Review

Functional diversity in plant communities: Theory and analysis methods

Jin-Tun Zhang\textsuperscript{1*}, Lihong Fan\textsuperscript{1} and Min Li\textsuperscript{2}

\textsuperscript{1}College of Life Sciences, Beijing Normal University, Beijing 100875, China.
\textsuperscript{2}Institute of Loess Plateau, Shanxi University, Taiyuan 030006, China.

Accepted 23 December, 2011

Plant functional diversity in community has become a key point in ecology studies recently. The development of species functional diversity was reviewed in the present work. Based on the former original research papers and reviews, we discussed the concept and connotation and put forward a new definition of functional diversity that refers to the change of species functions in communities, and species functions are reflected by functional traits during the completion of their life histories. The ecological process in ecosystems or ecosystem function is closely related to functional diversity. The present quantitative methods for functional diversity analysis were reviewed and their validity needs to be evaluated by more application studies, and new effective methods need to be developed. The questions and problems in functional diversity studies were discussed and will be solved in the future research, and the perspectives for functional diversity research were also discussed in this review.

Key words: Functional diversity, community structure, ecosystem function, quantitative methodology, ecology theory.

INTRODUCTION

General interest in biodiversity has grown rapidly in recent decades, in parallel with the growing concern about nature conservation generally, largely as a consequence of accelerating rates of natural habitat loss, habitat fragmentation and degradation, and resulting extinctions of species (Zhang, 2003; 2005). Biodiversity includes genetic variation within species (genetic diversity), the variety of species in a community or an area (species diversity), and the variety of habitat types within a landscape (ecosystem diversity). Species diversity is the main content of biodiversity, which study species composition and coexistence conditions in a community or ecosystem from taxonomy, systematics and biogeography (Thompson et al., 1996; Westoby et al., 2002). Status, formation, succession and mechanism of maintenance of species diversity are main research contents for species diversity. The species diversity is not just related to the number of species in a community, and also to the number of individuals of each species, distribution, mutual relations, but also to the respective function of species, that is, related to species functional diversity.

In recent years, the relationship between biodiversity and ecosystem function has become a major scientific problem in the field of ecology. With the global species extinction acceleration, the impact of species reduction on the ecosystem become a key topic of concern (Sun, 2003; Zhang and Zhang, 2007). For studying a number of key questions on species diversity and ecosystem function, some observations, experiments, theoretical analysis have been widely expanded, and some meaningful results have been obtained, but no conclusion has been generally recognized on many issues, and there are still heated debates (Loreau et al., 2001). For understanding the relationship between species diversity and ecosystem functioning, some ecologists thought that ecosystem function is subject to influence or control of species diversity, and they carried out some experiments to simulate the loss of species diversity, and monitor system function changes (system productivity, nutrition

*Corresponding author: E-mail: Zhangjintun@yahoo.com.cn. Tel: 86 10 58807647. Fax: 86 10 58807721.

Abbreviations: FD, Functional Diversity; FR, Functional richness; FE, Functional evenness; FTD, Functional trait diversity; FAD, Functional Attribute Diversity; CWM, community weighted mean; MST, minimum spanning tree.
maintenance, the decomposition rate, etc.) (Lawton, 2000; Naeem, 2002). While other ecologists believed that the effects of species diversity on ecosystem function are shared and confused with the effects of other factors in the studies of species diversity and ecosystem functioning. May be a “selection effect” (sampling effect), rather than species diversity itself lead to changes in ecosystem function (Tilman et al., 1997). They also believed that the ecosystem functions may be more controlled by species composition (species biological characteristics) and other factors rather than species diversity, and there is not existence of necessary connection or exist uncertainty relations between species diversity and ecosystem function (Tilman et al., 1997). This showed that the species functional diversity is more important. In fact, the functional diversity did not receive much attention in previous studies, and now the functional diversity as a crucial concept to ecological process and ecosystem function is proposed. In the past decade, the use of “functional diversity” is exponential growth in ecological literature and the widespread use of functional diversity in ecological research shows that functional diversity is gaining an increasingly important role (Zhang, 2011).

