



Species and trait compositions of freshwater nematodes as indicative descriptors of lake eutrophication



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ABSTRACT

In recent years, the analysis of single or multiple species trait patterns was regarded as a reliable biomonitoring tool alternative or in addition to the traditional taxon-based methods. Hitherto, the trait approach was overwhelmingly applied to macroinvertebrate assemblages to monitor anthropogenic induced degradations of freshwater ecosystems. However, little is known yet whether bio-ecological traits derived from speciose and functionally diverse meiobenthic taxa might also provide diagnostic descriptors for the assessment of ecosystem health. The aim of our pilot study was to assess if the trait composition (including life history, morphometrical and ecological attributes) of lake nematode assemblages can reflect signs of cultural eutrophication equally well as the concomitant change in the species composition. Sediment samples for the analysis of the nematodes assemblage structure were taken at littoral sites of 15 German and Swedish lakes. Lakes were assigned to three traditional classes along the trophic continuum—oligotrophic, mesotrophic, and eutrophic. Canonical correspondence analyses illustrated that both the nematode trait and species compositions were significantly altered to similar extents along the eutrophication gradient. A set of 7 out of 28 trait modalities and a group of 12 from 30 species could be defined as indicative of oligotrophic or eutrophic conditions, and enabled us to discriminate among the three trophic lake states, without confounding effects of pronounced trait inter-correlations. Trait modalities such as a high number of offspring per year and the feeding type suction feeder predominated at the upper range of the enrichment gradient, whereas for modalities such as the obligate asexual reproduction, the feeding type chewer and several specifying nematode morphometrics (short body length, slender body shape) the opposite trend was revealed. However, the observed trait replacement did not imply an increased potential of resilience or resistance to disturbance, suggesting that eutrophication effects rather indirectly shaped nematode assemblages. This first attempt to apply a trait-based analysis to nematode assemblages was found to be successful for distinguishing among different degrees of lake eutrophication. However, compared to macroinvertebrate taxa there remains a great paucity on bio-ecological trait data for nematode species. Therefore future research is demanded to expand and refine nematode trait specifications with the intention to gain further insights into the mechanistic link between responses of nematode populations to environmental alterations.

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1. Introduction

In recent years bio-ecological trait analyses, in particular of macroinvertebrates, are viewed as a promising biomonitoring tool to assess human impacts on freshwater habitats (e.g. Bonada et al., 2006; Doledec and Statzner, 2010; Culp et al., 2011). Trait analyses are based on a sound ecological theory, originating from the 'habitat temple' concept by Southwood (1977, 1988), which was

later refined by Townsend and Hildrew (1994). According to this theory, spatial and temporal habitat characteristics (e.g. physico-chemical factors), including anthropogenic disturbance, act as an array of filters which eliminate certain biological (e.g. body size and shape, reproductive mode, life cycle) or ecological (e.g. feeding habit, dispersal abilities) traits forming viable communities with similar sets of traits (Statzner et al., 2001b). Compared to the traditional taxon-based descriptors (based on the abundances of taxonomic entities, taxon diversity and richness) the trait approach is supposed to provide some major advantages (i) applicability across broad geographic regions, (ii) mechanistic understanding of changes in habitat conditions including a priori predictions about shifts in species traits along the gradient of environmental

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impairment, and (iii) ability to discriminate among different types and levels of human impacts (Statzner et al., 2001a; Liess et al., 2008; Menezes et al., 2010).

Thus far, trait analyses in freshwater systems have almost exclusively been conducted for macroinvertebrates and their response to anthropogenic-mediated habitat alterations in running waters at small and large spatial scales (e.g. Doledec et al., 1999; Gayraud et al., 2003; Liess, 2005; Feld and Hering, 2007). However, this approach could be basically applied to any taxon, as each of them encompasses a collection of environmentally filterable traits (Statzner et al., 2001a). Freshwater nematodes, in particular, are one of the most promising ones.

Sediment-dwelling nematodes are highly diverse and extremely numerous in all freshwater ecosystems, highlighted by the fact that in general 50–80 species per habitat form an assemblage of several hundred thousand individuals per m² (Traunspurger et al., 2006). The great diversity of freshwater nematodes is paralleled by a high ecological and functional importance within the benthic food web. Nematode graze on and/or stimulate benthic bacteria (Borchardt and Bott, 1995; Traunspurger et al., 1997; Schmid-Araya and Schmid, 2000), predate on other micro- and meiofaunal taxa, or use their stylet to suck the cell content of macrophytic roots and fungi (Meyl, 1961; Schmid-Araya and Schmid, 1995). As a food source for other benthic invertebrates and bottom-feeding fish (Muschiol et al., 2008; Spieth et al., 2011), nematodes are also essential for the linkage between lower and higher trophic levels. The great functional importance of free-living nematodes is accompanied by the evolution of complex life histories strategies (Evans, 1998) and an exceptional morphological diversity (Traunspurger, 2013), albeit nematodes are still often viewed as uniform worms (De Ley, 2000).

