

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

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19 **Abstract**

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

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

41

42 **Introduction:**

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

52 The group of roundworms (i.e., the nematodes; phylum Nematoda) represents a major component of
53 the belowground fauna diversity. Nematodes include more than 27'000 described species (Hugot et
54 al., 2001; Hodda, 2011), are found almost in every inhabitable place on Earth, and represent about
55 80% of belowground bulk metazoan taxonomic and functional diversity (Bongers and Bongers, 1998;
56 Hodda et al., 2009). Nematodes can be assigned to practically all existing trophic groups, including
57 the herbivore, fungivore, bacterivore, predator, unicellular eukaryote feeder, parasite, and omnivore
58 trophic and functional group (Yeates et al., 1993). Nematodes can also be functionally assigned to a
59 wide gamut of ecological adaptations, ranging from being classified as “colonizer” (i.e., r strategists),
60 to being classified as “persister” (i.e., K strategists), and all in between, such along the colonizer-
61 persister (“cp”) scale as described by Bongers (1990). Nematodes, therefore, constitute a key
62 component of the soil microbiota and contribute to regulating several ecosystem processes, such as
63 mineral cycling, succession processes, and energy flow (Boström and Sohlenius, 1986; Andrén et al.,
64 1995; Bongers and Bongers, 1998).

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

76 In addition to climate, it is well established that soil nematode diversity, abundance, and composition
77 are also influenced by soil physico-chemical properties, such as soil temperature (de Ruiter et al.,
78 1998), relative humidity (Dinoor and Eshed, 2003), organic matter content (Cook et al., 1992; Collins
79 et al., 1995; De Deyn et al., 2003, 2004; Crawford et al., 2005), phosphorus (De La Peña et al., 2006),
80 texture, or salinity (Djigal et al., 2004), either from the local to the large scales (Chen et al., 2015; Liu
81 et al., 2016; Quist et al., 2019; van den Hoogen et al., 2019). As a consequence, the study of the
82 taxonomic and functional structure of nematode communities can, in turn, be used for assessing soil
83 quality (Sochová et al., 2006; Brinkman et al., 2008; Wilson and Kakouli-Duarte, 2009), as well as for
84 evaluating natural changes in soil ecological conditions, for instance along large-scale ecological and
85 climatic gradients (Kergunteuil, 2016). Accordingly, several indices have been developed that
86 summarize the functional role and the contribution of nematodes in the ecosystem (Bongers and
87 Ferris, 1999; Ferris et al., 2001; Ferris, 2010). For instance, the “Channel index”, the “Enrichment
88 index” and the “Structure index”, which are all derived from calculating the weighted functional
89 diversity components of the soil nematodes communities (Ferris et al., 2001; Berkelmans et al., 2003),
90 represent the predominant decomposition pathways, food web response to available resources and
91 state of food web affected by environmental stress, respectively (Ferris et al., 2001; Ferris and
92 Bongers, 2009). Moreover, the “Metabolic Footprint”, which quantifies the amplitude of C utilisation
93 by different components of the nematode soil food web, can function as an indicator of carbon and
94 energy flow in the soil (Ferris, 2010). Being integrators of ecosystems properties, we, therefore,
95 expected these indices to vary across habitat types, as well as local climatic and edaphic conditions.

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

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

112 2016) we hypothesized that 1) nematodes functional composition varies with elevation, 2) nematodes
113 functional beta-diversity co-vary with changes in soil and climatic conditions along the elevational
114 gradient, and 3) indices related to ecosystem properties, also vary, with nematode communities being
115 more associated with more productive and mature ecosystems at low versus high elevation.
116 Interestingly, it was previously shown that along the Alpine elevation gradients, several soil
117 nematodes trophic and functional groups, such as the herbivores, increase with elevation (Kergunteuil,
118 2016). These findings were to some extent in opposition with classic hypotheses of biodiversity
119 changes along elevation, in which, for most clades, theory predicts a decline in biodiversity with
120 elevation, indeed due to an increase of more constrained and stressful environmental conditions at
121 high elevation. By studying similar ecosystem dynamics but in an entirely different setting – the
122 Himalayas *versus* the Alps – we ultimately hope to draw broader conclusions about soil nematodes
123 biodiversity patterns and soil functioning in nature.

