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## RESEARCH ARTICLE

# Management effects on soil nematode abundance differ among functional groups and land-use types at a global scale

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## Abstract

1. Anthropogenic land use is threatening global biodiversity. As one of the most abundant animals on Earth, nematodes occupy several key positions in below-ground food webs and contribute to many ecosystem functions and services. However, the effects of land use on nematode abundance and its determinants remain poorly understood at a global scale.
2. To characterize nematodes' responses to land use across trophic groups, we used a dataset of 6,825 soil samples globally to assess how nematode abundance varies among regional land-use types (i.e. primary vegetation, secondary vegetation, pasture, cropland and urban) and local land-use intensities (i.e. human-managed or not). We also quantified the interactive effects of land use and environmental predictors (i.e. mean annual temperature, annual precipitation, soil organic carbon, soil pH, global vegetation biomass and global vegetation productivity) on nematode abundance.
3. We found that total nematode abundance and the abundance of bacterivores, fungivores, herbivores, omnivores and predators generally increased or were not affected under management across land-use types. Specifically, the most numerically abundant bacterivores were higher in managed than in unmanaged secondary vegetation habitats and urban areas, and herbivores were more abundant in managed than in unmanaged primary and secondary vegetation habitats. Furthermore, the numbers of significant environmental predictors of nematode abundance were reduced and the magnitude and the direction of the predictors were changed under management. We also found that nematode abundance was more variable and less determined by environmental factors in urban than in other land-use types.
4. These findings challenge the view that human land use decreases animal abundance across trophic groups, but highlight that land use is altering the trophic composition of soil nematodes and its relationships with the environment at the global scale.

## KEYWORDS

animal abundance, global scale, human land use, land-use intensity, management, soil community, soil nematodes, trophic groups

## 1 | INTRODUCTION

Species abundance is sensitive to environmental and human-induced changes. Global declines in species abundance have been widely documented, and such declines could cascade onto ecosystem functioning and ultimately human well-being (Bowler et al., 2017; Butchart et al., 2010; Dirzo et al., 2014). Changes in land-use type from natural to managed ecosystems usually result in a decline in abundance of many aboveground taxa (Seibold et al., 2019; Şekercioğlu et al., 2019; Wagner, 2020). Numerous studies have demonstrated that impacts of human land use vary among trophic groups, and those species at higher trophic levels are more threatened (Barnes et al., 2014, 2017; Le Provost et al., 2020; Newbold et al., 2014; Newbold, Bentley, et al., 2020; Purvis et al., 2000; Seibold et al., 2019; Simons et al., 2016; Soliveres et al., 2016). For example, fruit-, nectar-, and invertebrate-feeding birds are disproportionately decreasing under land-use change in tropical forests (Newbold et al., 2014), predacious invertebrates are most heavily affected after the transformation of land use from forests to plantations (Barnes et al., 2014). A global synthesis covering a wide set of animal species concludes that human land use reduces the abundance of carnivores more strongly than animals in lower trophic groups (Newbold, Bentley, et al., 2020). However, all these studies pay attention to aboveground biodiversity, while a comprehensive assessment on potential impacts of human land use on belowground biodiversity remains limited beyond the local scale (but see Johnston, 2019; Wan et al., 2021).

Belowground organisms represent a major fraction of life on Earth and contribute to many critical ecosystem functions and services (Bardgett & van der Putten, 2014; Paul, 2015). As an important part of soil biodiversity, nematodes are the most abundant and functionally diverse animals (Bongers & Bongers, 1998; van den Hoogen et al., 2019). Indeed, nematode species are placed across the entire soil food web and include bacterivores, fungivores, herbivores, omnivores and predators (Neher, 2001; Yeates et al., 1993). Our knowledge of large-scale biogeographic patterns of soil nematodes has increased substantially in recent years (Wu et al., 2011; Nielsen et al., 2014; Song et al., 2017; van den Hoogen et al., 2019; Li, Zhu, et al., 2020). Also, a wealth of studies have shown that nematodes are affected by human land use at the local scale (Bongers et al., 1997; Li, Peng, & Zhao, 2020; Neher, 2010; Pothula et al., 2019; Yeates & Bongers, 1999; Zhao & Wang, 2021). But not all functional groups and taxa respond in the same way to land use changes. For example, large-bodied omnivores and predators at higher trophic levels are reduced in managed than in natural sites, while the small-bodied bacterivores and herbivores at lower trophic levels often show opposite patterns (Bongers et al., 1997; Neher, 2010; Pothula et al., 2019; Yeates & Bongers, 1999). In addition, the physicochemical drivers of nematode abundance differ between functional groups, with bacterivorous and fungivorous nematodes being affected most strongly by soil characteristics, while herbivores are shaped predominantly by vegetation (Liu, Whalen, et al., 2016; Nielsen et al., 2014; van den Hoogen et al., 2019; Yeates & Bongers, 1999). This differential

sensitivity is the basis for nematode community-based soil health assessments (Bongers & Ferris, 1999; Neher, 2001; Yeates, 2003). Yet, all these knowledge are mainly tested in studies conducted at limited geographic scales. It remains unknown whether these trophic groups respond to environmental factors (e.g. climate, soil and vegetation) in a similar way across different land-use types at a global scale.

