

1 Soil nematode abundance and functional group composition at a global scale

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27 28 Summary

29 **Soil organisms are a crucial part of the terrestrial biosphere. Despite their importance for ecosystem**
30 **functioning, no quantitative, spatially-explicit models of the active belowground community**
31 **currently exist. In particular, nematodes are the most abundant animals on Earth, filling all trophic**
32 **levels in the soil food web. Here, we use 6,579 georeferenced samples to generate a mechanistic**
33 **understanding of the patterns of global soil nematode abundance and functional group composition.**
34 **The resulting maps show that $4.4 \pm 0.64 \times 10^{20}$ nematodes (total biomass ~0.3 Gt) inhabit surface soils**
35 **across the world, with higher abundances in sub-arctic regions (38% of total), than in temperate**
36 **(24%), or tropical regions (21%). Regional variations in these global trends also provide insights into**
37 **local patterns of soil fertility and functioning. These high-resolution models provide the first steps**
38 **towards representing soil ecological processes into global biogeochemical models, to predict**
39 **elemental cycling under current and future climate scenarios.**

40

41 As we refine our spatial understanding of the terrestrial biosphere, we improve our capacity to manage
42 natural resources effectively. With ever-growing functional information about the biogeography of
43 aboveground organisms, an outstanding gap in our understanding of the biosphere remains the activity and
44 distribution patterns of soil organisms^{1,2}. Soil biota, including bacteria, fungi, protists and animals, play
45 central roles in every aspect of global biogeochemistry, influencing the fertility of soils and the exchange
46 of CO₂ and other gasses with the atmosphere³. As such, biogeographic information on the abundance and
47 activity of soil biota is essential for climate modelling and, ultimately, environmental decision making^{2,4-6}.
48 Yet, the activity of soil organisms is not explicitly reflected in biogeochemical models due to our limited
49 understanding of their biogeographic patterns at the global scale.

50

51 In recent years, pioneering studies in soil biogeography have begun to provide valuable insights into the
52 broad-scale taxonomic diversity patterns of soil bacteria⁷⁻¹¹, fungi¹¹⁻¹³ and nematodes¹⁴⁻¹⁷, and patterns of
53 microbial biomass^{11,18,19}. However, until now, we have been unable to generate a high-resolution,
54 quantitative understanding of the abundance or functional composition of active soil organisms because of
55 two major reasons. First, due to the methodological challenges in characterizing soil biota, most previous
56 studies have focused on a relatively limited number of spatially distinct sampling sites (<500), and therefore
57 cannot detect high-resolution regional-scale patterns. Second, most global studies have used molecular
58 sequencing approaches, which provide valuable semi-quantitative information on taxonomic diversity, but
59 not information on absolute abundance or biomass that is essential to link biological communities to
60 ecosystem functioning and global biogeochemistry^{20,21}. DNA and RNA-based approaches cannot
61 unambiguously differentiate between living (being either active or dormant) and dead cells, so they cannot
62 be used to quantify the active component of the belowground community^{22,23}. To generate a robust, global
63 perspective of belowground biota and their roles in biogeochemical cycling, we need a sampling design
64 that provides a thorough global representation of the belowground community, and direct, quantitative
65 abundance data reflecting the active community. Here, we adopt this approach in order to generate a

66 quantitative understanding of a critical component of the soil food web, for which direct extraction methods
67 enable quantification of active organisms: nematodes.

68

69 Nematodes are a dominant component of the soil community and are by far the most abundant animals on
70 Earth². They account for an estimated four-fifths of all animals on land²⁴, and feature in all major trophic
71 levels in the soil food web. The functional role of nematodes in soils can be inferred by their trophic
72 position, and hence nematodes are often classified into trophic groups based on feeding guilds (i.e.
73 bacterivores, fungivores, herbivores, omnivores, predators). Given their pivotal roles in processing organic
74 nutrients and control of soil microorganism populations²⁵⁻²⁷, they play critical roles in regulating carbon
75 and nutrient dynamics within and across landscapes²⁶ and are a good indicator of biological activity in
76 soils²⁸. Yet, we still lack even a basic understanding of broad-scale biogeographic patterns in nematode
77 abundance and nematode functional group composition. Despite expectations that nematode abundances
78 may peak in warm tropical regions with high plant biomass^{14,15}, other studies suggest that the opposite
79 pattern might exist, with high nematode abundances in high-latitude regions with larger standing soil carbon
80 stocks^{16,17,29-31}. Disentangling the effects of these different environmental drivers of soil nematode
81 communities is critical to generate a mechanistic understanding of the global patterns of soil nematodes,
82 and for quantifying their influence on global biogeochemical cycling.

83

84 Here, we use 6,759 spatially distinct soil samples from all terrestrial biomes and continents to examine the
85 environmental drivers of global nematode communities. By making use of 73 global layers of climate, soil,
86 and vegetation characteristics, we then extrapolate these relationships across the globe to generate the first
87 spatially-explicit, quantitative maps of soil nematode density and functional group composition at a global
88 scale.

