



University of Dundee

A global database of soil nematode abundance and functional group composition

van den Hoogen, Johan; Geisen, Stefan; Wall, Diana H.; Wardle, David A.; Traunspurger, Walter; de Goede, Ron G. M.

Published in: Scientific Data

DOI: 10.1038/s41597-020-0437-3

Publication date: 2020

Document Version Publisher's PDF, also known as Version of record

Link to publication in Discovery Research Portal

Citation for published version (APA): van den Hoogen, J., Geisen, S., Wall, D. H., Wardle, D. A., Traunspurger, W., de Goede, R. G. M., Adams, B. J., Ahmad, W., Ferris, H., Bardgett, R. D., Bonkowski, M., Campos-Herrera, R., Cares, J. E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S. R., Creamer, R., da Cunha E Castro, J. M., ... Crowther, T. W. (2020). A global database of soil nematode abundance and functional group composition. *Scientific Data*, *7*, 1-8. [103]. https://doi.org/10.1038/s41597-020-0437-3

General rights

Copyright and moral rights for the publications made accessible in Discovery Research Portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from Discovery Research Portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain.
- You may freely distribute the URL identifying the publication in the public portal.

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

SCIENTIFIC DATA

Check for updates

OPEN A global database of soil nematode abundance and functional group DATA DESCRIPTOR composition

Johan van den Hoogen et al.#

As the most abundant animals on earth, nematodes are a dominant component of the soil community. They play critical roles in regulating biogeochemical cycles and vegetation dynamics within and across landscapes and are an indicator of soil biological activity. Here, we present a comprehensive global dataset of soil nematode abundance and functional group composition. This dataset includes 6,825 georeferenced soil samples from all continents and biomes. For geospatial mapping purposes these samples are aggregated into 1,933 unique 1-km pixels, each of which is linked to 73 global environmental covariate data layers. Altogether, this dataset can help to gain insight into the spatial distribution patterns of soil nematode abundance and community composition, and the environmental drivers shaping these patterns.

Background & Summary

To generate a global and quantitative understanding of the biogeography of soil organisms, critical players in global biogeochemistry, large and comprehensive datasets are needed. Due to methodological challenges and the labor-intensiveness of characterizing soil biota, many previous studies have focused on a relatively limited number of spatially distinct sampling sites. Whilst these studies are valuable to dissect local and regional scale patterns, they may not hold the depth of information that is needed to feed global-scale models¹.

Soil nematodes are present in all trophic levels in the soil food web, play central roles in regulating carbon and nutrient dynamics, control soil microorganism populations²⁻⁴ and, consequently, are good indicators of biological activity in soils⁵. Here, we present a dataset of 6,825 spatially distinct soil nematode samples from all terrestrial biomes and continents, an updated version of the dataset that was originally used to create a global map of soil nematode abundance and community composition⁶. The original version contained 6,759 samples; the updated version that we present here contains 66 additional samples located in Ireland. This dataset can prove useful to disentangle the effects of environmental drivers of soil nematode abundance and community composition across broad spatial scales. The original version of this dataset was used to create a high-resolution map of soil nematode abundance, which revealed that nematodes are present in higher densities in sub-Arctic regions compared to tropical and temperate regions⁶. Soil properties are the primary drivers of soil nematode abundance, whereas climatic conditions have an indirect effect by altering soil conditions⁶. The overall latitudinal gradient, with decreasing abundance towards the equator, is the inverse of patterns often observed in aboveground organisms, but is in line with what has been shown for other belowground biota^{7,8}.

Besides data on the total number of nematodes per sample, the dataset contains quantification of the abundance of individuals in different functional groups of soil nematodes classified according to five feeding guilds9: bacterivores, fungivores, herbivores, omnivores, predators. For geospatial mapping, these sampling data were aggregated into 1,933 unique 30 Arc-seconds pixels (~1 km² at the equator) and combined with 73 global covariate layers including information on soil physiochemical properties, and vegetation, climate, and topographic, anthropogenic, and spectral reflectance information. We intend to continue expanding the dataset and are open to contributions of additional data.

