



# Higher taxa vs. functional guilds vs. trophic groups as indicators of soil nematode diversity and community structure



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## ABSTRACT

Biodiversity surrogates are often used in ecology to save money and time. One such widely used surrogacy method is the higher taxon approach, also known in the literature as taxonomic sufficiency. This approach has rarely been applied to microscopic organisms like soil microfauna, although there is a lack of detailed taxonomic knowledge regarding the latter. We tested taxonomic sufficiency for genus alpha and beta diversity, as well as for community structure of soil nematodes. We also tested whether the functional classifications of nematodes into functional guilds and trophic groups can serve as efficient indicators of nematode diversity and community structure. We used data from soil nematode communities from five different microhabitats (soil, soil moss, rock moss, low tree trunk moss and high tree trunk moss) in forested and non forested areas at five different stations (differing in elevation and aspect). Our results showed that both the higher taxon approach and the functional surrogacy approach could serve as reliable indicators of alpha and beta diversity. Furthermore, our community analysis of both taxonomic and functional composition identified that the variability at the finer scales, and namely the habitat structure, played the leading role in shaping nematode communities.

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## 1. Introduction

Assessing biodiversity of microscopic organisms is a vital, but also a very difficult, task in ecology. Taxonomic identification of large organisms is relatively easy that even non-expert volunteers can perform it reliably (Devictor et al., 2010). However, soil communities are highly diverse and the identification of soil biota to species level is an extremely difficult task, even for soil animals (Jeffery et al., 2010). Furthermore, for such organisms, the number of specialists worldwide is extremely small. Though, considering the significant role of soil biodiversity in regulating important ecosystem services (De Vries et al., 2013) and the complexity of the soil food web, it is essential to use soil organisms as indicators for monitoring soil functions and conditions. In this respect, nematodes are among the most preferred bioindicators of soil functioning (Bongers and Ferris, 1999) and nematological indices are among

the most widely used ones for evaluating soil conditions. Nematodes belong probably to the most well studied group of soil animals. Still, it is a common practice to identify nematodes to genera or family level assuming that they reflect the taxonomic composition of the species assemblage. This is a manifestation of the higher taxon approach or taxonomic sufficiency (Balmford et al., 1996; Gaston and Williams, 1993). A number of nematological indices have been developed based on a classification to trophic groups (omnivorous, predatory, bacterial, fungal or plant feeding). Another functional classification scheme also takes into consideration life history strategies and defines functional guilds (Ferris et al., 2001). In most cases the assignment to a trophic group is relatively easy under the microscope (Yeates et al., 1993) but the classification into functional guilds is based on identification to genus. Genera of the same family may belong to different guilds along with other phylogenetically distinct genera and families.

In many studies of the higher taxon approach, it has been documented that it is not necessary to identify samples to species-level in order to analyze biodiversity (mainly species richness) patterns (Ellis, 1985; Terlizzi et al., 2003). More recently, the higher taxon approach has been applied to conservation biology issues (Balmford et al., 2000; Mazaris et al., 2010), as a short-cut

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method to quantify changes of species assemblages in environmental monitoring (Kallimanis et al., 2012; Landeiro et al., 2012). But its efficiency and reliability still remains a matter of discussion (Neeson et al., 2013). The higher taxon approach has been tested and studied extensively for well known taxa like plants and vertebrates (Grelle, 2002; Mazaris et al., 2008). Fewer studies examined the efficiency of the method to other more diverse and less well known taxonomic groups like invertebrates (Musco et al., 2009; Rosser and Eggleton, 2012). The functional classifications of nematodes have not been tested as a surrogate for biodiversity assessment.

The higher taxon approach has been rarely tested on how well it performs on other aspects of biodiversity (namely beta diversity) and community structure. Terlizzi et al. (2009) found that higher taxa could be used as a reliable surrogate for species at estimating patterns of beta diversity in marine invertebrate assemblages. Prinzing et al. (2003), on the other hand, found higher taxa (even at the genus level) to be an unreliable surrogate for species level beta diversity in plant diversity of Kenya. Similarly, limited attention has been paid to the efficiency of the higher taxon approach for community analysis, such as the separation of ecological assemblages, with most such applications originating from aquatic systems (Bevilacqua et al., 2012; Schmera and Eros, 2011). Also, the functional classifications of the nematodes have been used extensively to analyze soil food webs as well as the effects of various environmental factors on nematode communities (Liu et al., 2013; Tsiafouli et al., 2007), but it has not been tested as a surrogate for beta diversity assessment or for nematode community analysis.

