

Biodiversity: theory and quantification



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1. 3. 1 Biodiversity components

Biodiversity includes existing species in a place, within species phenotypic and genotypic variation, and also the spatial and temporal variation in the communities and ecosystems contributed by the constituent species (Tilman 2001). Quantifying such a broad concept that includes diversity from gene to ecosystem level has proven to be a quite difficult task. To bypass such unusual situation, ecologists have divided ‘ biodiversity’ into various quantifiable components: species diversity (SD), functional diversity (FD), and phylogenetic diversity (PD).

1. 3. 2 Biodiversity quantification – Classical approach

1. 3. 2. 1 Species diversity

SD refers to species richness (number) and evenness (relative abundance of species) in a community (Maurer & McGill 2011). SD-centric approach has dominated most of the research projects related to biodiversity distribution from local to global scale. SD measures assume that all species are evolutionarily independent and ecologically equivalent while they are not (Swenson et al. 2012). All species have functional differences. This approach is criticized for avoiding functional aspects of species. The knowledge on species number, their identity or the number of different roles they play has not been found adequate to explain resource dynamics, ecosystem productivity, complexity and stability (Diaz & Cabido 2001; Petchey & Gaston 2006; Podani et al. 2013; Zhang et al. 2012) or any other prevailing mechanisms of an ecosystem. However, SD-centric approach can form the basis for incorporating other approaches suitable for quantifying functional

and evolutionary signals of communities (Cavender-Bares et al. 2009; McGill et al. 2006; Swenson et al. 2011).

Three components of SD i. e. alpha (α), beta (β) and gamma (γ) are often measured and used to describe the spatial distribution of species assemblages. These diversity components were first described by Whittaker (1960, 1972). α diversity represents SD of a particular site, β diversity represents species compositional variation among sites, and γ diversity is the sum of diversity for the various sites within an ecosystem. α diversity is measured in a bewildering number of ways. Species richness and numerous indices that incorporate relative abundances of species are two principle measurement schemes of α diversity. Maurer & McGill (2011) have classified SD indices into six categories: (i) richness metrics (e. g. Margalef diversity, Menhinick diversity etc.), (ii) diversity metrics (e. g. Shannon diversity, Simpson diversity etc.), (iii) evenness metrics (e. g. Shannon evenness, Simpson evenness etc.), (iv) dominance or common species metrics (e. g. absolute dominance, relative dominance etc.), (v) high rarity metrics (e. g. LogSkew, % Singletons, PctRare 1% etc.), (vi) semi-parametric metrics (e. g. Fisher's α , lognormal CV etc.). Despite presence of such variety of indices, Shannon's index of diversity and measures based on Simpson's concentration has been the most extensively used indices. However, Jost (2006, 2007) has strongly criticized the usage of index values of these indices in making ecological statements and suggested using the 'effective number of species' which he termed 'true diversity'.

β diversity can be defined in two ways: directional turnover and non-directional variation. In case of directional turnover, species compositional

change is measured along a specified gradient (e. g. spatial, temporal or environmental), and in case of non-directional variation, variation in species composition is measured without reference to any specific gradient (Legendre & De Cáceres 2013). Both β diversity versions are frequently used to explain the connections between local and regional diversity, and to visualize spatial patterns of species assemblages (De Cáceres et al. 2012). Various β diversity indices have been proposed to quantify species compositional variation (directional or non-directional) in a single number. Whittaker (1960) first proposed a non-directional β diversity index for species richness ($\beta = \gamma/\alpha$), and Nekola & White (1999) developed a directional β index by introducing the slope of the similarity decay in species composition with geographic distance. After these initial approaches, the number of indices for measuring beta diversity has been increasing (for details see Vellend 2001; Tuomisto 2010a & 2010b; Anderson 2011). At present, the most popular indices belong to two families: additive ($\alpha + \beta = \gamma$) (McArthur et al. 1966; Lande 1996; Veech et al. 2002) and multiplicative ($\alpha \times \beta = \gamma$) (Whittaker 1960, Jost 2007; Chao et al. 2012). However, debate on different statistical and measurement aspects of both of these broader approaches is still ongoing (see Forum section published by Ecology (2010: 1962-92). Moreover, species-centric β diversity approach has been criticized for ignoring functional similarities between communities and its inability to capture the processes underlying community assembly compared to functional turnover between ecological communities (i. e. functional beta diversity) (Siefert et al. 2013).

1. 3. 2. 2 Functional diversity

FD quantifies the functional differences between species by focusing on their functional traits' value and range (Tilman 2001). Functional traits are quantifiable phenotypic characteristics that regulate species performance and ultimately influence ecosystem processes (Pérez-Harguindeguy et al. 2013). Numerous studies have reported strong relationships between ecosystem functions and FD, rather than SD (reviewed in Díaz et al. 2013, Loreau et al. 2001; Tilman et al. 1997) and also acknowledge the influences of FD in affecting ecosystem processes (e. g. energy cycle, mineral cycle, community dynamics etc.) (Grime 1988; Lavorel & Grigulis 2012; Odum 1969).