89

90 **Results and Discussion**

91 **Biome-level patterns of soil nematodes**

92 By compiling soil sampling data from all major biomes and continents we aimed to generate a representative
93 dataset to capture the variation in global nematode densities. Within each sample, we quantified the total
94 abundance of each trophic group using microscopy. In order to standardize sampling protocols, we focus
95 on the top 15 cm of soil, which is the most biologically active zone of soils^{6,32}. In line with previous
96 reports³³, nematode abundances are highly variable within and across terrestrial biomes, ranging from dozen
97 to thousands of individuals per 100 g soil (Fig. 1b). This variation highlights the necessity for large datasets
98 in soil biodiversity analyses to reliably predict large-scale patterns, as the accuracy of our mean estimates
99 for any region improves considerably with increasing number of samples (Fig. 2a). Specifically, the
100 confidence in our mean estimates for nematode abundance in any region is relatively low at the individual
101 sample scale, but high only when calculated with larger (i.e. >400) sample size.

102
103 Overall, we observed the highest nematode densities in tundra (median = 2,329 nematodes per 100 g dry
104 soil), boreal forests (median = 2,159) and in temperate broadleaf forests (median = 2,136), while the lowest
105 densities are observed in Mediterranean forests (median = 425), Antarctic sites (median = 96) and hot
106 deserts (median = 81) (Fig. 1b, Supplementary Table 2). To examine the mechanisms driving the patterns
107 of soil nematode density and functional group composition across biomes, we integrated the nematode
108 abundance data with 73 global datasets of soil physical and chemical properties, and vegetative, climatic,
109 topographic, anthropogenic, and spectral reflectance information (Supplementary Table 3). Antarctic
110 sampling points were excluded from the modelling dataset due to limited coverage of several covariate
111 layers. To match the spatial resolution of our covariates, all samples were aggregated to the 1-km² pixel
112 level to generate 1,876 unique pixel locations across the world. We analysed a suite of machine-learning
113 models (including random forest, L1 and L2 regularised linear regression) to determine the environmental
114 drivers of the variation in nematode abundance and functional group composition across the globe. We
115 iteratively varied the set of covariates and model hyperparameters across 405 models and evaluated model
116 strength using *k*-fold cross validation (with *k* = 10). This approach allowed us to select the best performing
117 model which had high predictive strength (mean cross-validation $R^2 = 0.43$, overall $R^2 = 0.86$), whilst taking

118 into account issues surrounding multicollinearity, and model overparameterization and overfitting. This
119 final model, an iteration of random forests using all 73 covariates, was then used to create a per-pixel mean
120 and standard deviation values. Mapping the extent of extrapolation highlighted that our dataset covered
121 most environmental conditions, with the least represented pixels and highest proportion of extrapolation in
122 the Sahara and Arabian Desert (Extended Data Figs. 1a, 1b). We acknowledge that our models cannot
123 accurately predict nematode abundances at fine spatial scales, as local environmental heterogeneity can
124 cause considerable variation in nematode abundances, even within individual locations. However, the
125 strength of these predictions increases at the larger scales where our modelled estimates are informed by
126 more data observations (Fig. 2b), ensuring confidence in our estimates. Predicted *vs.* observed plots
127 revealed that, despite the high accuracy in most regions, the models tended to marginally over-represent
128 the observed numbers at low densities and underrepresent at higher nematode densities (Figs. 2c-h).
129 Moreover, our cross-validation accuracy calculations may be optimistically biased, as we cannot entirely
130 account for the potential impacts of overfitting. Our analyses would have ideally included a subset of data
131 removed at the beginning of the analyses for fully independent accuracy assessment. However, as the
132 removal of a subset would mean a loss of geographic representation, we chose instead to maintain the
133 integrity of the entire dataset and generate spatially explicit maps of model confidence that allow for error
134 propagation throughout the final global calculations (Fig. 2i, Extended Data Fig. 1a). These maps provide
135 spatial insight into the prediction uncertainties rather than a single accuracy measure for overall model
136 accuracy.

137

138 Our statistical models reveal the dominant drivers of nematode abundance across global soils. As with
139 aboveground animals, climatic variables (i.e., temperature and precipitation) played an important role in
140 shaping the patterns in total soil nematode abundance. However, soil characteristics (e.g. texture, soil
141 organic carbon (SOC) content, pH, cation-exchange capacity (CEC)) were by far the most important factors
142 driving nematode abundance at a global scale, with effects that largely overwhelmed the climate impacts
143 (Supplementary Table 3). Linear models enabled us to assess the directionality of these relationships,

144 revealing that both SOC content and CEC had strong positive correlations, whilst pH had a negative effect
145 on total nematode density (Extended Data Fig. 2). These trends support the suggestion that soil resource
146 availability is a dominant factor structuring belowground communities at broad spatial scales, overriding
147 the impact of climate, in structuring belowground communities at broad spatial scales^{2,12,15}.