Functional diversity has become a crucial and controversial concept in the biodiversity and ecosystem function debate (Wardle et al., 2000). There is an increasing body of work demonstrating its importance. Yet it is still unclear what functional diversity is, or how it should be measured (Mason et al., 2003). The aim of this paper was to review the development of functional diversity studies including its definition and contents, to discuss the relationships of functional diversity with ecosystem function, to introduce and evaluate quantitative measurement methods of functional diversity, and to present perspectives in future study.

CONCEPT AND CONNOTATION OF SPECIES FUNCTIONAL DIVERSITY

Despite the importance of functional diversity is increasingly being recognized and the studies of functional diversity is also increasing, there are still a lot of controversy about the definition of functional diversity. Different scholars have different interpretations.

For species functional diversity, Tesfaye et al. (2003) defined it as the functional multiplicity within a community. The concept is simple and clear, but no detailed interpretation of its meaning and connotation. It is difficult to be measured quantitatively (Zhang, 2011). Diaz and Cabido (2001) defined it as the number, type and distribution of functions performed by organisms within an ecosystem. This definition includes the roles of all organisms in a community. Tilman (2001) defined it as functional diversity which refers to those components of biodiversity that influence how an ecosystem operates or functions. This definition believed that the connotation of biodiversity is more abundant in a habitat, which includes all the species, all differences between genotype and phenotype of species, and all differences in time and space of species in communities and ecosystems. According to this definition, ecosystem with a high functional diversity will have a higher productivity, a strong resilience and a strong resistance to invasion (Petchey and Gaston, 2006). However, this concept is more complex, which can cover all the aspects of biological communities or ecosystems, such as the changes of microbial or plant functional characteristics, the complexity of the food chain, the quantity of plant functional groups and so on. According to this definition, it is also difficult to give functional diversity a quantitative measurement (Wang and Zhang, 2010).

Currently, the definition more widely accepted by researchers is that functional diversity refers to the value and scope of species functional traits in a special ecosystem, also called Functional trait diversity (FTD). It stresses the differences of functions among species in communities (Tilman et al., 2001; Petchey and Gaston, 2002). Accordingly, it can be said that functional diversity is the most important part of biological diversity, which is an important feature reflecting ecosystem function (Diaz and Cabido, 2001; Mason et al., 2005).

We believe that functional diversity refers to the change of species functions in communities, and species functions are reflected by functional traits during the completion of their life histories. The differences in types, change amplitude and stability of these functional traits reflect the quantity of species functional diversity in community. They play certain roles to community function or ecosystem function. Therefore, species functional diversity and ecosystem function are different concepts, but is linked to each other (Zhang, 2011).

Species functional diversity can be divided into functional richness and functional evenness (Mouillot et al., 2005). Functional richness and evenness have their own unique ecological significance, and the two also share a common characteristic to show the properties of the same community or ecosystem. Mason et al. (2005) suggested that the components of functional diversity need to be divided to link ecosystem function, and so that functional diversity can effectively test the mechanism of interactions between diversity and ecosystem function. Thus they divided functional diversity into functional richness, functional evenness and functional divergence.

The functional richness of community depends not only on the functional niche occupied by species, but also on the range of values of functional trait, that is, species functional richness shows the size of the functional space occupied by species in a community. While species functional evenness reflects the efficiency in utilizing the full range of effective resources in the community. It illustrates that the distribution uniformity of species functional characteristics in the ecological space within communities (Mouillot et al., 2005). Functional divergence reflects the probability of two random sampling species with the same functional characteristics, and also reflects the degree of niche complementarity among species and quantitative
heterogeneity of functional traits in communities. A higher degree of functional divergence implies that niche overlap is weak, and competition for resources is relatively weak in the ecosystem. Therefore, a high degree of functional divergence can increase ecosystem functions of communities, due to the higher efficiency of resource utilization.

RELATIONSHIP BETWEEN FUNCTIONAL DIVERSITY AND ECOSYSTEM PROCESSES

The roles of plant functional diversity to ecosystem function has been the research focus in recent years. The effects of functional diversity on ecosystem or community productivity and on resource short-term dynamics, as well on ecosystem stability and long-term resistance are mainly the research topics. There were many different research results and hypotheses from these studies. Actually, different research results are due to many causes such as functional process selection, functional trait selection, experimental design, statistical analysis of results, experimental control measures and scale effects and so forth, which results in different theories and mechanisms (Diaz and Cabido, 2001).

