Methods in Ecology and Evolution

British Ecological Society

Methods in Ecology and Evolution 2011, **2**, 233–237 doi: 10.1111/j.2041-210X.2010.00082.x

APPLICATION

FDiversity: a software package for the integrated analysis of functional diversity

Fernando Casanoves[1]*, Laura Pla[2], Julio A. Di Rienzo[3] and Sandra Díaz[4]

[1]*Headquarters, CATIE 7170, Cartago, Turrialba 30501, Costa Rica;* [2]*Complejo docente el Hatillo UNEFM, Apdo. 7434, Coro 4101, Venezuela;* [3]*FCA –UNC, Av. Valparaíso s/n, Ciudad Universitaria, Córdoba 5016, Argentina; and* [4]*IMBIV (CONICET-UNC) and FCEFyN, Av. Vélez Sarsfield 299, Córdoba 5000, Argentina*

Summary

1. The growing interest in functional diversity has been accompanied by a proliferation of indices proposed to calculate its different components; however, empirical studies have been hampered by a lack of integrated tools for their easy calculation based on field data sets.

2. We present FDiversity, a free, user-friendly, open source-based software package for the calculation and integrated statistical analysis of most functional diversity indices and metrics published to date.

3. This tool greatly facilitates the analysis of functional diversity patterns and also the links of different dimensions of functional diversity with environmental factors and ecosystem properties and services.

Key-words: abundance-trait profile, biodiversity, ecosystem properties, ecosystem services, free software, functional traits, linear models, R Project

Introduction

Functional traits are morphological, physiological, phenological or behavioural features measurable at the individual level, which impact fitness of the organism via their effects on growth, reproduction and survival (Violle *et al.* 2007). Functional diversity can be broadly defined as the value, range, distribution and relative abundance of the functional traits in a given ecosystem (Díaz *et al.* 2007). Functional diversity is an increasingly used concept in the analysis of biodiversity patterns and their links with various ecosystem properties and services (Tilman *et al.* 1997; Hooper & Vitousek 1998; Garnier *et al.* 2004; Díaz *et al.* 2007), as well as their responses to environmental drivers (Flynn *et al.* 2009; De Bello *et al.* 2010). As a consequence, a growing number of indices have been proposed to quantify its various aspects. These indices differ in mathematical properties, the features they capture, their emphasis on location or dispersion measures, the consideration of single or multiple traits and the inclusion of abundances of the trait values. Although some useful comparative reviews have been produced (Petchey & Gaston 2002, 2006, 2007; Mason *et al.* 2003; Petchey, O'Gorman, & Flynn 2009; Mouchet *et al.* 2010), the field is too young and fast-moving to draw definitive conclusions on the best indices for different purposes.

Also, because they capture different aspects of functional diversity, it makes sense to use several indices and statistics to characterize a situation or to answer different ecological questions. Mouchet *et al.* (2010) have compared functional diversity indices and provide recommendations to select appropriate indices for the different aspects of functional diversity. However, the application of different indices has been constrained by the lack of appropriate practical tools, hampering progress in both the empirical knowledge of functional diversity patterns and their associated ecosystem properties, and the understanding of the properties and the performance of the indices themselves. There are several software applications to calculate diversity indices, but they focus on species-based diversity (e.g. EstimateS, Colwell 2009; EcoSim, Gotelli & Entsminger 2009), on phylogenetic diversity (e.g. PHYLIP, Felsenstein 2005; PHYLOCOM, Webb, Ackerly, & Kembel 2008) or on specific functional diversity indices (e.g. the FD-R language package, Laliberté & Legendre 2010). The procedures to calculate functional diversity indices are scattered and involve carrying out separate analyses, often with different input formats like the script written by Petchey & Gaston (2002) and the FD R-library (Laliberté & Legendre

*Correspondence author. E-mail: casanoves@catie.ac.cr
Correspondence site: http://www.respond2articles.com/MEE/

2010). None of them covers a wide range of functional diversity indices. We rose to this challenge by building a tool for the integrated assessment of functional diversity, including the vast majority of functional diversity indices and metrics published to date.