148

149 **Global biogeography of soil nematodes**

150 The high predictive strength of the top model enabled us to extend the relationships across global soils to
151 construct high-resolution (30 arc-seconds, $\sim 1 \text{ km}^2$), quantitative maps of total nematode densities. These
152 maps reveal striking latitudinal trends in soil nematode abundance, with the highest densities in sub-arctic
153 regions (Fig. 3), a trend that is consistent across all trophic groups (Extended Data Figs. 3a-e). Specifically,
154 as with the regional averages, the highest abundances of soil nematodes are found in boreal forests across
155 North America, Scandinavia and Russia. Whether nematode abundance is expressed as density per gram of
156 soil or per unit area (thereby controlling for the differences in soil bulk density), the models reveal a striking
157 latitudinal gradient in soil nematode abundance (Fig. 3, Extended Data Figs. 4, 5). Whether soil animals
158 exist at highest abundances in the high or low latitudes has been a contentious issue in the soil ecology
159 literature, with some studies highlighting highest abundances in boreal forests, and others suggesting that
160 tropical forests support the greatest abundance^{29,31,14}. Our extensive sample data from every biogeographic
161 region allows us to see beyond these contrasting results to reveal a striking latitudinal pattern of nematode
162 abundance, providing conclusive evidence that soil nematodes are present in considerably higher densities
163 in high-latitude arctic and sub-arctic regions (Fig. 3).

164

165 Along with the latitudinal gradient in nematode abundance, our nematode density map also reveals regional
166 contingencies that stand out against the global trends. Although nematode abundances were relatively low
167 in tropical regions, our sampling data and models reveal high nematode abundance in certain tropical
168 peatlands such as the Peruvian Amazon (Fig. 1a; Fig. 3). These regions are characterized by high SOC
169 stocks, which support high microbial biomasses that serve as the basic resource for most nematode groups.

170 Similarly, increased SOC stocks at high altitude compared to lowland regions drive higher nematode
171 abundances in mountainous regions and highlands, such as the Rocky Mountains, Himalayan Plateau and
172 the Alps (Fig. 1a; Fig. 3). Although the respective climates of these regions exhibit large differences in
173 mean annual temperature ($<0^{\circ}\text{C}$ to $>10^{\circ}\text{C}$), their soils are all characterized by relatively high SOC stocks
174 (i.e. $>50\text{ g kg}^{-1}$). In contrast, the lowest nematode densities were predicted in hot deserts such as the Sahara,
175 Arabian Desert, Gobi Desert, and Kalahari Desert (Fig. 3), regions characterized by very low SOC stocks.
176 As such, the spatial variability in nematode abundance is highest in equatorial regions, which exhibit the
177 full range of possible abundances from desert to biomes characterized by high SOC stocks. This is reflected
178 by the spatial patterns in our model uncertainty, in which low-latitude arid regions with low sampling
179 density and soil nematode abundances are characterized by larger uncertainty (Fig. 2i, Extended Data Fig
180 1).

181
182 The strong correlation between temperature and SOC content at a global scale¹⁹ makes it challenging to
183 identify the primary driver of the latitudinal gradient in nematode abundances. However, regional
184 deviations from the global biogeographic pattern help to disentangle their relative roles, as they decouple
185 the effects of climate and soil characteristics. For example, low temperatures and high moisture content in
186 high-latitude regions restrict annual decomposition rates, leading to the accumulation of soil organic
187 material^{19,30}. But the positive effect of SOC in tropical peatland regions (with high soil carbon but also
188 warm temperatures) suggests that it is organic matter content, rather than climate conditions, that ultimately
189 determines nematode abundance in soil. These models reinforce the dominant role of soil characteristics in
190 driving nematode abundances. These trends suggest that the impacts of climate on nematode density are
191 not direct, but instead act indirectly by modifying soil characteristics.

192
193 We next examined how nematode community structure varied across landscapes by exploring the
194 abundance of each trophic group across our dataset. At the global scale, all trophic groups were positively
195 correlated with one another (Extended Data Fig. 6a), suggesting that biogeographic regions with high

196 nematode abundances are generally hospitable for members of all trophic groups. Despite the distinct
197 feeding habits, the global consistency across trophic groups provides some unity in the biogeography of the
198 soil food web. That is, although different nematodes rely on distinct food sources for their energetic
199 demands, the size of the entire food web is ultimately determined by the availability of soil organic matter.
200 Nevertheless, the relative composition of nematode communities did vary across samples. To characterize
201 the main nematode community types, we clustered the observed relative abundances into four types, based
202 on the relative abundance of each trophic group (Extended Data Fig. 6b). Although there were no clear
203 spatial patterns in these community types, vector analysis revealed that the indices of vegetation cover (e.g.,
204 NDVI, EVI) were the best predictors of herbivore-dominated communities, while edaphic factors (sand
205 content, pH) were strong predictors of communities dominated by bacterivores (Extended Data Fig. 6c).

