Ann. For. Res. 56(1): 43-52, 2013

ANNALS OF FOREST RESEARCH
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Evaluation of nine distance-based measures of functional diversity applied to forest communities

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Zhang J.T., Song N., Fan L., 2013. Evaluation of nine distance-based measures of functional diversity applied to forest communities. Ann. For. Res. 56(1): 43-52, 2013.

Abstract. Several methods for the estimation of functional diversity are employed in plant communities. However, it is hard to select the most suitable measures in practice. This work presents comparisons of nine distance-based measures applied to functional diversity analysis in forest communities (36 plots) along an elevational gradient in the Pangquangou Reserve, China. The employed indices and methods were: functional attribute diversity (*FAD*), Rao's functional diversity (Rao's index), single linkage (*SL*), complete linkage (*CL*), Unweighted Pair Group Method with Arithmetic Mean (UPGMA), Unweighted Pair-Group Method using Centroids (UPGMC), Median linkage (Median), fuzzy equivalence diversity (Fuzzy index) and minimum spanning tree index (*MST*). The results showed that all the nine measures successfully quantified the functional diversity in plant communities and described the changes along environmental gradient. It was concluded that all the employed indices and methods were equally effective and significantly correlated. Comparatively, fuzzy index, *MST*, UPGMC, UPGMA and Median were more suitable and should have priority over the other four measures in functional diversity analysis. A combination of a few measures of functional diversity within the same study was recommended. Functional diversity indices were significantly decreasing with elevation and correlated with species richness in the studied forest communities.
Keywords elevation gradient, functional traits, *Larix principis-rupprechtii* communities, linear mixed models, performance ranking, slope, species richness.

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Manuscript received May 22, 2012; revised October 29, 2012; accepted October 08, 2012; online first November 16, 2012.

Introduction

Biodiversity has become a central and recurring topic in ecology in recent decades, because it is important for community structure and development, in parallel with the growing concern about nature conservation (Zhang

2005). The relationship between biodiversity and ecosystem function has become a major scientific topic in biodiversity studies. Functional diversity in communities is a key driver of ecosystem processes, ecosystem resilience to environmental change, and ecosystem services (Diaz et al. 2007, Laliberte & Legendre 2010, Zhang et al. 2012). Functional diversity refers to the change of species functions in communities, and species functions are reflected by functional traits as well as the change of these traits during their life histories. The differences in types, amplitude change and stability of these functional traits reflect the quantity of functional diversity in community (Petchey & Gaston 2002, Zhang et al. 2012). The measures of functional diversity in community are essential in studies of functional diversity (Villeger et al. 2008).

Functional diversity is a measure of species trait diversity, which should allow it to predict the changes in ecosystem processes based on changes in community composition (Hillebrand & Matthiessen 2009). During the recent years, indices and quantification methods of functional diversity based on species traits have received much attention, and many studies tried to develop methodology in this area (Ackerly & Cornwell 2007, Suding et al. 2008). Villeger et al. (2008) have proposed three multidimensional functional diversity indices for continuous functional traits, each exploring a different aspect of functional diversity: functional richness, functional evenness, and functional divergence. Laliberte and Legendre (2010) provided a distance-based framework for measuring functional diversity from multiple functional traits. Although many indices and methods for measuring functional diversity based on functional traits of species in communities have been put forward and applied to the practical studies (Zhang et al. 2012), it is difficult for researcher to choose most suitable approach in their studies. Therefore comparison studies of different quantification of functional diversity are necessary (Zhang et al. 2012).

The main purpose of this paper is to compare the results of the nine distance-based measures for quantification of functional diversity applied to forest communities.

Materials and methods

Study site

The cold-temperate forest (*Larix principis-rupprechtii* forest) in the Pangquangou Reserve, Guandi Mountain, Shanxi of China was used as a case of functional diversity analysis. Guandi Mountain with the highest peak of 2831 m is located at N 37°20’-38°20’, E 110°18’-111°18’, and is a part of Luliang mountain range. The study area was included within the main distribution area of *Larix principis-rupprechtii* forests in the reserve.

