

Agricultural intensification and urbanization negatively impact soil nematode richness and abundance: a meta-analysis

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Abstract

Human activity has extensively transformed the land surface by agricultural intensification and urbanization. In soil, nematodes are the most abundant invertebrates. The effect of human interventions was assessed on overall richness, overall abundance, richness and abundance of nematodes of each trophic group and colonizer-persister (c-p) guild by comparing urban, agriculture and disturbed grassland (DGL) with natural grassland (NGL) and forest ecosystems. Meta-analyses were conducted to generate quantitative summaries from 111 published articles that met the inclusion criteria, 91 expressed data in grams and 20 expressed data in cm³. Results from data expressed per 100g of soil indicated that overall richness was higher in forest than in NGL, DGL, urban, and agriculture ecosystems. The richness of all c-p guilds and of all trophic groups except herbivores was highest in forest ecosystems. In contrast, overall abundance was highest in DGL, agriculture and forest ecosystems. The abundance of c-p 1, c-p 2 and c-p 3 guilds and bacterivores, fungivores and herbivores was highest in disturbed ecosystems, while the abundance of c-p 4 and c-p 5 guilds and predators and omnivores was highest in relatively undisturbed ecosystems. Results from data expressed as nematodes per 100 cm³ of soil indicated that abundance followed a similar pattern, but richness often differed between the two methodologies. These meta-analyses strengthen the concept that human interventions adversely impact both richness and abundance using nematodes as soil health bioindicators.

Key words

c-p guild, Ecology, Ecosystem, Meta-analysis, Richness, Trophic group.

Biodiversity plays pivotal roles in ecosystem functioning and provision of ecosystem services that are crucial to human well-being. These services include providing food and water; managing floods, pests, and diseases; and supporting photosynthesis, nutrient cycling, soil formation, and crop pollination that sustain all other services (Millennium Ecosystem Assessment (MEA), 2003). Unfortunately, modern human civilization occurs at the expense of biodiversity. Land transformation is the principal driving force for biodiversity loss. Human activity has extensively transformed the land surface by agricultural intensification and urbanization

(Vitousek et al., 1997). Urbanization and agricultural practices such as burning, tillage, fertilizer applications, and mono-cultural cropping practices affect below-ground biodiversity and its functions including decomposition, nutrient cycling, bioremediation, and pest and disease regulation (Giller et al., 1997). Despite its diverse benefits, biodiversity in soils is understudied compared to above-ground biodiversity.

Soil is a dynamic system in which organisms interact with each other and form complex food webs (Hunt and Wall, 2002). Nematodes are at the central place in the soil food web because they represent

Table 1. Heterogeneity statistics for the summary effect sizes per 100 g and per 100 cm³ of soil.

Summary effect	100 g			100 cm ³		
	Q_i	P_{hetero}	I^2	Q_i	P_{hetero}	I^2
Overall richness	740.37	0.000	23.37	49.75	0.103	12.42
Overall abundance	525.42	0.007	2.67	320.94	0.000	10.28
Richness of c-p 1	347.88	0.000	8.50	129.66	0.000	66.24
Richness of c-p 2	486.97	0.000	15.43	79.06	0.000	34.16
Richness of c-p 3	453.61	0.000	32.25	147.73	0.000	73.73
Richness of c-p 4	520.05	0.000	29.18	42.39	0.357	7.62
Richness of c-p 5	390.74	0.001	4.56	54.84	0.025	17.00
Abundance of c-p 1	553.15	0.009	2.43	330.58	0.000	6.07
Abundance of c-p 2	422.77	0.028	2.57	186.77	0.000	27.30
Abundance of c-p 3	1,299.77	0.000	2.07	224.18	0.000	43.86
Abundance of c-p 4	609.75	0.000	13.95	70.48	0.088	9.27
Abundance of c-p 5	730.70	0.000	9.33	159.32	0.000	14.05
Richness of bacterivores	584.92	0.000	17.00	76.29	0.000	29.57
Richness of fungivores	392.01	0.000	18.47	105.16	0.000	57.06
Richness of herbivores	358.48	0.000	15.42	69.50	0.000	37.84
Richness of predators	267.55	0.000	18.34	50.88	0.061	14.51
Richness of omnivores	446.01	0.000	18.48	48.12	0.135	11.56
Abundance of bacterivores	519.91	0.001	3.80	396.91	0.000	9.81
Abundance of fungivores	645.08	0.034	1.61	357.16	0.000	17.18
Abundance of herbivores	762.77	0.015	1.62	430.30	0.001	3.92
Abundance of predators	768.10	0.000	6.72	144.93	0.000	18.25
Abundance of omnivores	747.91	0.000	11.09	344.69	0.000	12.77

Notes: Q_i , total observed variation among studies, P_{hetero} , probability of true variation among studies; I^2 , the proportion of true observed variation.

