Functional richness: Overview of indices and underlying concepts

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ABSTRACT

Functional richness, currently defined as the amount of niche space occupied by the species within a community, is one of the three major components of functional diversity. Different indices have been developed in order to quantify this component. However, the range of indices available for assessing functional richness, often mathematically complex and based on different rationales, can cause confusion for field ecologists and lead to misinterpretation of the results obtained. In this context, we have provided the first study exclusively focused on the comparison of the definitions, advantages and drawbacks of a large set of functional richness indices. The first part of this work is focused on four indices ($FD_{P\&G}$, FRic, TOP and N-hypervolumes indices) that are currently the most commonly used for assessing functional richness. We have completed our study by including recently developed indices that enable us to take into account the intraspecific trait variability (i.e. FRim index and TDP framework), because there is currently a growing scientific consensus regarding the necessity of including this aspect in the assessment of the functional diversity of communities.

We demonstrate that although authors have argued that their index describes the functional richness, each of them describes only part of it, and this part may strongly differ from one index to another. Rather than advocating the general use of a single index and/or systematically avoiding others, our study highlights the need for selecting indices in close relation with the context, the available data and the aims of each study. Such a strategy is an essential preliminary step for preventing misunderstanding and artefactual controversies. Along these lines, we propose some guidelines to help users in selecting the most appropriate indices according both to the facet of functional richness on which they wish to focus and to the characteristics of the available data.

1. Introduction

Assessing functional diversity, which is now recognized as a main driver of the functioning of ecosystems and their responses in both terrestrial and aquatic environments, has become a crucial challenge in community ecology. This broad concept is now usually split into three major components: functional richness, functional evenness and functional divergence (Mouillot et al., 2005, 2013; Mason et al., 2005). The assessment of functional richness is probably the oldest and the most widely used way of investigating functional diversity (see Blondel, 2003). However, behind this term, simple in appearance, lies a much more complex component which may vary widely in its definitions according to the authors. Some approaches define the concept of functional richness as the number of species sharing the same characteristics, whereas other approaches have used the distribution of species trait values in the functional space. Consequently, combining all these definitions, and the associated indices, within a single general concept (i.e. functional richness) can cause confusion for field

ecologists, and misinterpretation of the results obtained (Battisti and Contoli, 2011; Contoli and Luiselli, 2015). However, there has to date been no survey reviewing all methods and indices used to assess functional richness and what facet of this concept they really measure (and how).

Initially, functional richness was mainly defined as the number of species sharing similar taxonomic, phylogenetic or morphological characteristics (Blondel, 2003). The first method used to estimate this concept of functional richness was based on the number of predefined functional groups in a given assemblage (Magurran, 2013). This approach consisted of grouping together all species sharing similar characteristics (Blondel, 2003). It was then assumed that all species belonging to the same functional group have similar effects on or responses to ecosystems (Chapin et al., 1996; Petchey and Gaston, 2002; Lavorel and Garnier, 2002). Although some studies have demonstrated that the number of functional groups was highly correlated with the ecosystem productivity (Tilman et al., 1997; Hector et al., 1999; Reich et al., 2001), and might be a good proxy of ecosystem

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functioning (Petchey et al., 2004), assessing the functional richness through the assessment of pre-defined functional groups can be problematic. The methods used to assign species to each group are in fact highly subjective because they are based on the user's choices (Holmes et al., 1979; Chapin et al., 1996; Diaz and Cabido, 2001). The definition of the boundaries between each group determines the number of functional groups and by consequence, may impact which species are included within each group. If we assume that the number of functional groups is in direct relation with the ecosystem functioning, defining this number in a non-standardized way can produce undesirable variability in the results obtained (Loiseau and Gaertner, 2015). Furthermore, the use of functional groups ignores all possible differences between species belonging to a single group, whereas these differences can be important notably when the functional traits are quantitative (Petchey and Gaston, 2002; Petchey et al., 2004; Ricotta, 2005). Due to these shortcomings, new approaches based on analyses of the trait values of species have been developed to assess the functional richness of communities. The aim of these approaches is to evaluate the functional richness according the position of species and the distribution of species trait values in the functional space. The first approach developed along these lines refers to the FR index of Mason et al. (2005) and describes the amount of niche filled by the community (Mason et al., 2005). This index considers only a single functional trait in its computation. However, many studies have demonstrated that considering just one functional trait may induce oversimplified conclusions because the major part of the ecosystemic functions cannot be summarized by a single functional trait (Villéger et al., 2008; Schleuter et al., 2010; Hortal et al., 2015).

For these reasons, the new approaches developed in recent years for assessing the functional richness of communities are based on simultaneous consideration of several functional traits. Following the definition offered by Mason et al. (2005), the great majority of studies consider functional richness as "the amount of niche space occupied by the species within a community". These approaches take into account the degree of difference among species with reference to functional variables (i.e. functional traits, Petchey and Gaston, 2002, Mason et al., 2003, Mouillot et al., 2005), and aim to estimate their distribution within the community studied. For that purpose, various indices have been developed, based on different mathematical formulas and concepts (e.g. FD index of Petchey and Gaston, 2002, FRic index of Villéger et al., 2008, TOP index of Fontana et al., 2015). In this context, the aim of this paper is to clearly identify which index characterizes what (in accordance with their respective mathematical construction), and to highlight how we can use this information to achieve a better – and sometimes more complete - view of the functional richness of a community. On this basis, we propose some guidelines to help users in selecting indices according to the concept of functional richness on which they wish to focus and to the properties of the available data.