Functional diversity indices

Faith (1996) proposed a functional diversity index based upon application of the environmental diversity index (ED) to a functional space, constructed using phylogenetic information for the set of species. Another attempt to define a functional diversity index was by identifying the number of different combinations of trait values (FAD1, Walker, Kinzig, & Langridge 1999). Most of the later approaches are based on dissimilarity among species in trait space (the T-dimensional space defined by the T traits). Functional attribute diversity (FAD 2) is the sum of all dissimilarities among pairs of species using ecological distance (Walker, Kinzig, & Langridge 1999). To overcome the direct dependence of FAD2 on richness, Schmera, Erős, & Podani (2009) proposed an average version obtained using the distance matrix among the unique profiles divided by the number of functional units (MFAD). Cornwell, Schwilk, & Ackerly (2006) proposed another index not based on the distance matrix, using the volume of the 'convex hull' defined by the relative position of species in the trait space to summarize the dispersion of species in this space.

The use of species abundance to weight trait profiles was first proposed for indices based on single traits, such as the community weighted mean (CWM, Grime 1998; Garnier *et al*. 2004; Díaz *et al*. 2007; Lavorel *et al*. 2008), functional divergence (FDvar, Mason *et al*. 2003) and functional regularity (FRO, Mouillot *et al*. 2005). The use of quadratic entropy (Rao 1982) to quantify functional biological diversity was the first attempt to incorporate species abundance with species multitrait profiles (Shimatani 1999, 2001; Botta-Dukát 2005). Petchey & Gaston (2002) proposed the use of a dendrogram to obtain functional diversity indices using multitrait profiles without abundance. The original method constructs a unique dendrogram for the set of species found in the community. The functional diversity of each sample is the sum of all branches in the dendrogram corresponding to the subset of species in the sample. Podani & Schmera (2006) proposed to recalculate this index using one dendrogram for the subset of species in each plot (FDp). Petchey & Gaston (2006), on the other hand, recommended to keep the dendrogram for all species and estimate the index (FDc) by summing the branches for the species subset only up to their own rooting node (Petchey & Gaston 2006, 2007).

Pla *et al*. (2008) proposed a modification of this dendrogram-based approach, which incorporates the relative abundance of each species by computing the weighted distance matrix as a first step in index calculation. The weighted FD can be calculated based on either a community dendrogram (wFDc) or a plot dendrogram (wFDp).

All the FD indices derived from dendrograms are most often calculated using one observation per species. However, intraspecies variability can be incorporated following the individual-level FD (iFD) approach of Cianciaruso *et al*. (2009), which considers several observations per species.

It is also possible to derive another index from the distance matrix among species in the trait space by summing all the distances weighted by the product of the species relative abundance. This index, first proposed by Rao (1982), may also be expressed on a 0–1 scale, by dividing the observed value by the Rao maximum to obtain the relative Rao (RaoR). This index is also known as quadratic entropy (Pavoine, Ollier, & Pontier 2005).

Each of the functional diversity indices described earlier gives a partial picture of the relationship among species abundance, trait variability and trait values (Mason *et al*. 2005; Mouillot *et al*. 2005). A way to overcome this limitation is to approach functional diversity using more than one measure. Villéger, Mason, & Mouillot (2008) proposed functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) as different, independent measures of biodiversity in the trait space. Recently, Laliberté & Legendre (2010) proposed a fourth measure, functional dispersion (FDis), to complement this approach.

Software capabilities

We present a new software package, FDiversity, that allows the integrated analysis of functional diversity. FDiversity is free and can be downloaded at http://www.fdiversity.nucleodiversus.org/. It allows the calculation of a comprehensive list of both well-established and recently proposed functional diversity indices (Table 1), as well as traditional species-based diversity indices, and provides tools for statistical analysis. The analytical tools include a module for the modelling of the estimated values of different indices of functional diversity with general linear models (ANOVA and ANCOVA). This module can be used to determine the relative importance of different dimensions of functional diversity for a particular ecosystem property or service, as suggested for example by Díaz *et al*. (2007). The software can handle its own data sets and read and write from/to different standard file formats, such as *.xls, *.txt, *.db and *.r, among others. It contains tools to edit, sort and rearrange rows and columns of the data matrix, select cases and perform basic descriptive analyses. Several data transformation options are available, including both standard and user defined. Importantly, it has tools to merge traits-by-species data matrices with species-by-plot data matrices.

