

Short Note

FEEr: An R package for calculating functional extension and evenness index

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ABSTRACT

Since the 1990s, functional diversity has attracted growing attention from biodiversity scientists. In recent years, various functional diversity indices have been proposed; but many of them presented conceptual and/or practical limitations. We recently developed a functional diversity index, Functional Extension and Evenness (FEE), to overcome some of the limitations. In this paper, we describe the content and major features of a new R package, FEEr, which serves as a tool for calculating the FEE index. The FEEr package includes one major core function to accomplish the FEE calculation and several support functions to provide important intermediate results relevant to the FEE calculation. To demonstrate the usage of this package, we present an abbreviated case study of quantifying the taxonomic and functional diversities of national forest inventory plots in the state of Tennessee, United States. In this application, we compare the correlations between species richness and FEE values in these plots. We also briefly summarize how species richness and FEE values vary among forest types and ecoregions in Tennessee. The results indicate that species richness and the FEE index reflect complementary aspects of the biodiversity profile in Tennessee's forests. The functional diversity package outlined in this work provides a comprehensive foundation for subsequent analyses to address the needs of biodiversity conservation.

1. Introduction

Biodiversity underpins ecosystem functioning and the provision of ecosystem services critical for human beings (Convention on Biological Diversity, 2010). The worldwide loss of biodiversity is one of the most profound challenges that humanity is facing (United Nations, 2015). Community ecologists and conservation biologists evaluated biodiversity from multiple perspectives, of which taxonomic diversity (e.g., species richness) may be the most used (Davies and Cadotte, 2011). However, taxonomic diversity does not adequately reflect functional differences among species. Scientists realize that a trait-based, causal view of community diversity may be more reasonable than species richness in studying how species interact in a community and how biodiversity affects ecosystem functioning (McGill et al., 2006), such as productivity, resilience to disturbances or invasion, and regulation of matter flux (Legras et al., 2019). In this context, research interest on functional diversity has rapidly increased over the last two to three decades. As Fig. 1 shows, the earliest articles on the topic of functional diversity appeared sporadically in 1960s; and the literature noticeably increased after 1990 and exponentially grew since then.

A common approach to measuring functional diversity of a species

assemblage is quantifying the overall difference of functional traits among species. Although a wide array of functional diversity indices have been developed or proposed in the literature, many of them presented conceptual and/or practical limitations (Legras et al., 2019; Mouchet et al., 2010; Pavoine et al., 2013; Pavoine and Bonsall, 2011). Some common issues include that they might be intrinsically correlated with species richness, focus only on a single facet of functional diversity (i.e., there is no consideration of other facets), focus only on the community of interest (without reference to species pool or regional context), and even provide counterintuitive inferences or fail to function in some scenarios (Zhang et al., 2021).

To overcome these limitations, Zhang et al. (2021) proposed a new functional diversity index named the Functional Extension and Evenness (FEE) index. By combining two aspects of functional diversity and applying a null model method in index design, the FEE index overcomes the limitations mentioned above and presents several desired properties and considerable application potential (Zhang et al., 2021). One important property of FEE is that it allows a fair comparison of functional diversity across different species richness because FEE is intrinsically independent from species richness.

Open-source software is used intensively in ecological studies (Kaya

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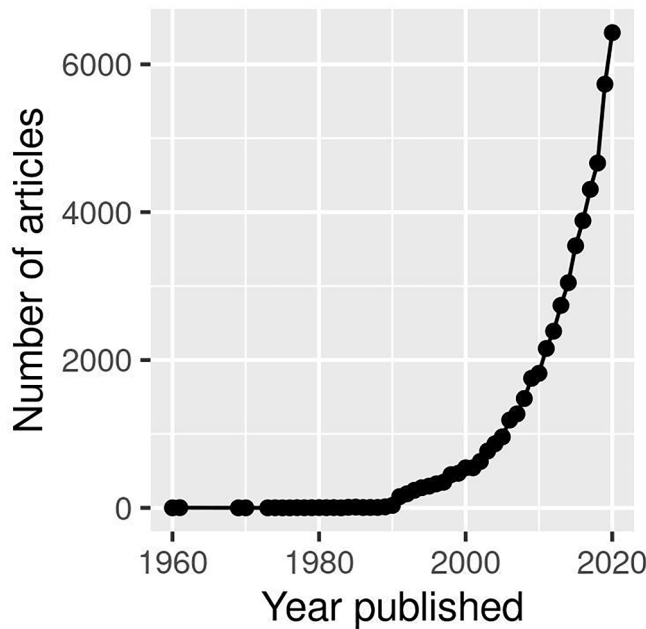


Fig. 1. Increasing body of literature on the topic of functional diversity from 1960 to 2020. Number of articles (y-axis) is based on the search results in Web of Science Core Collection database (Clarivate Analytics, 2021), with the topic of “functional diversity” as the search criteria.

et al., 2019). However, applications of functional diversity indices sometimes were hampered by a lack of calculation tools for the indices (Casanoves et al., 2011). To make FEE more accessible to a large audience and promote innovative applications of the index, we developed an R package, FEER, to facilitate the index calculation.