Numerous measureable concepts of FD have been provided by different scientists at different times (see Mason & Bello 2013; Petchey & Gaston 2006). The first published index measuring FD was Functional Diversity Attribute (Langridge et al. 1999). Later another index (FD) was proposed by Petchey & Gaston (2002b). This dendrogram-based index has been used by several scientists (Lepš et al. 2006; Petchey et al. 2004). In 2004, Garnier et al. proposed an index – 'community-weighted mean trait values' (CWMs) – to summarize the functional composition of single trait within a community. This index has been used to describe the relationships between community structure and ecosystem functioning (Lepš et al. 2006; Lavorel et al. 2008; Ricotta & Moretti 2010). In 2005, Botta-Dukat (2005) proposed Rao's quadratic entropy following Rao (1982). This multivariate index of diversity (Schleuter et al. 2010) has certain advantages over the previous indices because it considers abundance data (Botta-Dukat 2005; Petchey & Gaston 2006). In the same year (2005), Mason et al. proposed a measurement of FD

with a set of three components: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). The major advantage of this set of indices is that it identifies all aspects of functional diversity in single numbers (Mason & Bello 2013). Disintegrating FD based on the above three components helps plotting a structure to identify variation in FD along ecological gradients (Mason et al. 2013, Pavoine et al. 2013, Mason & Bello 2013). Multivariate measurements for these three FD components were defined by Villeger et al. (2008). In recent years, several discrete methods have been developed to measure FD (Mouchet et al. 2008; Schmera et al. 2009; Zhang et al. 2012). Very recently, a new method has been described by Song & Zhang, (2013), which is based on neural network theory and use self-organizing feature map (SOFM index) for FD measurement.

So far, known definitions of FD focus much on within community trait variation rather than between communities or among regions (Mason et al. 2005; Mason & Bello 2013). Hence, consideration of FD in β or γ level is required which can provide much insight on community structure over spatial and temporal scales. Very recently, some methods have been developed which allows measurement and comparison of the α and β components of species, functional and phylogenetic diversity (Bernard-Verdier et al. 2013; Carboni et al. 2013; Janecek et al. 2013). But a unified method is still required. Though Mason et al. (2005) and Villeger et al. (2008) claimed that unified index for the measurement of FD would not be attainable; later in 2011, Ricotta and Moretti incorporated CWM and Rao Q indices into a unifying framework and emphasized the benefits of using such combined index.

1. 3. 2. 3 Phylogenetic diversity

PD refers to the evolutionary distinctness of individual species or groups of species. More specifically, PD specifies the total extent of phylogenetic distance among species in an ecological community (Srivastava et al. 2012). There has been growing interest in measuring PD because of its importance in conservation prioritization and understanding community structure (Bernard-Verdier et al. 2013; Mi et al. 2012). Conservationists are now giving more emphasis on protecting the group of relatively distinct species with variety of biological features (Cadotte & Davies 2010). Phylogenetic information of species and communities can serve this conservation purpose.

Various methods are for quantifying the PD of a species assemblage (Hardy 2008). Faith (1992) proposed the first quantitative measure of PD that did not take species abundance into account. Both ecologists' and conservation biologists' have extensively used Faith's PD. Hardy & Senterre (2007) developed a set of metrics for partitioning phylogenetic community structure into α and β components. MPD (mean pair-wise phylogenetic distance) and MNND (mean nearest phylogenetic neighbor distance) (Webb 2000) are another two commonly used methods. For statistical validation of observed PD patterns, observed PD values are compared against randomly generated null expectations (e. g. Cavender-Bares et al. 2006, 2009; Kembel and Hubbell 2006; Swenson et al. 2006). NRI (Net Relatedness Index) and NTI (Nearest Taxon Index NTI) are the two commonly used indices for this.

1. 3. 3 Biodiversity quantification – Unified approach

While debate on several aspects of diversity measurements (e. g. partitioning diversity, scale, theoretical clarity, biological meaning) are ongoing, couple of approaches have been taken by ecologists (Jost 2006, 2007, 2010, Mendes et al 2008, Tuomisto 2010a, b, Olszewski 2004, Veech and Crist 2010) to develop a unified index of diversity measurement. Most of these approaches, abundance-based in nature, have tried to integrate several components of diversity (e. g. evenness, scale etc.) into a single unified equation. This kind of approach was first put forwarded by Hill (1973). One of the major motivations behind such approach is to overcome the limitations (e. g. measure different properties of a concept in different units) of traditional diversity indices and to make diversity comparisons easier and informative.

The number of studies attempting to relate abundance-based, phylogeny-based and function-based measures of diversity (Devictor et al. 2010, Stegen and Hurlbert 2011, Swenson et al. 2011) has been increasing for the last couple of years. But a unified equation for measuring species, functional and phylogenetic diversity was still lacking. As current theories of diversity mainly focus on species richness or abundance-based metrics, an integrated metric that focuses on the abundance of organisms, the phylogenetic relationships among those organisms, and the ecological functions that they perform and ecosystem functions that they affect, can provide much biological information for future management and conservation decision making, and can also help to expand ecological theory. In 2012, Scheiner first developed an equation that combines three key components of biodiversity – abundance, phylogeny, and ecological function. This metric has

‘ the ability to understand how the various components of diversity covary with each other and how management to maximize one component may trade off against another’ (Scheiner, 2012). However, the metric has not yet been tested with real world data.

In 2012, Leinster and Cobbold criticized previous approaches of abundance-based diversity measures for not incorporating the differences in abundances between species in natural communities. Following a similarity-sensitive approach, they developed a single formula that incorporates many popular indices (e. g. Shannon, Simpson, species richness, Rao’s quadratic entropy, the Gini-Simpson index, the Berger-Parker index, the Hill numbers, the Patil-Taillie Tsallis entropies etc.) which can be used in a unified way, and the measures provide effective numbers. This unified equation can be used for measuring different components of diversity: genetic, morphological, functional etc. They also suggested using diversity profiles to compare communities, to visualize the shape of a community, to understand how diversity changes when the emphasis shifts from rare to dominant species.