Based on a global database of soil nematode abundance including trophic group information (van den Hoogen et al., 2019, 2020a), we aimed to test the hypothesis that human land use, particularly increasing land-use intensity will reduce nematode abundance at a global scale with especially strong effects on higher trophic level organisms. We also examined whether the relationships between nematode abundance and environmental factors are consistent among land uses and trophic groups.

## 2 | MATERIALS AND METHODS

### 2.1 | Data collection

#### 2.1.1 | Nematode abundance

This study did not require ethical approval. Nematode data were obtained from van den Hoogen et al. (2020b). This dataset contains global information about soil nematode abundance (number of nematodes per 100g dry soil) and functional group composition (i.e. bacterivores, fungivores, herbivores, omnivores and predators). It is the most comprehensive and up-to-date dataset about soil nematodes at a global scale, which includes 6,825 samples collected in the top 15 cm of soils from all continents and almost all biomes (Figure S1).

#### 2.1.2 | Land uses

As it is a great challenge to gather and standardize detailed land use information of nearly 7,000 samples collected from a wide range of published and unpublished studies (van den Hoogen et al., 2019), we adopted two steps to classify land uses of all soil samples. First, as ecological processes could be mediated by large-scale controls (e.g. the generation of global biomes and realms), we supposed that nematode abundance could be affected by regional differences in land use. Therefore, the land-use type of each soil sample was determined based on a spatial dataset at a relatively coarse resolution relative to nematodes. Specifically, we adopted five regional land-use types, namely primary habitat (undisturbed natural habitat), secondary habitat (recovering, previously disturbed natural habitat), pasture (land used for the grazing of livestock), cropland (land used for crop production) and urban (land converted to dense urban settlement). We labelled each soil sample as one of these five types (i.e. the predominant land-use type) according to a land-use map at 30 arc-seconds ( $\approx 1 \text{ km}^2$ ) resolution (Hoskins et al., 2016). This global dataset is refined from the 0.5° Land-use Harmonization data with

fine-grained climate, land cover, landform and anthropogenic influence layers, making it a meaningful and comparable land-use dataset at a spatial grain relevant to many ecological processes (Hoskins et al., 2016). As this dataset was also validated using PREDICTS, a widely used global database of how local terrestrial biodiversity responds to human impacts (Hudson et al., 2014), findings based on this dataset might be comparable with some other land-use research (Millard et al., 2021; Newbold et al., 2015; Newbold, Oppenheimer, et al., 2020). Additionally, the five classes used here are formerly defined in representative concentration pathways harmonized land-use estimates for land use projections in the future (Hurtt et al., 2011). Therefore, this classification has the potential to connect current patterns with future predictions in land-use research (Hoskins et al., 2016).

Second, we used precise land use information provided by data contributors, which were originally obtained in a binary format (managed or not). The samples were conservatively assigned as unmanaged (no documented or observed direct human disturbance) or managed (more or less disturbed by various human activities like fertilization, tillage, grazing, logging, etc.) (treated as land-use intensity here) within each land-use type (Figure S1). We adopted this simple classification mainly because it is difficult to consistently quantify the intensity across different categories (e.g. fertilization vs. grazing; fertilization with nitrogen vs. with phosphorus) of human activity, although this classification may potentially reduce the difference in land-use intensity among samples. As the land-use type and intensity were obtained from different sources and in different resolutions, we suggest that it is possible to find some unusual combinations of land-use type and intensity. For instance, a regional cropland could have some unmanaged natural forest, and a regional urban area may contain unmanaged countryside. Nevertheless, caution should be exercised in explaining the direct impacts of the land uses adopted in current study, as the actual land-use type and intensity are determined by the local climatic and socio-economic conditions of the sampling time, although the uncertainties might be limited at a global scale (Tuanmu & Jetz, 2014). The factors of land-use type and intensity were further combined as a single variable (i.e. land use index, LUI) (Millard et al., 2021), because models including only LUI were far better than those models with only land-use type or intensity, and were statistically equivalent to the models containing land-use type, intensity, and their interaction (Table S1). Generally, the number of sites was considerable in each LUI level (103–1,721 sites) in our study (Table S2).

### 2.1.3 | Climatic, soil and vegetation variables

The following variables were also compiled by van den Hoogen et al. (2020a). Specifically, annual mean temperature (AMT) and annual precipitation (AP) were originally obtained from WorldClim (version 2; <http://www.worldclim.org>). Soil organic carbon (SOC) and soil pH were extracted from SoilGrids (<https://www.soilgrids.org/>). Vegetation information including global vegetation biomass (carbon density) and

productivity (NDVI, the normalized difference vegetation index) was obtained from Google Earth Engine (<https://developers.google.com/earth-engine/datasets>). All these spatial layers were re-sampled and re-projected to a unified pixel grid at 30 arc-seconds resolution first, and then were used to extract the values of the predictors for each sampling site (van den Hoogen et al., 2020a). We did not consider more variables in this study as other variables are normally highly correlated with the above-mentioned. Moreover, including too many terms in a statistical model may cause overfitting especially when the interactions between predictors are considered (see Section 2.2.2).