124

125 **MATERIALS AND METHODS:**

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

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

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

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

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

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

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

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

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

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

213

214 **RESULTS**

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

217 conductivity ($t_{39} = -11.34$, $p\text{-value} < 0.001$), and pH ($t_{39} = -2.04$, $p\text{-value} = 0.047$) all decreased with
218 elevation. From the lowest to the highest elevations, soil temperature decreased on average by $12.6 \pm$
219 0.4 degrees, conductivity decreased by a factor of 3.86 ± 1.14 mS/m, and pH decreased from 6.35 to
220 6.10. Soil moisture ($t_{39} = 23.90$, $p\text{-value} < 0.001$) increased along the elevational gradient, and ranged
221 between 25.69 ± 7.21 . For climatic conditions, we found that high elevation sites were at an average
222 9.25 ± 4.8 degrees colder, 16 % more humid, and 10 % less seasonal variation in precipitation than
223 low elevation sites (Table S2). We also found that climatic and soil properties across sites were
224 significantly correlated (Figure S1, Monte-Carlo test based on 999 replicates, $r = 0.71$, simulated p -
225 $\text{value} = 0.001$). Finally, we found a positive correlation between the first axis of the soil/climate
226 coinertia analysis (as a proxy of soil and climatic variables' correlation) and elevation (Figure S2,
227 Type III ANOVA with Satterthwaite's method, $F_{1,35,01}$, $p\text{-value} < 0.001$)

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

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

261

262 **DISCUSSION**

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

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

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

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

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

311

312 *Elevational variation in soil nematode functional indices related to ecosystem properties*

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

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

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

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

353 Finally, the metabolic footprints (MF) of nematode communities increased with elevation. The MF
354 provides information on the energy flow channelled by the nematodes in the soil food web (Ferris,
355 2010). Accordingly, the MF show that nematodes play a crucial role in the functioning of soil

356 ecosystems and energy flow at high elevations, and demonstrate the predominant role of soil
357 mesofauna in integrating carbon within soil food webs in comparison to macrofauna (Ostle et al.,
358 2007). Future work could thus focus on deciphering the extent to which nematodes replace other
359 members of the soil fauna for carbon cycling in alpine and arctic soils.

360

361 **CONCLUSIONS**

362 Changes in ecological factors like soil quality (Bongers, 1990), soil characteristics (de Goede and
363 Bongers, 1994), habitat stability (Wasilewska, 1994), and climate (Crawford et al., 1991; Ruess et al.,
364 1999; Sohlenius and Bostrom, 1999; Papatheodorou et al., 2004) strongly reflect on soil nematode
365 functional composition, and therefore, it has been predicted that different ecosystems or habitats should
366 sustain different communities of soil nematodes. Accordingly, we here showed that along elevation
367 gradients, soil nematodes are particularly good bioindicators of local ecosystem properties (Overgaard,
368 1949; Procter, 1984; Yeates, 2003; Yeates and Bongers). Particularly, we showed that alpine
369 ecosystems sustain a wider range of functional and taxonomic diversity than their respective low-
370 elevation sites. Indeed, mountain ranges are unusually biodiverse, with copious accumulations of
371 endemic species, which is the reflection of high variation in hydrology, meteorology, as well in
372 ecological and evolutionary processes (Hoschitz and Kaufmann, 2004; Rahbek et al.). Accordingly,
373 mountains play an important role in sustaining Earth's biodiversity and ecosystem functioning (Körner,
374 2004). Soil nematodes contribute tremendously to such diversity, both in term of taxonomic and
375 functional diversity. Therefore, a better understating of the causes that generate nematodes biodiversity
376 can inform on the impact of climate change and land-use change on ecosystem functioning worldwide.

