$)	k	R^2
Temperate zone	HZ	$y = 1.3977x^{0.5024}$	0.5024±0 a[‡]	0.9999
	LS	$y = 5.894x^{0.5281}$	0.5281±0.0075 bc	0.9995
	CB	$y = 7.8935x^{0.5315}$	0.5315±0.0063 c	0.9998
Subtropics	DL	$y = 4.9451x^{0.5168}$	0.5168±0.0023 b	0.9997
	TY	$y = 3.426x^{0.5284}$	0.5284±0.0163 b	0.9993
	SN	$y = 17.892x^{0.5199}$	0.5199±0.0050 b	0.9998
Tropic	JL	$y = 26.969x^{0.5251}$	0.5251±0.0020 bc	0.9997
	DH	$y = 14.092x^{0.5233}$	0.5233±0.0018 bc	0.9999
	JF	$y = 43.226x^{0.5338}$	0.5338±0.0015 c	0.9996

Note: [†] HZ, HuZhong; LS, LiangShui; CB, ChangBai; DL, DangLing; TY, TaiYue; SN, ShenNong; JL, JiuLian; DH, DingHu; JF, JianFengLing.

[‡] There is no significant difference between data with the same alphabet in each column ($P < 0.01$).

Appendix Ⅲ

The formula of trait diversity index

1. *FAD* is commonly calculated as Eq. 1 and Eq. 2:

$$ED_{ij}=\sqrt{\sum_{t=1}^{T}\left(x_{tj}-x_{ti}\right)^2} \tag{1}$$

$$FAD=\sum_{i=1}^{S}\sum_{j>1}^{S}ED_{ij} \tag{2}$$

where T is the number of traits, and x_{ti} and x_{tj} are the values of species i and species j for trait t, respectively. ED_{ij} is the Euclidean distance between species i and species j, and S is the number of species.

2. *MFAD* is a multidimensional trait richness index derived from the development of the *FAD* index, which considers the impact of species diversity (Eq. 3).

$$MFAD=\frac{FAD}{S} \tag{3}$$

3. *FRic* is calculated by the area or volume of the smallest polygon generated within the multidimensional convex hull volume formed by multiple traits (Villeger *et al.* 2008). This is a complex calculation that can be done in both Qhull software (http://www.Pricklysoft.org/software/ raithull. html) and R languages (http: //www.ecolag. univmontp2. fr/index. php? option = com _ content & task = view & id=219 & Itemid=125).

4. The evenness of traits (*FEve*) is the distribution law of the mean value of species traits in the trait space (Eqs.4–6).

$$FEve=\frac{\sum_{b=1}^{S-1}\min\left(PEW_b\times\frac{1}{S-1}\right)-\frac{1}{S-1}}{1-\frac{1}{S-1}} \tag{4}$$

$$PEW_b=\frac{EW_b}{\sum_{b=1}^{S-1}EW_b} \tag{5}$$

$$EW_b=\frac{d_{ij}}{w_i+w_j} \tag{6}$$

where S is the number of species, PEW_b is the local weighted average uniformity, EW_b is the weighted average uniformity, w_i is the relative abundance of species i, and d_{ij} is the Euclidean distance between species i and species j.

5. *FDiv* was calculated as follows:

$$g_k=\frac{1}{S}\sum_{i=1}^{S}x_{ik} \tag{7}$$

$$dG_i=\sqrt{\sum_{k=1}^{T}\left(x_{ik}-g_k\right)^2} \tag{8}$$

$$\overline{dG}=\frac{1}{S}\sum_{i=1}^{S}dG_i \tag{9}$$

$$\Delta d=\sum_{i=1}^{S}w_i\times\left(dG_i-\overline{dG}\right) \tag{10}$$

$$\Delta\left|d\right|=\sum_{i=1}^{S}w_i\left|dG_i-\overline{dG}\right| \tag{11}$$

$$FDiv=\frac{\Delta d+\overline{dG}}{\Delta\left|d\right|+\overline{dG}} \tag{12}$$

where S is the number of species, x_{ik} is the value of species i trait k, g_k is the center of trait k, T is the number of traits, dG_i is the average distance between species i and the center of gravity, and d is the dispersion degree with multiple degrees as the weight, w_i is the relative abundance of species i; $\overline{dG}$ is the mean of dG_i .

6. *FDis* is a new index from *FDiv*'s further improvement.

$$c=\left[c_i\right]=\frac{\sum a_j x_{ij}}{\sum a_j} \tag{13}$$

$$FDis=\frac{\sum a_j z_j}{\sum a_j} \tag{14}$$

where a_j is the relative abundance of species j and x_{ij} is the ith trait of species j. z_j is the weighted distance from species j to center c. Where a_j is the relative abundance of species j and x_{ij} is the i^{th} trait of species j. z_j is the weighted distance from species j to center c.

7. *Rao* defines a quadratic entropy equation that can be used to quantify the diversity and variability within a system.

$$d_{ij}=\sum_{t}^{T}\left(x_{tj}-x_{ti}\right)^2 \tag{15}$$

$$RaoQ=\sum_{i=1}^{S-1}\sum_{j=i+1}^{S}d_{ij}p_ip_j \tag{16}$$

where S is the number of species, x_{ij} is the t-characteristic of species i, p_i is the relative abundance of species i, and d_{ij} is the distance of species i and j in the trait space.