The software uses the R package (R Development Core Team 2010) through a user-friendly interface written in Delphi® (Fig. 1). The software operates under Windows® platforms, but it can also be run in MacOS® and Linux®.

The menus File and Edit include the options to handle files and edit entries. The Data menu allows access to a special tool to transform variables, concatenate data bases, perform several actions over rows and columns, search and select cases, define new variables using formulae, deactivate cases and rearrange rows and columns.

The Statistics menu includes an option to perform summary statistics. It also includes the core option to calculate functional

Table 1. Functional diversity indices calculated by FDiversity software

Type	Species weight	Names given by the authors	Source	Code
Single-trait	Yes	Community weighted mean	Garnier *et al.* 2004; Díaz *et al.* 2007; Lavorel *et al.* 2008	CWM
	Yes	Functional divergence	Mason *et al.* 2003	FDvar
	Yes	Functional regularity	Mouillot *et al.* 2005	FRO
Multi-trait	No	Functional attribute diversity	Walker, Kinzig, & Langridge 1999; Walker & Langridge 2002	FAD1 FAD2
	No	Modified FAD2	Schmera, Erős, & Podani 2009	MFAD
	No	Community-based functional diversity	Petchey & Gaston 2002, 2006	FDc
	No	Plot-based functional diversity	Podani & Schmera 2006	FDp
	No	Convex hull hypervolume	Cornwell, Schwilk, & Ackerly 2006	Chull
	No	Individual-level FD	Cianciaruso *et al.* 2009	iFD
	Yes	Quadratic entropy	Rao 1982	Rao
	Yes	Relative quadratic entropy	Rao 1982; Pavoine, Ollier, & Pontier 2005	RaoR
	Yes	Weighted FDc	Pla *et al.* 2008	wFDc
	Yes	Weighted FDp		wFDp
	No	Functional richness	Villéger, Mason, & Mouillot 2008	FRic
	Yes	Functional evenness		FEve
	Yes	Functional divergence		FDiv
	Yes	Functional dispersion	Laliberté & Legendre 2010	FDis

