

The functional role and diversity of soil nematodes are stronger at high elevation in the lesser Himalayan mountain ranges

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Abstract

Soil nematodes are a foremost component of terrestrial biodiversity, they display the whole gamut of trophic guilds and life strategies, and by their activity, affect major ecosystem processes, such as organic matter degradation and carbon cycling. Based on nematodes' functional types, nematode community indices have been developed and can be used to link variation in nematode community composition and ecosystem processes. Yet, the use of these indices has been mainly restricted to anthropogenic stresses. In this study, we propose to expand the use of nematodes' derived ecological indices to link soil and climate properties with soil food webs, and ecosystem processes that all vary along steep elevation gradients. For this purpose, we explored how elevation affects the trophic and functional diversity of nematode communities sampled every 300 m, from about 1000 m to 3700 m above sea level, across four transects in the lesser Himalayan range of Jammu and Kashmir. We found that (1) the trophic and functional diversity of nematodes increases with elevation; (2) differences in nematodes communities generate habitat-specific functional diversity; (3) the sigma maturity index, the channel index, and the metabolic footprint of nematodes increase with elevation, indicating less mature and less productive ecosystems, enhanced fungal-based energy flow, and a predominant role of nematodes in generating carbon influxes at high elevation sites, respectively. We thus conclude that the functional contribution of soil nematodes to belowground ecosystem processes, including carbon and energy flow, is stronger at high elevation. Overall, this study highlights the central importance of nematodes in sustaining soil ecosystems and brings insights into their functional role, particularly in alpine and arctic soils.

Keywords: Alpine environment, elevation gradient, function trophic structure, soil biodiversity, soil ecology, metabolic footprint.

Introduction:

It has been estimated that soils of terrestrial ecosystems sustain about 25% of the world biodiversity (Decaëns et al., 2006; Decaëns, 2008; Bach et al., 2020), consequently, soils function as biodiversity reservoirs, and have the potential to majorly contribute to ecosystem functioning (Fitter et al., 2005; Decaëns, 2010; Bardgett and van der Putten, 2014). Indeed, soil fauna functional diversity has been shown to contribute to ecosystem functioning by impacting on different processes, such as primary production and nutrient cycling of carbon, phosphorous, or nitrogen (Brussaard, 1997), the decomposition of organic matter, or the assimilation of carbon in food webs, which in turn regulates energy movements between the below and the aboveground compartments of the ecosystems (Hunt and Wall, 2002; Krumins et al., 2013).

The group of roundworms (i.e., the nematodes; phylum Nematoda) represents a major component of the belowground fauna diversity. Nematodes include more than 27'000 described species (Hugot et al., 2001; Hodda, 2011), are found almost in every inhabitable place on Earth, and represent about 80% of belowground bulk metazoan taxonomic and functional diversity (Bongers and Bongers, 1998; Hodda et al., 2009). Nematodes can be assigned to practically all existing trophic groups, including the herbivore, fungivore, bacterivore, predator, unicellular eukaryote feeder, parasite, and omnivore trophic and functional group (Yeates et al., 1993). Nematodes can also be functionally assigned to a wide gamut of ecological adaptations, ranging from being classified as “colonizer” (i.e., r strategists), to being classified as “persister” (i.e., K strategists), and all in between, such along the colonizer-persister (“cp”) scale as described by Bongers (1990). Nematodes, therefore, constitute a key component of the soil microbiota and contribute to regulating several ecosystem processes, such as mineral cycling, succession processes, and energy flow (Boström and Söhlenius, 1986; Andrén et al., 1995; Bongers and Bongers, 1998).

Numerous studies have demonstrated the critical role of climate in the development and maintenance of soil nematode diversity (Nielsen et al., 2014; Chen et al., 2015; Song et al., 2017). For instance, Nielsen et al. (2014) showed that nematode community composition was strongly related to two main climatic factors, mean annual rainfall and temperature, which accounted for 65% and 58% of the total variation in community differences, respectively. Similarly, mean annual precipitation has been shown to influence nematode assemblage at the regional scale (Chen et al., 2015). In addition, climate can directly impact local soil and vegetation characteristics (Rodríguez-Iturbe et al., 1999), and thus climate, indirectly, can influence soil invertebrate communities via changes in vegetation and soil properties (Kergunteuil, 2016). Therefore, contemporary and historical climatic factors can be used to study changes in species and functional diversity of soil nematodes across large geographic scales (Li et al., 2020).

In addition to climate, it is well established that soil nematode diversity, abundance, and composition are also influenced by soil physico-chemical properties, such as soil temperature (de Ruiter et al., 1998), relative humidity (Dinoor and Eshed, 2003), organic matter content (Cook et al., 1992; Collins et al., 1995; De Deyn et al., 2003, 2004; Crawford et al., 2005), phosphorus (De La Peña et al., 2006), texture, or salinity (Djigal et al., 2004), either from the local to the large scales (Chen et al., 2015; Liu et al., 2016; Quist et al., 2019; van den Hoogen et al., 2019). As a consequence, the study of the taxonomic and functional structure of nematode communities can, in turn, be used for assessing soil quality (Sochová et al., 2006; Brinkman et al., 2008; Wilson and Kakouli-Duarte, 2009), as well as for evaluating natural changes in soil ecological conditions, for instance along large-scale ecological and climatic gradients (Kergunteuil, 2016). Accordingly, several indices have been developed that summarize the functional role and the contribution of nematodes in the ecosystem (Bongers and Ferris, 1999; Ferris et al., 2001; Ferris, 2010). For instance, the “Channel index”, the “Enrichment index” and the “Structure index”, which are all derived from calculating the weighted functional diversity components of the soil nematodes communities (Ferris et al., 2001; Berkelmans et al., 2003), represent the predominant decomposition pathways, food web response to available resources and state of food web affected by environmental stress, respectively (Ferris et al., 2001; Ferris and Bongers, 2009). Moreover, the “Metabolic Footprint”, which quantifies the amplitude of C utilisation by different components of the nematode soil food web, can function as an indicator of carbon and energy flow in the soil (Ferris, 2010). Being integrators of ecosystems properties, we, therefore, expected these indices to vary across habitat types, as well as local climatic and edaphic conditions.