Methods

Data collection. The methods described here are expanded versions of descriptions in our related work⁶. The dataset encompasses georeferenced data on soil nematode abundances according to trophic groups, which were assigned according to Yeates et al.9. In total, the dataset contains 6,825 georeferenced samples collected in

#A full list of authors and their affiliations appears at the end of the paper.

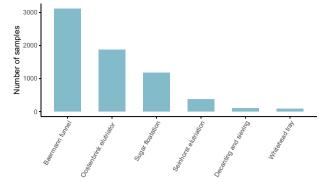


Fig. 1 Nematode extraction methods used. The majority of the samples were processed using the Baermann funnel method and Oostenbrink elutriation.

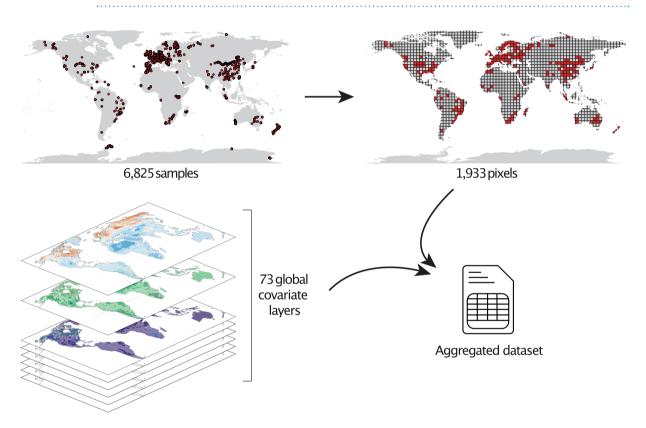


Fig. 2 Data processing approach. 6,825 georeferenced samples are included in the raw dataset. These sampling locations represent 1,933 unique 30 arc-seconds pixels (~1 km at the equator), or 1,895 pixels excluding locations falling off the covariate grid. To gain mechanistic insights and discern the major environmental drivers of nematode abundance, these pixels were sampled across 73 global covariate layers.

the top 15 cm of soils, including 66 additional samples compared to the dataset used in our related work⁶. Across all samples, 67.2% originate from natural sites and 32.8% from agricultural or managed sites. Nematodes were extracted from soil using standard elutriation methods, including the Baermann funnel method¹⁰, sugar-floata-tion/centrifugation^{11,12}, decanting and sieving¹³, Oostenbrink elutriation¹⁴, Whitehead tray¹⁵ and Seinhorst elutriation¹⁶. These methods may include variations of the original methods. Most samples present in the dataset were obtained using the Baermann funnel method, followed by Oostenbrink elutriation and sugar-floation (Jenkins/Freckman) (Fig. 1). Per-sample method descriptions, sampling depth, and data provider information are available via figshare¹⁷. For previously published data, we provide references to the original publications of the respective samples.

Environmental metadata: soil, climate, topography, vegetation, anthropogenic characteristics. For all sampling locations we provide paired environmental metadata, which can be used to provide insight into the environmental drivers of soil nematode abundance and community composition across spatial scales. To do so, we first prepared a covariate stack of 73 layers, for which we downloaded the covariate layers as geotiff files.

Group	mean	median	n
Bacterivores	1052	250	6788
Fungivores	438	84	6782
Herbivores	656	171	6784
Omnivores	325	41	6787
Predators	119	6	6706
Total_Number	2653	857	6825

Table 1. Mean and median nematode abundances, per trophic group. Values are reported as the number of nematodes per 100 g dry soil.

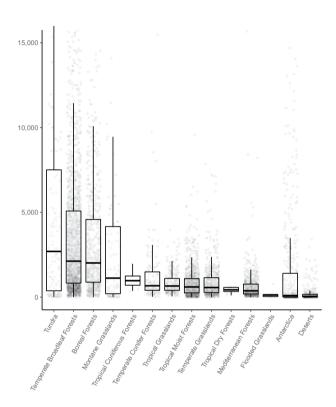


Fig. 3 Nematode communities vary across biomes. The median and interquartile range of nematode abundances (n = 6,825) per biome from all continents.

.....