Sampling design. Along the elevation gradient of 1800-2600 m, eighteen sampling points separated by 50 meters in altitude were recognized, and two plots of 10 m × 20 m were randomly set up at each sampling point. Species name, its cover, height, basal area and individual abundance for tree species were recorded in each plot. Two 4 m × 4 m and three 2 m × 2 m quadrats were randomly placed and sampled to record species name, cover, abundance and height for shrubs and herbs respectively within each plot of 10 m × 20 m (Zhang & Dong 2010). There were totally 127 species (see Appendix I) in 36 plots recorded. Elevation, slope, aspect, slope position, soil depth and the depth of litter for each plot were also measured and recorded. The elevation in each plot was measured by using a GPS (Garmin 39KB GIF), the slope and slope aspect were measured by using a compass meter, slope position was identified visually, soil depth was measured by using a soil depth instrument with five random points in a plot, and the depth of litter was measured by using a ruler directly with five random points in a plot (Zhang et al.

2006). The elevation, slope and litter thickness were reading values, while the aspect measurements were classified from 1 to 8 in the following way: 1 (337.6°-22.5°), 2 (22.6°-67.5°), 3 (292.6°-337.5°), 4 (67.6°-112.5°), 5 (247.6°-292.5°), 6 (112.6°-157.5°), 7 (202.6°-247.5°), and 8 (157.6°-202.5°). The slope position was recorded as 1 for upper slope, 2 for middle slope, 3 for lower slope and 4 for the valley floor (Zhang et al. 2011).

Eleven functional traits were selected to illustrate plant species roles in community (Table 1). Habitat type, leaf form, plant height, plant cover, flowering date, flowering period and life cycle were observed or measured in field, and seed dispersal, life-form, pollination type and nitrogen-fixing ability were identified from previously local flora (Zhang et al. 2012). Therefore the data matrix contains the functional trait values of species in a plot, i.e. each row is a species and each column is a functional trait and cells are filled by their values. Totally there are 36 data matrices for 36 plots.

Measures used for quantifying functional diversity

There are many choices for distance-based measurement of functional diversity based on species traits in ecology (Suding et al. 2008, Zhang et al. 2012). We used the following nine common measures.

Functional attribute diversity index. Functional attribute diversity (FAD) aimed at estimating the dispersion of species in trait space as the sum of the pairwise species distances (Walker et al. 1999):

$$FAD = \sum_{i,j} d_{ij} \tag{1}$$

where d_{ij} is functional distance between species i and j in functional trait space; $D = \{d_{ij}\}$ is Euclidean distance matrix and calculated based on the matrix of functional trait (N) by species (S).

Rao's index. Rao's index indicates the expectation of trait dissimilarity between two randomly chosen individuals in a community (Rao 1982, Lepš et al. 2006).

$$FD = \sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij}\, p_i\, p_j \tag{2}$$

where FD is functional diversity index for a community (plot), d_{ij} is the functional distance between species i and j, p_i and p_j are the relative abundances of species i and species j, and S the total number of species in the community.

Clustering methods. Dendrogram indices, a group of methods, use cluster analysis of species calculated from a matrix of functional

Table 1 The geographical and soil characteristics of the sampling stands

Functional trait type	Functional traits and values
Habitat type	1 Bare land, 2 cropland, 3 grassland, 4 scrubland, 5 forest
Seed dispersal type	1 Automatic spreading, 2 gravity spreading, 3 wind spreading, 4 animals spreading
Pollination manner	1 Anemophilous, 2 entomophilous
Nitrogen-fixing ability	0 No nitrogen-fixing, 1 nitrogen-fixing
Life cycle	1 Annual, 2 Biennial, 3 perennial
Life-form	1 Tree, 2 shrubs, 3 woody vine, 4 perennial herb, 5 annual herb
Leaf form	1 Coniferous, 2 Broadleaved
Plant height	Measured value in cm
Plant cover	Measured percentage cover
Flowering date	Start month of flowering
Flowering period	Flowering months