While studies relating nematodes’ functional structure and soil functioning remain mostly restricted to anthropogenic systems (Freckman and Ettema, 1993; Šalamún et al., 2014; Zhao et al., 2015), studying the functional variation of soil nematode communities in natural systems can inform on the potential natural co-structuration between belowground diversity, ecosystem function, soil properties and climate (van den Hoogen et al., 2019). In this context, we here propose to expand the use of nematodes’ derived ecological indices to the study of natural populations’ variation along large-scale ecological gradients, which in turn, it will allow increasing our understanding of how soil nematodes contribute and inform on the changes in ecosystem functioning across contrasted landscapes (Ritz and Trudgill, 1999; Yeates, 2003; Wilschut et al., 2019). In this regard, studying nematode communities’ functional variation along steep elevation gradients can be used to dissect the link between climate and soil conditions and nematode functional properties within a homogenous biogeographical and evolutionary background (Körner, 2007; Kergunteuil, 2016).

The purpose of this study is thus to investigate whether, along steep elevation gradients, nematodes communities and functionalities vary predictably with soil and climatic properties. For this, we studied the soil community’s composition along four elevation transects of Northern India (Jammu and Kashmir region). Based on previous studies along elevation gradients in the Alps (Kergunteuil,

2016) we hypothesized that 1) nematodes functional composition varies with elevation, 2) nematodes functional beta-diversity co-vary with changes in soil and climatic conditions along the elevational gradient, and 3) indices related to ecosystem properties, also vary, with nematode communities being more associated with more productive and mature ecosystems at low versus high elevation. Interestingly, it was previously shown that along the Alpine elevation gradients, several soil nematodes trophic and functional groups, such as the herbivores, increase with elevation (Kergunteuil, 2016). These findings were to some extent in opposition with classic hypotheses of biodiversity changes along elevation, in which, for most clades, theory predicts a decline in biodiversity with elevation, indeed due to an increase of more constrained and stressful environmental conditions at high elevation. By studying similar ecosystem dynamics but in an entirely different setting – the Himalayas *versus* the Alps – we ultimately hope to draw broader conclusions about soil nematodes biodiversity patterns and soil functioning in nature.

MATERIALS AND METHODS:

Study area - We surveyed soil nematode communities along the Pir Panjal mountain range, a group of mountains in the Lesser Himalayan region, running from east-southeast to west-northwest, and including the Indian Territory of Jammu and Kashmir, where this study was conducted, and where the average elevation varies from 1'000 m to 4'000 m. Within this region, four elevation transects were selected viz., Darhal, Thanamandi, Budhal and Bakori transects (Figure 1, Table S1). The transects span elevations ranging as low as about 1000 m above sea level (asl), which are characterized by evergreen forests dominated by arboreal plant species, such as *Quercus leucotricophora*, *Pinus wallichiana*, *Pyrus pashia*, *Rhododendron arboreum*, and *Priensepia utilis*, and to almost 3700 m asl; habitats which are characterised by alpine meadows and recent glacial retreats (Table S1).

Extraction of climatic variables - To characterize the climatic conditions present at each site along the elevational transects, we extracted the 19 BIOCLIM variables from the Chelsa global climate data set (<https://chelsa-climate.org/bioclim/>) at 30-second resolution (Karger et al., 2017). For statistical analyses, we removed overly correlated variables from the full list using the package *caret* (Kuhn et al., 2020) and ended up with 10 variables describing the climatic niche of each site (Table S2).

Soil and nematode sampling - Nematodes were sampled between June and October 2020 across the four transects. Within each transect, we sampled 10 sites, separated from one another about 300 m in elevational distance, so to yield a total of 40 sites (Table S1). At each site, a sampling quadrat of 2 × 2 m was randomly chosen within the characteristic and homogenous vegetation type of the site. In sub-alpine areas, soil samples were predominantly collected within *Fagus sylvatica*, *Abies pindrow*, *Pinus spp.*, *Quercus spp.*, or *Castanea sativa* dominated forests, whereas sampling in the alpine elevation stage was performed in alpine grasslands found above the timberline. Everywhere, agricultural or

urban lands were avoided. At each site, about 10–12 soil cores of 10 cm diameter and 10-20cm deep were collected until reaching a sufficient amount of soil (about 1 Kg fresh weight) after the removal of big (> 2 cm in diameter) rock particles. From this well-homogenized bulk soil material, a sub-sample of 100 g of fresh soil was used for extracting soil nematodes using the sieving and Baermann funnel method (Barker, 1985). All nematodes in each sample were then counted under an Olympus Stereo-zoom SZX16 microscope, mounted into slides for identification to the genus level, and assigned to various functional guilds based on their trophic group and life-histories strategies (Yeates et al., 1993) (Table S3). Next, another sub-sample of the bulk soil was used for measuring soil parameters, including soil humidity, pH, conductivity and temperature. For soil humidity, we calculated the difference between soil fresh weight and soil dry weight after 7 days at 70°C. pH and conductivity were measured using a pH meter/Conductometer (HANNA HI-98129 pH, EC and TDS Meter, HANNA Instruments AG, Langnau bei Reiden, Switzerland), after mixing 50 g of this subsample with 100ml of deionized water. Soil temperature was measured on-site with a soil thermometer.