377

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647 **TABLES AND FIGURES**

648

649 **Table 1.** Type III Analysis of Variance Table with Satterthwaite's method for measuring the effect of
 650 the combined soil/climate variation (coinertia axis 1, Figure S3) on the different nematode trophic
 651 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	*

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

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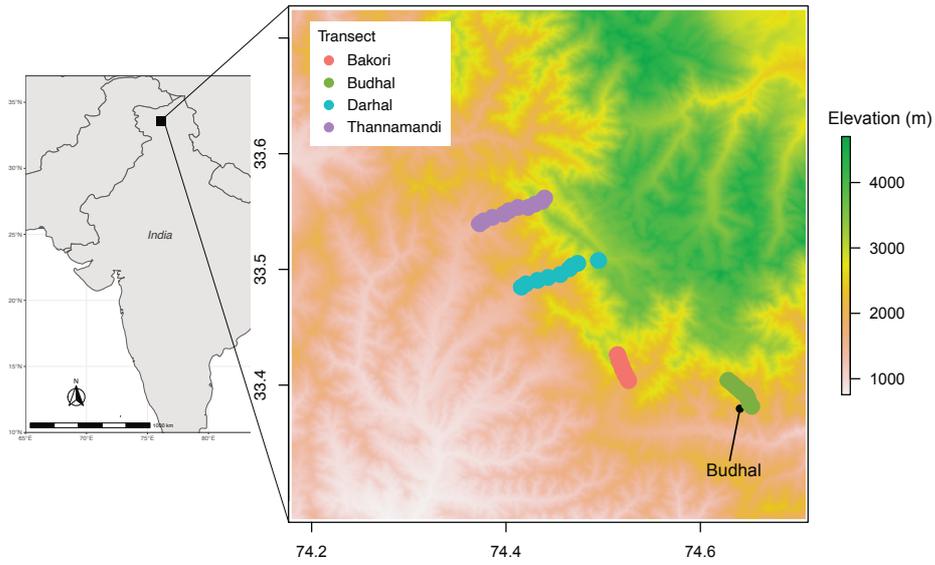
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655 **Table 2.** Type III Analysis of Variance Table with Satterthwaite's method for 1) the *sigma-maturity*
 656 *index*, 2) The *enrichment index*, 3) The *channel index*, and 4) The *metabolic footprints (MF)*

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	***

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

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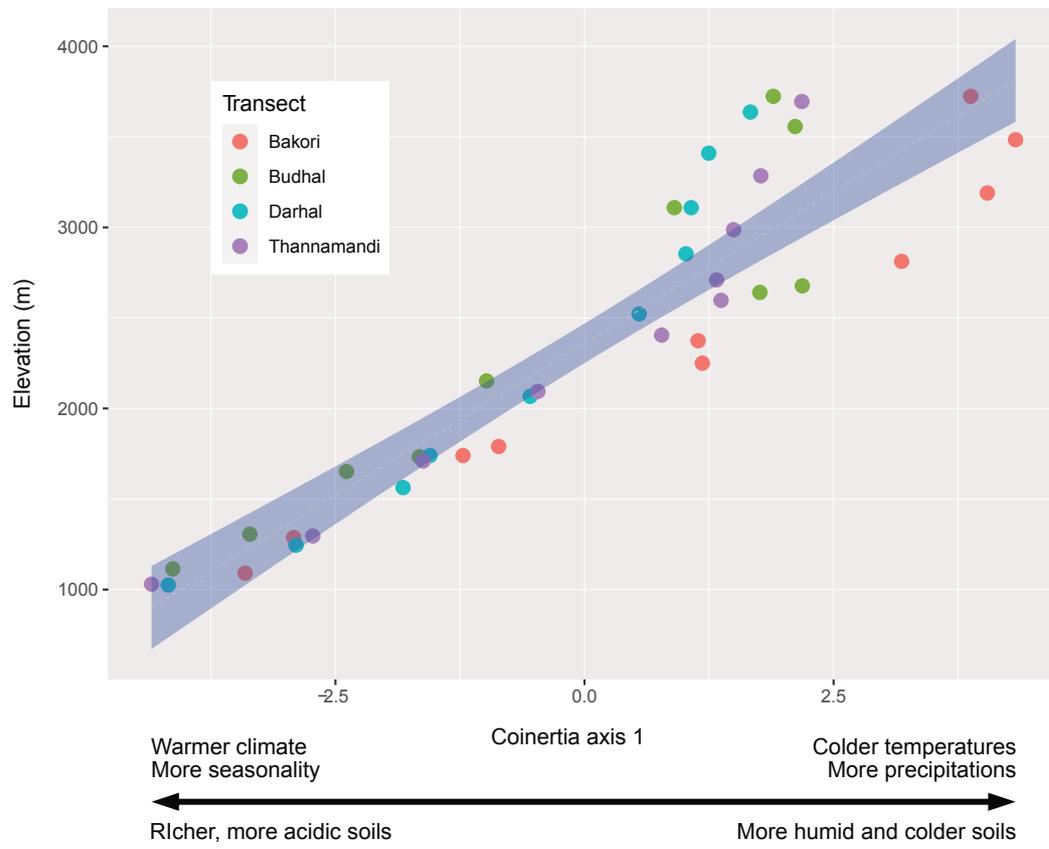
660 **Figure 1.** Sampling sites along elevation gradients. Shown is an elevation map of the Indian Jammu
 661 and Kashmir region in which four elevation transects were chosen for sampling nematode
 662 biodiversity.