Next, all layers were resampled and reprojected to a unified pixel grid in EPSG:4326 (WGS84) at 30 arc-seconds resolution. Layers with a higher original pixel resolution were downsampled using a mean aggregation method; layers with a lower original resolution were resampled using simple upsampling (i.e. without interpolation) to align with the higher resolution grid. Next, all layers were converted into a multiband image, i.e. the covariate stack, that was used for pixel sampling.

To prepare the dataset for this purpose, we first need to match the resolution of the dataset to that of the global covariate layer stack that contains the environmental metadata: 30 arc-seconds, which corresponds to approximately 1-km² at the equator. In this step, we aggregate all data points falling within the same pixel by taking the mean value, resulting in 1,933 unique pixels. We stress that the covariate layer stack has no coverage in Antarctica and therefore the 503 samples located in this region were dropped at the pixel aggregation step. Next, pixel values across the 73 layers were retrieved and stored as a csv file. This dataset is available via figshare¹⁷. We stress that, as some covariate layers were reprocessed since the publication of the nematode mapping study⁶, there are some slight differences in the sampled covariate data in this updated version. The approach is visualized in Fig. 2.

Full metadata, including descriptions, units, and source information of all global covariate layers are available via figshare¹⁷. In short, information about soil texture and physiochemical properties was obtained from SoilGrids¹⁸, limited to the upper soil layer (top 15 cm). Climate information was obtained from WorldClim¹⁹ (version 2), which includes climate data averaged across 1970–2000 (http://www.worldclim.org/). Plant productivity data (i.e. EVI, NDVI, Gpp, Npp) and spectral reflectance data were obtained from Google Earth Engine (https://developers.google.com/earth-engine/datasets/). Aridity index and potential evapotranspiration layers were obtained from CGIAR²⁰ (version 1) (http://www.cgiar-csi.org/data/global-aridity-and-pet-database). Anthropogenic information (i.e. human development, population density) was obtained from WCS²¹ (http:// wcshumanfootprint.org) and from Tuanmu and Jetz²². Aboveground biomass data was obtained from CDIAC²³

Biome	mean	median	n
Tundra	7298	2695	148
Temperate Broadleaf Forests	4465	2120	2175
Boreal Forests	3959	2016	669
Montane Grasslands	6096	1120	116
Tropical Coniferous Forests	1000	970	8
Temperate Conifer Forests	1800	670	158
Tropical Grasslands	863	657	272
Tropical Moist Forests	914	601	968
Temperate Grasslands	945	565	627
Tropical Dry Forests	430	431	11
Mediterranean Forests	619	374	704
Flooded Grasslands	183	124	7
Antarctica	2245	89	503
Deserts	193	44	361

Table 2. Mean and median nematode abundances, per biome. Values are reported as the total number of nematodes per 100 g dry soil.

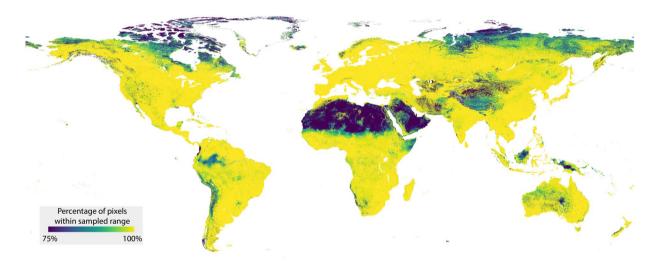


Fig. 4 Environmental representativeness of the dataset. The sampled locations represent a wide range of environmental conditions. For illustrative purposes, ten environmental variables were chosen from the full set of 73.

(https://cdiac.ess-dive.lbl.gov/epubs/ndp/global_carbon/carbon_documentation.html). Radiation data was obtained from CliMond²⁴ (https://www.climond.org/BioclimRegistry.aspx#BioclimFAQ). WWF Ecoregion classifications were used to categorize sampling locations into biomes (https://www.worldwildlife.org/biome-categories/terrestrial-ecoregions).