Nematode communities' functional characterization - Depending upon the abundance of functional guilds of nematodes, various indices were calculated, to analyse the functional role of nematode-based food webs along various mountain transects (Bongers and Bongers, 1998; Ferris et al., 2001). To do so, all identified nematodes were classified into five main trophic habits (bacterial-feeders, fungal feeders, plant-feeders, omnivores, and predators (Yeates et al., 1993)), and along the colonizer-persister (cp) scale (Bongers, 1990) (Table S3). We calculated three indices of relating nematodes functional groups to ecosystem functioning: (1) the *Sigma-maturity index* (Σ MI; Bongers, 1990), representing the proportions of the different cp groups for the whole nematode community, and higher values indicate that nematodes harbouring “persister” life-history traits are predominant within each of those different nematode categories. 2) The *Enrichment index* (EI; Ferris et al., 2001), which is based on the biomass of opportunistic nematodes that respond rapidly to the increase of bacterial and fungal populations that arise from organic matter decomposition. High values indicate high soil enrichment and high fertility. (3) The *Channel index* (CI; Ferris et al., 2001), which is calculated as the ratio between the biomass of fungivore to bacterivore nematodes, and greater values indicate that fungal decomposition (the fungal “channel”) predominates over bacterial decomposition for a given site. For specific calculation of each index see (Kergunteuil, 2016). Finally, we calculated (4) the *Metabolic footprints* (MF) according to the equation developed by (Ferris, 2010), and using the Nematode Joint Indicator Analysis tool (Sieriebriennikov et al., 2014) (<https://sieriebriennikov.shinyapps.io/ninja/>). The MF balances the mass of carbon used by nematodes for both production (growth and egg production) and respiration (metabolism activities) components. MF can be computed either for specific functional trophic guilds or the whole nematode community. In this latter case, the so-called “composite MF” represents an indicator of the energy flow channelled

by nematodes in general within soil food webs. High composite MF suggests that nematode assemblages facilitate the storage of high amounts of soil carbon (Ferris, 2010).

Statistical Analyses - All statistical analyses were performed using R software, version 4.0.3 (The R Foundation for Statistical Computing, 2020).

1) Soil-climate covariation – First, the effect of elevation on all individual soil and climate variables was tested using a mixed linear model (package *lme4* (Bates et al., 2015)) with “elevation” as fixed factor and “transect” as random factor. Second, we tested for a shared structure between soil properties and climatic conditions, which would represent a coupled soil-climate syndrome along elevation gradients, using a coinertia analysis. In other words, here we tested whether the matrices of soil parameters and climatic variables concomitantly vary across different sites. If this is the case, it would lead us to conclude that sites co-vary in their soil and climatic properties. The coinertia analyses were performed using the *ade4* package (Dray et al., 2003; Dray and Dufour, 2007), and the significance of the shared variance was assessed using a Monte Carlo test as implemented in *ade4*. When the coinertia analysis was significant (i.e., there is a significant soil/climate structuration across sites; see Figure S1), we performed a linear regression between combined soil-climate syndrome (coinertia 1) and elevation using a mixed linear model (package *lme4* (Bates et al., 2015)) with “elevation” as fixed factor and “transect” as random factor.

2) Nematodes trophic diversity co-vary with changes in soil and climatic conditions along the elevational gradient – First we assessed the effect of the coupled soil/climatic variables on the six major trophic groups of nematodes (herbivores, fungivores, bacterivores, predators, omnivores and parasites) using a mixed linear model (package *lme4*) with “coinertia axis 1” as fixed factor and “transect” as random factor. Second, we scored the effect of individual soil and climatic variables on the different trophic groups by performing a distance-based redundancy analysis (dbRDA) between nematode communities and i) the climatic variable matrix, and ii) the soil variable matrix. Distance matrices were built using Bray-Curtis dissimilarity values, and significances were tested using permutational analyses of variance function *capscale*, the package *vegan* (Oksanen et al., 2013).

3) Nematode functional indices change along elevation - We assessed the effect of the coupled soil/climatic variables on the four nematode function indices (sigma maturity index, channel index, enrichment index, and composite metabolic footprint) using a mixed linear model (package *lme4*) with “coinertia axis 1” as fixed factor and “transect” as random factor.