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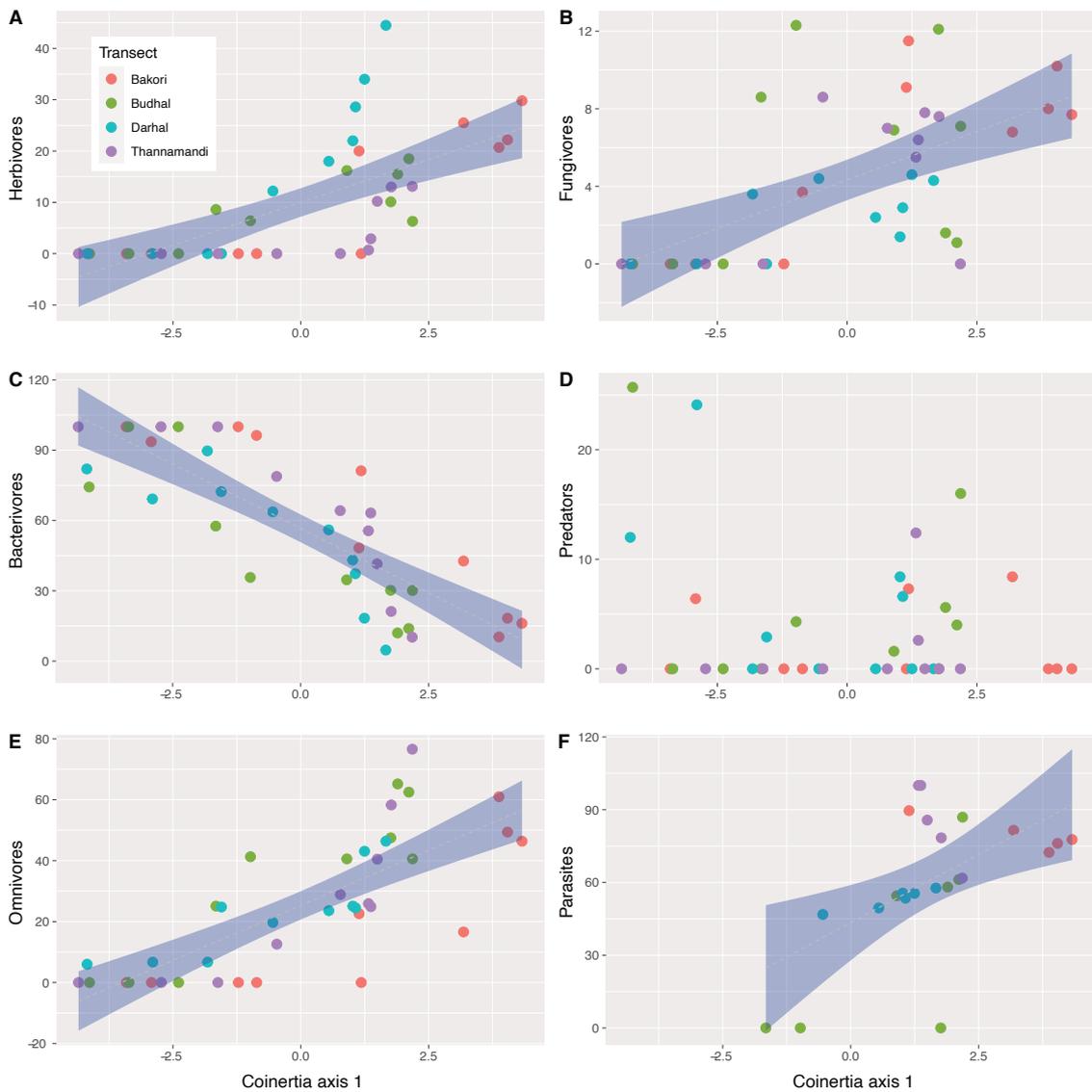
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669 **Figure 2.** Climate and soil properties co-variation along elevation. Grey shading shows the best fitting
670 of the linear model with confidence intervals when the correlation is significant ($p < 0.05$). Dots are
671 coloured for distinguishing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