Functional diversity and ecosystem productivity

Community productivity is a main reflection of ecosystem function (Zhang, 2003). Many studies showed that the diversity of species functional groups is the basis of community productivity. Tilman et al. (1997, 2001) studied the effects of species richness, functional diversity and functional group on community primary productivity of plants, plant N ratio, total N and plant photosynthetic rates and other ecological processes. The results showed that species richness, functional diversity and functional group composition all had obvious impacts on the ecosystem processes, but functional group composition and functional diversity were leading factors. Diaz and Cabido (2001) analyzed and summarized the results of 25 experiments in the effects of species diversity, functional diversity and functional group composition on ecosystem processes in the world, 17 experiments in the artificial ecosystem and eight experiments in controlled natural ecosystems, which also come to this conclusion: functional group composition and functional diversity had greater roles in ecosystem processes compared with species richness (Diaz and Cabido, 2001).

There are two main mechanisms which can explain the potential effect of functional diversity on productivity. One is sampling effects (selection effect) for species with extremely functional traits (Tilman, 1997). Species sampling effect model assumes that there are differences in the competitive ability among species, and highly competitive species will have high productivity. Community with higher functional diversity will have more opportunity for occurrence of species with higher competition ability, and so will have higher productivity (Tilman, 2001). In a community, the greater the difference between species is, the greater the effects of functional diversity on system function will be (Zhang and Zhang, 2002). The other is the niche complementarity effect. Each habitat has spatial and temporal heterogeneity, and the differences of species functional traits led them to have different reactions to heterogeneity. Any species in its best niche space must be a better competitor and a stronger producer. Therefore, the coexistence of many species with large ranges of functional traits in a habitat will lead to an increase in ecosystem productivity. For example, soil pH and soil nutrients will affect species richness. Different species have different requirements for these two environmental factors, and the difference of environmental factors allows the existence of different species in a community. A community with single species can not completely and effectively use environmental resources in the system (Zhang and Zhang, 2007; Suding et al., 2008).

The difference between Selection effect model and niche complementary effect model is that the community composed with a single species with the most competitive ability overall characteristics will have the maximum productivity in selection effect mode, and this case only exists in the agro-ecosystem of high productivity. While in the niche complementary effect model, the functional characteristics of two species are more than that of individual species, so the productivity of two species community is higher than that of individual species community. Similarly, the functional characteristics of three species are more than that of two species, and the former has more productivity than the latter, and so on. The more the mixture of system is, the greater productivity will be. This theory is suitable for all natural ecosystems (Tilman, 2001).

Functional diversity and resource dynamics in ecosystem

The quantity of functional diversity affects the resource dynamics within an ecosystem, and the mechanism can also be explained by use of sampling effects and niche complementary effects. Sampling effects believed that the higher the species richness in communities are, the more the probability of existence for species with special traits are, which will play dominant roles in ecosystem function (Wang and Zhang, 2010); it emphasized the value of characteristic species, while niche complementary effects thought that community with higher species richness will have a variety of plant species with different functional characteristics, and they effectively utilize all environmental resources in the temporal and spatial variation in community. Niche complementary theory emphasizes interspecies differences in the characteristics, which improves the efficiency of environmental resource utilization in amount and rate (Diaz and Cabido, 2001).
When the contributions of all species to ecosystem functions are unique and equal in an ecosystem, the increase of species diversity will lead to a linear increase for ecosystem processes. However, if the responses of different species (groups) to environmental factors and the impacts of different species on ecosystem processes are different, then the relationships between species richness and ecosystem functional processes are not linear. Thus, compared with single-function type, the ecosystem with multi-functional groups will increase the complementarity of resource utilization. At this time, the effects of functional diversity on ecosystem function are more apparent (Zhang, 2005).

In most cases, a small number of key species affect major ecosystem functions. That completely lost a functional group will have much greater impact on ecosystem than that lost the same number but derived from different functional groups of species. The experimental results of species addition also proved that the ecosystem added new functional group can lead to significant change of ecosystem function. The natural experiments of land use also support this theoretical speculation.