Data Records

All data are available via figshare¹⁷. Raw nematode abundance data (6,825 samples) are available as a csv file: "nematode_full_dataset_wBiome.csv". Sample IDs 20001–20066 are samples not present in our related work⁶. Abundance data aggregated into 30 Arc-seconds pixels (1,933 unique locations), combined with environmental covariate data are available as a csv file: "nematode_abundance_aggregated_wCovar.csv". Full metadata, including descriptions, units, and source information, of all global covariate layers are available as a csv file: "metadata.csv".

Technical Validation

Soil nematode abundances are highly variable within and across terrestrial biomes⁶. On average, the number of nematodes per 100 g dry soil is in the few hundred – few thousand range (median = 859, mean = 2,671), although the highest recorded abundances exceed 20,000 nematodes per 100 g dry soil. Across biomes, bacterivores are the most abundant trophic group and predatory nematodes the least abundant (Table 1). Overall, the highest abundances are observed in tundra (median = 2,695 nematodes per 100 g dry soil), temperate broadleaf forest (median = 2,119) and in boreal forest (median = 2,016) soils. The lowest abundances are observed in Mediterranean forest (median = 374), flooded grasslands (median = 124), Antarctic (median = 89) and hot desert

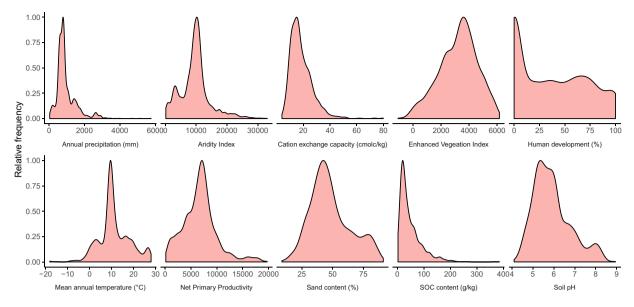


Fig. 5 Assessment of the representativeness of the dataset in multivariate environmental space. The map displays the percentage of pixels that fall within the convex hulls of the first 17 principal component spaces (collectively covering >90% of the sample space variation).

.....

(median = 44) soils (Fig. 3, Table 2). We stress that these numbers slightly differ from the values reported in our accompanying paper⁶, where we reported the aggregated pixel median values.

As with any global ecological dataset, combining data from many researchers across the world, there is inherent variation in the data. Also, the different nematode extraction methods may vary in their efficiencies^{25,26}. This underscores the need for large datasets for global scale analyses of ecological patterns. When a sufficiently large sample size allows to detect strong patterns through this statistical noise, we can be confident that a biological pattern exists⁶. As a consequence, there may be limitations to the use of the dataset at finer scales. Yet, by subsetting the dataset by extraction method or region, for example, it can serve as a starting point for local scale studies.

Environmental representativeness of the dataset. To evaluate the comprehensiveness of the dataset, we explored the environmental conditions that the sampling locations represent. Across individual environmental variables, the samples represent a wide range of environmental conditions (Fig. 4). To gain spatial insight into the environmental representativeness of the dataset, information that is important when comparing observations across spatial scales, we evaluated how the multidimensional environmental space covered by the dataset compares to the global environmental space. To do so, we used a similar approach as in our previous work⁶. First, we set out to reduce the computational load, as exploring the full stack of 73 global environmental covariate layers across ~210 million terrestrial pixels would require exorbitantly large computing power. To this end, we transformed the set of global environmental covariate layers into Principal Component (PC) space. We reduced the number of selected PCs to 17, collectively explaining more than 90% of variation. Next, we assessed the proportion of the world's terrestrial pixels falling within convex hulls of the 136 bivariate combinations of the 17 PCs. The resulting map provides a spatially-explicit depiction of the representativeness of the dataset, showing that the majority of the terrestrial pixels fall within these convex hulls, with most of the outliers existing in arid regions such as the Sahara and Arabian Deserts, and in sub-arctic regions such as the far north of Canada and Russia (Fig. 5).

Code availability

Code is available via https://github.com/hooge104/2020_global_nematode_dataset.