## 2.2 | Statistical analyses

### 2.2.1 | Responses of nematode abundance to LUI

General linear mixed-effects models were used to determine the responses of nematode abundance to LUI across trophic groups. Data provider was treated as a random effect to account for potential differences in sampling and analysis methods, and the selection of sampling sites. LUI was considered as a fixed effect. Nematode abundance was log<sub>10</sub>-transformed to improve normality (Millard et al., 2021; van den Hoogen et al., 2019). Likelihood ratio tests suggested that mixed models were indeed far better than models without random terms across trophic groups (Table S3). Pairwise comparisons were performed using R package EMMEANS at the levels of LUI in the mixed models, and *p*-values were adjusted with Tukey's correction (Lenth et al., 2019). We also calculated the percentage difference in nematode abundance among LUI levels, with the unmanaged primary habitat as baseline, to characterize effect sizes. Briefly, fixed effects were randomly simulated based on the variance-covariance matrix in the mixed model, and each fixed effect within each draw was expressed as a percentage of the baseline. Then, median values and 95% confidence intervals (2.5th and 97.5th percentiles) were calculated based on 1,000 simulations for each LUI level (Millard et al., 2021; Newbold et al., 2015).

### 2.2.2 | Interactive effects of LUI and environmental predictors on nematode abundance

As the relationships between nematode abundance and environmental factors could differ among LUI levels, we assessed the effects of interactions between LUI and main environmental factors (including climatic, soil and vegetation variables) on nematode abundance across trophic groups, using linear mixed-effects models with data provider as random variable. Two steps were adopted here. First, we evaluated the relative importance of each environmental factor on abundance through comparing the performance of models including LUI, each predictor, and their interaction based on models' Akaike Information Criterion (AIC) values (i.e. models with a single environmental predictor). Annual precipitation, SOC and vegetation biomass were log<sub>10</sub>-transformed before modelling.

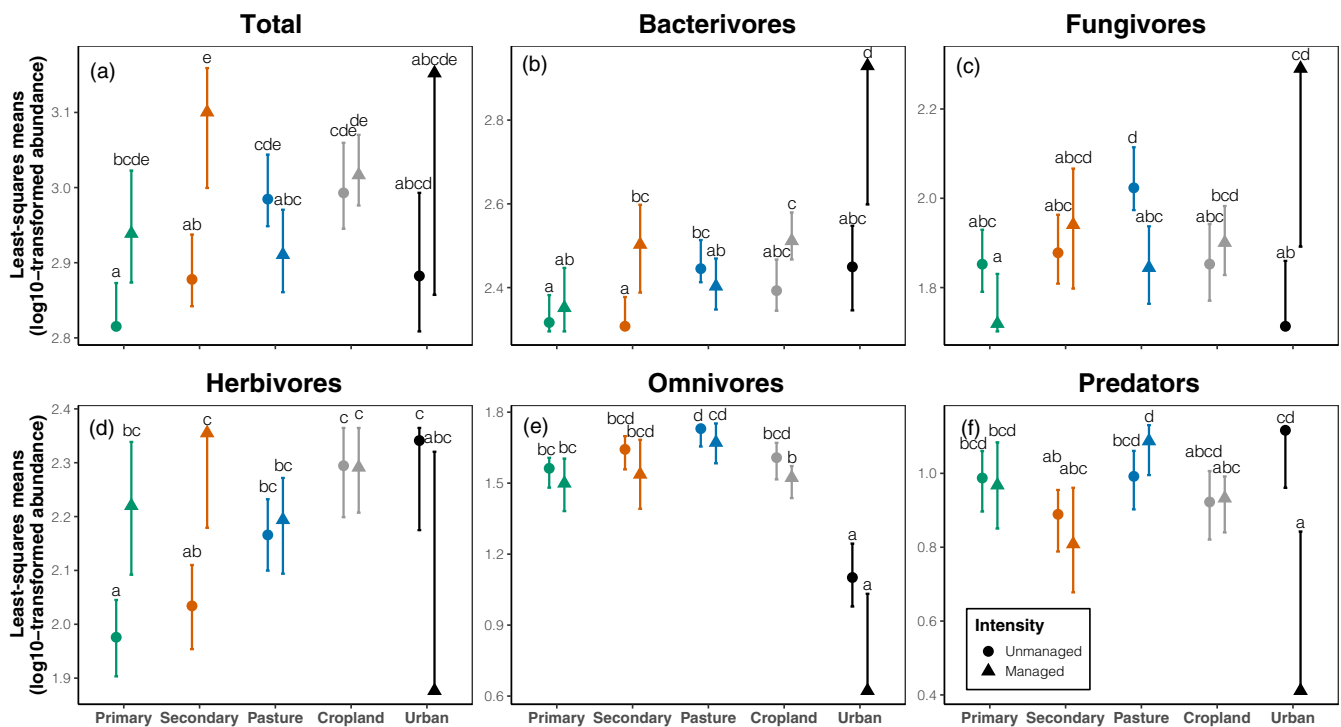
Second, to comprehensively model nematode abundance, we also built and simplified models including all the predictors simultaneously for each trophic group. Specifically, we first built a full model including LUI, all the six predictors, and the interactions between LUI and each predictor. Then, backward stepwise variable selection was conducted to simplify the model. The interaction terms were tested and removed first, and if an interaction term was significant then all its components were retained regardless of their significance as single terms. Fit of the candidate models was compared based on likelihood ratio tests using R package `STATISTICALMODELS` (Newbold et al., 2015; <https://github.com/timnewbold/StatisticalModels>). Furthermore, as interactions between LUI and each predictor were included in the final models (i.e. the relationship between each predictor and abundance depended on LUI level), the significance of slope of each predictor trend was determined for each LUI level using the `emmeans` package based on those best models (Lenth et al., 2019). The impacts of each predictor on nematode abundance across the LUI levels were also predicted and visualized using a randomization procedure. Specifically, we randomly drew fixed effects of those predictors based on the variance-covariance matrix in the best mixed model. Then, these fixed effects were used to predict the abundance on a specific predictor with all other predictors held constant. This procedure was repeated 1,000 times. The median and 95% confidence intervals of the 1,000 predicted abundance values were calculated for visualization for each predictor (Millard et al., 2021; Newbold, Oppenheimer, et al., 2020).