The aim of this study is to examine if the identification of specimens to family level, functional guilds or trophic groups could be used as an indicator of the genus level identification for assessing alpha or beta diversity and for discriminating ecological assemblages.

## 2. Materials and methods

### 2.1. Sampling design

We selected 10 sites at the slopes around the “Vigla” peak (40°25'42.1", 23°9'55.89") of Mt. Holomontas, Chalkidiki, Greece. The sites differed by aspect (East, North and South), altitude (High and Low) and forest cover (Forest and Open) giving 12 combinations but the South-Low-Open and South-Low-Forest sites were not sampled. The vegetation of the area is a Mediterranean oak (*Quercus pubescens*) forest but in the East-Low sites the vegetation is evergreen shrubland dominated by *Quercus coccifera*. In each site we distinguished three microhabitats namely soil (SL), soil mosses (SM) and rock mosses (RM) but in the forested sites we also sampled tree trunk dwelling mosses taken from the base (TL) or from the upper-most moss covered position on the trunk (TU). We were careful to sample moss carpets of the dominant moss species *Hypnum cupressiforme* Hedw. (Sabovljević et al., 2008) in all cases. In each site, we took samples from three sampling plots with a minimum distance of about 30 m among them but in the South-High-Open site the minimum distance was 15 m due to restrictions in the surface area and shape of that site. In each plot we took one sample from each microhabitat. We used a soil corer 5 cm in diameter and 15 cm depth for soil sampling. For mosses we separated the moss carpet from the substrate and cut a piece of about 20 cm × 20 cm in area. Samples were collected in January of 2010 (5 sites × 5 microhabitats × 3 replicates from forested areas and 5 sites × 3 microhabitats × 3 replicates from open areas).

### 2.2. Extraction and identification of nematodes

Soil samples were gently mixed by hand and soil aggregates were broken. From this mixture we used a subsample of 150 ml and extracted nematodes by Cobb's sieving and decanting method as proposed by S'Jacob and Van Bezooijen (1984). Mosses were gently cut into smaller pieces by hand and were placed into a Modified Baermann funnel for extraction. Nematodes were collected in water, counted under the stereoscope, heat killed, and fixed with formaldehyde 4%. Abundance of nematodes was expressed as number of individuals per substrate volume. From each extracted sample we selected randomly 150 nematodes under the microscope (Nikon-Ci-L) and identified them to genus level by the identification key of Bongers (1994). They were subsequently allocated to a trophic group (bacterivorous, fungivorous, plant parasitic, and plant associated, predatory-omnivorous) according to Yeates et al. (1993) and to life history strategies (*c-p* values) according to Bongers (1990). Functional guilds were assigned according to Ferris et al. (2001) by combining the trophic groups to the *c-p* value.

### 2.3. Analysis

For each sample we analyzed its community composition at each classification level (i.e. genus, family, functional guild and trophic group). We analyzed patterns of alpha and beta diversity as well as the ordination of nematode assemblages. In order to test the efficiency of higher classification levels to estimate the genus diversity patterns we used Pearson correlation coefficient. As alpha diversity indices we used richness (number of taxa or groups per sample), Shannon and Simpson diversity indices.

For beta diversity, we made all the possible pairwise comparisons among our samples. We used beta diversity indices that rely only on presence (i.e. Jaccard) but also indices that rely on the relative abundance of each class (Bray Curtis and Euclidean distance). Also to account for the difference in alpha diversity among samples we used the beta diversity index of Lennon as proposed by Koleff et al. (2003). For each index we compiled a distance matrix and estimated the congruence of those matrices with the Mantel test with 1000 permutations. Besides the pair-wise comparisons for beta diversity we also used across scale beta diversity indices including Whittaker's index, the first formulation of the beta diversity concept (Whittaker, 1960), and  $N^*$  (Lazarina et al., 2013) which reflects the rate of redundancy in a dataset, depending on the slope of the species accumulation curve. These indices were calculated for genera, families, functional guilds and trophic groups using the Nstar function under R (Lazarina et al., 2013). The above indices provide a unique value for each classification level so in order to test for correlation among classification levels we estimated their values in random subsets of samples (100 random subsets formed) each containing half of the available samples. In each subset we estimated beta diversity of every classification level.