Received: 5 November 2019; Accepted: 2 March 2020; Published online: 26 March 2020

References

- 1. Crowther, T. W. et al. The global soil community and its influence on biogeochemistry. Science 365, eaav0550 (2019).
- Crowther, T. W., Boddy, L. & Jones, T. H. Species-specific effects of soil fauna on fungal foraging and decomposition. *Oecologia* 167, 535–545 (2011).
- 3. Ferris, H. Contribution of nematodes to the structure and function of the soil food web. J. Nemat. 42, 63-67 (2010).
- Ingham, R. E., Trofymow, J. A., Ingham, E. R. & Coleman, D. C. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. *Ecol. Monogr.* 55, 119–140 (1985).
 - 5. Neher, D. Role of nematodes in soil health and their use as indicators. J. Nemat. 33, 161-168 (2001).
 - 6. van den Hoogen, J. et al. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194–198 (2019).
 - 7. Bahram, M. et al. Structure and function of the global topsoil microbiome. Nature 560, 233–237 (2018).
 - 8. Phillips, H. R. P. et al. Global distribution of earthworm diversity. Science 366, 480-485 (2019).

- 9. Yeates, G. W., Bongers, T., De Goede, R. G. M., Freckman, D. W. & Georgieva, S. S. Feeding habits in soil nematode families and genera-an outline for soil ecologists. J. Nematol. 25, 315-331 (1993).
- 10. Baermann, G. Eine einfache methode zur auffindung von Ancylostomum (Nematoden) larven in erdproben. Geneeskd Tijdschr Ned Indie 57, 131-137 (1917).
- 11. Jenkins, W. R. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Dis. Rep. 48, 692 (1964).

12. Freckman, D. W. & Virginia, R. A. Low-diversity antarctic soil nematode communities: distribution and response to disturbance. Ecology 78, 363-369 (1997)

- 13. Flegg, J. J. M. Extraction of Xiphinema and Longidorus species from soil by a modification of Cobb's decanting and sieving technique. Ann. Appl. Biol. 60, 429-437 (1967).
- 14. Oostenbrink, M. Estimating nematode populations by some selected methods. Nematology 6, 85-102 (1960).
- 15. Whitehead, A. G. & Hemming, J. R. A comparison of some quantitative methods of extracting small vermiform nematodes from soil. Ann. Appl. Biol. 55, 25-38 (1965).
- 16. Seinhorst, J., others. The relation between nematode density and damage to plants. Nematologica 11, 137-154 (1965).
- 17. van den Hoogen, J. et al. A global database of soil nematode abundance and functional group composition. figshare, https://doi. org/10.6084/m9.figshare.c.4718003 (2020)
- 18. Hengl, T. et al. SoilGrids250m: Global gridded soil information based on machine learning. PLoS ONE 12, e0169748 (2017).
- 19. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol 37, 4302-4315 (2017).
- 20. Zomer, R. J., Trabucco, A., Bossio, D. A. & Verchot, L. V. Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. Agr. Ecosyst. Environ. 126, 67-80 (2008).
- 21. Venter, O. et al. Global terrestrial human footprint maps for 1993 and 2009. Sci. Data 3, 160067 (2016).
- 22. Tuanmu, M.-N. & Jetz, W. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling: Consensus land cover. Global Ecol. Biogeogr. 23, 1031-1045 (2014).
- 23. Ruesch, A. & Gibbs, H. K. New IPCC Tier-1 global biomass carbon map for the year 2000, https://cdiac.ess-dive.lbl.gov (2008).
- 24. Kriticos, D. J. et al. CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling: CliMond: climate surfaces for bioclimatic modelling. Methods Ecol. Evol. 3, 53-64 (2012).
- De Goede, R. G. & Verschoor, B. The nematode extraction efficiency of the Oostenbrink elutriator-cottonwool filter method with special reference to nematode body size and life Strategy. *Nematology* 2, 325–342 (2000). 26. Cesarz, S., Schulz, A. E., Beugnon, R. & Eisenhauer, N. Testing soil nematode extraction efficiency using different variations of the
- Baermann funnel method. Soil Org. 91, 61-72 (2019).