All the analyses were conducted for total abundance (including unidentified individuals) and for the abundance of five trophic groups (i.e. bacterivore, fungivore, herbivore, omnivore and predator) separately in R v.4.0.3 (R Core Team, 2020).

### 3 | RESULTS

#### 3.1 | Soil nematode abundance among LUI levels

Medians of raw abundance were generally higher in managed than in unmanaged soils across trophic groups, especially in those highly human-disturbed habitats such as pasture, cropland and urban ones (Table S4). Mixed models showed that nematode abundance was significantly influenced by LUI across trophic groups (total nematodes,  $F = 10.275$ ; bacterivores,  $F = 8.556$ ; fungivores,  $F = 6.767$ ; herbivores,  $F = 10.605$ ; omnivores,  $F = 17.552$ ; predators,  $F = 5.015$ ; all  $p < 0.001$ ). Least-squares means based on the mixed models suggested that managed primary and secondary lands supported greater total and herbivorous nematodes than the corresponding unmanaged lands (all adjusted  $p < 0.05$ ; Figure 1). Correspondingly, results of our predicted models based on randomization of the fixed effects also demonstrated that abundances of total (percentage increase: primary, 32%; secondary, 67%) and herbivorous (percentage increase: primary, 75%; secondary, 108%) nematodes were higher in primary and secondary habitats in managed than in unmanaged soils (Figure S2). Similarly, more bacterivores were found in managed than



**FIGURE 1** Differences in nematode abundance among land-use types and intensities across trophic groups; (a) total, (b) bacterivore, (c) fungivore, (d) herbivore, (e) omnivore and (f) predator. The least-squares means were calculated based on mixed-effects models. Please notice the bars are based on the statistical properties of differences (not the confidence intervals) of least-squares means that are used to demonstrate whether they differ significantly. Different letters indicate significant difference (Tukey's HSD test,  $p < 0.05$ ).

in unmanaged secondary vegetation (percentage increase: 56%) and urban (percentage increase: 201%). Fungivores were more abundant in urban regions (percentage increase: 270%) but less abundant in pasture lands (percentage decrease: 33%) under management. Less predatory nematodes were detected in managed than in unmanaged urban areas (percentage decrease: 80%;  $p < 0.05$ ; Figure 1; Figure S2).

Cropland supported more total, bacterivorous and herbivorous nematodes than the primary and secondary habitats, when the land-use intensity was not considered in the mixed models (all  $p < 0.05$ ; Figure S3). Secondary habitat, pasture, cropland and urban favoured higher abundances of total, bacterivorous and herbivorous nematodes compared with primary habitats (percentage increase: 25%, 32%, 48% and 27% for total; 7%, 26%, 37% and 64% for bacterivores; 17%, 41%, 81% and 89% for herbivores) (Figure S4). Urban areas decreased omnivorous nematodes by 70%–80% (Figures S3 and S4), but did not affect total, fungivorous and predatory abundance compared with other land-use types due to high variations of abundance in urban regions (Figure S3). We also found that managed lands harboured more total, bacterivores and herbivores but fewer omnivores than unmanaged lands, irrespective of the influence of land-use types (all  $p < 0.05$ ; Figure S5). Generally, management raised the abundance of total, bacterivorous and herbivorous nematodes by 18%, 23%, and 40%, but decreased omnivores by 19% (Figure S6).