Finally for the community level analysis we used DCA ordination, one for each classification level. We used the procrustes test (protest function in vegan) to test the correlations between ordinations. We also used adonis (implementing PERMANOVA, Anderson (2001)) for the evaluation of altitude, cover and aspect effects on the multivariate data stratified by microhabitat. For estimating beta diversity indices, Mantel tests, procrustes tests, adonis and for producing DCA ordinations we used the vegan package (Oksanen et al., 2013) under R version 3.0.1 (R Core Team, 2013).

## 3. Results

We found 63 Nematode genera, belonging to 30 families in our samples. The most abundant genera were *Plectus*, *Aphelenchoides*,

**Table 1**  
Correlation (Pearson correlation coefficients and Mantel tests) among classification levels of Nematodes for alpha and beta diversity indices.

Index	Genus–family	Genus–functional	Genus–trophic	Family–functional	Family–trophic	Functional–trophic
<b>Pearson's correlation coefficients</b>						
Richness	0.927	0.812	0.590	0.908	0.698	0.822
Shannon	0.977	0.864	0.746	0.904	0.778	0.902
Simpson	0.958	0.882	0.806	0.939	0.844	0.917
N*	0.86	0.77	0.56	0.74	0.54	0.75
Whittaker	0.68	0.40	0.44	0.35 (NS)	0.41	0.79
<b>Mantel test correlation coefficients</b>						
Jaccard	0.791	0.594	0.446	0.701	0.536	0.628
Lennon	0.716	0.459	0.122	0.645	0.228	0.375
Bray Curtis	0.989	0.980	0.968	0.988	0.975	0.994
Euclidean	0.973	0.885	0.853	0.924	0.893	0.975

*Filenchus* and *Monhystera*. Nematode total abundance and genus richness were highest in the soil (SL) and lowest in the upper trunk mosses (TU). Average richness per sample was 14.02 Genera (range 2–28), 9.96 Families (range 2–18), 6.76 functional guilds (range 2–12) and 4.86 trophic groups (range 1–6).

### 3.1. Alpha and beta diversity indices

All indices were correlated significantly but genera to family were more strongly correlated than genera to functional guilds or trophic groups (Table 1). Generally, the correlations were higher when proximate classification levels (taxonomic or functional) were compared and declined constantly with the distance between classification levels. Indices involving abundances were more strongly correlated (Table 1) than the qualitative ones (Shannon and Simpson vs. Richness; Bray–Curtis and Euclidean vs. Jaccard and Lennon). Finally, between the two across-scales beta diversity indices, N\* provided higher correlations than Whittaker's index except in the case of functional guild to trophic group comparison. This is due to the higher sensitivity of Whittaker's index on variations of alpha and gamma among subsets of data.

### 3.2. Community structure

The ordination plots for genera and for families were very similar (Fig. 1a and b, protest  $r=0.921$ ,  $p=0.001$ ), and the same holds for the plots for functional guilds and trophic groups (Fig. 1c and d, protest  $r=0.95$ ,  $p=0.001$ ). The major difference between genera–families and functional guild–trophic group ordinations, was the clear separation of SL from SM in the former but not in the latter. Still, the ordination based on genera is significantly correlated with that based on trophic groups (protest  $r=0.73$ ,  $p=0.001$ ). Thus, there is congruence among all ordinations. In all cases, microhabitat is recognized as the main differentiating factor with the first axis reflecting a gradient from SL to SM to RM to TL and TU. But this was more distinct for the genera and family ordination than for the functional and trophic group ordination. Using microhabitat as strata the factors affecting community structure variations were altitude (adonis,  $p=0.001$  for genera and  $p=0.005$  for families) and cover ( $p=0.015$  for genera,  $p=0.032$  for families) but only altitude for functional guilds and trophic groups ( $p=0.021$  for both). The ordination results indicate that nematode community structure varies significantly, but this variation is driven mainly by habitat heterogeneity (fine spatial scale) than distance among samples. Other environmental factors like altitude and vegetation cover type seem to play secondary role to the microhabitat.

