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Essays and Perspectives

Functional diversity: an overview of its history and applicability

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ABSTRACT

Ecological investigations are increasingly using functional diversity in order to understand different patterns, such as species occurrence, species competitive abilities, and the influence of biological communities on ecosystem functioning. Here we provide an overview of the history and applicability of functional diversity in ecological studies. We found that the idea of functional diversity emerged many times and in distinct fields over the years. Functional diversity was conceived as an alternative classification to measure the ecological importance of species in a community, as well as a way to understand how biodiversity affects specific ecosystem functions. Gradually, new questions regarding functional traits emerged. Some examples include understanding species competitive abilities, patterns of species co-occurrence, community assembly, and the role of different traits on ecosystem functioning. The increasing use of functional-based approaches fueled the search for new metrics aiming at accurately estimating functional diversity and, consequently, categorical-based classifications of functional traits have been gradually replaced by continuous multi-trait approaches. More recently, the role of functional diversity was recognized as a key factor to maintain important functions and services of ecosystems. We present empirical evidence supporting this statement.

Introduction

Recent decades have been especially notable in the rapid accumulation of functional diversity studies. Still, functional diversity is in need of a consensual definition (Petchey and Gaston, 2006). A widely adopted definition is "the value and the range of those species and organismal traits that influence ecosystem functioning" (Tilman, 2001). Functional diversity studies may also focus on the importance of specific traits for

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individual fitness (Bradshaw, 1987). In this sense, the use of the term "function" may apply both to trophic levels and to evolutionary process (i.e. considering the function of adaptations). Regardless of the definition used, it is a consensual point that functional diversity studies always consider organisms as "dynamic entities that interact with their environment" (Calow, 1987).

Functional diversity studies were historically conducted to respond two main questions: (a) how do species influence ecosystem functioning, and (b) how do species respond to environmental change (Hooper et al., 2000). Currently, the applicability of the functional approach was expanded to answer questions related to assembly rules (Díaz et al., 1998; Kraft et al., 2008; Cornwell and Ackerly, 2009), organismal strategies facing severe abiotic conditions (Raunkiær, 1934; Grime, 1974; Westoby, 1998; Lavergne et al., 2003; Golodets et al., 2009), interspecific competition (Grime, 1973), and biodiversity conservation (Petchey and Gaston, 2002a).

Here we review the development of functional diversity studies since their conception to the present day, addressing how concepts and applicability of functional diversity measures changed over time. In addition, we discuss the relationship between functional diversity and ecosystem functioning and services.

The history of functional diversity

The perception that organisms could be categorized in functional groups is not new. The Greek Theophrastus likely took the first step toward the idea of functional diversity, 300 B.C., in *Enquiry into Plants*. Theophrastus created the first botanical systematization by classifying plants according to their height and stem density (see Weiher, 1999). New ideas about this topic emerged only on the 19th century, but now focusing on another functional goal: the influence of biodiversity on ecosystems. The emergence of this view was reported by Darwin in *On the Origin of Species* (Darwin, 1859) through observations of higher productivity in areas holding higher plant diversity.

In the early 20th century Charles Elton introduced a new definition of ecological communities, focusing on the different ways in which species use resources (Elton, 1927). Later, the functional view based on species traits was revisited by Raunkiær (1934), who classified plants into life-forms (i.e. groups of organisms that respond similarly to biotic or abiotic conditions) aiming to understand plant strategies to face cold climates. At the end of the 1950s, G. Evelyn Hutchinson reinforced Elton's view of community ecology by also assuming that communities are formed by groups of organisms sharing similarities regarding resource use (see Blondel, 2003). This idea was further expanded by Root (1967), suggesting the term guild to designate groups of animals exploiting similar resources (see Blondel, 2003). However, it did not take long before a similar, but more widely applicable term emerged, the so-called "functional groups" (Cummins, 1974).

During the 1970s, ecologists were mainly interested in understanding how species traits were influenced by different biotic and abiotic factors (Grime, 1973, 1974), fueling the development of new classification systems (Cummins, 1974; Grime, 1974). These approaches aimed to classify species with respect to their roles in ecosystem processes (such as the functional group classification of stream ecosystems based on trophic interactions; Cummins, 1974) and their interaction with other species (such as the classification of plants based on competitive ability and tolerance to stress and disturbance by species; Grime, 1974).