2. Methods

2.1. The FEE index

The concept of the FEE index was documented in detail in Zhang et al., (2021). Briefly, the goal of the FEE index is to quantify functional diversity of a species assemblage (or community) by measuring the overall extension of species traits and interspecific differences in trait space, which is represented by a unit hypercube. The FEE index leverages the concept of minimum spanning tree (MST) to obtain the essential distribution properties for the species assemblage in trait space. Specifically, the total length of MST branches is used to characterize the overall species extension in the trait space; and the variation of branch lengths is used to characterize the evenness of species' distribution in the trait space. These two aspects of species distribution properties are integrated into a raw FEE₀ metric, which is defined as follows:

$$FEE_0 = \text{sum}(l) \cdot \sum_{i=1}^{n-1} \min\left(\frac{l_i}{\text{sum}(l)}, \frac{1}{n-1}\right) = \sum_{i=1}^{n-1} \min(l_i, \bar{l}) \quad (1)$$

where n is the species richness of the species assemblage; l is the vector of MST branch lengths for the species assemblage (l has $n-1$ elements); l_i is the i th branch element in l ; and $\bar{l}$ is the mean length of the branches.

When applying Eq. (1) to species presence-absence data (i.e., when the factor of species abundance is not considered), MST branch lengths are based on the raw interspecific distances in trait space. If variation of species abundance needs to be addressed in quantifying the functional diversity, the abundance-adjusted interspecific distances are adopted in the MST and FEE₀ calculations:

$$\begin{aligned} \text{dist}_a(p_i, p_j) &= \min(K_1 K_2, 1) \cdot \text{dist}(p_i, p_j) \\ &= \min\left(\frac{4}{n \cdot (w_i + w_j)} \cdot \frac{k_{ij}}{k_{ij} + 1}, 1\right) \cdot \text{dist}(p_i, p_j) \end{aligned} \quad (2)$$

where $\text{dist}_a(p_i, p_j)$ is the abundance-adjusted distance for a pair of species i and j ; $\text{dist}(p_i, p_j)$ is the raw distance between the two species; w_i or w_j is the relative abundance of species i or j ; and k_{ij} is the abundance ratio between the two species (the higher abundance over the lower abundance). More detailed explanations of this distance-adjustment scheme were given in Zhang et al., (2021).

After FEE₀ is calculated based on the MST derived from either the raw interspecific distances (e.g., for presence-absence data) or the adjusted interspecific distances (e.g., for abundance data), the FEE index is calculated as the empirical cumulative distribution function (eCDF) of FEE₀ among the null models of equi-abundant species assemblage that has the same species richness as the species assemblage of interest:

$$FEE = F_Q(X) = \frac{\sum_{i=1}^Q 1\{x_i \leq X\}}{Q} \quad (3)$$

where $F_Q(X)$ is the empirical cumulative distribution function of FEE₀ estimated from Q realizations of a null model of species assemblage; x_i is the value of FEE₀ from the i th realization of the null model; X is the observed value of FEE₀ in the species assemblage of interest; and $1\{x_i \leq X\}$ is the indicator function (equal to 1 if, and equal to 0 otherwise). In other words, FEE is the proportion of null model realizations that produce FEE₀ values less than or equal to the observed FEE₀. Depending on the assumption about trait distributions of the species pool, species traits in the null model could be random samples from a uniform trait distribution (no prior knowledge), observed trait distribution of real species pool, or other forms of trait distributions that comply with specific prior knowledge (Zhang et al., 2021).

2.2. R package framework

We designed the FEER package to facilitate the calculation and applications of the FEE index. In the package development, we followed the major workflow of calculating the FEE index described above (refer to Zhang et al., (2021) for more details) and provided one core function and three support functions. The core function `computeFEE` is for calculating the FEE indices for species assemblages given their species abundance (or presence-absence) information (argument `abund`) and functional traits of species in the species pool (argument `pool_traits`). This function calls the three support functions, which provide important intermediate results in the process of calculating FEE: species richness (`computeNSP`), branch lengths of its MST (`communityMST`), and the null model's eCDF (FEE₀_eCDF) (Fig. 2).

Besides the two key input arguments (`pool_traits` and `abund`), the function `computeFEE` contains three essential arguments and three auxiliary arguments (Table 1 and Fig. 2). The essential arguments together define the FEE calculation scheme. The auxiliary arguments do not affect the FEE calculation results; but could influence the efficiency of calculations or slightly alter the output format.