RESULTS

1) Soil-climate covariation along elevation. We found that elevation was correlated with soil moisture, pH, temperature and conductivity. Particularly, soil temperature ($t_{39} = -31.70$, p-value < 0.001),

conductivity ($t_{39} = -11.34$, $p\text{-value} < 0.001$), and pH ($t_{39} = -2.04$, $p\text{-value} = 0.047$) all decreased with elevation. From the lowest to the highest elevations, soil temperature decreased on average by 12.6 ± 0.4 degrees, conductivity decreased by a factor of 3.86 ± 1.14 mS/m, and pH decreased from 6.35 to 6.10. Soil moisture ($t_{39} = 23.90$, $p\text{-value} < 0.001$) increased along the elevational gradient, and ranged between 25.69 ± 7.21 . For climatic conditions, we found that high elevation sites were at an average 9.25 ± 4.8 degrees colder, 16 % more humid, and 10 % less seasonal variation in precipitation than low elevation sites (Table S2). We also found that climatic and soil properties across sites were significantly correlated (Figure S1, Monte-Carlo test based on 999 replicates, $r = 0.71$, simulated $p\text{-value} = 0.001$). Finally, we found a positive correlation between the first axis of the soil/climate coinertia analysis (as a proxy of soil and climatic variables' correlation) and elevation (Figure S2, Type III ANOVA with Satterthwaite's method, $F_{1,35.01}$, $p\text{-value} < 0.001$)

2) Nematodes trophic composition varies with elevation. Across 40 sites, we retrieved 15'091 nematodes, belonging to 47 genera (Table S3). Nematode communities observed along the elevational transects varied considerably in their composition. Low-elevation soils found in forested areas, ranging from altitude 1000 m to 2500 m, were mainly composed of genera like *Plectus*, *Acrobeles*, *Mesorhabditis*, *Mylonchulus*, *Aphelenchus*, *Alaimus*, *Wilsonema* and *Eudorylaimus*, while those found between the range of 2500 m to 3500 m were composed of genera like *Mesodorylaimus*, *Prodorylaimus*, *Aphelenchoides*, *Teratocephalus*, *Panagrolaimus*, *Tylencholaimus*, *Paratylenchus*, *Helicotylenchus*. However, in the transition zones of elevation transects, various genera coexist, e.g., *Helicotylenchus* and *Eudorylaimus*, which were found both in lower transects as well as in the middle transects, whereas genera like *Teratocephalus*, *Panagrolaimus*, *Prodorylaimus* were found in both mid-elevation transects and in the upper-elevation transects, at an altitude of 3500 m asl. Some genera were completely absent in some sites but present in others. For example, the bacterivore genera *Cuticularia*, *Curvicitis*, *Rhabditis* were not found at high elevations, while *Longidorella*, *Nagelus* were not found at low elevations. Furthermore, above 3500 m, nematode communities mostly consisted of few herbivore and omnivore genera like *Pratylenchus*, *Longidorella*, *Prodorylaimus*, *Panagrolaimus*. Overall, we observed a general increase in the number of nematodes along the elevational gradient, but the diversity of nematode communities declined at the highest elevations (above 3500 m), which mostly consisted of herbivore and omnivore genera (Figure 3). Among climatic variables, diurnal temperature range, isothermality, were significantly associated with more bacterivores and predators, while seasonality was significantly correlated with more omnivores and herbivores (Figure S3, Table S4). Among soil variables, pH was negatively associated with fungivores, but positively associated with herbivores, while conductivity and temperature were positively associated with bacterivores, and finally, soil moisture was positively associated with omnivores (Figure S3, and Table S4).

3) We found that indices related to ecosystem properties varied with elevation, with nematode communities being associated with more productive and mature ecosystems found more likely living at low versus high elevation. Specifically, i) the Σ MI showed an increase along the elevational gradient (Table 2, Figure 4A), depicting an increase in the relative abundance of persister nematodes when moving up along the elevational gradient. ii) The CI also showed an increase with elevation, with the highest values mostly above 1600m asl (Table 2, Figure 4B), while iii) the EI showed a decline with elevation (Table 2, Figure 4C). Finally, iv) the MF of nematodes showed an increase with elevation, thus highlighting high influxes of carbon through nematode with increasing in elevation (Table 2, Figure 4D).

DISCUSSION

Abiotic variation along elevational gradients shapes species diversity patterns, both for above- and belowground organisms, but the generalities of these patterns are still a matter of debate and vary across guilds of taxa (Sundqvist et al., 2013). Here, we studied elevational gradients in soil nematode functional structure in the lesser Himalayan range and found that variation in nematode communities' functional composition along the elevational gradient was related to a shared structure of climatic and edaphic variables. Second, we found an increase in functional diversity and nematodes footprints with elevation. Third, functional indices analyses highlighted a more stable ecological successional status and high amplitude of carbon utilisation at high elevation sites, respectively. Below, we expand on these findings and extrapolate on the relevance of soil nematodes functional indices for characterizing ecosystems changes along ecological gradients.

Elevation effect on soil nematodes trophic groups in relation to edaphic and climatic variables

We analysed nematode communities' linkages to ecosystem function by studying site-specific soil and climatic variables along the elevational gradient. First, our results show an increase in soil moisture content along the elevation, which can be attributed to the increase in mean annual climatic precipitation and a decrease in precipitation seasonality. These properties were in turn related to an increase in the abundance and diversity of nematodes along the elevation (Li et al., 2020). Indeed, we observed that most trophic groups of nematodes, except the bacterivores, which showed a decline, and the parasites, which showed no variation in abundance along elevation, all increased with elevation. Similarly, it was previously observed that soil nematodes' diversity is higher in cooler, more humid soils (Kergunteuil, 2016; Dong et al., 2017). Such trends might be counterintuitive since the diversity and abundance of most taxonomic groups studied so far; e.g., plants (Bryant et al., 2008), arthropods (Hodkinson, 2005), or birds (Patterson et al., 1998; Duclos et al., 2019), all show either a steady decline or a hump-shaped relationship with elevation (Brehm et al., 2007; Godschalx et al., 2019;