### 3.2 | Interactions between LUI and environmental predictors on nematode abundance

Including a climatic, soil or vegetation predictor in a model significantly improved its performance compared with a model that included only LUI across trophic groups (likelihood-ratio test, all  $\chi^2 > 50$ , all  $p < 0.001$ , Table 1). Generally, SOC was the most important predictor of nematode abundance across trophic groups as models containing SOC had relatively small AIC values (ranking first or second among the predictors), although bacterivores and predators were best explained by AMT and NDVI respectively (Table 1).

The results of backward stepwise selection based on models including all the predictors showed that nearly all the fixed terms were retained, except that the interaction between LUI and NDVI was removed for predators (Table S5). The best models showed that the relationships between nematode abundance and environmental predictors differed among LUI levels and trophic groups (Figures 2 and 3; Figures S7–S13). Generally, more significant predictors were found in unmanaged (especially in primary habitats) than in managed areas, and most of the predictors were positively correlated with nematode abundance except that MAT was negatively correlated with nematode abundance (Figure 2; Figure S7). MAT only had a positive effect on abundance under management in certain land-use types for specific trophic groups, such as fungivores in pasture, omnivores in secondary vegetation, pasture, cropland and urban regions, and predators in urban regions (Figure 3; Figure S8). Similarly, the

generally positive effects of AP were changed under management. For instance, bacterivores in cropland, omnivores and predators in both secondary vegetation and urban were all negatively correlated with AP under management (Figure 3; Figure S9). In contrast, the effects of SOC were not always positive across land-use types in unmanaged lands. For example, nematodes in unmanaged pastoral lands were negatively associated with SOC (Figures 3; Figure S10). Soil pH was positively related with nematode abundance in unmanaged areas (excluding fungivores and predators in pastoral areas, and herbivores in secondary lands), but negatively related with nematode abundance in managed lands (excluding fungivores and predators in pastoral areas) (Figures 3; Figure S11). The effects of vegetation biomass varied substantially. For instance, bacterivores and herbivores largely declined, but fungivores and predators mainly increased with increasing vegetation biomass (Figure 3; Figure S12). NDVI generally had positive effects on nematode abundance in most situations, except for fungivores in primary habitats under management (Figure 3; Figure S13).

## 4 | DISCUSSION

Overall, we found that nematode abundance was generally higher in managed than in unmanaged primary and secondary habitats, and was comparable between land-use intensities in other land-use types. This finding did not support our hypothesis that human land use generally reduces nematode abundance at a global scale, and contrasts with findings from aboveground biodiversity (Barnes et al., 2014; Le Provost et al., 2020; Newbold, Bentley, et al., 2020; Seibold et al., 2019; Şekercioglu et al., 2019; Soliveres et al., 2016; Wagner, 2020). Our results also suggest that the numerically dominant bacterivores and herbivores are especially benefiting from human influence such as management and urbanization. Since human activities always introduce additional nutrients (e.g. fertilizers and cover crop) to promote plant growth, the increased substrates are supposed to favour more microbes, thereby boosting the growth of microbial consumers (Gurr et al., 2003; Liu, Chen, et al., 2016; Neher, 2010; Ratnadass et al., 2012; Yeates, 1999). The hypothesis that nematodes at higher trophic levels (e.g. omnivores and predators) would be more negatively affected by management is only observed in urban regions. This could be because the increase in their food resources like microbivorous nematodes (e.g. bacterivores and fungivores) may offset the negative disturbance of human activities on those nematodes at higher trophic levels. In addition, a decrease in the relative abundance of omnivores and predators could be simply due to the fact that opportunistic nematodes (e.g. microbivores) have higher population turnover than those that persist (e.g. omnivores and predators), while the absolute abundance of omnivores and predators do not always decrease under management (Bongers & Ferris, 1999; Ferris et al., 2001).

