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Functional diversity in nematode communities across terrestrial ecosystems

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Abstract

Functional diversity can be defined as the distribution of trait values within a community. Hence, functional diversity can be an indicator of habitat filtering and a reliable environmental predictor of ecosystem functioning. However, there is a serious lack of studies that test how functional diversity indices change depending on the environmental conditions. The aim of this study is to provide such evidence by analyzing the distribution and variation of continuous body-mass values (i.e. functional diversity) and related shifts in body length and width in a nematode community.

We used a large online dataset on nematode traits to analyze: (i) the distribution of body mass using three functional diversity indices, i.e. functional richness, functional divergence and functional evenness; (ii) the shifts in body-size traits (length and width); and (iii) the body-mass distributions of five trophic groups and of the entire nematode community.

Managed grasslands exhibited the widest range of body-mass values while body-mass distribution in arable fields covered the greatest area in comparison to the other ecosystem types. The shift in body size revealed environmental filters that could not have been identified by the study of functional diversity indices per se. We found low values of functional evenness to be associated with high values of functional richness. We provide novel empirical evidence that body-mass distribution within a trophic group mirrors the effects of habitat filtering more than the distribution in the community as a whole. Hence, our trait-based approach, more than functional diversity itself, disclosed soil food-web structure and identified community responses.

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Keywords: Body-size distribution; Functional divergence; Functional evenness; Functional richness; Functional trait; Trophic groups

Introduction

Functional traits capture characteristics of organisms (i.e. morphological, physiological, phenological or behavioral)

that are linked to life-history and ecological functioning, and determine individual responses to pressures and subsequent effects on ecological processes and services (Violle et al. 2007; Díaz et al. 2007, 2013). Hence, traits are suitable as indicators of specific ecological processes (e.g. Lavorel, McIntyre, Landsberg, & Forbes 1997; Harrington et al. 2010; Lavorel & Grigulis 2012). Changes in means and distri-

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butions of trait values within a community can be seen as early warning signals of disturbance and can be described by functional diversity indices (Mulder et al. 2012; Mouillot, Graham, Villéger, Mason, & Bellwood 2013). Functional diversity can be defined as the distribution of trait values within a community (Díaz & Cabido 2001) and has therefore been suggested to reflect habitat filtering (Villéger, Mason, & Mouillot 2008) and ecosystem functioning (Petchey & Gaston 2002). In particular, functional diversity is assumed to be a better predictor of ecosystem functioning than classical species diversity (Gagic et al. 2015) because competitive interactions and responses to habitat filtering reflect, at least partly, functional traits (Mouillot et al. 2013). In the last decades, many indices have been proposed to quantify functional diversity and to capture the different aspects of trait distributions within and between species assemblages (Tilman et al. 1997; Hooper & Duker 2004). Originally, functional diversity was assessed mainly as functional group richness (Hooper et al. 2002). Although it is generally much easier to identify functional group classifications than to measure continuous traits, gathering species into groups imposes a discrete structure on functional differences that can result in information loss (Petchey & Gaston 2002). More recently, indices based on either continuous or multiple (discrete and continuous) traits and their abundance have been formulated (Botta-Dukát 2005; Mason, Mouillot, Lee, & Wilson 2005; Villéger et al. 2008; Laliberté & Legendre 2010), but until now the performance of functional diversity indices has been assessed using artificial data only (Mouillot & Wilson 2002; Villéger et al. 2008; Mouchet, Villéger, Mason, & Mouillot 2010). Therefore, there is still a lack of studies testing how functional diversity indices based on continuous traits, change in response to specific environmental pressures in real ecosystems (despite the plea by Pakeman in 2011). In Mason et al. (2005), three main components of functional diversity have been defined and the related indices, which are in principle independent from each other, are formulated: (1) functional richness, i.e. the amount of functional space, i.e. the range of values of the trait considered, filled by species in a community. Low functional richness may indicate that some of the resources potentially available to the community are unused. (2) Functional evenness, i.e. the evenness of the abundance distribution in filled functional space. Assuming resource availability is even throughout niche space, low functional evenness indicates that some parts of niche space, whilst occupied, are under-utilized. (3) Functional divergence, which is the degree to which the abundance distribution in functional space enhances the divergence in functional characters within a community. High functional divergence indicates a high degree of niche differentiation, and thus low resource competition. These indices have the additional advantage of enabling comparisons of site-independent trait measurements grouped in bins instead of averaged trait values, hence they can depict higher resolution. Moreover, they are based on one single trait, making their interpretation potentially easier

than if based on multiple traits. Our main aim is to analyze the aforementioned components of functional diversity to explore the structure of biological communities, to determine how empirical functional diversity varies with environmental conditions, and to investigate if single trait can mirror environmental variation like soil and ecosystem types. To perform and test these indices, we used an online dataset on individual body sizes of nematodes across three contrasting terrestrial ecosystem types, i.e. arable fields, managed grasslands, and shrublands/woodlands (Mulder & Vonk 2011). Nematodes are a phylum in the animal kingdom and, due to their broad taxonomic range, are excellently suited to test and evaluate changes in functional diversity. We selected body mass as a suitable trait for our aim. In fact, body mass is a continuous trait measurable in all organisms. It determines most of the multitrophic interactions, shaping the structure and the function of communities (Elton 1927; Kleiber 1932). Body mass is related to many life-history traits and reflects both life strategies and individual adaptations and, together with taxonomic and functional identity, determines the species interactions that shape community structure across the food web (Peters 1983; Calder 1984; Hendriks & Mulder 2008).

As it has been recently demonstrated that functional diversity of nematodes is strongly mirroring soil abiotics like molar C:N ratio (Mulder & Maas 2017), we hypothesize here that the functional diversity of soil nematodes has to mirror the land management intensity. According to Pakeman (2011), in less disturbed habitats high richness and divergence and low evenness indicate that competition is of higher importance in structuring the community than habitat filtering. Therefore, we expect to find high functional richness and divergence, and low evenness in less disturbed shrublands/woodlands than in managed grasslands and arable fields. Given that the soil microfauna often seems functionally redundant (i.e. high species richness but low functional richness) and that the body mass only partially reflects trophic levels (Mulder & Elser 2009; Sechi, Brussaard, De Goede, Rutgers, & Mulder 2015), we hypothesized that species belonging to different trophic groups will overlap along a trait-based functional gradient. This means that the effect of environmental pressure on a specific trophic group may be hidden by the overlap with body size ranges of other trophic groups. Hence, we also hypothesized that individual body-mass distribution within each group, more than that of the whole community body-mass distribution may better mirror the habitat filtering acting on all the organisms within the soil food web. Therefore, (i) we applied the functional indices for the whole community and for each trophic group separately. In addition, (ii) we analyzed histograms of body-mass distribution of the nematode community as a whole and of five trophic groups separately to better interpret and visualize the meaning of the calculated indices (Cadotte, Arnillas, Livingstone, & Yasui 2015). Finally, (iii) we studied the shifts in body length and width traits to provide detailed information on the potentially observed differences in body-mass values and test whether or

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