Pilar et al., 2020). This is thought to be the reflection of the climate becoming colder and harsher, and growing seasons becoming shorter at high elevation (Chapin and Korner, 1995), a pattern that we also observed: a decrease in mean diurnal temperature range, along with the increase in mean precipitation and a decrease in precipitation seasonality with the increasing elevation. Nematodes, in contrast, we observed to increase in abundance and functional (trophic) diversity with elevation. Other studies have shown the ability of nematodes to inhabit the harshest environments, such as the extreme polar regions (Loof, 1971; Yeates, 2010). Accordingly, we might speculate that nematodes can thrive more at high elevation, since they display adaptations to low temperatures, such as the ability of supercooling and anhydrobiosis (Pickup, 1990; Pickup and Rothery, 1991; Wharton, 1995, 1996), while on the other hand, they might suffer from desiccation in warmer and drier conditions of low elevation sites (Procter, 1990).

Along with climatic variables, we also observed that soil conditions varied with elevation, and, independently from climate, were also correlated with variation in nematodes trophic groups. This is in line with previous results showing that soil variables are indeed important determinants of the composition of soil nematode communities (Wu et al., 2011; Nielsen et al., 2014; Song et al., 2017; Li et al., 2020). For instance, increased free water availability at high elevation is an important aspect for nematode movement and might thus a contributing factor for promoting nematode populations in the alpine environment (Landesman et al., 2011). Taken together, we could argue that variation in nematode community composition and diversity along the elevation gradient could be explained by the shared effects of soil and climatic factors, highlighting the crucial role of interaction among multiple ecological factors on soil biodiversity. Nonetheless, the climatic and edaphic factors only explained a small proportion of the total variation in nematode diversity and composition (from 20% to 68%), suggesting that other potential and indirect explanatory variables, such as the vegetation characteristics or soil microbes, providing the habitat as well as food for nematodes, could also influence soil nematode diversity (Wardle, 2006; Decaëns, 2010).

Elevational variation in soil nematode functional indices related to ecosystem properties

While studies of taxonomic variation can inform on biodiversity changes along ecological gradients, the functional characterization of major players in the community, such as nematodes, are necessary to link biodiversity to ecosystem functioning (Wall and Lynch, 2000; Tilman, 2001; van den Hoogen et al., 2019, 2020). We here addressed the functional composition of nematodes by studying multiple integrative functional indices, including the Sigma maturity index (ΣMI), which increased with elevation. Such patterns were likely driven by an increase in plant-parasitic nematodes index (PPI) and stable soil conditions i.e., less disturbed environment (Bongers, 1990) at high elevating. We suspect that the reason for the observed increase in PPI with elevation is the occurrence of higher

numbers of herbivorous nematodes at high elevation, which goes hand in hand with changes in soil moisture, conductivity and the climatic variables, particularly seasonality, precipitation and temperature. Such conditions provide a convenient environment for soil-dwelling nematodes of larger body size, longer life cycles i.e., 'persistent group' of nematodes. That said, the increase in ΣMI along the elevational gradient depends on both the free-living and the plant-parasitic nematodes, however, high elevations were mostly inhabited by plant-parasitic and omnivore nematode genera, likely due to their better tolerance to stress conditions (Bongers, 1990). A general decrease in the temperatures can also contribute to the maintenance of nematodes with long life cycles and low reproduction rates, thus, favouring the persister groups at high elevations. Furthermore, at high elevations, a denser root system provides a more suitable environment for herbivore and omnivore nematodes, by providing shelter from various kinds of abiotic stress, as well as potentially providing enemy-free zones (Kergunteuil, 2016).

In addition to the ΣMI , we also observed that the channel index (CI) increased with elevation, highlighting a switch from more bacterial-driven to more fungal-driven decomposition pathways when moving from low to high elevation. Plant adaptations to high elevations include a long leaf lifespan and slow growth. Moreover, high elevation soil organic matter decomposition is slow, likely due to thermal inhibition of the metabolic machinery (Pellissier and Rasmann, 2018). All together these patterns result in decreased mineralization processes, and decreased soil fertility (e.g., as shown by a decrease in soil conductivity at high elevation) (Wardle, 2006), and thus favouring enhanced fungal-based energy flow (Wardle and Yeates, 1993; Zhao and Neher, 2014). Together, soil and climatic properties at high elevation thus shift energy transformation pathways from the bacteria to the fungi (Pritchard, 2011), and the nematodes functional index CI was able to detect this major ecosystem property shift.

Another index portraying the functional structure of nematode communities is the enrichment index (EI), which, in contrast with the previous two indices, showed a negative correlation with elevation, although we detected strong variability right above the tree line (Figure 4C). Higher EI values indicate resource enrichment and can be used to classify more undisturbed and more stable habitats (Ferris et al., 2001). Therefore, our findings suggest that across the elevational transects, soil resources are richer at lower than at higher altitudes. This might be explained by the slower erosion processes at lower elevations, which leads to the concentration of nutrients in the soil. Therefore, the EI can be used to extrapolate at which elevation the soil was sampled, as well as the quality of the soil in relation to productivity (Tsiafouli et al., 2017).