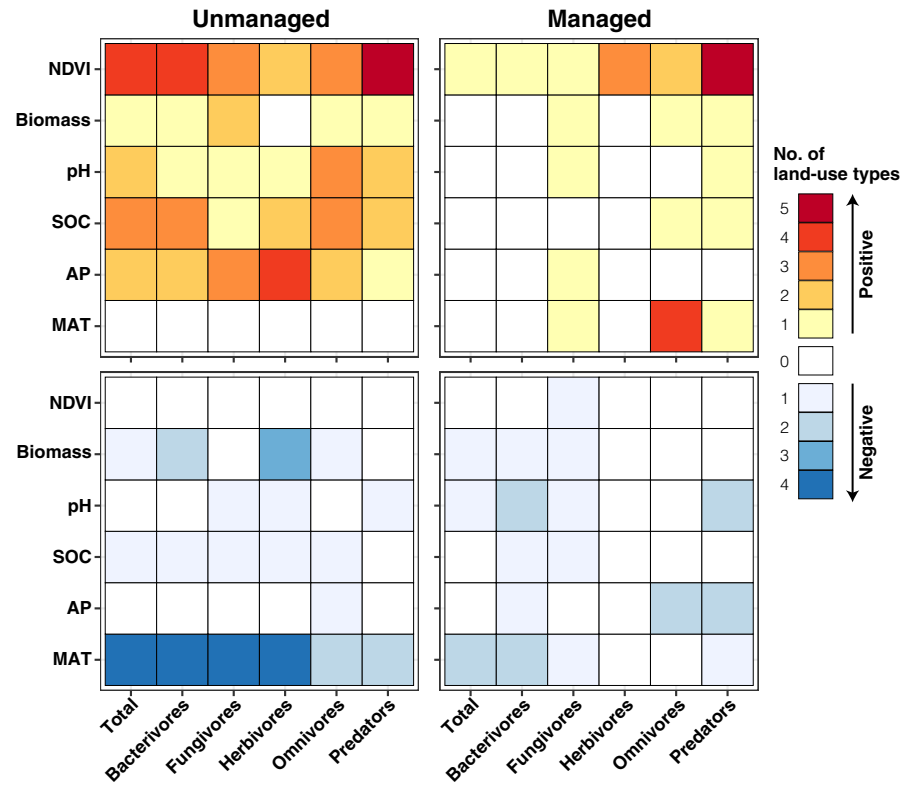
It is worth mentioning that although total nematode abundance was similar between urban and other land-use types or between land-use intensities within urban regions, the trophic composition



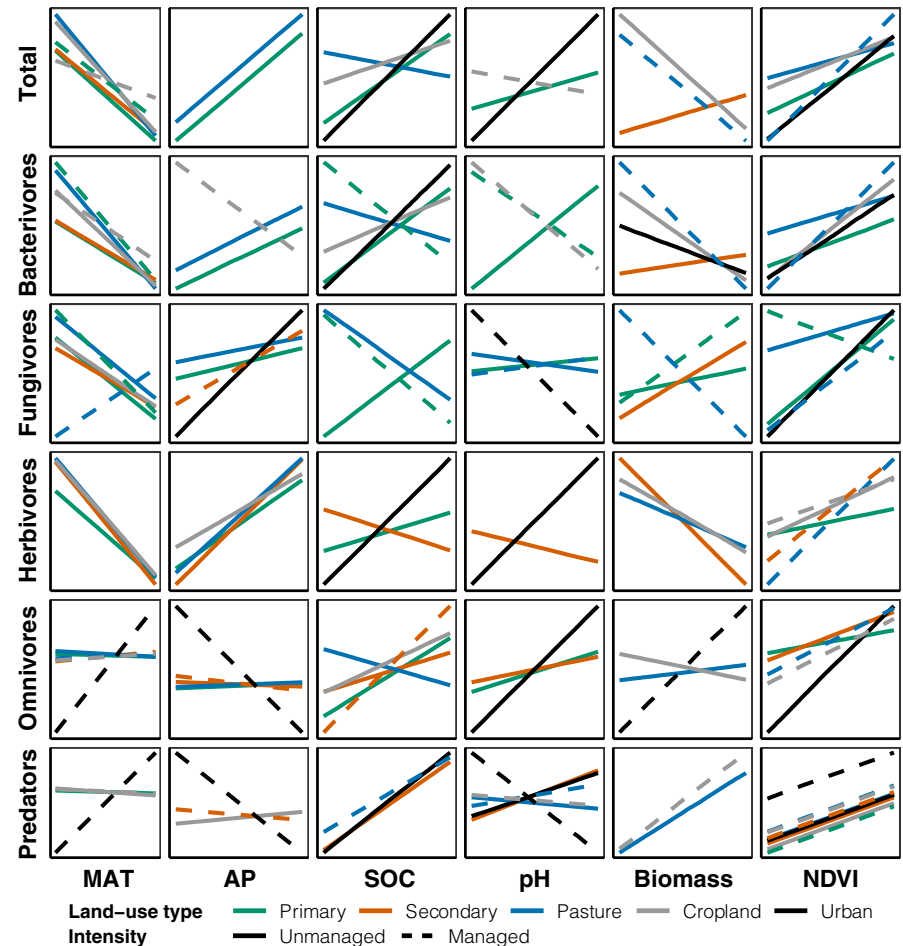
**TABLE 1** Comparisons of mixed models including LUI (a combined variable of land-use type and intensity), a single environmental predictor, and their interaction across trophic groups. The models were sorted according to AIC (Akaike information criterion) values for each trophic group. Models with smaller AIC values are better, and the best models were shown in bold. The statistics ( $\chi^2$ , chi-squared value) obtained from likelihood-ratio tests are used to determine if including a specific predictor is better than using LUI alone in explaining nematode abundance. AMT, annual mean temperature; AP, annual precipitation; biomass, vegetation biomass carbon density; *df*, degrees of freedom; logLik, log-likelihood value; NDVI, the normalized difference vegetation index; SOC, soil organic carbon