**Functional diversity and ecosystem complexity and stability**

The ecosystem complexity and stability are closely related functional diversity. Generally, scientists believed that the richer the functional diversity is, the more the complex of system, the closer to climax and the stronger the stability of system will be (Mokany et al., 2008). But its impact process, there are still controversial. Mokany et al. (2008) studied the effects of species diversity and species functional characteristics on net primary productivity, litter decomposition rate, soil moisture and plant photosynthetic rate, in natural ecosystems and found that functional characteristics of dominant species had significant impacts on the ecosystem processes and dynamics, that is, functional diversity has an important roles in ecosystem stability and complexity. There are several hypotheses for interpreting the mechanism of functional diversity and ecosystem stability and complexity.

**Diversity - stability hypothesis**

This hypothesis was proposed by MacArthur (1955) and believed that the ecosystem stability and functional trait diversity has a strict linear relationship and ecosystem stability will be characterized as species richness increases.

**Rivet hypothesis**

Ehrlich and Ehrlich (1981) proposed a rivet hypothesis. They thought that each species existing in ecosystem is unique in contribution to ecosystem function, and all species has small but important roles in the maintenance of system functions. Any ecosystem functions (machine) will be influenced by the loss of functional characteristics of species (rivets), and the reduction in the number of species functional characteristics, will cause the extent of system damage to accelerate gradually.

**Ecological redundancy or ecological insurance hypothesis**

These two concepts are two sides of one issue and are debate focus on diversity and ecosystem function relations. Ecological redundancy hypothesis believed that there is a low limitation for species functional diversity in an ecosystem, and this limitation is necessary for ecosystem to maintain its normal function. When functional diversity is higher than the limitation, the increase or decrease of species number do not have much effect on the system function, and these increase or decrease species are called redundant species (Huang et al., 2001). Walker et al. (1999) thought that functional redundancy plays a role as insurance, which can prevent the loss of functions resulting from species loss. In this sense, redundancy is not redundant. In communities, the more the species with different functions are, the more the probability of species able to survive under environmental change and the greater the probability of maintaining ecosystem stability will be (Diaz and Cabido, 2001).

That close contact with the concept of functional redundancy is that of insurance hypothesis. Species are not synchronized in responses to environment, meaning that there is differentiation of temporal niche. When ecosystem withstands exquisite changes of environment, niche differences can make species different in risk-sharing (Zhang, 2002). In this case, functional diversity can play insurance role in ecosystem, because increase of functional diversity can increase the probability of species responses under different conditions and in the turbulent environment (Diaz and Cabido, 2001). Functional redundancy and functional insurance reflect the difference between functional roles and functional responses, which reflect different aspects as a funda-mental link between functional diversities, that is, there is a certain degree of redundancy for particular function types in ecosystem. The loss of a small amount of species will not cause major change in ecosystem function in short term, because the subsistence species will respond differently to the change of environment. Although functional redundancy plays a buffer role to dramatic changes in ecosystems, a combination of different functional types is significant to maintain ecosystem function stability in long-term (Sun, 2003).

**MEASUREMENT OF FUNCTIONAL DIVERSITY**

In recent years, measurement methods of functional diversity based on species traits have attracted much
attention in ecology, and there are many studies tried to
develop methodology in this area (Ackerly and Cornwell,
2007; Suding et al., 2008). Functional diversity is a mea-
sure of species trait diversity, which should allow it to
predict the changes in ecosystem processes based on
changes in community composition (Hillebrand and
Matthiessen, 2009). Instead of defining functional groups
classified according to a priori defined schemes, func-
tional diversity can also be described in continuous
ecological-gradients of different traits, which are directly
linked to certain functions of species and ecosystems
(Hillebrand and Matthiessen, 2009; Griffin et al., 2009;
Wacker et al., 2009). The several present methods of
functional diversity measurement are available to calcu-
late the functional diversity indices based on functional
traits of species in communities.