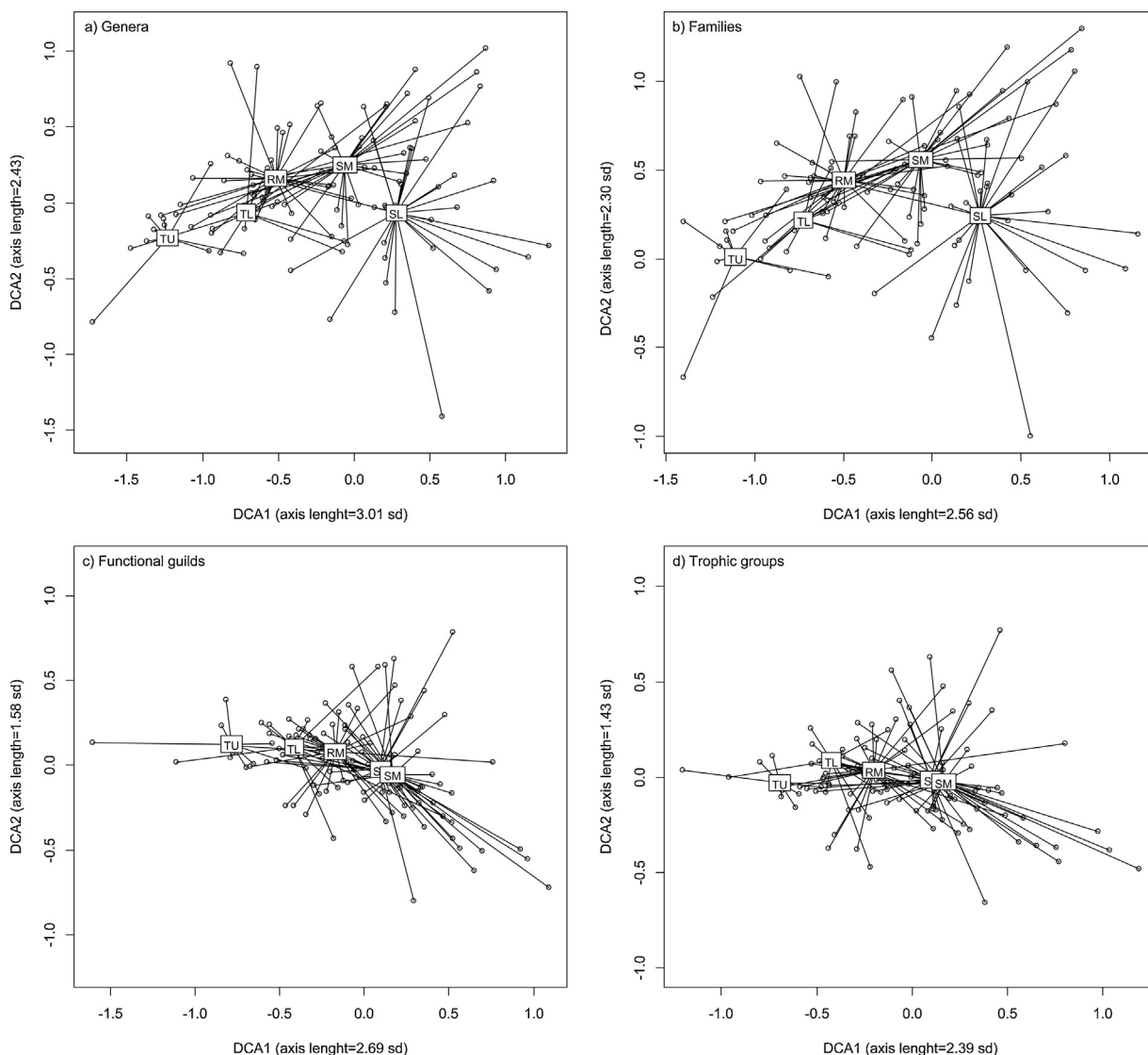
## 4. Discussion

Our analyses of alpha diversity patterns verify the reliability of the higher taxon approach for nematodes. We found that family