206
207 By summing the nematode density information in each pixel, we can begin to generate a quantitative
208 understanding of soil nematode abundances and biomass at a global scale. We estimate that approximately
209 $4.4 \pm 0.64 \times 10^{20}$ nematodes inhabit the upper layer of soils across the globe (Table 1, Supplementary Table
210 5). Of these, 38.7% exist in boreal forests and tundra, 24.5% in temperate regions and 20.5% in tropical
211 and sub-tropical regions (Supplementary Table 6). By combining our estimates of nematode abundance
212 with mean biomass estimates of each functional group (using a database containing 32,728 nematode
213 samples^{34,35}), we can approximate that global nematode biomass in the global topsoil is approximately 0.3
214 Gt (Table 1). This translates to approximately 0.03 Gt of carbon (C) (Table 1, Supplementary Table 7),
215 which is three times greater than a previous estimate of soil nematode biomass³⁶, and represents 82% of
216 total human biomass on Earth (see Supplementary Methods). Using the same database of nematode
217 metabolic activity^{34,35}, we estimate that nematodes may be responsible for a monthly C turnover of 0.14 Gt
218 C within the global growing season, of which 0.11 Gt C is respired into the atmosphere (Table 1). For a
219 comparison, the amount of C respired by soil nematodes is equivalent to roughly ~15% of C emissions
220 from fossil fuel use, or ~2.2% of the total annual C emissions from soils (approximately 9 and 60 Gt C per

221 year, respectively³⁷). As such, our findings indicate that soil nematodes are a major, and to date poorly
222 recognised, player in global soil C cycling.

223

224 Despite high confidence in our estimates of total nematode abundance and community composition, these
225 approximations of metabolic footprint retain several assumptions that might lead to considerable
226 uncertainty in our estimates. For example, seasonal climatic variation in metabolic activity could influence
227 the values we present here, and total activity levels might be lower than expected based on these growing
228 season estimates. On the other hand, extraction efficiency can be lower than 50% in some samples, which
229 could lead to underestimation of the actual activity levels. Local variation in land use types and bias in our
230 sampling data could cause variation in soil nematode abundances at local scales. Further, even though our
231 sampling locations cover the vast majority of environmental conditions on Earth (Extended Data Figs. 1c,
232 1e), our data underrepresented certain regions such as the Sahara and Arabian Desert, leading to relatively
233 high uncertainties in these regions (Fig. 2i, Extended Data Figs. 1a, 1b, 6). Also, as our sampling approach
234 focusses on the top soil layer, we stress that our analysis will underestimate total nematode abundances, for
235 example in tropical regions where high nematode densities are found in litter layers³⁸. Yet, the metabolic
236 footprint that we provide enables us to approximate the magnitude of soil nematode contributions to global
237 carbon cycling and highlights their contribution to the total soil C budget. Further, our findings emphasize
238 the importance of high-latitude regions, characterized by high soil nematode abundances, in our
239 understanding of soil carbon and feedbacks to on-going climate change. These regions compose a major
240 reservoir of soil carbon stocks⁶, and may release much more carbon as a result of increased soil animal
241 activity and a prolongation of the plant-growing season due to human-induced climate change.

242

243 In conclusion, our maps provide the first spatially-explicit, quantitative information of belowground biota
244 at a global scale. Besides providing baseline information about soil nematodes as a fundamental component
245 of terrestrial ecosystems, it also alters some of our most basic assumptions about the terrestrial biosphere
246 by highlighting that soil animal abundances peak in high latitude zones. The high nematode numbers that

247 are present across all global soils highlights their functional importance in global soil food web dynamics,
248 nutrient cycling terrestrial ecosystem functioning. This quantitative understanding of these belowground
249 animals enables us to begin to comprehend the order of magnitude of their influence on the global carbon
250 cycle, and the spatial patterns in these processes. By providing quantitative information about the variation
251 in biological activity in soils around the world, our models can provide the information necessary to
252 explicitly represent soil biotic activity levels in spatially-explicit biogeochemical models. That is, this
253 information can now be used to parameterize, scale or benchmark spatially-explicit model predictions of
254 organic matter turnover under current or future climate change scenarios. We highlight that this global
255 nematode study can and should be supplemented with similar future efforts to understand the biogeography
256 of other important soil organisms, including fungi, bacteria and protists. Our unique soil nematode
257 abundance and biomass data can serve as a stepping stone to facilitate future modelling efforts that add
258 additional layers of soil biodiversity information to build a thorough understanding of the overwhelming
259 abundance of life belowground and its impact on global ecosystem functioning.

260

261

262 **Table 1 | Total nematode abundance, biomass and carbon budget.**

Trophic group	Computed individuals (x 10²⁰)	Fresh biomass (Mt)	Biomass (Mt C)	Monthly respiration (Mt C)	Monthly production (Mt C)	Monthly carbon budget (Mt C)
Bacterivores	1.92 ± 0.208	68.57 ± 7.42	7.13 ± 0.77	34.17 ± 3.69	12.22 ± 1.31	46.39 ± 5.02
Fungivores	0.64 ± 0.065	9.56 ± 0.97	0.99 ± 0.10	6.49 ± 0.66	0.91 ± 0.09	7.40 ± 0.75
Herbivores	1.25 ± 0.114	83.41 ± 7.59	8.67 ± 0.79	26.74 ± 2.43	7.01 ± 0.64	33.75 ± 3.07
Omnivores	0.39 ± 0.046	96.50 ± 11.40	10.25 ± 1.19	27.38 ± 3.17	6.08 ± 0.70	33.46 ± 3.87
Predators	0.20 ± 0.031	42.25 ± 6.59	4.39 ± 0.68	15.06 ± 2.35	3.00 ± 0.46	18.06 ± 2.82
Total	4.40 ± 0.643	302.30 ± 33.99	31.44 ± 3.54	109.82 ± 12.31	29.24 ± 3.23	139.06 ± 15.54

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367

368 **Author contributions**

369 J.vdH., S.G., D.R. and T.W.C. designed and performed the data analyses. J.vdH, D.R., T.W.C. designed
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377 the paper.