Finally, the metabolic footprints (MF) of nematode communities increased with elevation. The MF provides information on the energy flow channelled by the nematodes in the soil food web (Ferris, 2010). Accordingly, the MF show that nematodes play a crucial role in the functioning of soil

ecosystems and energy flow at high elevations, and demonstrate the predominant role of soil mesofauna in integrating carbon within soil food webs in comparison to macrofauna (Ostle et al., 2007). Future work could thus focus on deciphering the extent to which nematodes replace other members of the soil fauna for carbon cycling in alpine and arctic soils.

CONCLUSIONS

Changes in ecological factors like soil quality (Bongers, 1990), soil characteristics (de Goede and Bongers, 1994), habitat stability (Wasilewska, 1994), and climate (Crawford et al., 1991; Ruess et al., 1999; Sohlenius and Bostrom, 1999; Papatheodorou et al., 2004) strongly reflect on soil nematode functional composition, and therefore, it has been predicted that different ecosystems or habitats should sustain different communities of soil nematodes. Accordingly, we here showed that along elevation gradients, soil nematodes are particularly good bioindicators of local ecosystem properties (Overgaard, 1949; Procter, 1984; Yeates, 2003; Yeates and Bongers). Particularly, we showed that alpine ecosystems sustain a wider range of functional and taxonomic diversity than their respective low-elevation sites. Indeed, mountain ranges are unusually biodiverse, with copious accumulations of endemic species, which is the reflection of high variation in hydrology, meteorology, as well in ecological and evolutionary processes (Hoschitz and Kaufmann, 2004; Rahbek et al.). Accordingly, mountains play an important role in sustaining Earth's biodiversity and ecosystem functioning (Körner, 2004). Soil nematodes contribute tremendously to such diversity, both in term of taxonomic and functional diversity. Therefore, a better understating of the causes that generate nematodes biodiversity can inform on the impact of climate change and land-use change on ecosystem functioning worldwide.

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TABLES AND FIGURES

Table 1. Type III Analysis of Variance Table with Satterthwaite's method for measuring the effect of the combined soil/climate variation (coinertia axis 1, Figure S3) on the different nematode trophic guilds.

	SQ	NumDF	DenDF	F	Pr(>F)	
Herbivores	2646.7	1	35.67	49.17	< 0.001	***
Fungivores	221.8	1	37.77	20.93	< 0.001	***
Bacterivores	29906	1	35.54	129.46	< 0.001	***
Predators	72.663	1	38	1.79	0.187	
Omnivores	13012	1	35.67	84.63	< 0.001	***
Parasites	2650.3	1	20.71	6.43	0.019	*

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 2. Type III Analysis of Variance Table with Satterthwaite's method for 1) the *sigma-maturity index*, 2) The *enrichment index*, 3) The *channel index*, and 4) The *metabolic footprints* (MF)

Indices	SQ	NumDF	DenDF	F	Pr(>F)	
sigma-maturity	24.202	1	35.441	169.38	4.60E-15	***
channel	2854.3	1	37.365	9.2445	0.0043	**
enrichment	4548.9	1	37.727	18.323	0.0001231	***
MF	46968	1	38	36.046	5.62E-07	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