diversity is a good surrogate for genus diversity when estimating richness, Shannon or Simpson diversity indices. This finding is in accordance with existing literature for a variety of organisms from different biogeographic regions (Carneiro et al., 2010; Heino, 2014). This pattern has rarely been tested for the soil ecosystem (Pik et al., 1999; Rosser and Eggleton, 2012), and even then with disappointing results leading Rosser and Eggleton (2012) to discourage the use of this approach. We found that other indicators (the diversity of functional guilds or trophic groups) could also serve as a surrogate for genus diversity, but they are slightly less efficient than the higher taxon approach. The scheme we analyzed is widely used in nematode studies since it offers insights on the functional structure of the nematode community, which in turn is indicative of the functional performance of the soil (Ferris et al., 2001). Similar functional surrogates based on feeding types, reproductive strategies, and trophic states were strongly correlated to species diversity in freshwater ecosystems (Mueller et al., 2013).

We analyzed beta diversity patterns as pair-wise comparisons among samples using both qualitative (like Jaccard and Lennon) and quantitative indices (like Bray–Curtis and Euclidean distance) or as across-scales estimates (like Whittakers and N\*). For all indices analyzed, family level beta diversity patterns were in congruence with genus level beta diversity patterns. The reliability of the higher taxon approach for beta diversity estimates remains unclear with the few available studies reaching contradictory results; Terlizzi et al. (2009) argue in favor of the surrogacy while Prinzing et al. (2003) argue against it. Our results support the applicability of the higher taxon approach to beta diversity patterns. When analyzing the beta diversity pattern for the diversity of nematode functional guilds or trophic groups, we found that these patterns were associated with the beta diversity patterns of family or genus level but less strongly. If abundance was taken into consideration the correlation was stronger than in the case of presence only.

The analysis of community structure provided similar results. It verified the higher taxon approach for this task, with genus and family level ordinations providing almost identical inferences. The same holds for ordinations according to functional guilds and trophic groups. To a large extent, the functional guilds or trophic groups ordinations are congruent with the ones from genera or family. In all cases, the variability at fine spatial scales (at our study reflected as microhabitat structure) was the key factor in defining nematode community structure. The properties of the microhabitat seem to drive this pattern with a gradient from soil communities to tree moss communities, in accordance with other studies examining nematode community differentiation (Lazarova et al., 2004; McSorley, 2013). The relationship between soil properties and soil biota across spatial scales and land-use types is complex and only few principles have been unravelled (Birkhofer et al., 2012). In our study, after microhabitat structure, other environmental factors like altitude or vegetation coverage seem to play a secondary role in defining nematode communities. So samples located km



**Fig. 1.** DCA ordination of all plots according to their (a) genera, (b) families, (c) functional guilds and (d) trophic group composition of nematodes. The labels refer to microhabitat the samples taken from (SL: soil, SM: soil mosses, RM: rock mosses TL: mosses from the base of tree trunk, and TU: mosses from the upper part of their distribution on the tree trunk).

apart in the same type of microhabitat had more similar community structure than samples located next to each other but in distinct microhabitats, something that has been observed in other soil animals also (Kallimanis et al., 2002). Our findings suggest that microhabitat structure apart from species composition affects the functional composition of the nematode community but this effect is slightly weaker (no distinction between SL and SM). Such effect of environmental conditions on soil nematode communities has been reported in the literature (Ekschmitt et al., 2001; Neher et al., 2005; Sanchez-Moreno et al., 2011; Yeates et al., 1999). However, this is the first application on the higher taxon approach to community structure in soil (at least to our knowledge), i.e. the comparison of community structure and environmental drivers as perceived from different taxonomic levels and compared also to the structure deduced by functional guilds and trophic groups. The higher taxon approach has been documented to produce similar results in aquatic ecosystems (Smale et al., 2010).

Summarizing our findings, the higher taxon approach seems to be working reliably in nematode communities for estimating alpha and beta diversity patterns and in detecting community assemblages. Functional guild or even trophic group alpha and beta

diversity estimates could be used as a reliable indicator of taxonomic alpha and diversity estimates (even if weaker than the higher taxon approach), at least in our case, but more studies are needed before reaching a general conclusion. Finally, functional guild community structure is also an indicator of taxonomic community structure, and might be used as its surrogate.

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