We leveraged several R functions and packages to implement specific calculations and develop the package. Specifically, the package was developed and released using the “devtools” package (Wickham et al., 2021). We achieved MST of a species assemblage through the `mst` function in the “ape” package (Paradis and Schliep, 2019) and parallel calculations with the “doSNOW” package (Microsoft and Weston, 2020a), a “foreach” parallel adaptor (Microsoft and Weston, 2020b) for the “snow” package (Tierney et al., 2018). For raw interspecific distance in trait space and eCDF implementation, we relied on the `dist` and

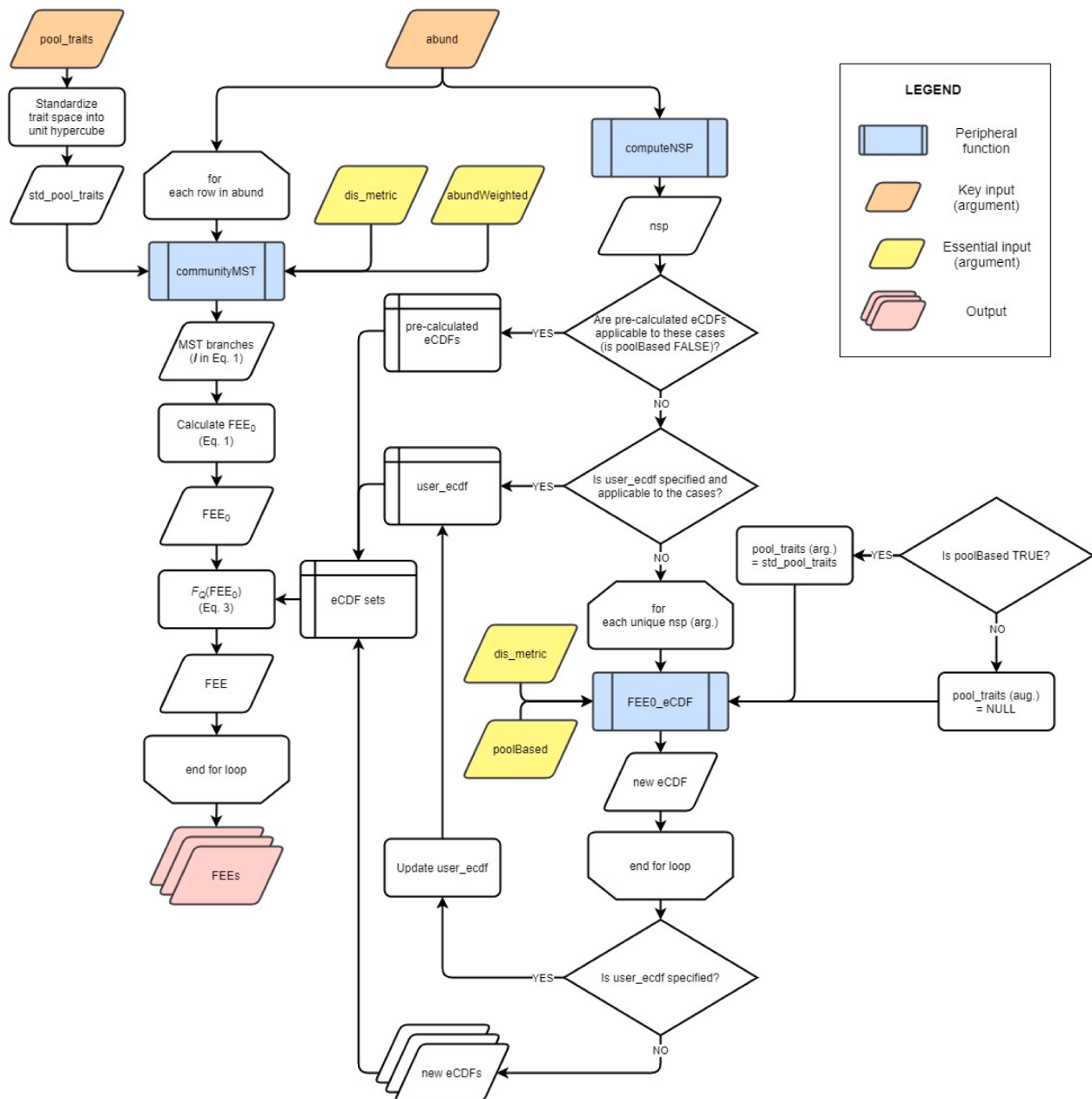


Fig. 2. Simplified flowchart of the core function `computeFEE` in the FEER package. The three support functions are highlighted in blue; the two key arguments (inputs) are highlighted in orange; the three essential arguments (inputs) are highlighted in yellow; and the FEE result (output) is highlighted in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

`ecdf` functions in the R core package “stats” (R Core Team, 2021), respectively.

2.3. Application example

A vignette in the FEER package used a small artificial dataset to demonstrate the package’s usage. Here, we introduce the utility of the FEER package in quantifying biodiversity by assessing actual forest stands in the state of Tennessee, USA. The state was selected because of its diversity in tree species, forest vegetation types, and varying topography. We used data from systematically-sampled Forest Inventory and Analysis (FIA) plots (USDA Forest Service, 2021) to retrieve species composition and abundance information in the stands. We adopted two species traits in our calculation: drought tolerance and shade tolerance, which we obtained from Niinemets and Valladares (2006). These two

tolerance indices or their relevant traits have been widely used to evaluate functional diversity of forests (e.g., Curzon et al., 2017; Granda et al., 2018; Rueda et al., 2017; Strahan et al., 2016).