378

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382

383 Competing interests

384 One of the co-authors (WSA) recently became an employee of Nature Communications, a sister journal
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479 **Main figure legends**

480 **Figure 1 | Map of sample locations and abundance data.** **a**, Sampling sites. A total of 6,759 samples
481 were collected and aggregated into 1,876 1-km² pixels that were used for geospatial modelling and
482 abundance data from 39 1-km² pixels from Antarctica. **b**, The median and interquartile range of nematode
483 abundances (n = 1,875) per trophic group (top) and per biome (bottom) from all continents. Axes have been
484 truncated for increased readability. Biomes with observations from more than 20 1-km² pixels are shown.

485

486 **Figure 2 | Model and data validation.** The standard error of the observed (**a**) and predicted (**b**) mean
487 values of nematode density decrease with increasing sample size. The operation was repeated with 100 and
488 1,000 random seeds for the observed and predicted mean values, respectively, and the mean calculated
489 standard errors are shown. **c-h**, Heat plots showing the relationships between predicted versus observed
490 nematode abundance values, for total nematode number and each trophic group. Dashed diagonal lines
491 indicate fitted relationships (R^2 values are indicated in the bottom right), solid diagonal lines indicate a 1:1
492 relationship between predicted and observed points. **i**, Bootstrapped (100 iterations) coefficient of variation
493 (standard deviation divided by mean predicted value) as a measure of prediction accuracy. Sampling was
494 stratified by biome. Overall, our prediction accuracy is lowest in arid regions and in parts of the Amazon
495 and Malay Archipelago.

496

497 **Figure 3 | Global map of soil nematode density at the 30 arc-seconds (~1 km²) pixel scale.** Nematodes
498 per 100 g dry soil. Pixel values were binned into seven quantiles to create the colour palette.

499

500 **Methods**

501 Data acquisition

502 We collected data on soil nematode abundances that morphologically quantified nematodes and determined
503 taxa to the level of trophic groups or taxonomic groups. Rather than taxonomic diversity, we decided to
504 focus on trophic groups as this gives more functional information. Trophic groups were assigned based on
505 Yeates, et al. ³⁹. We only collected samples that contained the following metadata: longitude and latitude,
506 season or date sampled, sampling depth, information on land use (agriculture or natural sites) and if samples
507 were collected from soils or litter. We then standardized our efforts by focusing on all samples that were
508 derived from soils and in which samples were representative for nematode functional group composition in
509 the top 15 cm of soils. This resulted in a final subset of 6,759 samples that were used for further analyses.
510 Of these, 32.8% originate from agricultural or managed sites, and 67.2% from natural sites. All data points
511 falling within the same 30 arc-seconds (~1-km²) pixel were aggregated via an average, resulting in a total
512 of 1,915 unique pixels across the globe as inputs into the models (Extended Data Table 1). 39 pixels located
513 in Antarctica were removed from the dataset as the covariate layers have limited coverage in these regions.
514 This resulted in a total of 1,876 unique pixels that were used for geospatial modelling.

515

516 Acquisition of global covariate layers

517 To create spatial predictive models of nematode abundance, we first sampled our prepared stack of 73
518 ecologically relevant, global map layers at each of the point locations within the dataset. These layers
519 included climatic, soil nutrient, soil chemical, soil physical, vegetative indices, radiation and topographic
520 variables and one anthropogenic covariate (Extended Data Table 2). All covariate map layers were
521 resampled and reprojected to a unified pixel grid in EPSG:4326 (WGS84) at 30 arc-seconds resolution
522 (\approx 1km at the equator). Layers with a higher original pixel resolution were downsampled using a mean
523 aggregation method; layers with a lower original resolution were resampled using simple upsampling (i.e.,
524 without interpolation) to align with the higher resolution grid.