The use of nematodes to indicate the quality and environmental conditions of rivers and lakes dates back to the initial works of Zullini (1976) and Prejs (1977) and recent results from several field and experimental studies support their general suitability to trace various anthropogenic impacts on sediment quality (e.g. Beier and Traunspurger, 2001; Brinke et al., 2010; Höss et al., 2011). Nevertheless, to this day no widely accepted metric for biomonitoring purposes with regard to freshwater ecosystems exists, so that the so-called Maturity Index (MI), originally developed by Bongers (1990) primarily for soil nematode assemblages, was most frequently applied as a measure of lake or river habitat condition. Even though the MI was designed more than 20 years ago, it follows the modern approach to integrate species traits for the assessment of ecosystem health. According to their life history traits (e.g. reproductive rate, colonization ability, resistant life stage) nematode families are assigned to one of five categories along a colonizer (*r*-strategist) to persister (*K*-strategist) scale, with the first group being most tolerant and the latter being most sensitive in respect to environmental disturbances. Early on, the MI was criticized for losing predictive power due to aggregating species on family level, and thereby summarizing trait information in just a single *cp*-value (Dmowska and Ilieva-Makulec, 2004; Danovaro et al., 2009). In addition, there is growing evidence that the MI is not applicable to detect environmental degradation of freshwater systems (Heininger et al., 2007; Brinke et al., 2011).

The first aim of our initial study is to give baseline information on the bio-ecological traits of freshwater nematodes and how these traits are intercorrelated. This aspect addresses the fact that traits are not necessarily independent autecological features, but are often linked as a result of evolutionary and physiological constraints thereby representing a complex of traits termed *syndrome* (Blomberg et al., 2003; Poff et al., 2006). The knowledge of such trait correlations is a prerequisite for the separation of robust and statistical independent measures from redundant ones. The second aim is to evaluate the performance of multivariate trait analyses in

comparison to the species-based approach using freshwater nematode assemblages to study eutrophication-related impacts on lake ecosystems. We used a recent data set showing shifts in nematode species composition in response to eutrophication (Ristau and Traunspurger, 2011) extended by the data of 7 additionally sampled lakes. This resulted in information for 15 German and Swedish lakes, ranging from oligotrophic to eutrophic conditions. The existence of trait linkages was evaluated by a fuzzy correspondence analysis (Chevenet et al., 1994). Based on canonical correspondence analysis and the resulting ordination scores we assessed the effect of eutrophication on the distribution of species and biological traits and tested the prediction that the trait composition data would be more efficient to discriminate among different levels of lake eutrophication than the abundance structure of species.

2. Materials and methods

2.1. Study site

Nematode assemblages in the littoral zone of 15 European lakes covering a gradient from oligotrophic to eutrophic conditions were analyzed either during spring 2007 or 2008. Eight lakes are located in the southern area of Sweden and another seven in northern or eastern Germany (information on limnological data are given in Table 1).

2.2. Species composition

Sediment samples including the nematode assemblage were collected in the littoral zone at a water depth between 0.4 and 0.6 m. The number of sampling sites per lake varied between four to eight sites (three replicates per site), depending on the accessibility of littoral areas. For each replicate the uppermost 3 cm of the sediment layer were collected using an acrylic tube (internal diameter of 2.5 cm) and directly preserved in formaldehyde (final concentration 4%). Meiobenthic organisms were stained with Rose Bengal, and extracted by the density centrifugation technique in colloidal silica (Ludox TM 50 [Sigma-Aldrich Chemie GmbH, Steinheim, Germany]: density adjusted to 1.14 g mL⁻¹, mesh size 35 μm, two re-runs) described by Pfannkuche and Thiel (1988). Nematode abundances in each replicate were quantified at 40× magnification and, when present, the first 30 individuals mounted in glycerin according to the method of Seinhorst (1959, 1962). In total nearly 9000 individuals were identified to species level (1000× magnification, oil immersion).

2.3. Trait composition

The data set included seven bio-ecological traits related to morphology, life history, feeding type, and habitat preference, with 28 modalities for 30 nematode species (Table 2). The dataset was restricted to the 30 most abundant species; together accounting for >80% of all identified specimens, as only for them complete and reliable information of traits could be assembled. Information on species traits was compiled from the literature (Tsalolikhin, 1983; Andrassy, 1984; Bongers, 1987; Swart et al., 1991; Loof, 1999) and using personal knowledge (Walter Traunspurger). The degree of linkage between a species and each modality within a single trait was fuzzy-coded, thereby accounting for intraspecific variation and incongruent specification from the used literature sources (see Chevenet et al., 1994). The affinity of each species to a single modality was expressed by scores on a scale from 0 indicating no affinity to 4 indicating high affinity. The affinity scoring for each trait-species combination was transformed into a frequency distribution that was finally standardized to 1. For example, an affinity scoring of “0, 0, 1, 3” for a set of four modalities for a given trait

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