traits, and then use the sum of branch lengths of the dendrogram as a multivariate measure of functional diversity (Petchey & Gaston 2006, Podani & Schmera 2006). We use five common clustering methods, Single Linkage (*SL*), Complete Linkage (*CL*), Unweighted Pair Group Method with Arithmetic Mean (UPGMA), Unweighted Pair-Group Method using Centroids (UPGMC), and Median Linkage (Zhang 2011).

Fuzzy equivalence index. Fuzzy equivalence index (fuzzy index) is also a dendrogram index which clusters species into a dendrogram based on fuzzy equivalence relations calculated from a matrix of functional traits, and then used the sum of branch lengths of the dendrogram as a multivariate measure of functional diversity (Zhang 2011). This is a new trial for measuring functional diversity in plant community (Zhang & Li 2011).

Minimum spanning tree index. Minimum Spanning Tree index (*MST*) is also derived from the matrix of pairwise species functional distances d_{ij}. 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. 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* (Ricotta & Moretti 2008).

Statistical analysis

All functional trait data were standardized by deviation before calculation of functional diversity to avoid scale effects (Petchey & Gaston 2006).

Three species diversity indices, one for species richness, one for species heterogeneity, and one for species evenness, were used to calculate diversity estimates (Pielou 1975, Zhang 2011). These indices were species richness:

$$R = S$$

The Shannon-Wiener heterogeneity index:

$$H' = -\sum P_i \ln P_i \tag{3}$$

and the Pielou evenness index:

$$E = \frac{H'}{\ln(S)} \tag{4}$$

where P_i is the relative importance value of species *i*, P_i- N_i/N, N_i the importance value of species *i* and N_i - (relative cover + relative abundance + relative height)/3, *N* the sum of importance values for all species in a plot, *S* the species number present in a plot (Pielou 1975, Zhang 2011).

Spearman’s rank correlation and linear mixed models were used to analyse the relationships among functional diversity, species diversity and environmental variables (Zhang 2011). Principal component analysis (PCA, Greig-Smith 1983, ter Braak & Šmilauer 2002) based on functional trait data was used to analyse relationships of the nine measures for quantifying functional diversity.

The analyses were carried out by SPSS 16.1.

Results

The estimates of functional diversity varied significantly in forest communities in the Pangquangou Reserve and all the nine measures employed for quantifying functional diversity described these changes successfully. FAD was the greatest in value and Rao’s index was the least in value.

The nine measures for estimating functional diversity were significantly correlated (Table 2), which suggests that they provide similar results on the analyses of functional diversity of forest communities. Except Rao’s index, that was negatively correlated with other measures, all the others were positively correlated. The variance explained by the first two PCA axes was rather low (15.07% and 9.89% respectively), which shown that these measures were very similar and significantly correlated with each other (Fig. 1). The *FAD* (1) and Rao's index (2) were the farthest away in the ordination space and consequently, the most different, but their correlation was also significant (Fig. 1, Table 2). In the studied forest communities, functional diversities estimated by the nine indices or methods were all significantly correlated with elevation and seven out of the nine measures were also correlated with slope (Table 3). Other variables such as aspect, slope position, soil depth and litter depth had no obvious relationships with functional diversity in the studied forest communities (Table 3). The functional diversity of *Larix principis-rupprechtii* forests along the elevation gradient, as expressed by the nine measures, showed similar patterns, i.e. it decreased with elevation, except for Rao's index (Table 3). Among the nine metrics, UPGMA, UPGMC and fuzzy index displayed the best linear fit with altitude, whereas the Rao's index and *FAD* were the worst fitted (Table 4).

Functional diversities measures were all significantly correlated with species richness and heterogeneity (Shannon-Wiener index), and marginally correlated with evenness (Table 5).