525

526 Geospatial modelling

527 Using the ClustOfVar package⁴⁰ in R, we reduced the covariates of interest to the most representative and
528 least collinear few. As we did not have a specific number of variables defined *a priori* to use as a parameter
529 for the clustering procedure, we put a range of cluster numbers (i.e., 5, 10, 15, 20) into the ClustOfVar
530 functions in order to compute multiple covariate groups for testing machine learning models. Using these
531 selections of variables, we used a “grid search” procedure to iteratively explore the results of a suite of
532 machine learning models trained on each group of covariates computed from the ClustOfVar function.
533 Moreover, following recent advancements in machine learning for spatial prediction⁴¹, we tested models
534 using all covariates with and without latitude/longitude data as well as a specific selection of covariates
535 representing principal ecosystem components plus satellite-based spectral reflectance. In addition to grid
536 searching through models trained on different groupings of the covariates, we also explored the parameter
537 space of multiple machine learning algorithms (including random forests and regularized linear regression
538 with both L1 and L2 regularization) and optional post-hoc image convolution using kernels of various pixel
539 sizes. During the grid search procedure, we assessed each model using *k*-fold cross validation, to test the
540 performance and overfitting across each of the 405 models. For each fold, a 10% subset of the data was
541 extracted and held back for validation. Then, the model was trained on the remaining data, and tested on
542 the validation data. To test each model on the entire dataset, this process was performed 10 times for each
543 model (i.e., *k* = 10). computing coefficient of determination values for each fold that were then used to
544 compute mean and standard deviation values for the cross validated model. These mean and standard
545 deviation values were the basis for choosing the “best model” of all 405 models explored via the grid search
546 procedure, which was an iteration of random forests using all 73 non-spatial covariates. The grid search
547 procedure was performed using the total nematode abundance data, and this final model was then used to
548 model the sub-functional group abundance. The final R² value for the ensembled total nematode abundance
549 model (also assessed using 10-fold cross validation) was 0.43.

550

551 Model uncertainty

552 To create a per-pixel mean and standard deviation we ensembled multiple versions of the “best model”; as
553 the “best model” was an iteration of random forests using all 73 non-spatial covariates, the ensemble
554 procedure was to rerun this model 10 times (each with different random seed values) then averaging the
555 model results. Using these values we calculated the coefficient of variation (standard deviation divided by
556 the mean predicted value) as a measure of the prediction accuracy of our model (Fig 2i).

557

558 To create statistically valid per-pixel confidence intervals, we performed a stratified bootstrapping
559 procedure with the “total number” collection of nematode point data. The stratification category was the
560 sampled biomes of each point feature (to avoid biases), and the number of bootstrap iterations was 100.
561 Each of the bootstrap iterations required the classification of the composite raster data i.e., 209,000,000
562 pixels classified 100 times. Doing so allows us to generate per pixel, statistically robust 95% confidence
563 intervals (Extended Data Fig 1c).

564

565 Next, we tested the extent of extrapolation in our models by examining how many of the Earth’s pixels
566 exist outside the range of our sampled data for each of the 73 global covariate layers. To evaluate the
567 sampled range, we extracted the minimum and maximum values of each covariate layer of the pixels in
568 which our sampling sites were located. Then, using the final model, we evaluated the number of variables
569 that fell outside the sampled range, across all terrestrial pixels. Next, we created a per-pixel representation
570 of the relative proportion of interpolation and extrapolation (Extended Data Fig. 1b). This revealed that our
571 samples covered the vast majority of environmental conditions on Earth, with 84% of Earth’s pixels values
572 falling within the sampled range of at least 90% percent of all bands (Extended Data Fig. 1e). Across all
573 environmental layers, the percent of pixels with values within the sampled range is generally above 85%
574 (Extended Data Fig. 1f).

575

576 To evaluate how well our data spread throughout the full multivariate environmental covariate space, we
577 performed a Principal Components based approach. After performing a PCA on the sampled data, we used

578 the centering values, scaling values, and eigenvectors to transform the composite image into the same PCA
579 spaces. Then, we created convex hulls for each of the bivariate combinations from the first 11 principal
580 components (which collectively covered more than 80% of the sample space variation). Using the
581 coordinates of these convex hulls, we classified whether each pixel falls within or outside each of these
582 convex hulls. 62% of the world's pixels fell within the entire set of 55 PCA convex hull spaces computed
583 from our sampled data, with most of the outliers existing in arid regions (Extended Data Fig 1 e).

584

585 Geospatial analyses and extrapolation were performed in Google Earth Engine⁴². Additional model results
586 can be found in the Extended Data.

587

588 Nematode density values

589 To compute the original nematode density values (which were in “number of nematodes per 100 grams of
590 soil”), we performed the following calculations at a per-pixel level. First, we multiplied the value by 10 in
591 order to compute nematodes per 1 kg of soil; the new units, per-pixel, became “number of nematodes per
592 1kg of soil”. Then, we multiplied this value by the per-pixel bulk density values as produced by SoilGrids⁴³;
593 bulk density values were then produced in “kg of soil per 1 cubic meter”. Finally, the new units after
594 multiplication are the “number of nematodes per 1 cubic meter of soil”. Next, we multiplied this value by
595 0.15 meters to compute the “number of nematodes per 1 square meter of soil (in the top 15 cm)”. For pixels
596 that had a soil layer shallower than 15 cm, the pixel value was multiplied by the depth to bedrock values as
597 produced by SoilGrids⁴³. These respective pixel values were then multiplied by the area of each pixel
598 presumed to have soil (i.e., we exclude areas of “permanent snow/ice” and “open water” from the
599 calculations, following the Consensus Land Cover classes found here:
600 <https://www.earthenv.org/landcover>); the units at this point, per-pixel, are the total number of nematodes
601 (in the first 15cm of soil). Finally, all pixel values were summed to compute the final nematode abundance
602 values across all pixels (i.e., across the entire globe).

