



Diversity and distribution of soil micro-invertebrates across an altitudinal gradient in a tropical montane rainforest of Ecuador, with focus on free-living nematodes



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ABSTRACT

Here we describe the community structure of soil micro-invertebrates at three altitudes (1000, 2000, and 3000 m) and two soil layers (upper L/F layer and deeper H/Ah layer) of a tropical montane rainforest situated on the eastern slope of the Andes (southern Ecuador) with special focus on nematodes. Nematodes dominated the micro-invertebrate assemblage (average density 1.82×10^3 ind. m^{-2}), accompanied by populations of typical aquatic invertebrates, such as harpacticoid copepods and rotifers, which increased with increasing altitude. Among 1217 nematode individuals inspected, 143 morphospecies were identified. The equitability index was remarkably high. Sample rarefaction curves suggested that up to 244 nematode species dwell in soils of the studied area. Nematode diversity was affected neither by altitude nor by layer; however, the community structure changed with altitude. Bacterial-feeding nematodes dominated throughout the altitudinal gradient whereas at higher altitude populations of plant-feeding nematodes were replaced by hyphal-feeding nematodes, presumably because of changes in habitat and resource availability. Canonical correspondence analysis identified litter C/N ratio and fungal biomass as major drivers of the changes in nematode community composition with altitude. Abundant and diverse assemblages of large predacious and omnivorous nematode species were found at each of the study sites, suggesting that omnivory and animal predation compensate for the lower abundance/quality of basal resources.

1. Introduction

Nematodes are the most abundant and one of the most species-rich metazoan phyla on Earth (Wilson 2000; Hodda et al., 2009) and play a key role as intermediaries in soil ecosystems (Ettema 1998; Scheu 2002; Bardgett and van der Putten, 2014). Communities of free-living nematodes are also functionally diverse, as shown by the presence of marked feeding specialization and a wide range of body-sizes (e.g. Ettema, 1998). The former include bacterial- and algal-feeders, predators of small invertebrates and protozoans, and stylet-bearing species able to suck out the inner contents of plant roots or fungal hyphae (Yeates et al., 1993; Traunspurger 1997; Yeates and Bongers 1999).

Procter (1984) suggested that the species richness, density, and biomass of free-living soil nematodes is higher at high latitudes than in tropical zones, due to abundant microbial prey and a lack of specialized invertebrate competitors. However, for diversity this statement does

not seem to hold true, as tropical regions contain a very high diversity of nematode species: In their study of a primary rainforest in the Republic of Cameroon, Lawton et al. (1996) identified 204 morphospecies among 1009 specimens and estimated that a sample of 200 individuals would yield 72 different species. Based on a comparison of 24 sites along a gradient of forest disturbance also in Cameroon, Bloemers et al. (1997) detected 431 species from 5000 individuals (although 90% could not be assigned to known species), with samples of 200 individuals yielding 61 species on average. Interestingly, those authors found that forest disturbance only moderately reduced nematode diversity, as slash-and-burn or clear-cut sites showed ~40% fewer species than primary forest sites. Powers et al. (2009) used molecular barcoding to estimate that 500 nematode species could be expected in 1600- m^2 rainforest plots in Costa Rica. Tropical litter and understory habitats harbor the most diverse assemblages, with some species forming unique associations with other soil invertebrates (e.g., nine

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species of termites are typically associated with eight nematode species). So far, however, free-living nematode communities have been evaluated in much more detail in temperate than in tropical regions, which could have led to an under-appreciation of the species richness and basic distribution patterns.

Both the density/biomass patterns and the structure of nematode communities are affected by soil characteristics, such as soil type, pH, and nutrient content, but presumably more intensively by climatic constraints, such as temperature and rainfall regimes (Yeates and Bongers 1999; Ruess 2003; Nielsen et al., 2014; Bhusal et al., 2015; Tsiafouli et al., 2017). For example, Yeates and Bongers (1999) reported a consistent reduction of nematode density with increasing altitude in grassland soils forming a climosequence in New Zealand (from 4195 ind. 50 g⁻¹ soil at 300 m asl, to only 120 ind. 50 g⁻¹ soil at 1500 m). Tsiafouli et al. (2017) recently concluded that, among the landscape properties that affect nematode community indices, altitude rather than vegetation cover was the most predictable because altitudinal climatic conditions strongly constrain the availability and turnover of basal resources.

In this study we analyzed the changes in the density, diversity, and community structure of soil invertebrates, especially free-living nematodes, along an altitudinal gradient (1000, 2000 and 3000 m) in a tropical rainforest of the Andes of Ecuador. We specifically asked (1) whether the density of soil micro-invertebrates declines with altitude and soil layer (2) whether and how nematode species richness, feeding-types, and community structure respond to altitudinal and/or soil layer gradients, and (3) how nematode species richness in tropical montane rainforests compares with that of high-latitude forest ecosystems.