Acknowledgements

We are thankful to Walter S. Andriuzzi and Louise E. Jackson for help in the initial phases of this study and for providing data. This research was supported by a grant from DOB Ecology to T.W.C., a grant from the Netherlands Organization for Scientific Research (grant 016.Veni.181.078) to S.G., grants from NSF (OPP 1115245, 1341736, 0840979) to B.J.A., by a Ramon y Cajal fellow award (RYC-2016-19939) to R.C.H., a grant from UNEP & Global Environment Facility to J.E.C., grants from NERC's Soil Security Programme to R.D.B. (NE/M017028/1) T.C. (NE/M017036/1), a grant from FAPEMIG/FAPESP/VALE S.A. (CRA-RDP-00136-10) to L.B.C., through the strategic programme UID/BIA/04050/2013 (POCI-01-0145-FEDER-007569) awarded to S.R.C., a grant from CNPq PROTAX (562346/2010-4) to J.M.d.C.C., a grant from DFG (CRC990) to V.K. and S.S., a grant from the MSHE of Russia (AAAA-A17-117112850234-5) to A.A.K., grants from the Chinese Academy of Sciences (XDB15010402) and the National Natural Science Foundation of China (41877047) to Q.L., grants from the National Natural Science Foundation of China (31330011, 31170484) to W.L., grants from NERC (NE/ M017036/1) to M.M., grants from the Spanish Ministry of Innovation (CGL2009-14686-C02-01/02, CGL2013-43675-P) to J.A.R.M., grant from the Spanish Ministry of Innovation (RYC-2016-19939) to R.C.H., grants from NSF (DEB-0450537, DEB-1145440) to P.M., T.O.P. and K. Powers, grants from the German Academic Exchange Service (PKZ 91540366) and NAFOSTED (106.05-2017.330) to T.A.D.N., by an ARC Discovery project (DP150104199) to U.N.N., by the National Key Research and Development Program of China (2016YFC0502101) and the National Natural Science Foundation of China (31370632) to K. Pan, a ERC Research Council Advanced grant (ERC-Adv 323020 SPECIALS) to W.H.v.d.P, a grant from the Natural Environment Research Council (NERC) to D.G.W., a grant from BAPHIQ (106AS-9.5.1-BQ-B3) to J.-i.Y., a grant from the Russian Foundation for Basic Research (18-29-05076) to A.V.T. The James Hutton Institute receives financial support from the Scottish Government Rural and Environment Science and Analytical Services (RESAS) division. Investigations in Northwest Russia were carried out under state order for IB KarRC RAS and are partially supported by the Russian Foundation for Basic Research (18-34-00849).

Author contributions

J.v.d.H., S.G., D.R. and T.W.C. designed and performed the data analyses. S.G., H.F., W.T., D.A.W., R.G.M.d.G., B.J.A., W.A., W.S.A., R.D.B., M.B., R.C.H., J.E.C., T.C., X.C., S.R.C., R.C., J.M.C.C., M.D., L.B.C., D.D., M.E., B.S.G., C.G., K.H., D.K., P.K., A.K., G.K., V.K., A.A.K., Q.L., W-J.L., M.M., M.M., J.A.R.M., E. Matveeva, E.H.M., E. Mzough, C.M., P.M., R.N., T.A.D.N., U.N.N., H.O., J.E.P.R., K.P., V.P., L.P., J.C.P.S., C.P., T.O.P., K.P., C.W.Q., S.R., S.M., S.S., H.S., A.S., A.V.T., J.T., W.H.v.dP, M.V., C.V., L.W., D.H.W., R.A.W., D.G.W., J.-I.Y., O.S. R.B., Z.F., and A.M.K. contributed data. J.v.d.H., S.G. and T.W.C. wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to J.v.d.H., S.G. or T.W.C.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/.

The Creative Commons Public Domain Dedication waiver http://creativecommons.org/publicdomain/zero/1.0/ applies to the metadata files associated with this article.