603

604 Clustering

605 To delineate main nematode 'community types', i.e. the relative frequency of each trophic group in a given
606 sample, we first defined the number of clusters for the analysis. Based on pairwise distances and Partitioning
607 Around Medoids (*k*-medoids) clustering we chose to select four clusters. Each of the four community types
608 was then plotted (Extended Data Fig. 6b) to reveal their composition. To examine which environmental
609 variables best explained each of the community types, we plotted each of the samples using a non-metric
610 multidimensional scaling (stress = 0.0691) and fitted environmental variables as vectors (Extended Data
611 Fig. 6c).

612

613 Biomass estimates

614 Using publicly available data^{34,35}, a database with taxon-specific body size values (i.e. length, width) of
615 32,728 nematode taxa (including 9,497 observations of adult nematodes and 23,231 observations of
616 juveniles) was created to calculate the biomass, and respiration and assimilation rates for each trophic
617 group. A nematode community typically contains numerous juveniles³⁵, we assume the presence of 70%
618 juveniles and 30% adults. For all calculations described in this section, we calculated per-trophic group
619 means using per-taxon observations. To produce the final values, we multiplied the mean calculated values
620 per trophic group with the predicted number of individuals per trophic group and per biome. The biomass
621 of an assemblage of nematodes can be calculated as the sum of the weights of the number of individuals of
622 each species present. According to Andrassy⁴⁴, the fresh weight of individual nematodes is calculated by

623
$$W_{\text{fresh}} = \frac{L \cdot D^2}{1.6 \cdot 10^6}$$

624 where W_{fresh} is the fresh weight (μg) per individual, L is the nematode length (μm) and D is the greatest
625 body diameter (μm)⁴⁴. Assuming a dry weight of nematodes as 20% of fresh weight and the proportion of
626 carbon in the body as 52% of dry weight^{45,46}, the dry weight (W_{dry}) of an individual nematode can be
627 calculated as

628
$$W_{\text{dry}} = \frac{0.104 \cdot L \cdot D^2}{1.6 \cdot 10^6}$$

629

630 Daily carbon used in production

631 To calculate the total carbon utilized per nematode per day, we assumed that life cycle length in days can
632 be approximated as 12 times the colonizer-persister (cp) scale^{47,48} and that the accumulation of fresh weight
633 is linear. Then, the daily increase in fresh weight is

634
$$R_w = \frac{W_t}{12 \cdot cp_t}$$

635 where W_t and cp_t are the adult weight and cp value for a nematode of trophic group t , respectively. Then,
636 we calculate the normalized daily carbon used in production (P_c) as

637
$$P_c = \frac{0.104 \cdot W_t}{12 \cdot cp_t}$$

638 where cp_t is the mean cp value of the respective trophic group. For a nematode assemblage, the daily carbon
639 used in production can be calculated as

640
$$P_c = \sum N_t \frac{0.104 \cdot W_t}{12 \cdot cp_t}$$

641 for N_t individuals of each trophic group present in the assemblage.

642

643 Carbon respiration

644 To estimate the carbon respiration rates of an assemblage of nematodes, we assume relationships between
645 respiration rates and body weights for poikilothermic organisms, so that

646
$$R = a \cdot W^b$$

647 where R is the respiration rate, W is the fresh weight (μg) per individual, and a and b are regression
648 parameters^{49,50}. Following literature, we assume that b is equal to 0.75^{51,52}. The parameter a varies with
649 temperature and the time interval on which the rate is based. For example, Klekowski, et al.⁵³ determined
650 an average a -value of approximately 1.40 nl O₂ h⁻¹ for 68 nematode species. This converts to an a -value of

651 2.43 ng CO₂ h⁻¹ at 15 °C. To estimate CO₂ respiration in µg per day, we make the assumption of an *a*-value
652 of 2.43 × 24/1000 (= 0.058) for our calculations. Using the relative molecular weights of carbon and oxygen
653 in CO₂ (12/44 = 0.273), we can calculate the total rate of carbon respiration for all nematodes in the system
654 as

$$655 \quad R = \sum N_t \cdot 0.273 \cdot 0.058 W_t^{0.75}$$

656 or

$$657 \quad R = \sum N_t \cdot 0.0159 W_t^{0.75}$$

658 where N_t is the number of individuals and W_t the median body weight of each of the trophic groups summed
659 over t trophic groups.

660

661 Total daily carbon budget

662 The total carbon budget (in µg per day) for each trophic group is the sum amounts that are respired and
663 used for production, that is:

$$664 \quad C_{\text{tot}} = \sum \frac{N_t \cdot 0.104 \cdot W_t}{12 \cdot c_{p_t}} + N_t \cdot 0.0159 \cdot (W_t)^{0.75}$$

665

666

667 **Data and code availability**

668 All raw data, source code, sampled covariate layer data, models and maps are available under:

669 https://gitlab.ethz.ch/devinrouth/Crowtherlab_Nematode

670

671

672 **Additional References**

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716 **Extended Data Legends**

717 **Extended Data Fig. 1 | Model accuracy assessment and extent of interpolation and extrapolation**
718 **across all terrestrial pixels in 73 global covariate layers. a,** coefficient of variation (standard deviation
719 as a fraction of the mean predicted value) as a measure of the prediction accuracy of our model. **b,**
720 proportional extent of interpolation (purple) *vs.* extrapolation (red) in univariate space. **c,** Percentage of
721 pixels that fall within the convex hulls of the first 11 principal component spaces (collectively covering
722 >80% of the sample space variation). **d,** percentage of pixels interpolated as a function of the percent of
723 global environmental conditions covered by the sample set. On the global scale, 86% of the Earth's pixels
724 have at least 90% of the covariate bands falling within the sampled range of environmental conditions. **e,**
725 percentage of pixels falling within the 55 convex hull spaces of the first 11 Principal Components
726 (collectively explaining >80% of the variation. On the global scale, 62% of the Earth's pixels fell within
727 100% of 55 PCA convex hull spaces. **f,** percent of terrestrial pixels falling within the sampled range, per
728 covariate band.