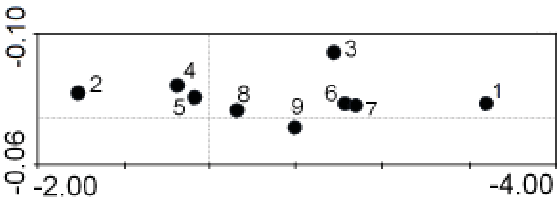

Figure 1 PCA ordination diagram of the nine measures for quantifying functional diversity in 36 plots of forest communities in the Pangquangou Reserve, China. 1-9 refer to functional attribute diversity, Rao's functional diversity, single linkage, complete linkage, UPGMA dendrogram, UPGMC dendrogram, median linkage, fuzzy functional diversity and minimum spanning tree index respectively

Discussion and conclusions

FAD, as a sum of distances within the matrix, is the greatest in value and may overestimate functional diversity (Mason et al. 2005). Rao's index uses relative abundance as weights and may increase functional evenness but underestimate functional diversity (De Bello et al. 2009). *SL*, *CL*, UPGMA, UPGMC and Median are all based on the same model of clustering analysis with different strategies in

Table 2 Correlation coefficients of the nine measures for functional diversity applied to forest communities in the Pangquangou Reserve, China

Measures	*FAD*	Rao's index	*SL*	*CL*	UPGMA	UPGMC	Median	Fuzzy index	*MST*
FAD	1.000								
Rao's index	-0.619***	1.000							
SL	0.729***	-0.534**	1.000						
CL	0.823***	-0.580***	0.927***	1.000					
UPGMA	0.825***	-0.616***	0.949***	0.961***	1.000				
UPGMC	0.794***	-0.546**	0.922***	0.910***	0.911***	1.000			
Median	0.804***	-0.536**	0.926***	0.916***	0.918***	0.959***	1.000		
Fuzzy index	0.396*	-0.321*	0.728***	0.614***	0.639***	0.677***	0.695***	1.000	
MST	0.721***	-0.582***	0.916***	0.916***	0.940***	0.902***	0.897***	0.702***	1.000

Note. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. *FAD*, Rao's index, *SL*, *CL*, UPGMA, UPGMC, Median, Fuzzy index and *MST* refer to functional attribute diversity, Rao's functional diversity, single linkage, complete linkage, UPGMA dendrogram, UPGMC dendrogram, median linkage, fuzzy functional diversity and minimum spanning tree in dex, respectively.

calculation of distances between new groups and should provide similar results. Comparatively, UPGMA, UPGMC and Median are better than *SL* and *CL* because *SL* overestimate

Table 3 Correlation coefficients of the nine measures for quantifying functional diversity with environmental variables in forest communities in the Pangquangou Reserve, China (see Table 2 for abbreviations)

Measures	Elevation	Slope	Aspects	Slope position	Soil depth	Litters
FAD	-0.599***	-0.232	0.219	0.100	-0.305*	0.063
Rao's index	0.342*	0.206	0.155	0.170	0.077	0.001
SL	-0.706***	-0.335*	0.240	0.089	-0.236	-0.114
CL	-0.740***	-0.344*	0.195	0.105	-0.303*	-0.110
UPGMA	-0.674***	-0.361*	0.241	0.032	-0.241	-0.089
UPGMC	-0.667***	-0.324*	0.032	0.155	-0.241	-0.126
Median	-0.706***	-0.324*	0.095	0.110	-0.241	-0.134
Fuzzy index	-0..592***	-0.265*	0.300*	0.228	-0.245	-0.195
MST	-0.646***	-0.261	0.184	0.045	-0.212	-0.095

Note. **p* < 0.05, ** *p* < 0.01, *** *p* < 0.001.