3. Results

3.1. Load library and example data

The FEER package is currently hosted by GitHub (Zhang, 2021b). The following commands can be entered into an R console to install and load the package:

```
install.packages("devtools")
Sys.unsetenv("GITHUB_PAT")
devtools::install_github("tz05/FEER")
library(FEER)
```

Table 1

Summary of the arguments in core function `computeFEE`. In the “Role” column, K means key arguments, E means essential arguments, and A means auxiliary arguments. Key and essential arguments are highlighted in Fig. 2.

Arguments	Role	Meaning	Note
<code>pool_traits</code>	K	Species pool and the functional traits of these species	Each row represents a species in the pool; each column represents a functional trait
<code>abund</code>	K	Species composition information (abundance or presence-absence) in the species assemblages	Each row represents a species assemblage (community); each column represents a species in the pool
<code>dis_metric</code>	E	The distance measure to be used in quantifying interspecific distance (dissimilarity) in trait space	Currently, the function supports two distance metric options: <code>euclidean</code> (default) and <code>manhattan</code> . The trait space is a unit hypercube because each trait is standardized into the 0–1 range.
<code>abundWeighted</code>	E	Whether species' abundance is considered in the FEE calculation or not	If <code>TRUE</code> (default), the MST and FEE calculations are based on abundance-adjusted interspecific distances ($dist_a$ in Eq. (2)). If <code>FALSE</code> , the MST and FEE calculations are based on raw interspecific distance in trait space ($dist$ in Eq. (2)), i. e., only species presence and absence information is considered.
<code>poolBased</code>	E	Whether traits of pooled species are used as the prior knowledge of trait distribution or not	If <code>TRUE</code> , pooled species and their traits specified in <code>pool_traits</code> are used to define the null models. If <code>FALSE</code> (default), no prior knowledge about species trait distribution is presumed (the null models are based on the uniform trait distribution).
<code>doFEE0</code>	A	Whether or not to include the FEE_0 in the function outputs	FEE_0 is an intermediate result (Eq. (1)) in the FEE calculation.
<code>user_ecdf</code>	A	Path of the file that saves user's results of eCDF of FEE_0 (Eq. (3))	Many pre-calculated eCDFs under the assumption of no prior knowledge about trait distribution are enclosed in the FEE package. For other scenarios, especially in species-pool-based calculations (<code>poolBased=TRUE</code>), eCDFs are not prepared. Using <code>user_ecdf</code> can save eCDFs that are not pre-calculated. Then for calculating FEE of species assemblages under the same pool setting (<code>pool_traits</code>) as the saved eCDFs, these saved eCDFs will be loaded and reused to substantially save calculation time.
<code>doParallel</code>	A	Whether or not to conduct FEE calculations in parallel	When size of species pool (rows of <code>pool_traits</code>), number of species assemblages (rows of <code>abund</code>), and/or number of new eCDFs are very large, setting <code>doParallel=TRUE</code> can save time if the computer backends support parallel computation.

The raw FIA data (FIADB_1.9.0) for Tennessee was downloaded using the `rFIA` package (Stanke et al., 2020). We preprocessed the FIA data and species trait data for the purpose of demonstration. The plots included here are the base intensity forested plots remeasured in 2017. The plots being harvested and plots containing unidentified species were excluded in this study. We then prepared the tree species composition data for the stand communities in these plots (471 plots). Species pool was defined as the set of species found in these plots (91 species). The relevant datasets were packed into an RData file and hosted in a GitHub repository (Zhang, 2021a) for downloading:

```
url <- "https://github.com/tz05/FEEr_TN_Example/
blob/main/TN_FEEr.RData?raw=true"
download.file(url, destfile = "/TN_FEEr.RData")
load("/TN_FEEr.RData")
```

The `comm` variable is a 471×91 data frame which specifies the abundance (in pound/acre) of the 91 species in the 471 FIA plots. Each row represents a forest plot in FIA and its row name is the plot sequence numbers (PLOT_CN), a unique value documenting each plot in the FIA database (Burrill et al., 2018). An element with a value of 0 or NA means the species is absent in the corresponding plot. The `pool` variable is a 91×2 data frame which specifies the two traits of the 91 species in the pool: drought tolerance (DT) and shade tolerance (ST) (Niinemets and Valladares, 2006) (Fig. 3). The row names of `pool` and the column names of `comm` are the species codes (SPCD) used in the FIA database (Burrill et al., 2018). To call functions in the FEEr package, the orders of species in the two variables (columns of `comm` and rows of `pool`) must remain the same.