Group	Predictor	AIC	$\Delta$ AIC	logLik	$\chi^2$ ( <i>df</i> , <i>p</i> )
Total	<b>SOC×LUI</b>	<b>8,215.78</b>	<b>0.00</b>	<b>-4,085.89</b>	<b>651.18 (10, &lt;0.001)</b>
	AMT×LUI	8,350.37	134.60	-4,153.19	516.58 (10, <0.001)
	AP×LUI	8,407.23	191.46	-4,181.62	459.72 (10, <0.001)
	NDVI×LUI	8,465.45	249.68	-4,210.73	401.50 (10, <0.001)
	pH×LUI	8,491.53	275.76	-4,223.77	375.42 (10, <0.001)
	Biomass×LUI	8,699.43	483.65	-4,327.71	167.52 (10, <0.001)
	LUI	8,846.95	631.18	-4,411.48	-
Bacterivores	<b>AMT×LUI</b>	<b>9,758.97</b>	<b>0.00</b>	<b>-4,857.48</b>	<b>402.93 (10, &lt;0.001)</b>
	SOC×LUI	9,770.56	11.59	-4,863.28	391.33 (10, <0.001)
	NDVI×LUI	9,931.41	172.44	-4,943.71	230.48 (10, <0.001)
	AP×LUI	9,965.73	206.76	-4,960.87	196.16 (10, <0.001)
	pH×LUI	9,990.09	231.12	-4,973.05	171.80 (10, <0.001)
	Biomass×LUI	10,015.65	256.68	-4,985.82	146.25 (10, <0.001)
	LUI	10,141.90	382.93	-5,058.95	-
Fungivores	<b>SOC×LUI</b>	<b>12,366.50</b>	<b>0.00</b>	<b>-6,161.25</b>	<b>281.21 (10, &lt;0.001)</b>
	pH×LUI	12,382.07	15.57	-6,169.03	265.65 (10, <0.001)
	AP×LUI	12,398.48	31.98	-6,177.24	249.24 (10, <0.001)
	NDVI×LUI	12,402.85	36.35	-6,179.43	244.86 (10, <0.001)
	AMT×LUI	12,438.75	72.25	-6,197.38	208.96 (10, <0.001)
	Biomass×LUI	12,481.97	115.47	-6,218.99	165.74 (10, <0.001)
	LUI	12,627.71	261.21	-6,301.86	-
Herbivores	<b>SOC×LUI</b>	<b>13,697.6</b>	<b>0.00</b>	<b>-6,826.8</b>	<b>452.91 (10, &lt;0.001)</b>
	AP×LUI	13,764.24	66.64	-6,860.12	386.27 (10, <0.001)
	AMT×LUI	13,783.35	85.74	-6,869.67	367.16 (10, <0.001)
	pH×LUI	13,832.97	135.37	-6,894.48	317.54 (10, <0.001)
	NDVI×LUI	13,885.36	187.76	-6,920.68	265.15 (10, <0.001)
	Biomass×LUI	13,921.61	224.00	-6,938.8	228.90 (10, <0.001)
	LUI	14,130.51	432.91	-7,053.26	-
Omnivores	<b>SOC×LUI</b>	<b>12,598.20</b>	<b>0.00</b>	<b>-6,277.10</b>	<b>208.80 (10, &lt;0.001)</b>
	AMT×LUI	12,627.14	28.93	-6,291.57	179.86 (10, <0.001)
	AP×LUI	12,668.76	70.55	-6,312.38	138.24 (10, <0.001)
	NDVI×LUI	12,708.19	109.99	-6,332.10	98.81 (10, <0.001)
	pH×LUI	12,708.51	110.30	-6,332.25	98.49 (10, <0.001)
	Biomass×LUI	12,756.32	158.12	-6,356.16	50.68 (10, <0.001)
	LUI	12,787.00	188.80	-6,381.50	-
Predators	<b>NDVI×LUI</b>	<b>13,372.30</b>	<b>0.00</b>	<b>-6,664.15</b>	<b>223.29 (10, &lt;0.001)</b>
	SOC×LUI	13,433.79	61.49	-6,694.90	161.80 (10, <0.001)
	pH×LUI	13,436.08	63.78	-6,696.04	159.51 (10, <0.001)
	AP×LUI	13,449.22	76.92	-6,702.61	146.37 (10, <0.001)
	AMT×LUI	13,487.02	114.72	-6,721.51	108.57 (10, <0.001)
	Biomass×LUI	13,496.47	124.17	-6,726.24	99.12 (10, <0.001)
	LUI	13,575.59	203.29	-6,775.80	-

**FIGURE 2** Number of land-use types where nematode abundance was significantly affected by a predictor across trophic groups in unmanaged and managed areas. The significance of slope of each predictor for each LUI level was determined using the emtrends function in EMMEANS library based on the best mixed-effects models when all the predictors were considered simultaneously. Warm colours show positive effects, and cold colours show negative effects ( $p < 0.05$ ). Darker colours (warm or cold) indicate that nematode abundance was significantly affected in more land-use types. AMT, annual mean temperature; AP, annual precipitation; biomass, vegetation biomass carbon density; NDVI, the normalized difference vegetation index; SOC, soil organic carbon.