Table 4 Linear mixed models of the nine metrics of functional diversities by elevation in forest communities in the Pangquangou Reserve, China (the intercept estimates are not shown)

Measures	F	Parameter estimate	*t*	Goodness of fit	AIC
FAD	134.22***	78.359	11.594***	62.089***	364.089
Rao's index	485.32***	0.341	69.663***	34.120***	-142.122
SL	1362.01***	3.970	36.904***	14.307***	74.313
CL	826.85***	3.092	28.756***	14.233***	74.232
UPGMA	1373.02***	2.243	36.511***	9.048***	35.049
UPGMC	1836.01***	2.786	42.847***	10.044***	39.043
Median	1096.01***	5.239	33.111***	21.270***	101.027
Fuzzy index	838.36***	3.239	28.954***	19.006***	36.989
MST	1558.00***	2.493	39.469***	12.898***	77.006

Note. **p* < 0.05, ** *p* < 0.01, *** *p* < 0.001.

Table 5 Correlation coefficients of the nine measures for functional diversity with species richness, diversity and evenness in forest communities in the Pangquangou Reserve, China (see Table 2 for abbreviations)

Measures	Richness (*R*)	Shannon-Wiener index (*H'*)	Evenness (*E*)
FAD	0.988***	0.856***	0.253
Rao's index	-0.656***	-0.583***	-0.167
SL	0.694***	0.773***	0.427**
CL	0.797***	0.835***	0.410*
UPGMA	0.783***	0.819***	0.398*
UPGMC	0.605***	0.637***	0.294
Median	0.632***	0.663***	0.307*
Fuzzy index	0.382*	0.395*	0.164
MST	0.702***	0.783***	0.435**

Note. **p* < 0.05, ** *p* < 0.01, *** *p* < 0.001.

and *CL* underestimate the distances between new groups (Petchey & Gaston 2006, Podani & Schmera 2006, Zhang 2011). Fuzzy index is based on fuzzy mathematical theory, which has advantages in solving non-linear problem and in studying complicated and fuzzy system (Zhang & Li 2011) and should be a good measure in evaluation of functional diversity in plant communities (Zhang & Li 2008). *MST* is based on minimum spanning tree which supposes to provide optimum functional diversity (De Bello et al. 2007, Ricotta & Moretti 2008). According to the results of this study, fuzzy index, *FAD* and Rao's index provided some different information and therefore, their conjoint use seem to be justified, and among the clustering methods *MST*, UPGMC, UPGMA and Median should be priority over *SL* and *CL*.

The nine measures used were all significantly correlated. This fact suggests that these metrics provide similar results in the analysis of functional diversity in forest communities (Zhang et al. 2012), and indicated that all were effective in quantifying and assessing functional diversity (Petchey & Gaston 2006). *SL*, *CL*, UPGMA, UPGMC, Median, Fuzzy index and *MST* were closely correlated in describing the amount of functional diversity along altitude gradient. These measures should be employed in the first place in functional diversity studies (Dıaz et al. 2007, Zhang 2011). The AIC values in linear mixed models also support this point.

Functional diversities measured in forest communities by the nine metrics were all significantly correlated with species richness. This contradicts other authors' idea that functional diversity and species richness should be independent, which implies that measures employed for estimation of functional diversity are also independent of species richness (Mason et al. 2005, Laliberte & Legendre 2010). These autors considered that if an estimation method for functional diversity was significantly correlated with species richness, it was, in theory, a shortcoming (Ricotta & Moretti 2008). According to this opinion, the less species richness is correlated to functional diversity, the better the method is. According to this criteria, the decreasing suitability of indices and methods is: Fuzzy index > UPGMC> Median > *SL* > *MST* > UPGMA > *CL* > *FAD*. Rao's index is not recommended due to its negative correlation to species richness (Zhang 2011).

Through the theoretical and application analyses above, we can conclude that the nine measures are all useful in quantifying and assessing functional diversity in forest communities. Among these measures, fuzzy index, *MST*, UPGMC, UPGMA and Median should have priority over *SL*, *CL*, Rao's index and *FAD*. Several measures of functional diversity should be employed and their values compared in future studies (Villeger et al. 2008, Zhang et al. 2012).