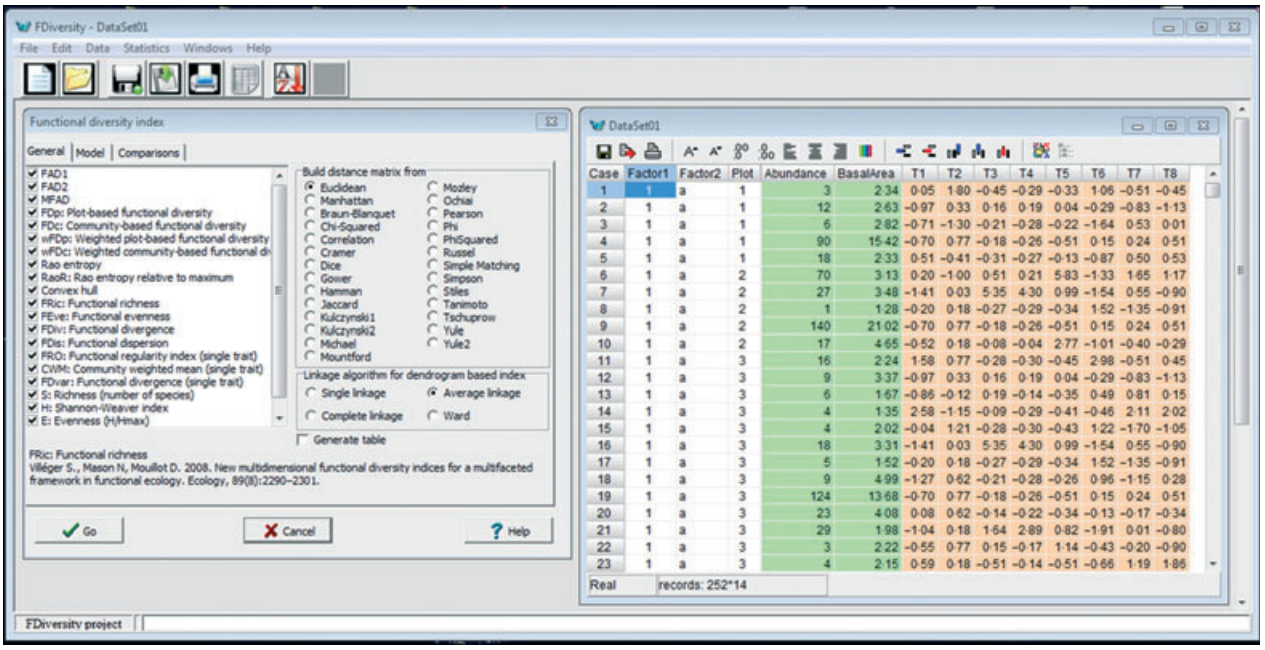

Fig. 1. Main frame of FDiversity. The General tag (left) is used to select indices to be estimated and distance measures to be used. The data base (right) is displayed with class variables (Factor1, Factor2, and Plot), weight measures (Abundance and BasalArea) and trait values after standardization (T1 to T8).

diversity indices based on a set of traits for each species in each plot or experimental unit. All the indices summarized in Table 1 can be computed simultaneously or by subsets; when an index is selected, the original reference is copied to the clipboard to assist identification of the original source. The preferred distance or similarity measure, as well as the linkage algorithms for those indices based on dendrograms, can be selected from a comprehensive list. Two tabs complete this option: one to select the model to perform ANOVA and ANCOVA when a classificatory or factor variable has been included, and the other to choose an appropriate method for comparison of means for main effects and interactions.

The Results panel shows the calculated values for all functional diversity indices selected, the ANOVA or ANCOVA tables and the results of comparisons of means. It is possible to save the content of this panel with a single command for future inspection, copy the text to a word processor or transform it in a data table. By enabling the Generate table option in the General

tab, a new table can be produced, with one row per plot and one column per index.

FDiversity has an interface to run R scripts, read data bases from R libraries and exchange tables. The user may define particular indices or analyses using any of the R capabilities within the same software environment and take advantage of FDiversity's versatility in the handling of data tables. The user may also modify some of the routines used to calculate functional diversity indices if it is appropriate for a particular analysis.

The software includes additional productivity tools. A comprehensive User Manual (Casanoves, Di Rienzo, & Pla 2008) contains systematic descriptions and examples of data handling, calculation of functional diversity indices and the general linear model specification to fit models for the estimated indices. It also includes a brief description of each index, a guide to interpret it, and the mathematical expression used to calculate it. Guidelines are provided to assist the selection of the appropriate index for each particular study. Additional support to users is given in the form of e-mail assistance, regular update announcements and special assistance for analysis of data bases. For details of math expressions and algorithms used for each index, see Appendix S1 in Supporting Information.

Acknowledgement

This project was supported by the Inter-American Institute for Global Change Research, IAI-CRN 2015 (supported by National Science Foundation, Grant GEO-0452325). This is an initiative of Núcleo DiverSus, supported by CONICET, FONCYT, Universidad Nacional de Córdoba, DIVERSITAS and the IGBP Global Land Project.

References

Botta-Dukát, Z. (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, **16**, 533–540.

Casanoves, F., Di Rienzo, J.A. & Pla, L. (2008) *User Manual f-Diversity: Statistical Software for the Analysis of Functional Diversity*, 1st edn. Argentina. URL http://www.fdiversity.nucleodiversus.org [accessed 13 June 2010].

Cianciaruso, M.V., Batalha, M.A., Gaston, K.J. & Petchey, O.L. (2009) Including intraspecific variability in functional diversity. *Ecology*, **90**, 81–89.

Colwell, R.K. (2009). EstimateS: statistical estimation of species richness and shared species from samples. Version 8.2. User's Guide and application published at: http://purl.oclc.org/estimates.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006) A trait-based test for habitat filtering: convex hull volume. *Ecology*, **87**, 1465–1471.