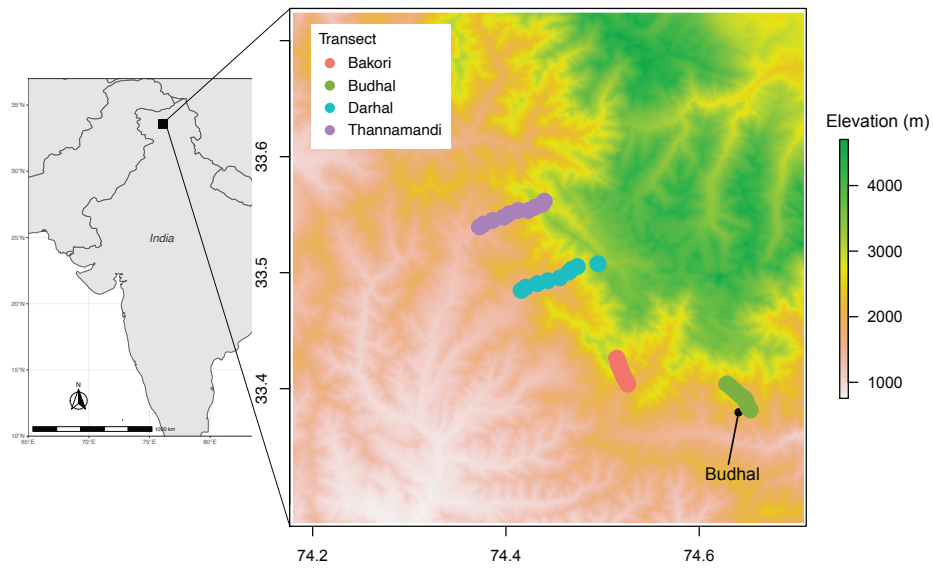
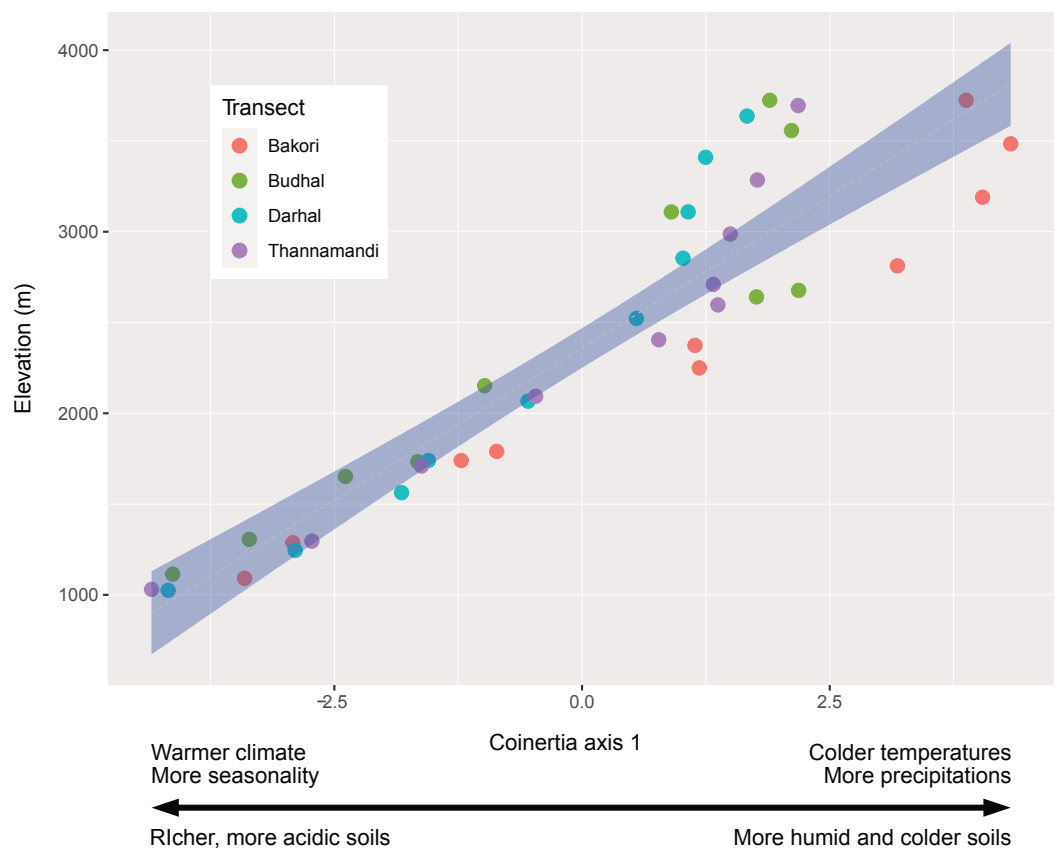


Figure 1. Sampling sites along elevation gradients. Shown is an elevation map of the Indian Jammu and Kashmir region in which four elevation transects were chosen for sampling nematode biodiversity.

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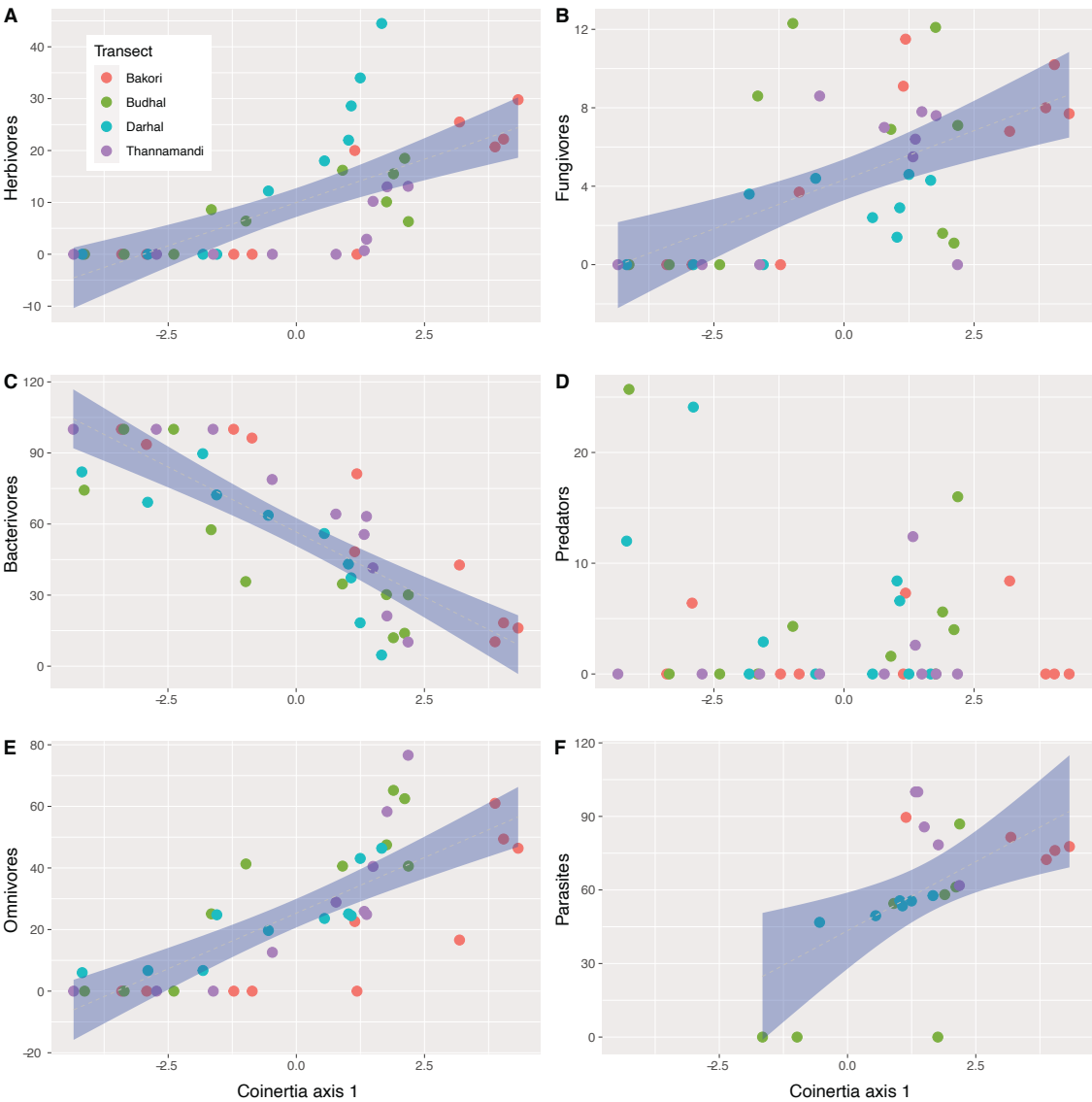
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669 **Figure 2.** Climate and soil properties co-variation along elevation. Grey shading shows the best fitting
670 of the linear model with confidence intervals when the correlation is significant ($p < 0.05$). Dots are
671 coloured for distinguishing the four different elevation transects.