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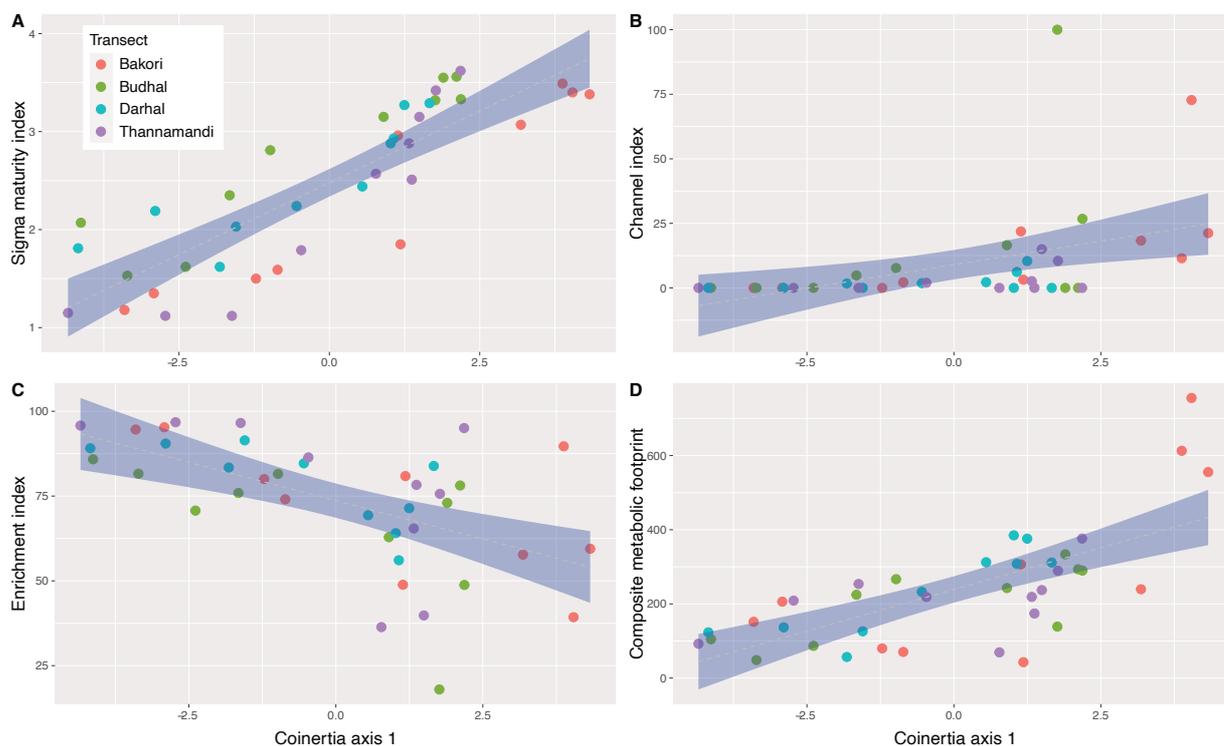
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677 **Figure 3.** Effect of the coupled climate/soil variation along elevation and the abundance of different
 678 nematodes' trophic groups. (A) herbivores, (B) fungivores, (C) bacterivores, (D) predators, (E)
 679 omnivores, (F) parasites. Shown 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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