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Relationships between functional diversity and ecosystem functioning: A review

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ABSTRACT

Functional diversity, which is the value, variation and distribution of traits in a community assembly, is an important component of biodiversity. Functional diversity is generally viewed as a key to understand ecosystem and community functioning. There are three components of functional diversity, i.e. functional richness, evenness and divergence. Functional diversity and species diversity can be either positively or negatively correlated, or uncorrelated, depending on the environmental conditions and disturbance intensity. Ecosystem functioning includes ecosystem processes, ecosystem properties and ecosystem stability. The diversity hypothesis and the mass ratio hypothesis are the two major hypotheses of explaining the effect of functional diversity on ecosystem functioning, diversity hypothesis reflects that organisms and their functional traits in a assemblage effect on ecosystem functioning by the complementarity of using resources, and mass ratio hypothesis emphasises the identify of the dominant species in a assemblage. These two hypotheses do not contradict each other and instead they reflect the two different sides of functional diversity and functional composition. The effect of functional diversity on ecosystem functioning also depends on abiotic factors, perturbation, management actions, etc. Function diversity potentially influences ecosystem service and management by effecting on ecosystem functioning. Ecosystem management groups should include functional diversity in their scheme and not just species richness.

Contents

1. Introduction

Human activities have extensively altered the global environment, biogeochemistry cycles, land coverage and biota changes [1]. As a result, biodiversity is lost at an unprecedented speed on a global scale [2]. The loss of biodiversity potentially threatens ecosystem processes and ecosystem services [3]. Therefore, the relationship between biodiversity and ecosystem functioning has been one of the core ecological topics [4,5], although it still remains highly in dispute [6]. Biodiversity is usually measured by species richness [4,7,8]. Adler et al. [9] found that there was no clear relationship between species richness and productivity within

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sites, regions, or across the global by conducting standardized sampling in 48 herbaceous dominated plant communities on 5 continents.

In the last decade, phrases that contain 'functional diversity' increased exponentially in literature [8,10]. More and more researchers show that functional diversity plays an important role in ecosystem functioning [11–13]. Furthermore, Journal of Applied Ecology by the British Ecological Society had published a special issue about applying functional diversity in 2011, inspiring people to consider the role of functional diversity on ecosystem management [14]. In order to better understand and cognize the effect of functional diversity on ecosystem functioning, we review functional diversity, relationship between functional diversity and species richness, and relationship between functional diversity and ecosystem functioning, to promote further development of the functional plant ecology.

2. Functional diversity

2.1. Concept of functional diversity

Functional diversity is an important component of biodiversity [11,15], but there is no standard definition of functional diversity at present. Functional diversity was defined as "the distribution and range of functional traits of the organisms present in a community or ecosystem" [3], "functional diversification within the community" [16], "the components of biodiversity impact on ecosystem working or functioning" [17], "the value, range and relative abundance of traits of organism in a community" [2], or "the variation or distribution of traits in an assemblage [14]". In general, the definitions of functional diversity could be summarized into two categories: the first one is to treat the organism as a unit, and it emphasizes on the quantity and properties of the organism, such as the diversity of functional groups; and the other is to regard the trait as a unit, and it emphasizes the range and distribution of traits, such as functional traits diversity. In fact, the functional traits diversity is paid more and more attention [5,10].

The concept of functional diversity is relatively easy to understand, however, researchers have attempted to calculate the functional diversity in different ways [10]. A common method of calculating functional diversity is expressed by functional group richness [4]. However, functional group richness is overestimated the functional redundancy when there are few variations within functional groups [18]. Walker et al. expanded the concept of functional diversity, and they firstly used species traits for calculation of the functional diversity in an assemblage [19]. The simplest functional diversity index is the sum of the Euclidean distance between any two species within the assemblage [19]. However, this index depends strongly on species richness [20]. To overcome this drawback, Schmera et al. suggested that functional diversity should be calculated by the distance matrix divided by the number of functional units [21]. With the increased knowledge of functional diversity, the indices include species abundance weight (such as the community weighted mean CWM) [12], functional divergence [23], functional regularity [20], multiple traits [24], intraspecific variation [10], and many more indices [25] were developed over time. In addition, Petchey and Gaston proposed the functional dendrogram based on multi-trait distance to calculate functional diversity [11,15,26]. Cornwell created an index which did not depend on the distance matrix, but calculated by the volume of convex hull of the trait space [27].

Similar to the composition of species diversity, functional diversity consists of functional richness, evenness and divergence. Functional richness measures the present species occupying the amount of niche space within an assemblage, functional evenness measures the distribution of species traits occupying the trait space, and functional divergence measures the maximum degree of divergence of abundance distribution of functional trait in trait space within an assemblage [10,28,29]. Laliberté and Legendre suggested that functional dispersion should be the fourth component of functional diversity [25]. Scheuter et al. summarized and compared the functional diversity indices and developed new functional diversity indices (Table 1). They also gave the suggestions on application of the functional diversity indices [10]. Song et al. [30] and others have introduced the method of calculation of these indices, the selection of functional traits, and weight of traits [30–32].

With the development of functional diversity index, some authors developed various programs to calculate the functional diversity index, such as R program (http://www.ecolag.univ-montp2.fr/software) [10,25], "EstimateS" (http://purl.oclc.org/estimates), "EcoSim" (http://garyentsminger.com/ecosim/index.htm), "PHYLOCOM" (http://phylodiversity.net/phylocom/) [38], and so on. However, those programs just calculated or analysed one single functional diversity index, and different programs required different data format, which were inconvenient to users [39]. To address the above problems, Casanoves et al. developed a free software, "FDiversity", available at http://www.fdiversity.nucleodiversus.org, which has a user-friendly interface, and it can calculate and/or analyse most of the functional diversity indices. In addition, the software supports multiple data formats of *.xls, *.txt, *.db, *.r, etc., and it can run on the operating systems of Windows, MacOS, Linux, etc. [39,40].

2.2. Relationship between functional diversity and species richness

The relationship between functional richness and species richness puts forward challenges to compare their relative roles on ecosystem functioning [8,41]. Functional diversity is often positively correlated with species richness, and in this case the functional richness could be replaced by species richness [4,17]. In natural communities, species richness can be higher or lower than functional diversity because of niche overlap between species and intraspecific variation [3]. One explanation of the significantly positive relationship between functional diversity and species richness is the "selection effects" [7]. It assumes that the value or range of traits increase with the regional species pool increasing randomly [4]. However, this positive correlation has rarely been tested in natural ecosystem [3,7,42]. In natural communities, functional redundancy, local species pool, environmental filter, etc. could affect the relationship between diversity and ecosystem functioning [8]. Mayfield et al. illustrated that functional diversity and species richness had 8 possible directions with land use changes [7]. It may be more complex in natural ecosystems. For example, results along the 24 small streams of boreal forests in Ontario, Canada showed that the relationships between functional diversity and species diversity under different disturbance intensities were from positive correlation to the unrelated [42]. Furthermore, the slopes of the relationship were significantly different under different disturbance intensities [42]. Flynn et al. found that both the plant functional diversity and species richness did not change significantly with different intensity of land use [43], while the relationship between functional diversity and species richness changed significantly between the forested and deforested habitats [44]. The relationship between functional diversity and species richness is also affected by the number of functional traits and their properties [15,44], the meaning of the special functional traits [45,46], the calculation methods of functional diversity index, etc. [8,45,47].