Advances in functional ecology included the creation of a specific journal, Functional Ecology, first published in 1987. At that time, research topics focused mainly on species strategies for survival and tolerance of distinct environmental conditions (Noble and Slatyer, 1980). In the same decade, a clear definition of functional diversity was provided for the first time, highlighting that "function" is synonymous with "adaptation", in the Darwinian sense of the concept (Bradshaw, 1987; Calow, 1987).

In the 1990s, a growing concern regarding how the Earth would respond to human-induced global changes motivated new ecological questions. The initial concern in explaining distribution of species was gradually replaced by understanding how species affect ecosystem functioning, widening the focus and applicability of functional diversity. The role of species in ecosystem functioning began to be considered a key component of biodiversity (Walker, 1992; Chapin, 1997) and the effects of different components of diversity were assessed (Tilman, 1997). The need to estimate functional diversity in a quick, easy and ecologically meaningful way led to new schemes of classification (Westoby, 1998).

By the 2000s, classification schemes such as the leaf-height-seed strategy scheme – LHS (Westoby, 1998) began to be used to understand species response to disturbance (Golodets et al., 2009) and predict species occurrence along environmental gradients (De Frenne et al., 2010). At the same time, the emergence of a standardized method for measuring functional traits facilitated comparisons among studies (Cornelissen, 2003). In addition to the increasing evidence highlighting the importance of functional diversity in maintaining the functions and services of ecosystems (Hooper et al., 2005; Balvanera et al., 2006), during the 2000s researchers also began to address questions such as how does the order of traits lost affects functional diversity (Petchey and Gaston, 2002b). At the same time, trait-based approaches, although used earlier (e.g. Weiher and Keddy, 1995), became a common tool for understanding community assembly (Ackerly and Cornwell, 2007; Kraft et al., 2008; Pakeman et al., 2011). The popularity of functional diversity investigations associated with a growing consensus about limitations of functional group approaches (Petchey and Gaston, 2002b) in turn fueled the search for new measures of functional diversity (Petchey and Gaston, 2002b; Mason et al., 2005; Botta-Dukát, 2005; Cianciaruso, 2009a).

Measuring functional diversity

The rapid growth of the functional ecology discipline during the past two decades promoted the development of a plethora of indices to measure functional diversity. Debates concerning ecological meaningful ways to choose species traits for ecosystem functioning investigations (Chapin, 1997) and the development of functional indices based on continuous variables (Walker et al., 1999) were particularly fruitful topics at the time. Here, we present a brief overview on the main methodological issues related to functional diversity. However, readers interested in reviews of other aspects of the subject can find them elsewhere (Pavoine and Bonsall, 2011; Petchey et al., 2004, 2009).

Which traits should we consider?

Correct estimates of functional diversity mainly depend on the choice of ecologically meaningful traits. Functional traits may be defined as organismal characteristics that influence fitness and the functioning of ecosystems (Petchey and Gaston, 2006; Cianciaruso, 2009b; Swenson, 2014). However, choosing traits that are truly functional may represent a difficult task and will depend on the study question. When focusing on ecosystem processes it is fundamental to understand how the process of interest operates and which organisms and traits are more influenced by this process (Petchey and Gaston, 2006). For investigations about species interactions and performance, information regarding organism–environment and organism–organism interactions are fundamental, as well as the variation in traits along environmental gradients (Díaz and Cabido, 1997; Petchey and Gaston, 2006; Vandewalle et al., 2010).

The number and type of traits are also key aspects to be considered when measuring functional diversity. By including several traits one will enhance species functional uniqueness, whereas by using only a few traits one will enhance the probability of detecting redundancy of species (Petchey and Gaston, 2006). Therefore, the number of traits included in the analysis must be adequate to capture the specific function of interest (Petchey and Gaston, 2006). Due to the inherent variation in species traits, however, quantitative traits must be preferred over categorical or qualitative ones (Weiher, 1999). In this sense, continuous traits are more effective at capturing interspecific variability in trait values than categorical traits.

Partitioning functional diversity at different spatial scales

We can measure functional diversity using categorical or continuous indices and currently there are many measures available in the literature (see Pavoine and Bonsall, 2011 for a review). Similarly for the traditional measures of diversity, it is also possible to decouple functional diversity in α and β components (De Bello et al., 2009); a useful approach for assembly rules and macroecological studies. Considering that assembly processes acting on natural communities may differ depending on the spatial scale considered, separating functional diversity in within-community (α) and among-community (β) components will improve the detection of all the processes acting on community assembly. Here, α represents the diversity of trait values within one community, whereas β represents how diverse are species trait values among different communities (Bryant et al., 2008; De Bello et al., 2009; Lozupone and Knight, 2005; Swenson, 2014).