729

730 **Extended Data Fig. 2 | Linear regression models of the most important variables from the final**
731 **random forest model and annual mean temperature.** Soil organic carbon and cation-exchange capacity
732 have a positive correlation with total nematode abundance, pH is negatively correlated. These linear
733 regression models (n = 1,809) were not used to create global perspectives of nematode distribution patterns.
734 The grey area represents the 95% confidence interval for the mean.

735

736 **Extended Data Fig. 3 | Global maps of nematode trophic group abundance. a,** bacterivores. **b,**
737 fungivores. **c,** herbivores. **d,** omnivores. **e,** predators. Scales differ per map. Most trophic groups show
738 similar patterns, but predators (**e**) are predicted to be present in particularly high abundances in some arid
739 soils e.g. in the Sahara and Arabian Desert. Pixel values were binned into seven quantiles to create the
740 colour palette.

741

742 **Extended Data Fig. 4 | Global map of total nematode abundance per unit area (m²).** Correcting for the
743 lower bulk density in soils high in organic matter, this map shows the same global patterns of nematode
744 abundance as in Fig. 3. Hence, it is not low soil bulk density in boreal regions resulting in the observed
745 patterns, but rather the high nematode abundances. Pixel values were binned into seven quantiles to create
746 the colour palette.

747

748 **Extended Data Fig. 5 | Global maps of nematode trophic group abundance per unit area (m²).** **a,**
749 **bacterivores. b,** fungivores. **c,** herbivores. **d,** omnivores. **e,** predators. Scales differ per map. Correcting for
750 the lower bulk density in soils high in organic matter, these maps show the same global patterns of nematode
751 trophic group abundance as in Extended Data Figs. 3a-e. Pixel values were binned into seven quantiles to
752 create the colour palette.

753

754 **Extended Data Fig. 6 | Community types and driving variables of community type composition. a,**
755 **Correlations between trophic groups.** Overall, correlations of predators with other trophic groups are the
756 least positive. **b,** based on the relative abundance of each trophic group, soil nematode communities can be
757 classified in four distinct types. We find that these soil nematode communities are dominated by either
758 herbivores (1), herbivores and bacterivores (2), bacterivores (3), or have a mixed composition (4). **c,** non-
759 metric multidimensional scaling to highlight environmental conditions that drive the composition of each
760 of the four main community types. Vegetation-type indices, such as NDVI and Fpar, drive the dominance
761 of herbivores in nematode communities (type 1), while edaphic characteristics are correlated with
762 communities dominated by microbivores (types 3 and 4). The names of the environmental variables are
763 listed in Supplementary Table 3.

764

765 **Supplementary Table 1 | Nematode abundance data and corresponding metadata values.** Abundance
766 data for each trophic group and associated metadata from 1,876 1-km² pixels that were used for geospatial
767 modelling and abundance data from 39 1-km² pixels from Antarctica. (.csv file)

768

769 **Supplementary Table 2 | Summary of mean, median and sample size values per biome.** The number
770 of sites corresponds to the number of 1-km² pixels into which the samples were aggregated. (.csv file)

771

772 **Supplementary Table 3 | Global covariate layers used for geospatial modelling.** A total of 73 global
773 covariate layers was used in our modelling approach. The 7 Nadir Reflectance Band layers (i.e.,
774 MCD43A4.005 BRDF-Adjusted Reflectance 16-Day Global 500m) are summarised as one entry in the
775 table. (.xlsx file)

776

777 **Supplementary Table 4 | Variable importance metrics.** Edaphic characteristics emerged as the most
778 important variables. As the full dataset includes collinear variables leading to a false representation of the
779 variable importance metrics, analysis was performed on a selection of main variables. (.xlsx file)

780

781 **Supplementary Table 5 | Number of soil nematodes per trophic group, per biome.** Summing the
782 predicted number of nematodes per 1 km² pixel across biomes we estimate a total of 4.4×10^{20} nematodes
783 are present in the top 15 cm of soil across the globe. (.csv file)

784

785 **Supplementary Table 6 | Relative abundance of soil nematodes per trophic group, per biome.** (.csv
786 file)

787

788 **Supplementary Table 7 | Nematode biomass per trophic group, per biome.** Note that values are
789 presented in megatons (10^6 tons) carbon. (.csv file)

790

791 **Supplementary Table 8 | Relative nematode biomass per trophic, per biome.** (.csv file)

792