© The Author(s) 2020

Johan van den Hoogen 1,61 , Stefan Geisen 2,61 , Diana H. Wall , David A. Wardle⁴, Walter Traunspurger⁵, Ron G. M. de Goede⁶, Byron J. Adams⁷, Wasim Ahmad⁸, Howard Ferris⁹, Richard D. Bardgett ¹⁰, Michael Bonkowski ¹¹, Raquel Campos-Herrera¹², Juvenil E. Cares¹³, Tancredi Caruso 1⁴, Larissa de Brito Caixeta¹³, Xiaoyun Chen¹⁵, Sofia R. Costa¹⁶, Rachel Creamer⁶, José Mauro da Cunha e Castro¹⁷, Marie Dam¹⁸, Djibril Djigal¹⁹, Miguel Escuer²⁰, Bryan S. Griffiths²¹, Carmen Gutiérrez²⁰, Karin Hohberg²², Daria Kalinkina²³, Paul Kardol ²⁴, Alan Kergunteuil²⁵, Gerard Korthals², Valentyna Krashevska²⁶, Alexey A. Kudrin²⁷, Qi Li²⁸, Wenju Liang²⁸, Matthew Magilton²⁹, Mariette Marais³⁰, José Antonio Rodríguez Martín³¹, Elizaveta Matveeva²³, El Hassan Mayad ³², E. Mzough³², Christian Mulder ³³, Peter Mullin³⁴, Roy Neilson³⁵, T. A. Duong Nguyen^{11,36}, Uffe N. Nielsen³⁷, Hiroaki Okada³⁸, Juan Emilio Palomares Rius³⁹, Kaiwen Pan⁴⁰, Vlada Peneva⁴¹, Loïc Pellissier^{42,43}, Julio Carlos Pereira da Silva ⁶⁴, Camille Pitteloud⁴², Thomas O. Powers³⁴, Kirsten Powers³⁴, Casper W. Quist^{45,46}, Sergio Rasmann 10⁴⁷, Sara Sánchez Moreno⁴⁸, Stefan Scheu^{26,49}, Heikki Setälä⁵⁰, Anna Sushchuk²³, Alexei V. Tiunov⁵¹, Jean Trap⁵², Mette Vestergård⁵³, Cecile Villenave^{52,54}, Lieven Waeyenberge 55, Rutger A. Wilschut², Daniel G. Wright 56, Aidan M. Keith 56, Jiue-in Yang ⁵⁷, Olaf Schmidt ⁵⁸, R. Bouharroud ⁵⁹, Z. Ferji⁶⁰, Wim H. van der Putten ^{2,46}, Devin Routh¹ & Thomas W. Crowther ¹[∞]

¹Department of Environmental Systems Science, Institute of Integrative Biology, ETH Zürich, Zürich, Switzerland. ²Department of Terrestrial Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands. ³Department of Biology and School of Global Environmental Sustainability, Colorado State University, Fort Collins, CO, USA. ⁴Asian School of the Environment, Nanyang Technological University, Singapore, Singapore. ⁵Animal Ecology, Bielefeld University, Bielefeld, Germany. ⁶Soil Biology Group, Wageningen University & Research, Wageningen, The Netherlands. ⁷Department of Biology, Evolutionary Ecology Laboratories, Monte L. Bean Museum, Brigham Young University, Provo, UT, USA. ⁸Nematode Biodiversity Research Laboratory, Department of Zoology, Aligarh Muslim University, Aligarh, India. ⁹Department of Entomology & Nematology, University of California, Davis, CA, USA. ¹⁰Department of Earth and Environmental Sciences, The University of Manchester, Manchester, UK. ¹¹Institute of Zoology, Terrestrial Ecology, University of Cologne and Cluster of Excellence on Plant Sciences (CEPLAS), Cologne, Germany. ¹²Instituto de Ciencias de la Vid y del Vino (Universidad de La Rioja, CSIC, Gobierno de La Rioja), Logroño, Spain. ¹³Department of Phytopathology, Institute of Biological Sciences, University of Brasília, Brasília, Brazil. ¹⁴School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland. ¹⁵Soil Ecology Laboratory, College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing, China. ¹⁶Centre of Molecular and Environmental Biology, University of Minho, Braga, Portugal. ¹⁷Empresa Brasileira de Pesquisa Agropecuária (Embrapa), Centro de Pesquisa Agropecuária do Trópico Semiárido, Petrolina, Brazil. ¹⁸Zealand Institute of Business and Technology, Slagelse, Denmark. ¹⁹Institut Sénégalais de Recherches Agricoles/ CDH, Dakar, Senegal. ²⁰Instituto de Ciencias Agrarias, CSIC, Madrid, Spain. ²¹Crop and Soil Systems Research Group, SRUC, Edinburgh, UK. ²²Senckenberg Museum of Natural History Görlitz, Görlitz, Germany. ²³Institute of Biology of Karelian Research Centre, Russian Academy of Sciences, Petrozavodsk, Russia. ²⁴Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden. ²⁵Laboratory of Functional Ecology, Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland. ²⁶J. F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Göttingen, Germany. 27 Institute of Biology of the Komi Scientific Centre, Ural Branch of the Russian Academy of Sciences, Syktyvkar, Russia. ²⁸Erguna Forest-Steppe Ecotone Research Station, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China.