Selection of traits

Functional diversity comprises different descriptors of
variation in traits (Mouillot et al., 2005). Species traits are
considered to be functional traits, which are defined as
morphological, physiological, reproductive, ecological or
phenological characteristics of a species affecting its
individual performance in its life history (Vielle et al.,
2007; Hillebrand and Matthiessen, 2009). Body size,
resource uptake rates, growth rates or life history phases
(for example, resting stage production) can be consid-
ered such functional traits (Litchman and Klausmeier,
2008). Thus, functional traits influence species fitness by
affecting survival, growth and reproduction. By upscaling
from the individual to the community level, functional
traits are characterized as components of species pheno-
type that influence ecosystem processes (Petchey and
Gaston, 2006). Thus, different functional traits used in
measurement will affect the quantity of functional diver-
sity (Zhang, 2011). Generally, there are three categories
of plant traits: (1) plant morphology, such as growth form,
life form, plant height, cloning capacity and underground
storage organs, stabs or coats, flammability, leaf size,
leaf hardness, leaves life, bark thickness, root length and
diameter, (2) plant reproductive characteristics, such as
number and size of pollen, diffusion, seed shape and
size, seed weight, ability to sprout, and (3) plant physio-
logical characteristics: N and P content in leaf, chlorophyll
content, photosynthetic rate, respiration rate, biomass,
nitrogen-fixing capability etc. All these traits have been
considered and used in functional studies, but morpho-
logical and reproductive traits were more commonly used
than physiological traits because the former two are easy
to be measured and more stable (Zhang, 2011).

Methods for measuring functional diversity

Functional richness

Functional richness (FR) of a community depends not
only on the functional niche size occupied by species, but
also on the range of values of functional traits. Functional
richness reflects the size of functional space occupied by
species. It is calculated as follows (Mason et al., 2005):

\[
FR_{ci} = \frac{SF_{ci}}{R_c}
\]  (1)

Where, \(FR_{ci}\) refers to the functional richness of functional
character \(c\) in community \(i\), \(SF_{ci}\) is the niche space filled
by species within the community, \(R_c\) is the absolute range
of the character. If the absolute range of a character is
not known, \(Rc\) may be taken as the largest range in the
set of communities being studied which will make the
calculations consistent within the study, or it may be
taken as the range of values reported in the literature
(Mason et al., 2005).

Functional evenness

Functional evenness (FE) (or called functional regularity)
measures how evenly-spaced species are in functional
space, weighted by species abundances (e.g. density or
biomass). Functional regularity is one of a set of
measures that may be used to estimate the functional
evenness component of functional diversity (Mouillot et
al., 2005). Regularity in species abundances (evenness)
has already been related to fundamental community
functions such as species complementarity, resistance to
invasion and productivity (Wiseley and Potvin 2000;
Mouillot et al., 2005). For categorical functional traits (e.g.
flower colour, C4/C3 photosynthesis, seed size), and for
functional groups, functional regularity index can be
calculated as:

\[
FRO = \sum_{i=1}^{C} \min\left(P_i, \frac{1}{C}\right)
\]  (2)

with \(p_i\) the proportion of community abundance (e.g.
biomass) belonging to the \(i\)th category or group and \(C\) the
total number of categories or groups.

Functional divergence

A method for calculating functional divergence was pre-
sented by Mason et al. (2003) based on an abundance-
weighted sum of squares. It uses the mean character
value for each of the species in a community. The
formula is:

\[
FD_{c,x} = \frac{2}{\pi} \arctan\left[ 5 \times \sum_{i=1}^{N} \left( \ln \bar{C}_i - \ln x \right) \times A_i \right]
\]  (3)
where, $FD_{car}$ is the functional divergence across functional character categories, $C_i$ the character value for the $i^{th}$ functional character category, $A_i$ the proportional abundance of the $i^{th}$ functional character category, $\ln x$ the abundance-weighted mean of the natural logarithm of character values for the categories. That is, the sum of category proportional abundances multiplied by the natural logarithm of category character values. $N$ refers to category number in community. The arc tangent is taken of the abundance-weighted sum of squares for the categories, and multiplied by $2/\pi$ so that the index is constrained to vary between 0 and 1. The inclusion of the value 5 allows a more even use of the 0 to 1 scale (Mason et al., 2005).

High functional divergence indicates a high degree of niche differentiation, and thus low resource competition. Thus communities with high functional divergence may have increased ecosystem function as a result of more efficient resource use (Mason et al., 2003).

**Walker functional diversity (FAD)**

Walker et al. (1999) proposed an index termed ‘Functional Attribute Diversity’ (FAD) aimed at estimating the dispersion of species in trait space as the sum of the pairwise species distances in $D$:

$$FAD = \sum_{i,j} d_{ij}$$

$d_{ij}$ is functional distance between species $i$ and $j$ in functional trait space and $d_{ij}$ varied from 0 (two species have the same characteristics) to 1 (two species have completely different characteristics).

