Review

Functional diversity assessment in riparian forests – Multiple approaches and trends: A review

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ABSTRACT

Measures of functional diversity are increasingly being used in ecological research to understand and predict vegetation ecosystem changes. However, there is currently no summary of how, why and where these indicators have been used in riparian forest studies around the world. The present article addresses the key concepts and their evolution across ti me and reviews the relevance of the use and application of functional trait-based approaches in riparian forests in the last two decades (1997–2017; 70 SCI articles). Our overview contains five sections: I. Evolution of concepts, applications, and methods; II. Functional diversity measures: application in riparian forests; III. Plant functional traits: which traits, how many and why; IV. Functional diversity responses and drivers of change; and V. Future research directions. It would appear that the advances in functional diversity frameworks in the last 20 years have led to an increase in the number of studies using riparian plant guilds and functional diversity indices, with a widespread distribution across Europe and the USA. The use of easily measurable ('soft') traits is more prevalent than that of 'hard traits' consisting of direct measurements of individual processes. Specific Leaf Area (SLA), plant height, and seed mass were the most common traits used in riparian studies. The number of traits per case study varied greatly, ranging from 1 to 36 traits (median = 6), most of which were selected with the goal of describing ecosystem processes. Among the functional diversity indices, Functional Richness was the most common metric, usually coupled with indices that incorporate trait abundances such as Functional Evenness, Functional Divergence, Functional Dispersion, Rao, and Functional Redundancy. Future research should seek to integrate ecological networks and connectivity in such a way as to produce guidance with regard to trait selection, applications to large spatial scales, and comparable frameworks (guilds, index values) across regions. Novel approaches are emerging in this field of science, seeking to improve both the connection to both prevailing ecological networks and biotic and abiotic interactions.

1. Introduction

The use of functional traits and measures of functional diversity to quantify and/or represent the diversity of species niches or functions is increasingly serving to link species to ecosystem functioning and its dynamics (Díaz et al., 1999). The frequency of distribution of functional traits that are important to community assembly processes means that functional diversity can also account for biotic interactions (McGill et al., 2006). In addition, it has been suggested that prediction of the relationship between biodiversity and ecosystem functioning can be improved by focusing on the diversity of functional attributes rather than on taxonomic diversity (Hooper et al., 2005; Mokany et al., 2008; Gagic et al., 2015).

The functional attributes of plants are determined by the latter's distinctive strategies manifested as functional traits (Violle et al., 2007),

which vary according to abiotic factors in the environment, thereby providing insights into the prevailing local environmental filters. This can help anticipate which species from a regional pool might colonize and survive in a given area (Keddy, 1992a). For instance, it is predicted that in the tropics, the warmer temperatures and less precipitation in future climate-change scenarios will support shorter trees with smaller leaves (Madani et al., 2018). Besides trait variation due to abiotic factors, biotic factors such as facilitation or competition should be taken into account as well (Kraft et al., 2015). Otherwise, it is difficult to assess whether trait variation it is a result of abiotic tolerance of species or it is a result of biotic interaction. In the case of ecosystem functions, the use of functional diversity relies on the extent to which organisms extract resources from the environment (McGill et al., 2006) and on the species coexistence (Kraft et al., 2015). As the diversity of functional traits increases, the ecosystem increases both its portion of the total

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available resources and thus the efficiency with which those resources are used (Díaz and Cabido, 2001). This in turn determines the stability of the ecosystem, enabling it to serve as a buffer against abiotic variation (Walker et al., 1999) and resist invasions (Mason et al., 2005). By assessing the functional diversity in natural communities, researchers improve their understanding of the spatial and temporal distribution of biodiversity, and this can ultimately facilitate conservation prioritization (Petchey and Gaston 2002; Devictor et al., 2010). At the same time as recognition of the concept of functional diversity is growing (Petchey et al., 2004; Flynn et al., 2011), various new indicators have appeared, such as functional diversity indices and the distribution of 'plant guilds' (hereinafter referred to as 'functional diversity measures'). Functional diversity measures have been applied worldwide in diverse plant community types ranging from mountain vegetation, grasslands and arable fields to wetlands and riparian forests. They have been used to provide ecological understanding at the habitat level (Kumordzi et al., 2015), serve as a predictable link for environmental changes (e.g. Aguiar et al., 2013; de la Riva et al., 2016a), assess the effects of human disturbance (e.g. Janeček et al., 2013; Brice et al., 2017), prioritize management and conservation practices (e.g. Brym et al., 2011; Bejarano et al., 2017), and evaluate restoration projects (e.g. D'Astous et al., 2013; Hedberg et al., 2013; Laughlin et al., 2017). Functional diversity measures were initially based on a few common traits within a community (e.g. Root, 1967) and on linkages to resources (Grime, 1977), and then later on the trait range of both rare and dominant species (Villéger et al., 2008) or on the average trait range of the most dominant species (Garnier et al., 2004). However, it is still not clear which of these functional diversity measures perform best and how redundant they are among each other (Mouchet et al., 2010; Clark et al., 2012). Mason et al. (2005) and Villéger et al. (2008) emphasized that there may not be a single "best" metric for measuring functional diversity and advocated that the decision should be based on the objectives of each individual study.