²⁹School of Biological Sciences, Institute for Global Food Security, Queen's University of Belfast, Belfast, UK. ³⁰Nematology Unit, Agricultural Research Council, Plant Health and Protection, Pretoria, South Africa. ³¹Department of Environment, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain. ³²Laboratory of Biotechnology and Valorization of Natural Resources, Faculty of Science Agadir, Ibn Zohr University, Agadir, Morocco. ³³Department of Biological, Geological and Environmental Sciences, University of Catania, Catania, Italy. ³⁴Department of Plant Pathology, University of Nebraska-Lincoln, Lincoln, NE, USA. ³⁵Ecological Sciences, The James Hutton Institute, Dundee, UK. ³⁶Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam. ³⁷Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia. ³⁸Nematode Management Group, Division of Applied Entomology and Zoology, Central Region Agricultural Research Center, NARO, Tsukuba, Japan. ³⁹Institute for Sustainable Agriculture, Spanish National Research Council, Córdoba, Spain. ⁴⁰Ecological Processes and Biodiversity, Center for Ecological Studies, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China. ⁴¹Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria. ⁴²Landscape Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland. ⁴³Swiss Federal Research Institute WSL, Birmensdorf, Switzerland. ⁴⁴Department of Phytosanitary Defense, Universidade Federal de Santa Maria, Santa Maria, RS, Brazil.⁴⁵Biosystematics Group, Wageningen University, Wageningen, The Netherlands. ⁴⁶Laboratory of Nematology, Wageningen University, Wageningen, The Netherlands. ⁴⁷Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland. ⁴⁸Plant Protection Products Unit, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain.⁴⁹Centre of Biodiversity and Sustainable Land Use, University of Göttingen, Göttingen, Germany. ⁵⁰Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, University of Helsinki, Lahti, Finland. ⁵¹A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia, ⁵²Eco&Sols, University of Montpellier, CIRAD, INRA, IRD, Montpellier SupAgro, Montpellier, France. ⁵³Department of Agroecology, AU-Flakkebjerg, Aarhus University, Slagelse, Denmark. ⁵⁴ELISOL Environnement, Congénies, France. ⁵⁵Plant Sciences Unit, Flanders Research Institute for Agriculture, Fisheries and Food, Merelbeke, Belgium. 56 UK Centre for Ecology & Hydrology, Lancaster Environment Centre, Lancaster, UK. ⁵⁷Department of Plant Pathology and Microbiology, National Taiwan University, Taipei, Taiwan. ⁵⁸UCD School of Agriculture and Food Science, University College Dublin, Belfield, Dublin 4, Ireland. ⁵⁹Research Unit of Integrated Crop Production, Centre Regional de la Recherche Agronomique d'Agadir, Agadir, Morocco.⁶⁰Institut Agronomique et Vétérinaire Hassan II, Campus d'Agadir, Département de Protection des Plantes, Agadir, Morocco. ⁶¹These authors contributed equally: Johan van den Hoogen, Stefan Geisen. ¹²e-mail: johan. vandenhoogen@usys.ethz.ch; s.geisen@nioo.knaw.nl; tom.crowther@usys.ethz.ch