More comparison studies of different measures for quantifying functional diversity applied to different plant communities, e.g. grasslands, scrublands, wetlands, are needed (Hillebrand & Matthiessen 2009, Zhang et al. 2012).

Acknowledgements

The study was financial supported by the National Natural Science Foundation of China (Grant Nos. 31170494, 30870399).

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Appendix

Table 1 List of the species recorded during the field inventory

Larix principis-rupprechtii
Picea meyeri
Picea wilsonii
Populus davidiana
Populus maximowiczii
Salix wallichiana
Betula albo-sinensis
Betula dahurica
Betula platyphylla
Corylus mandshurica
Aconitum barbatum var. *puberulum*
Aconitum sinomontanum
Anemone vitifolia
Aquilegia yabeana
Cimicifuga foetida
Clematis brevicaudata
Paeonia obovata
Ranunculus japonicus
Ranunculus monophyllus
Thalictrum petaloideum
Trollius chinensis
Berberis amurensis
Corydalis curviflora
Cardamine tangutorum
Hylotelephium tatarinowii
Sedum aizoon
Hydrangea bretschneideri
Philadelphus pekinensis
Ribes burejense
Ribes mandshuricum
Agrimonia pilosa
Cotoneaster multiflorus
Crataegus wilsonii
Fragaria orientalis
Malus baccata
Potentilla anserina
Potentilla glabra
Polemonium coeruleum
Mertensia sibirica
Myosotis silvatica
Pulmonaria mollissima
Ajuga ciliata
Mentha haplocalyx
Phlomis umbrosa
Pedicularis muscicola
Pedicularis verticillata
Adoxa moschatellina
Galium aparine var. *tenerum*
Galium kinuta
Galium verum
Rubia cordifolia
Rubia membranacea
Lonicera chrysantha
Lonicera hispida
Lonicera tangutica
Triosteum pinnatifidum
Viburnum mongolicum
Valeriana officinalis
Adenocaulon himalaicum
Artemisia dubia
Artemisia lavandulaefolia
Aster ageratoides
Quercus wutaishanica
Urtica angustifolia
Urtica laetevirens
Polygonum lapathifolium
Polygonum suffultum
Dianthus chinensis
Dianthus superbus
Moehringia lateriflora
Pseudostellaria davidii
Stellaria media
Cerastium arvense
Potentilla simulatrix
Rosa bella
Rosa xanthina
Rubus pungens var. *oldhamii*
Sorbus koehneana
Spiraea pubescens
Lespedeza bicolor
Vicia unijuga
Vicia amoena
Geranium sibiricum
Euonymus fortunei
Acer ginnala
Viola biflora
Epilobium angustifolium
Angelica dahurica
Carum carvi
Heracleum moellendorffii
Ligusticum jeholense
Peucedanum terebinthaceum
Sanicula chinensis
Swida bretchneideri
Cortusa matthioli
Primula maximowiczii
Gentiana macrophylla
Carpesium cernuum

Table 1 (continuation)

Cirsium leo	*Poa annua*
Cirsium souliei	*Stipa bungeana*
Delphinium grandiflorum	*Carex lanciolata*
Dendranthema chanetii	*Allium macrostemon*
Heteropappus hispidus	*Allium ramosum*
Ligularia intermedia	*Allium victorialis*
Parasenecio hastatus	*Asparagus schoberioides*
Prenanthes macrophylla	*Convallaria majalis*
Prenanthes tatarinowii	*Maianthemum bifolium*
Saussurea parviflora	*Paris verticillata*
Senecio nemorensis	*Polygonatum odoratum*
Taraxacum mongolicum	*Polygonatum sibiricum*
Achnatherum splendens	*Veratrum nigrum*
Arundinella anomala	*Dioscorea nipponica*
Leymus secalinus	