De Bello, F., Lavergne, S., Meynard, C.N., Lepš, J. & Thuiller, W. (2010) FORUM The partitioning of diversity: showing Theseus a way out of the labyrinth. *Journal of Vegetation Science*, DOI: 10.1111/j.1654-1103.2010.01195.x.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, **104**, 20684–20689.

Faith, D.P. (1996) Conservation priorities and phylogenetic pattern. *Conservation Biology*, **10**, 1286–1289.

Felsenstein, J. (2005) *PHYLIP (Phylogeny Inference Package) Version 3.6. Distributed by the Author*. Department of Genome Sciences, University of Washington, Seattle.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M. & DeClerck, F. (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, **12**, 22–33.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.-P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.

Gotelli, N.J. & Entsminger, G.L. (2009) *EcoSim: Null Models Software for Ecology*. Version 7. Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT 05465. http://garyentsminger.com/ecosim.htm.

Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.

Hooper, D. & Vitousek, P. (1998) Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs*, **68**, 121–149.

Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A. & Bonis, A. (2008) Assessing functional diversity in the field – methodology matters! *Functional Ecology*, **16**, 134–147.

Mason, N.W.H., MacGillivray, K., Steel, J.B. & Wilson, J.B. (2003) An index of functional diversity. *Journal of Vegetation Science*, **14**, 571–578.

Mason, N.W.H., Mouillot, D., Lee, W.G. & Bastow, W. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**, 112–118.

Mouchet, M.A., Villeger, S., Mason, N.W. & Mouillot, D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**, 867–876.

Mouillot, D., Mason, N.W.H., Dumay, O. & Wilson, J.B. (2005) Functional regularity: a neglected aspect of functional diversity. *Oecologia*, **142**, 353–359.

Pavoine, S., Ollier, S. & Pontier, S. (2005) Measuring diversity from dissimilarities with Rao's quadratic entropy: are any dissimilarities suitable? *Theoretical Population Biology*, **67**, 231–239.

Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, **5**, 402–411.

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758.

Petchey, O.L. & Gaston, K.J. (2007) Dendrograms and measuring functional diversity. *Oikos*, **116**, 1422–1426.

Petchey, O.L., O'Gorman, E.J. & Flynn, D.F.B. (2009) A functional guide to functional diversity measures. *Biodiversity, Ecosystem Functioning, and Human Wellbeing* (eds S. Naeem, D.E. Bunker, A. Hector, M. Loreau & C. Perrings), pp. 49–59. Oxford University Press, Oxford.

Pla, L., Casanoves, F., Di Rienzo, J., Fernandez, F. & Finegan, B. (2008) *Confidence Intervals for Functional Diversity Indices Considering Species Abundance*. XXIV International Biometric Conference. Dublin, 2008.

Podani, J. & Schmera, D. (2006) On dendrogram-based measures of functional diversity. *Oikos*, **115**, 179–185.

R Development Core Team. (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org [accessed 18 May 2010].

Rao, C.R. (1982) Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology*, **21**, 24–43.

Schmera, D., Erős, T. & Podani, J. (2009) A measure for assessing functional diversity in ecological communities. *Aquatic Ecology*, **43**, 157–167.

Shimatani, K. (1999) The appearance of a different DNA sequence may decrease nucleotide diversity. *Journal of Molecular Evolution*, **49**, 810–813.

Shimatani, K. (2001) On the measurement of species diversity incorporating species differences. *Oikos*, **93**, 135–147.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.

Walker, B.H., Kinzig, A. & Langridge, J.L. (1999) Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, **2**, 95–113.

Walker, B.H. & Langridge, J.L. (2002) Measuring functional diversity in plant communities with mixed life forms: a problem of hard and soft attributes. *Ecosystems*, **5**, 529–538.

Webb, C., Ackerly, D. & Kembel, S. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098–2100.

Received 17 June 2010; accepted 11 November 2010
Handling Editor: Daniel Faith

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Definition of current measurement of diversity indices implemented in FDiversity.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.