**FIGURE 3** Relationships between environmental predictors and nematode abundance among land-use types and intensities. The relationships were determined using a randomization procedure based on the best mixed-effects models for each trophic group and each predictor when all the predictors were considered simultaneously. Only significant predictors are shown in the figure. See Figures S8–S13 for the confidence intervals for each trend.





of soil nematodes changed. For instance, higher numbers of bacterivores and fungivores, but lower numbers of predators were identified in managed than in unmanaged urban regions whereas more bacterivores and herbivores but fewer omnivores were found in urban than in other land-use types. These results suggest that continuous human land use (e.g. urbanization) might change soil nematode communities and possibly their community functioning, for example, through increasing fast-growing taxa at the expense of slow-growing predators. This is supported by tight links between nematode-based soil food web properties, particularly abundances of bacterivorous nematodes and leaching of nitrogen (N) and dissolved organic carbon (C) across land use systems (de Vries et al., 2013). However, the relative importance of increased abundances of bacterivorous nematodes and changes in nematode functional group compositions in driving N losses and reducing C sequestration in urban settings remains to be explored.

Generally, land-use intensity weakens environmental constraints on nematode abundance as fewer predictors were supported in those managed habitats. This is in line with studies showing that human activities such as agricultural management erase environmental constraints on nematode communities at a regional scale (Li, Zhu, et al., 2020; Vazquez et al., 2019). Specifically, management weakened the negative effect of annual mean temperature on nematode abundance, perhaps because land management disturbs the natural relationship between temperature and resource availability (i.e. soil organic matter accumulates at low temperature) (Crowther et al., 2019; van den Hoogen et al., 2019). Management also weakened the positive effect of annual precipitation on nematode abundance, which contrasts the general expectation that nematodes benefit from a high annual precipitation because they inhabit water films (Neher, 2010; Song et al., 2016). This contraction might be caused by management effects that often actively control soil moisture through irrigation. Besides, management weakened the positive effect of SOC on nematode abundance, although high correlations between SOC and nematode abundance across trophic groups were observed in unmanaged lands. This result confirmed that SOC is an important soil resource driving belowground communities (Freckman, 1988; van den Hoogen et al., 2019), but highlights that land management such as carbon input (Liu, Chen, et al., 2016; Page et al., 2020) may lead to considerable variation of SOC in managed soils. Nematodes were generally more abundant in neutral soils than in acidic soils under unmanaged regimes. This finding might be explained by higher bacterial biomass and plant productivity that support bacterivores and herbivores in neutral pH (Chen et al., 2013; Fierer & Jackson, 2006; Kitagami et al., 2020). The positive correlation between NDVI and nematode abundance across trophic groups supports the hypothesis that nematode population sizes increase with plant productivity, especially in unmanaged ecosystems (Cusens et al., 2012; Evans et al., 2005).

The determinants of nematode abundance also differed between trophic groups and land-use types. Specifically, nematodes in high trophic levels (i.e. omnivores and predators) were relatively less affected by climate (e.g. annual mean temperature and annual precipitation) in

unmanaged soils, indicating that these nematodes are more affected by biotic factors that are mediated by resource availability (e.g. SOC and NDVI). We also found that nematode abundance in primary habitats was more determined by environmental factors than those in highly human-disturbed ecosystems such as cropland and urban systems. A potential explanation is that some predictors have not been included in this study, for example, plant species identity and diversity (De Deyn et al., 2004; Penone et al., 2019) or biotic interactions with other species (Liu et al., 2019; Mueller et al., 2016).

Given the abovediscussed alleviation of environmental determinants on nematode abundance in managed soils and/or highly human-disturbed ecosystems, we suppose that the effects of global climate change on the nematode community and its function is currently not predictable. Effect-sizes might become disastrous in future human land use and climate. Nevertheless, further studies with detailed information on land use and nematode community composition obtained by standardized sampling across spatial scales are required to verify our findings and speculations.

In conclusion, our study provides valuable information for understanding and predicting land-use effects on the distribution and potential functioning of soil nematodes at a global scale. Future work should follow our suggestions to increase the efforts started here to better predict and forecast our impact on soils and soil functioning, especially given that the global land area is experiencing rapid land use changes (e.g. land conversions to residential and agricultural areas and increases in land-use intensity).

#### AUTHORS' CONTRIBUTIONS

X.L., H.L., S.G., F.H. and M.L. conceived the ideas and designed the study; S.G. and X.L. collected the data; X.L. analysed the data; X.L., T.L. and S.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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#### CONFLICT OF INTEREST

The authors declare no competing interest.

#### DATA AVAILABILITY STATEMENT

Data available from the Figshare Digital Repository <https://doi.org/10.6084/m9.figshare.c.4718003> (van den Hoogen et al., 2020b).

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