2. Material and methods

2.1. Study sites and sampling

This study was conducted on the eastern slopes of the Andes of southern Ecuador, along an altitude transect of 1000, 2000, and 3000 m asl. Samples were collected in June–July 2007. The maximum distance between sampling sites was 30 km. The sites at 1000 m were located in Bombuscaro (S4°6'54", W78°58'2"), those at 2000 m in the Reserva Biologica San Francisco (S3°58'18", W79°4'45"), and those at 3000 m in Podocarpus National Park (S4°6'711", W79°10'581"). The soil types were aluic Acrisol at 1000 m, gley Cambisol at 2000 m, and Podzol at 3000 m (Soethe et al., 2006). The climate was semi-humid, with 8–10 humid months per year and an annual rainfall of roughly 2200, 3500, and 4500 mm at 1000, 2000, and 3000 m, respectively (Röderstein et al., 2005).

The three sites were characterized by a high plant diversity, with at least 1117 species of vascular plants and more than 280 tree species typical of the montane rainforest of the southern Ecuadorian Andes (Röderstein et al., 2005; Homeier et al., 2008). Stand height decreased gradually with altitude; so that, at 3000 m a typical cloud forest comprising trees with crooked stems and a maximum stand height of only 9 m was present close to the timberline. The soil was nutrient-poor; the organic layers had a mass of 30–713 t ha⁻¹ and a thickness of ca. 6, 11, and 28 cm at 1000, 2000, and 3000 m, respectively (Wilcke et al., 2008).

At each site, a sampling area of 100–200 m² was selected and four sampling points were randomly chosen. The four sampling points at each elevation were pseudo-replicates: It was beyond the scope of this study to replicate entire mountain slopes. Samples were collected from the upper L/F layer and deeper H/Ah layer with a corer (5 cm diameter), for the layer description see Krashevska et al. (2008).

2.2. Extraction and identification of invertebrates

For each layer a soil volume (58.9 cm³ = $\pi \cdot 2.5^2 \times 3$ cm depth of the sample in the extractor) was placed into a modified Baermann

funnel extractor (Baermann, 1917) at 25 °C for 24 h. After extraction, invertebrates were treated with hot 4% formaldehyde solution, and then immediately cooled by a spill-over addition of cold 4% formaldehyde solution. For each sample, ~50 nematodes were sorted, gradually transferred to glycerin medium according to the method of Seinhorst (1959), and then mounted on slides for species-level identification. Densities were expressed per area. Nematode functional identity was assessed through classification of taxa into feeding-types according to mouth morphology and known feeding habits (Yeates et al., 1993).

2.3. Statistical analysis

Differences in the absolute and relative densities of the invertebrate groups as well as in nematode species richness and feeding-types were analyzed using a repeated-measures analysis of variance (RMANOVA), with altitude as a fixed factor and soil layer as a repeated factor. All data were checked for homoscedasticity using Levene's test and log-transformed if necessary. Data that, due to the small sample size, had still not achieved homoscedasticity after log-transformation were discarded from the RMANOVA models to avoid the risk of type-I errors. Tukey's HSD test was used for posterior comparisons of means at $P < 0.05$.

Changes in nematode community structure were assessed using non-metric multidimensional scaling (nMDS) ordination (set of 143 species, 24 samples, a total of 725 occurrences in the samples). In addition, a permutational multivariate analysis of variance (PERMANOVA) was performed to test for the main and interactive effects of altitude and soil layer on nematode community structure. A distance-based test for homogeneity of multivariate dispersion (PERMDISP2) was used to verify that the statistically significant effects were not due to a deviation from the condition of homogeneous dispersions (Anderson, 2006). P-values were determined based on 999 permutations. Similarity percentages analysis (SIMPER) was conducted to identify those species that contributed the most to the separation between communities at different altitudes. All community analyses were based on the Bray-Curtis distance calculated from untransformed nematode species densities in each sample. Statistical analyses were performed with R (R Development Core Team, 2016) using the 'vegan' and 'ade4' packages (functions: 'metaMDS', 'adonis', 'betadisper' and 'simper'; Oksanen, 2009).

Sample rarefaction curves (Mao Tau-type analytical solution) were performed for each altitude and soil layer condition and for the total sampling effort after all species data were transformed to a presence/absence data matrix. Two non-parametric species-richness estimators (Chao 2 and Jackknife 2) were chosen as they provide robust estimations of species richness (Colwell and Coddington, 1994). Sample rarefaction and richness were estimated with Past v1.93 (Hammer et al., 2001).

The influence of abiotic and biotic variables on nematode species was analyzed using canonical correspondence analysis (CCA) as implemented in CANOCO (Ter Braak, 1994). The following variables were included: soil moisture (wet:dry weight ratio), pH, total carbon content, C/N ratio, microbial biomass, total Gr+ and Gr- bacterial PLFAs, fungal PLFA biomarker, bacterial:fungal PLFA ratio (for details see Krashevska et al., 2008, 2014; for means, see Supplementary Table S1). The graphic representation was simplified by using the following inclusion rules: only species fitting > 10% and weighing > 10% were displayed (32 out of 143 species). Monte-Carlo permutation-test (999 permutations) was used to evaluate the significance of individual axes. Data were log-transformed prior the analysis.

3. Results

3.1. Micro-invertebrate community

Neither the absolute density of nematodes nor the total density of

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