This distance matrix $D = (d_{ij})$ is calculated based on the matrix of functional trait $(N)$ by species $(S)$. A number of distance coefficients can be chosen for calculation of $D$.

**Rao’s index**

Rao’s index indicates the expectation of trait dissimilarity between two randomly chosen individuals in a community (Ricotta, 2005; Lepš et al., 2006). If $d_{ij}$ is the dissimilarity between each pair of species $i$ and $j$, the $\alpha$ functional diversity calculated with the Rao index gives (Rao, 1982):

$$\alpha FD = \sum_{i=1}^{S} \sum_{j=i+1}^{S} d_{ij} P_i P_j$$

Where, $\alpha FD$ is $\alpha$ functional diversity index for a community, $d_{ij}$ is the functional distance between species $i$ and $j$, $P_i$ and $P_j$ the relative abundances of species $i$ and species $j$, and $S$ the total number of species in the community.

This index is the sum of the trait dissimilarity among all possible pairs of species, weighted by the product of the species relative abundance.

By considering species abundance, the index gives highest importance to the dissimilarity between dominant species (de Bello et al., 2007).

Similarly, for $\gamma$ functional diversity:

$$\gamma FD = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} P_i P_j$$

Thereinto $P_{it} = \sum_{k=1}^{N} P_{ik} / N$, $P_{jt} = \sum_{k=1}^{N} P_{jk} / N$

Here $\gamma FD$ is $\gamma$ functional diversity index, $k$ the serial number of quadrats, and $N$ is the number of quadrats.

**Mason functional diversity**

Mason $\alpha$ functional trait diversity could be defined as:

$$\alpha FD = \sum_{i=1}^{S} P_i \left( x_i - \bar{x} \right)$$

Where, $\alpha FD$ is $\alpha$ functional diversity index for a community, $P_i$ is the proportion of the $i^{th}$ species, $S$ is the number of species in the community (species richness), $x_i$ is the mean trait value of the $i^{th}$ species, and $\bar{x}$ is the community mean calculated as: $\bar{x} = \sum_{i=1}^{S} P_i x_i$. This $\alpha$ functional diversity represents the overall variance of a given trait in a community (de Bello et al., 2009). Following the same approach, Mason $\beta$ functional diversity is defined as:

$$\beta FD = \sum_{k=1}^{n} \frac{1}{n} \left( x_k - \bar{x}_{region} \right)^2$$

Where, $\beta FD$ is $\beta$ functional diversity index, $n$ is the number of communities (samples) in the region, $x_k$ is the average of the $k^{th}$ community ($k=1, 2, \ldots, n$) and $\bar{x}_{region}$ is the overall mean across all communities in a region. With this formula, the $\beta$ functional diversity represents the increase in variance resulting from pooling different communities together (de Bello et al., 2009).

**Community weighted mean index**

Community weighted mean (CWM) is defined as weighted
mean of plant traits in communities (Lavorel et al., 2008). For each trait, CWM is derived by combining species relative abundances with population-based trait measurements from the data base. CWM was calculated as:

$$CWM = \sum_{i=1}^{S} p_i \times trait_i$$  \hspace{1cm} (9)

where \(p_i\) is the relative contribution of species \(i\) to the community, and \(trait_i\) is the trait value of species \(i\), \(S\) is the number of species in community. Studies have shown that CWM index is important in evaluation of community dynamics and ecosystem processes.

**Dendrogram distance index**

Petchey and Gaston (2002; 2006) applied cluster analysis of species calculated from a matrix of functional characters, and then used the sum of branch lengths of the dendrogram as a multivariate measure of functional diversity. This method includes four steps: first, to obtain functional trait matrix \(S\), the matrix which contains all the functional characteristics of species; second, to calculate the functional distance matrix \((S \times S)\); to cluster species by hierarchical clustering method using functional distances and obtain the dendrogram; to add the lengths of dendrogram branches to get functional diversity (Petchey and Gaston, 2002). There are many distance coefficients and clustering methods can be applied in this measurement. Podani and Schmera (2006) suggested Gower’s formula and group average (UPGMA) clustering as a standard combination of techniques for calculating functional diversity.