Functional redundancy

In addition to the diversity of trait values, another important aspect of trait composition is functional redundancy, which represents the similarity among species in functional terms (De Bello et al., 2007), influencing the resilience of communities (Naeem, 1998; Pillar et al., 2013). Functionally redundant species are expected to play similar roles in ecosystem processes. Therefore, it is fundamental to select the species traits involved in the ecosystem process for correctly estimating functional redundancy (Pillar et al., 2013). Despite its great importance, an attempt to mathematically improve the measurement of functional redundancy was only made recently (see De Bello et al., 2007 for details).

Biodiversity and ecosystem functioning

The maintenance of life on Earth depends on an effective functioning of ecosystems. Likewise, several aspects of human well-being depend on benefits provided by ecosystems (the so-called ecosystem services; Millenium Ecosystem Assessment, 2005). Ecosystem functions represent processes that regulate the flux of energy and matter through the environment (e.g. primary productivity, nutrient cycling, and decomposition), whereas ecosystem services are the benefits provided by the ecosystems to humans (e.g. water and air quality, provision of food and wood; Cardinale, 2012).

The rapid growth of the human population is resulting in overexploitation of natural resources and increasingly causing ecosystem modifications. A growing concern for understanding the consequences of human-induced changes on natural systems has fostered research to investigate the relationship between biodiversity and ecosystem functioning. Important theoretical and empirical contributions were provided since then. Perhaps the most relevant was the accumulation of robust evidence supporting a positive effect of biodiversity on ecosystem processes (Cardinale, 2012). Nonetheless, many questions remain unsolved and researchers still seek for generalizations (Balvanera et al., 2006).

The importance of functional diversity for ecosystem functioning and services

Considering that biodiversity spans several organismal classifications (taxonomic, functional, and phylogenetic) and levels (from genes to ecosystems), identifying the components of biodiversity that are closely related to ecosystem functioning is a key step (Díaz et al., 2006). In this sense, functional diversity has proven to play an important role, since it is claimed to be the most effective diversity measure for detecting a positive effect of biodiversity on ecosystem functioning and services (Balvanera et al., 2006; Díaz et al., 2006).

The effects of biodiversity on ecosystem services occur as the properties of ecosystems related to carbon storage, water and nutrient cycling (Díaz et al., 2007; Cardinale, 2012). For example, food and wood provisioning are tightly related to increases in plant biomass (Balvanera et al., 2006). Other positive effects of plant diversity on ecosystem services include erosion control (due to larger plant roots and mycorrhizal networks), increases in decomposition (via greater diversity and activity of decomposers), and ecosystem resistance to pests (greater diversity of plants results in lower damage to plants) and invasive species (plant biodiversity reduces success of invaders; Balvanera et al., 2006).

There is a complex relationship between species traits and ecosystem services. While a trait may affect several ecosystem services, a given ecosystem service is in turn influenced by several traits. For example, there is a strong relationship between the size and structure of the canopy on climate regulation, but these traits also affect other ecosystem services such as water balance, soil stability, and fiber provisioning (De Bello et al., 2010). Climate regulation, in turn, is also affected by size and architecture of roots and animal body sizes (De Bello et al., 2010).

Biodiversity loss is not a random process (Dirzo et al., 2014). Species with larger body mass, slower growth rate, longer lifespan, and lower reproductive rate are generally lost at higher rates (Díaz et al., 2006). As a consequence, there is a biased impact on ecosystem functions and services linked to these traits (Díaz et al., 2006). For example, biomass production may be affected by loss of large bodied species, mainly due to changes in trophic interactions (Séguin, 2014). Therefore, efforts toward conservation of functional diversity may be a necessary approach to ensure ecosystem functioning and services.

Idiosyncrasies among research fields make it difficult to extrapolate the findings from ecosystem services and ecosystem functioning studies. The former is often conducted at larger scales and usually do not investigate the underlying ecosystem functions related to the specific services (Cardinale, 2012), whereas the latter is biased to grassland ecosystems and most often based on experimental designs (controlling several factors). Therefore, studies using different organisms other than plants, in different ecosystems, and using observational or less-controlled approaches will help to connect the findings among research fields (Balvanera et al., 2006). Furthermore, identifying trait-service clusters (i.e. the multiple connections between traits and ecosystem services involving different trophic levels, De Bello et al., 2010) will provide a more complete picture of how biodiversity affects ecosystems, representing an important tool for conserving ecosystem services and functions.

Conflicts of interest

The authors declare no conflicts of interest.

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