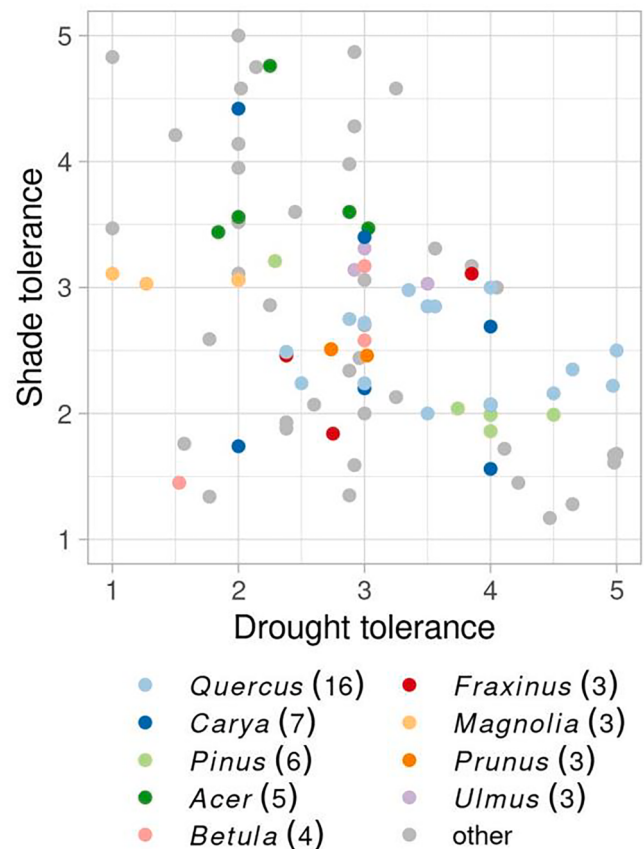


Fig. 3. Trait space of drought and shade tolerance for the species pool in our case study of Tennessee forests. The species are colored based on their genus. The parenthesized numbers in the legend are the number of species within the corresponding genus.

3.2. Species pool and trait space

The following code snippet creates a scatter plot between DT and ST of the 91 species in the pool (Fig. 3):

```
par(mar=c(3,3,0,0)+0.1, mgp=c(2,1,0))
plot(pool, main="", xlab="Drought tolerance",
ylab="Shade tolerance", xlim=c(1,5), ylim=c(1,5),
asp=1)
```

Species show an evident trade-off between shade and drought tolerance (Fig. 3; Niinemets and Valladares, 2006). Species tend to lie along the spectrum from low-DT and high-ST to high-DT and low-ST. In addition, species within a genus usually have similar values for DT and ST. For example, *Quercus* species (oaks) tend to have high DT but low ST, and in contrast, *Acer* species (maples) tend to have low DT but high ST.

3.3. Species richness and FEE

In the following code snippet, we used the computeNSP function to calculate species richness and the computeFEE function to calculate the FEE indices of the FIA plots; then we create a pairwise scatter plots between species richness and the FEE values (Fig. 4). We calculated multiple versions of FEE under different settings on the key arguments: *dis_metric*, *poolBased*, and *abundWeighted* (Table 1). In addition, to save calculation time, we specified a file path to *user_ecdf* (".ecdf_TN") in calling *computeNSP*, allowing pool-based eCDFs calculated from scratch to be loaded and reused in the following commands:

```
biodiv <- data.frame(PLT_CN=rownames(comm))
biodiv$nsp <- computeNSP(comm)
biodiv$fee1 <- computeFEE(pool, comm,
```

```
dis_metric="euc", poolBased=TRUE, user_ecdf =
"./ecdf_TN")
biodiv$fee2 <- computeFEE(pool, comm, dis_metric="-
man", poolBased=TRUE, user_ecdf="./ecdf_TN")
biodiv$fee3 <- computeFEE(pool, comm, dis_metric=
"euc", poolBased=FALSE, user_ecdf="./ecdf_TN")
biodiv$fee4 <- computeFEE(pool, comm, dis_metric="-
man", poolBased=FALSE, user_ecdf="./ecdf_TN")
biodiv$fee5 <- computeFEE(pool, comm, dis_
metric="euc", abundWeighted=FALSE, poolBased=TRUE,
user_ecdf="./ecdf_TN")
biodiv$fee6 <- computeFEE(pool, comm, dis_metric="-
man", abundWeighted=FALSE, poolBased=TRUE, user_
ecdf="./ecdf_TN")
biodiv$fee7 <- computeFEE(pool, comm, dis_
metric="euc", abundWeighted=FALSE, poolBased=FALSE,
user_ecdf="./ecdf_TN")
biodiv$fee8 <- computeFEE(pool, comm, dis_metric="-
man", abundWeighted=FALSE, poolBased=FALSE, user_
ecdf="./ecdf_TN")
biodiv[biodiv$nsp==1,3:10] <- 0.5 # assign mono-
cultures FEE of 0.5
pairs(biodiv[,2:10], pch=19)
```

As shown in Fig. 4, most FIA plots have a species richness (*n*) around 8. FEEs in different versions are significantly and positively correlated; but species richness has negative (some are weak) correlations with these FEEs.