More specifically, we have focused our discussion on the indices respecting three essential properties in the assessment of the functional richness of communities. Firstly, the index should conserve the continuous values of functional traits (because using functional groups would implicitly assume that species within a group are functionally identical and that the functional differences of species pairs drawn from different groups are equivalent, Ricotta, 2005). Secondly, the index should consider several functional traits (to limit the risk of oversimplification and misrepresentation arising from analyses restricted to a single functional trait, Villéger et al., 2008). Thirdly, the index should not consider the species abundance (to be consistent with the one of the criteria of functional richness index as defined by Mason et al., 2005: "a section of niche space is considered to be occupied even if only very little abundance occurs within it", i.e. a section of niche space is considered as occupied even if only one individual is present in this place).

Consequently, we focused our study on the FD $_{P\&G}$ index (Petchey and Gaston, 2002), the FRic index (Villéger et al., 2008), the TOP index (Fontana et al., 2015) and the N-hypervolume index (Blonder et al.,

2014), hereafter referred to as 'inter-entity approaches'. Furthermore, some recent studies have demonstrated the importance of taking into account the intraspecific trait variability (ITV) in the assessment of the functional richness of communities, because traits vary among genotypes within species and according to the environmental conditions (Messier et al., 2010; Albert et al., 2011; Clark et al., 2011; Laughlin and Laughlin, 2013; Auger and Shipley, 2013). Thus, we also included in our analyses the FRim index of Schleuter et al. (2010) and the TPD $_{Rich}$ index of Carmona et al. (2016a), which are two recent indices taking into account the ITV.

2. Inter-entity approaches

The indices presented in this section consider as basic unit in their computation the species or the functional entities (i.e. individuals sharing the same combination of trait values) but not the probabilistic nature of intraspecific variability.

2.1. The FD$_{P\&G}$ index of Petchey and Gaston (2002): a dendrogram-based measure

The FD index (FD$_{P\&G}$; Petchey and Gaston, 2002) has been one of the most widely used indices during the last decades (e.g. Petchey and Gaston, 2006; Flynn et al., 2009; Mendez et al., 2012; Cianciaruso et al., 2013). FD$_{P\&G}$ is based on functional dendrograms, i.e. trees where species are the tips and the length of branches between them reflects the functional dissimilarities between species (Petchey and Gaston, 2002; Maire et al., 2015). This concept is similar to that developed to compute the phylogenetic diversity (Faith, 1992; Petchey and Gaston, 2002). By consequence, many authors used FD because it is the only index that could be compared to the phylogenetic index (i.e. Faith's PD index) in a biodiversity assessment based on both ecological and evolutionary processes. FD$_{P\&G}$ is the total branch length of the functional dendrogram and consequently, this index measures the overall distance between the different functional units (i.e. all individuals or species sharing the same values of functional traits) of a given community. The greater the distance, the higher the functional richness of this community is considered to be. This index is computed in four steps: (1) obtaining a species * trait matrix (crossing species in lines by their respective trait values in columns), (2) converting the trait matrix into a distance matrix, (3) clustering the distance matrix to produce a dendrogram, and (4) calculating the total branch length of this dendrogram (Petchey and Gaston, 2002). This approach has the advantage of considering the functional difference between species: the more functionally different the species are, the higher the FD$_{P\&G}$. For example, Flynn et al. (2009) have demonstrated that the FDP&G index can be used to highlight the loss of functional richness in species assemblages composed of multiple taxa (e.g. birds, mammals and plants) after land use intensification. However, the faithfulness of fit between the initial distance matrix (i.e. the reality) and the final dendrogram (i.e. on which the FD$_{P\&G}$ index is based) can vary according to the clustering method (Pielou, 1984; Legendre and Legendre, 1998; Podani and Schmera, 2006). More generally, Mouchet et al. (2008) demonstrated that the same combination of distance metric (e.g. Euclidean or Gower metrics) and clustering methods (e.g. UPGMA, UMPMG or Ward clustering) used does not always achieve the best dendrogram. Furthermore, the congruence between the initial distance matrix and the matrix resulting from the classification may decline with a decrease in the number of functional traits and/or of the species richness (Sokal et al., 1992). With the aim of using the most faithful dendrogram to compute the FD$_{P\&G}$ of a community, Mouchet et al. (2008) developed an algorithm allowing its identification on the basis of the two-norm quality criterion (which assesses the similarity between the initial dissimilarity matrix and the dissimilarity matrix from different dendrograms, Mérigot et al., 2010). However, Maire et al. (2015) found that even the 'best' dendrogram (i.e. the most faithful dendrogram) could generate a functional space