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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