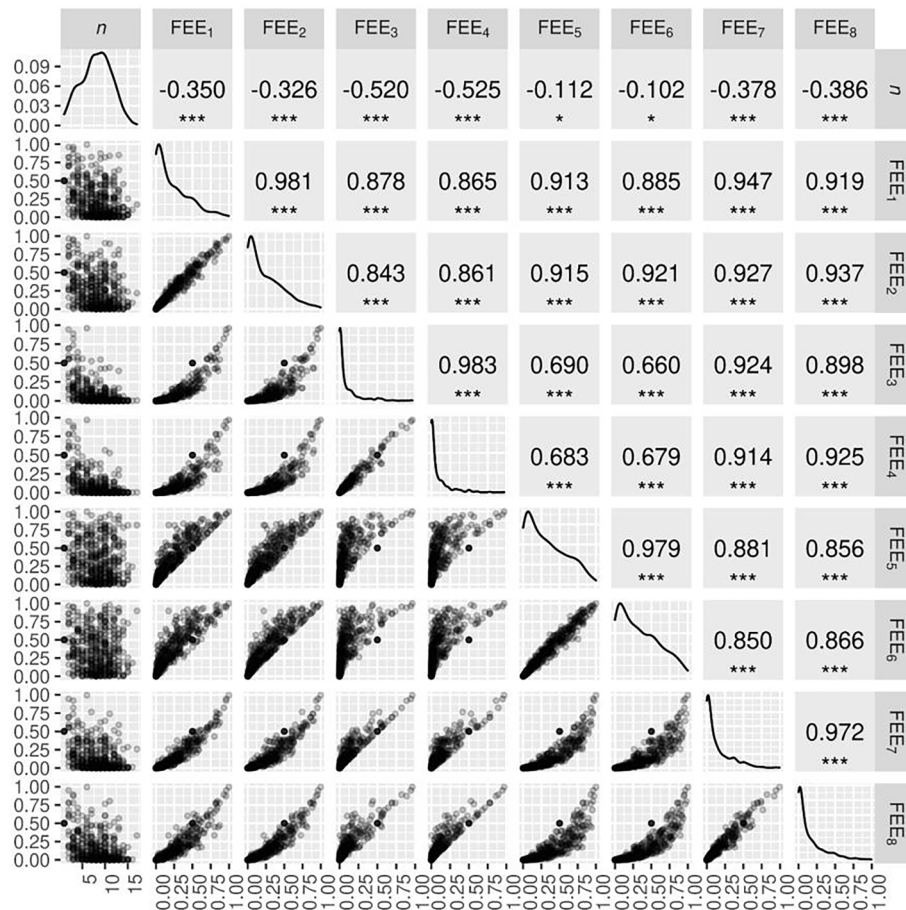


Fig. 4. Pairwise scatter plots (lower left) and Pearson's *r* correlations (upper right) among species richness (*n*) and FEE indices (see the code snippet above to find the meaning of FEE₁ to FEE₆). The diagonal cells show the distributions of the corresponding indices. Significance levels: ***, <0.001; *, <0.05.

3.4. Diversity in different forest types

We further investigated the distribution characteristics of individual plots' FEE index and species richness. In the following examples, we took FEE₂ above (with the argument setting of `dis_metric="manhattan"`, `abundWeighted=TRUE`, `poolBased=TRUE`) as the representative FEE index to examine how functional diversity varies among the FIA plots. In the following code snippet, we compared the biodiversity of these plots among different forest types, which was derived from the FORTYPECD variable in the FIA database (Burrill et al., 2018). In the dataset we prepared for this example, `plt_FORGRP` contains the FIA forest type code of the plots and `frttyp` provides the forest types' mapping relationship between their codes and names. Only 266 plots were included in this analysis because we excluded the plots with multiple forest types.

```
library(dplyr)
biodiv_FORGRP <- biodiv %>% right_join(plt_FORGRP)
%>% left_join(frttyp, by=c("FORGRP"="Code"))
par(mfrow=c(2,1), mar=c(4,11,1,1))
byfreq <- with(biodiv_FORGRP, reorder(GRP,FORGRP,
length)) # ordered by frequency (number of plots)
boxplot(biodiv_FORGRP$fee2~byfreq, xlab=expression(
FEE[2]), ylab="", horizontal=TRUE, las=1)
boxplot(biodiv_FORGRP$nsp~byfreq, xlab="species
richness", ylab="", horizontal=TRUE, las=1)
```

As shown in Fig. 5, the oak/hickory forest type is most common in Tennessee and has relatively high species richness; but its functional diversity is relatively low. This is probably because most *Quercus* (oak) and *Carya* (hickory) species have high DT and low ST (i.e., they are concentrated to a small portion of the trait space, as Fig. 3 shows). In contrast, the forest type "other eastern softwoods" has low species richness but high FEE. Softwood or conifer species in our pool includes six *Pinus* species, one *Juniperus* species, one *Taxodium* species, and one *Tsuga* species. These species spread much more widely in the trait space, from high DT and low ST (e.g., *Juniperus virginiana* with DT of 4.65 and ST of 1.28) to low DT and high ST (e.g., *Tsuga canadensis* with DT of 1 and ST of 4.83, see Fig. 3). Therefore, a species assemblage of conifers in Tennessee might have a higher probability to be functionally diverse in terms of drought and shade tolerance.