**Minimum spanning tree index**

Ricotta and Moretti (2008) put forwarded the minimum spanning tree (MST) index, which may be useful in revealing the functional structure of a given species assemblage. Like dendrograms obtained from hierarchical clustering, the MST is derived from the matrix of pairwise species functional distances \(d_i\). However, in MSTs, each vertex corresponds to a species, so there are no ‘abstract’ vertices in the graph. For \(S\) species, MSTs are composed of \(S-1\) edges, each weighted by the corresponding distance value, such that the total sum of edge length is minimized (Podani, 2000; Ricotta and Moretti, 2008). Based on MSTs, we can thus calculate the measure of functional diversity that is defined simply as the sum of branch lengths of the corresponding MST.

These methods mentioned above are main measurements of functional diversity appeared in the literature of ecology. They are rigorous in theoretical basis and recognized by most scholars in theory (Ricotta and Moretti, 2008). Some of them had practical applications in studies and had achieved good results; while others had only analysis using simulated data and their application results need to be further tested (Zhang, 2011). Functional diversity of species is limited in practice, one of that reasons is that there are not many effective research methods (Ackerly and Cornwell, 2007; Suding et al., 2008).

**DISCUSSION AND PERSPECTIVE**

Many of the aspects dealt with in the present work have been addressed in previous original research papers and reviews (Petchey and Gaston, 2006; Suding et al., 2008; Hillebrand and Matthiessen, 2009). It has been our intention to answer the question, what kind of information we need to successfully predict consequences of changing biodiversity in real ecosystems, and what kind methods we need to evaluate functional diversity in communities. This is essential to provide ecologists with the tool to transfer knowledge of functional diversity into conservation biology and ecosystem management (Hillebrand and Matthiessen, 2009).

Functional trait diversity is the value and scope of species functional traits in a special ecosystem. Selection of species traits is still a question, what kind of traits, how many traits depend on researcher’s selection. Among the three main kinds of traits, morphological and reproductive are more commonly used in practice. Some people argued that plant physiological traits are the best functional characteristics, but it is difficult to measure all physiological characteristics for all plant species simultaneously in a community, especially in multi-species community. In addition, physiological traits are vulnerable to environmental factors and not very stable, which is more suitable for experimental communities with fewer species such as the experimental microbial communities. In natural plant communities, plant morphological and reproductive characteristics are more commonly used (Wacker et al., 2009). In practice, the selection of traits should consider the study purpose, community type, complexity, etc. The comparison study of different traits will be a topic for future research (Cadotte et al., 2009; Zhang et al., 2010).

Functional diversity and species richness are different concepts, the former refers to the change of species functions in communities, and species functions are reflected by functional traits during the completion of their life histories; the latter refers to the number of species in communities. Some scholars believed that the functional diversity and species richness are the same, which is clearly inconsistent with their definition and meanings (Ricotta and Moretti, 2008). Other scholars believed that functional diversity and species richness are independent of each other and not necessarily linked. Therefore, the analysis methods of functional diversity should also be independent of species richness, that is, functional diversity should not be significantly correlated with species richness (Zhang and Zhang, 2007; Ricotta and...
Moretti, 2008). The existing measurement methods of functional diversity are correlated with species richness, and they thought, in theory, it is obvious short-coming (De Bello et al., 2006), but we believe that there are no any two species with the exactly same functional characteristics in a community, and so the greater the number of species are, the larger the change in functional characteristics and the greater the functional diversity are. Therefore, functional diversity and species richness should be interrelated. This point will be confirmed in future research (Zhang, 2011).

Functional diversity of species is one of the research hotspots currently, but the effective methods accepted by all scholars are small. The development of new analysis methods is one of the research directions in future (Suding et al., 2008; Zhang et al., 2011). For mathematical theory, fuzzy mathematics and SOFM neural network theory may provide new preferred method for functional diversity, because they are theoretically suitable for studies of complex ecosys-tems (Zhang and Yang, 2008; Zhang et al., 2008; Zhang and Li, 2008). In addition, the application and comparison of a variety of methods are necessary in future studies (Zhang, 2011).

ACKNOWLEDGEMENTS

The study was financial supported by the National Natural Science Foundation of China (Grant No. 31170494, 30870399).

REFERENCES