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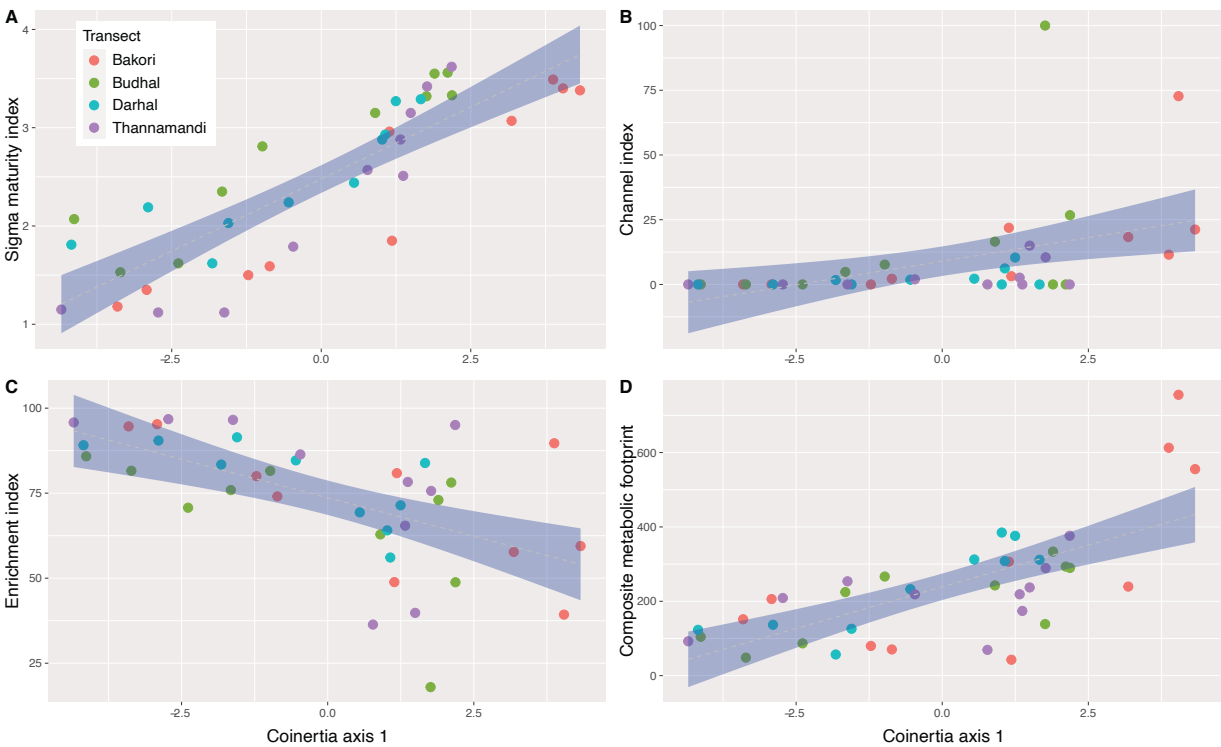
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677 **Figure 3.** Effect of the coupled climate/soil variation along elevation and the abundance of different
678 nematodes' trophic groups. (A) herbivores, (B) fungivores, (C) bacterivores, (D) predators, (E)
679 omnivores, (F) parasites. Shown are the sampling sites belonging to four mountain transects as shown
680 in Table S1. Grey shading shows the best fitting of the linear model with confidence intervals when
681 the correlation is significant ($p < 0.05$). Dots are coloured for distinguishing the four different
682 elevation transects.

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688 **Figure 4.** Effect of the coupled climate/soil variation along elevation and soil nematode functionality.
689 Shown are linear model regression between the climate/soil coinertia axis 1 (see Figure S1), and A)
690 the *Sigma maturity index*, B) the *Channel index*, C) the *Enrichment index*, and D) the *Metabolic*
691 *footprint*. Grey shading shows the best fitting of the linear model with confidence intervals when the
692 correlation is significant ($p < 0.05$). Dots are coloured for distinguishing the four different elevation
693 transects.

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