There are several reviews on the applicability of functional diversity in plant communities (e.g. Merritt et al., 2010; Cadotte et al., 2011; Kominoski et al., 2013). However, there is no summary of the knowledge on how, why and where these functional diversity indicators have been used in riparian forest studies around the world. The present study aims to respond to these questions and discuss the relevance of these indicators to the description and prediction of ecosystem responses to changing environments. Our overview is divided into five sections:

I. Evolution of concepts, applications, and methods
II. Functional diversity measures: applications in riparian forests
III. Plant functional traits: which traits, how many and why
IV. Functional diversity responses and drivers of change
V. Future research.

2. Methods

We collected data from the Scopus database. The search was performed using several combinations of keywords: "riparian forests" OR "riparian plant communities" OR "riparian vegetation" AND "functional diversity" OR "functional indices" OR "functional richness" OR "functional evenness" OR "functional divergence" OR "functional redundancy". The search returned 376 SCI articles starting in 1997, from which we removed both reviews and viewpoint articles and standard research studies targeting other communities (fish, invertebrates, birds, mammals, grasslands, wetland and herbaceous vegetation). The final dataset for the quantitive analyses included 70 original research articles for a 20-year period (1997-August 2017) (Supplementary Material – Appendix A). All proportions shown in this review were calculated using the routine Multiple Response Frequencies procedure available in the SPSS software. The procedure was applied to the overall dataset (n = 70 case studies) and quantifies the relative importance of frequency counts for a given issue when references for multiple responses

are collected. Reviews and viewpoint papers (n = 58) were used for Sections I and V.

3. Evolution of concepts, applications, and methods

3.1. From traits to concepts

There is a long history to the development of the concept of 'functional diversity'. It originated in ancient times (c. 300 BCE) with Aristotle and Theophrastus' use of the term 'trait' and the subsequent development of the first known plant classifications, based on plant height and stem density (Weiher et al., 1999). Efforts have also long been made to describe and classify vegetation from combinations of traits, in the so-called 'functional groups' (Grisebach, 1872; Raunkiaer, 1907). Vegetation assemblages have been classified according to life forms (Raunkiaer, 1934), and based on climatic data (Holdrige, 1947). Later, the concept of 'guild' as co-occurring species with similar traits gained recognition in community ecology. It was first used to describe groups of functionally similar species in a community (Root, 1967), and then for a mechanistic understanding of ecosystems and in predictive science. Another concept dealing with a functional grouping of plant species which incorporates plant responses to environmental conditions is 'plant functional types' (PFT). The term was coined by Walker (1992) and Skarpe (1996), although the same concept had already been published with different terminology by Grime (1977). By providing a morphological classification of plant life forms, Hutchinson (1975) represented a milestone in the functional ecology of wetland and riparian vegetation, and was followed by Menges and Waller (1983), who applied functional groups in order to describe wetland plants growing along an elevational gradient on a floodplain. In addition, the pioneering study by Boutin and Keddy (1993) used guilds for the functional classification and ecological understanding of wetland plants. However, the terminology for the various emergent functional diversity approaches remains challenging, especially following the introduction of functional ecology as a discipline (Calow, 1987; Keddy, 1992a). For instance, 'plant functional types' (Walker, 1992; Díaz and Cabido, 1997) has been used as a synonym for 'functional groups' (Hooper et al., 2005). Further confusion was generated by the use of the 'guild' approach, which often refers to 'plant functional types' and 'functional groups' (Leonard and Orth, 1988; Poff and Allan, 1995). What is more, Wilson (1999) introduced the term 'ecological groups' and Lavorel et al. (1997) used 'emergent groups', 'strategies' and 'functional groups' for plant classification purposes. However, the fact is that despite the varying terminology used by the different approaches, the objective is the same – to describe functional groups of plant species along environmental gradients (Fig. 1a).

Quantification of functional diversity relies on trait assessment, which can be obtained in different ways: as a community-weighted mean (CWM), using trait values weighted by the relative numerical abundance and biomass of species in order to calculate a community-aggregated trait value (Violle et al., 2007); and as functional diversity indices, based on the use of trait-range assessment to calculate distinct functional diversity attributes (Mason et al., 2005).

One of the first proposed methods for simplifying species assemblages into quantifiable units relied on using an *a priori* classification to divide species into various functional groups (Hooper and Vitousek, 1997; Tilman et al., 1997). However, the choice of functional groups was not based on objective (mathematical or statistical) methods, but on an arbitrary decision taken by the experimenter (Wright et al., 2006), and this arbitrariness underlined the need to work with objective measurements of functional diversity (Petchey et al., 2004). The first published index measuring functional diversity in an objective way was the Functional Diversity Attribute (FAD) (Walker et al., 1999). This index evaluates the average functional contribution of each species to the total diversity of a community and is extremely sensitive to species richness (Ricotta, 2005). Subsequent modifications of FAD led to the