3.5. Diversity in different ecoprovinces

Tennessee spans five ecoprovinces (Fig. 6), from the Mississippi riverine forests in the west to forests in Appalachian Mountain in the east. We evaluated the variations of species richness and FEE among these ecoprovinces in Tennessee, as the following code snippet demonstrates. The ecoprovince of plots was derived from the ECOSUBCD field in the FIA database (Burrill et al., 2018). In the dataset we prepared for this example, `plt_ECOPV` contains FIA ecoprovince code of the plots and `ecopro` provides the ecoprovinces' mapping relationship between their codes and names (Cleland et al., 2007).

```
biodiv_ECOPV <- biodiv %>% right_join(plt_ECOPV) %>%
left_join(ecopro, by=c("ECOPV"="Code"))
par(mfrow=c(2,1), mar=c(4,15,1,1))
byECOPV <- with(biodiv_ECOPV, reorder(ECOP,ECOPV,
unique)) # ordered from east to west
boxplot(biodiv_ECOPV$fee2~byECOPV, xlab=expression(
FEE[2]), ylab="", horizontal=TRUE, las=1)
boxplot(biodiv_ECOPV$nsp~byECOPV, xlab="species
richness", ylab="", horizontal=TRUE, las=1)
```

In general, plots in the Appalachian Mountains [M221] have relatively high species richness but low FEE (Fig. 7). This might relate to the environmental filtering effect in shaping tree communities in the mountainous region (Chapman and McEwan, 2018). In contrast, plots in the Southeastern Mixed Forest ecoprovince [231] have relatively high FEE while their species richness is lower than the plots in the

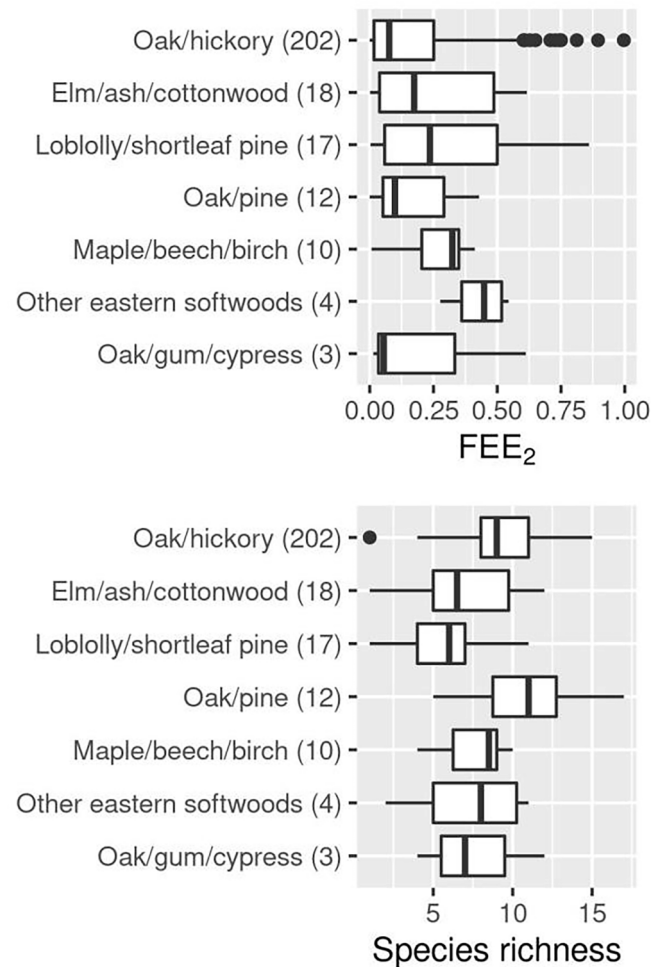


Fig. 5. Distribution of plot's FEE and species richness in the different forest types. The parenthesized numbers are the amounts of plots of the corresponding forest type. The boxes in the boxplots show the interquartile range, and the outliers are cases beyond 1.5 times the interquartile range.

ecoprovinces to the east ([223, 221, and M221]) (Fig. 7), which are dominated by broadleaf forests.

Decadal climate variability has induced widespread shifts of forest species composition in the eastern U.S. (Zhang et al., 2018). Conversions between softwood and hardwood forests have been observed in Tennessee in recent years (Oswalt et al., 2012). In the Southeastern Mixed Forest ecoprovince, some historical mixed forests (e.g., oak/pine) have transitioned to loblolly pine plantations and broadleaf forests (Hanberry et al., 2019). The total area of mixed forests in Tennessee has decreased 7.4% from 2004 to 2009 (Table 6 in Oswalt et al. (2012)). If this trend continues, the loss of mixed forests might imply a reduction of functional diversity in forest stands even if species richness might remain stable in Tennessee's forests. By applying the FEE calculation to historical forests and ecological inventory data, the FEEr package can be further extended to examine the trend of functional diversity over time and assess its link with natural and/or human disturbances.

4. Conclusion

Functional diversity is an important concept in studying the role of biodiversity in ecosystem function and vulnerability. The FEE index performs well in qualifying functional diversity by combining two aspects of species distribution (extension and evenness) in trait space and applying null models to standardize the comparison across species richness (Zhang et al., 2021). We developed this FEEr package to

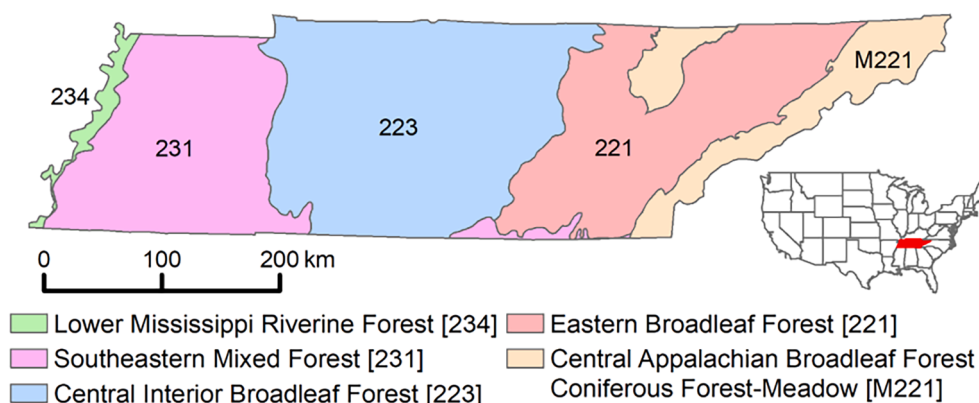


Fig. 6. Five ecoprovinces in Tennessee. The ecoprovince boundaries and their codes are defined in Cleland et al. (2007).

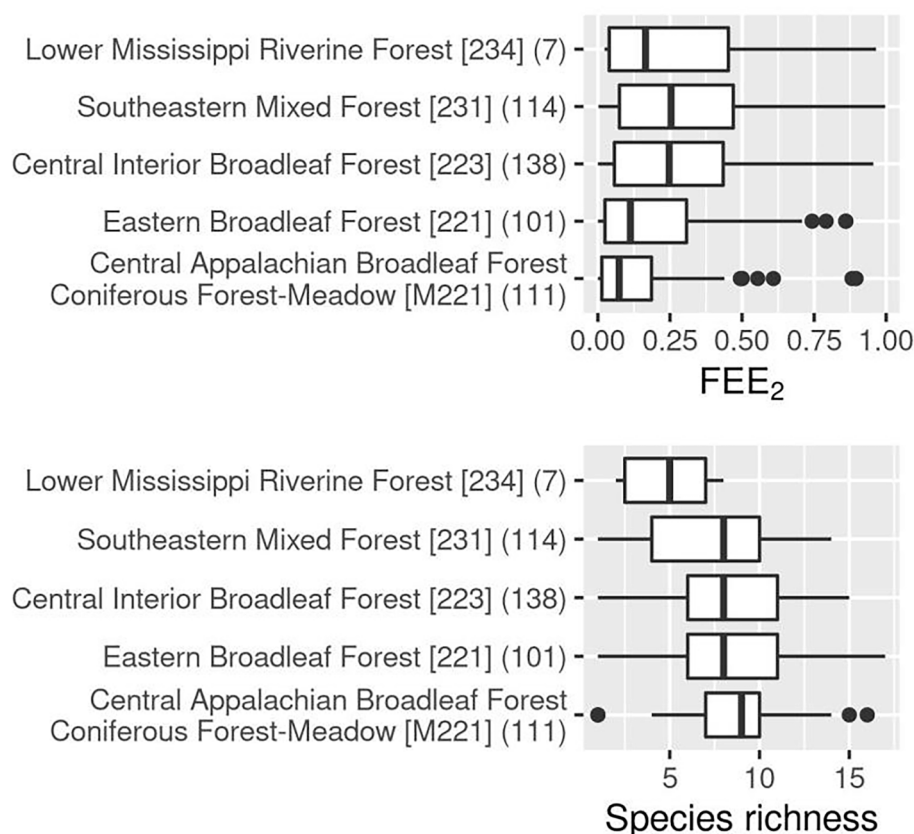


Fig. 7. Distribution of plot's FEE and species richness in the different ecoprovinces (the ecoprovince codes are shown in the brackets). The parenthesized numbers are the amounts of plots of the corresponding ecoprovince. The boxes in the boxplots show the interquartile range, and the outliers are cases beyond 1.5 times the interquartile range.

facilitate the calculations of FEE, intending to provide a convenient and reliable open-source tool for evaluating functional diversity. We used FIA plots in Tennessee, USA as a simplified case study to demonstrate the potential of the FEE index and the FEER package. Specifically, we showed the usage of FEER in decoupling measurement of functional diversity from taxonomic diversity.

CRediT authorship contribution statement

Tao Zhang: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Matthew B. Russell:** Validation, Writing – review & editing, Supervision, Funding acquisition. **Grant M. Domke:** Writing –

review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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