multiple trophic levels including primary, secondary, and tertiary consumer levels (Yeates et al., 1993). The structure of a nematode community provides good information on the condition of the soil food web since nematodes are specific in their food sources and are most abundant in all habitats where decomposition occurs (Bongers and Bongers, 1998). Yeates et al. (1993) assigned nematodes to different trophic groups such as bacterivores, fungivores, herbivores, predators, and omnivores based on their feeding habits. Bacterivores, fungivores, and herbivores are considered as nematode trophic groups in the lower hierarchy of the soil food web

and predators and omnivores are considered as nematode trophic groups in the higher hierarchy of the soil food web (Yodzis, 2001). Nematode trophic interactions contribute to regulating nutrient dynamics in soil. Bacterivores and fungivores promote N and C mineralization by feeding on decomposing bacterial and fungal biomass. Nematode trophic groups in the higher hierarchy of the soil food web maintain ecological balance between decomposition and mineralization by regulating bacterivores and fungivores (Ingham et al., 1985). In addition, predators act as biocontrol agents by feeding on plant feeding nematodes (Bilgrami and Brey, 2005).

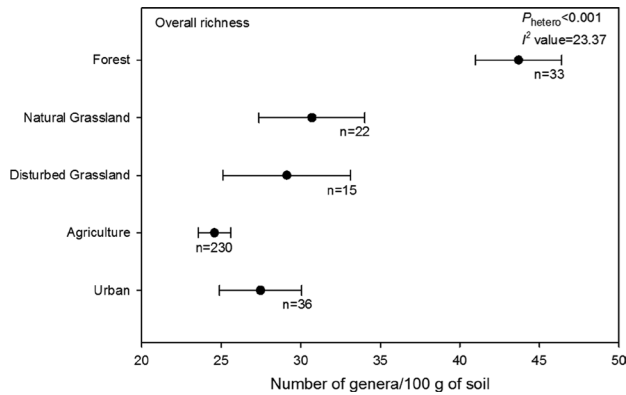


Figure 1: Effect of ecosystem on genus-level nematode richness. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing overall richness of nematodes per 100 g of soil in different ecosystems. Letter n is the number of studies reporting data at each ecosystem. $P_{hetero} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels.

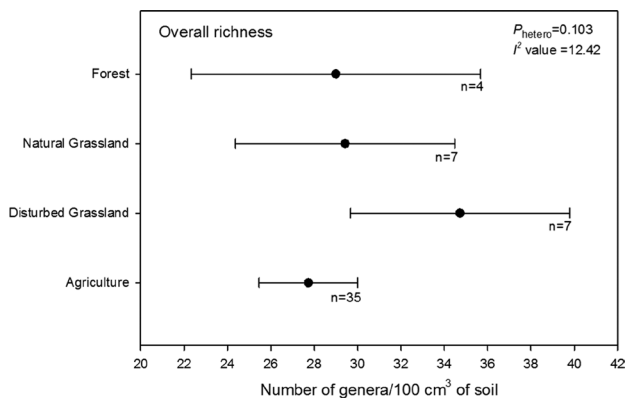


Figure 2: Effect of ecosystem on genus-level nematode richness. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing overall richness of nematodes per 100 cm³ of soil in different ecosystems. Letter n is the number of studies reporting data at each ecosystem. $P_{hetero} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels.

Bongers (1990) developed a colonizer-persister (c-p) scale for nematodes by allocating the nematode taxa to one of five c-p groups ranging from colonizers (c) with a c-p value 1 to persisters (p) with a c-p value 5 through intermediate values based on their life history characteristics and survival strategies. Nematodes with small size, short life span, and high fecundity are assigned to c-p 1, whereas those with the longest-lived nematodes, low fecundity, and slow in development are placed in c-p 5 (Bongers, 1990). Many useful indices for nematode faunal analysis have been developed based on trophic groups and c-p scale. Consequently, nematodes can be used as indicators of structure and function of soil food webs and overall ecosystem conditions (Ferris et al., 2001).

A plethora of published literature exists on how different ecosystems affect the abundance (number of nematodes) and richness (number of taxa) of nematodes. However, there is no single consensus about the pattern of nematode abundance and richness in different ecosystems across the published literature. Some authors have reported that richness is high in forest ecosystems and abundance is high in agricultural ecosystems (Yeates and Bongers, 1999; Ferris et al., 2001; Yeates, 2007; Cardoso et al., 2015) but others have stated the converse (Nehrer et al., 2005; Briar et al., 2007; Darby et al., 2007; Kimenju et al., 2009). The existence of a large body of literature with diverse results creates the need to synthesize quantitative summaries in order to draw general conclusions across studies and test key hypotheses regarding patterns and processes governing soil biodiversity. Meta-analysis is a tractable and powerful statistical tool developed to generate a quantitative summary of all the published literature and draw conclusions across multiple studies (Arnqvist and Wooster, 1995). Therefore, meta-analysis was chosen to address this issue.

The specific objective of this study was to assess the influence of agricultural intensification and urbanization on nematode richness and abundance compared to forest and grassland ecosystems through meta-analysis of published literature on a global scale. The richness and abundance of nematodes were compared using different moderator levels or explanatory variables. We hypothesized that overall richness, overall abundance, and richness and abundance of nematodes of each trophic group and c-p guild are greater in forest and natural grassland (NGL) ecosystems compared to urban, agriculture and disturbed grassland (DGL) ecosystems.

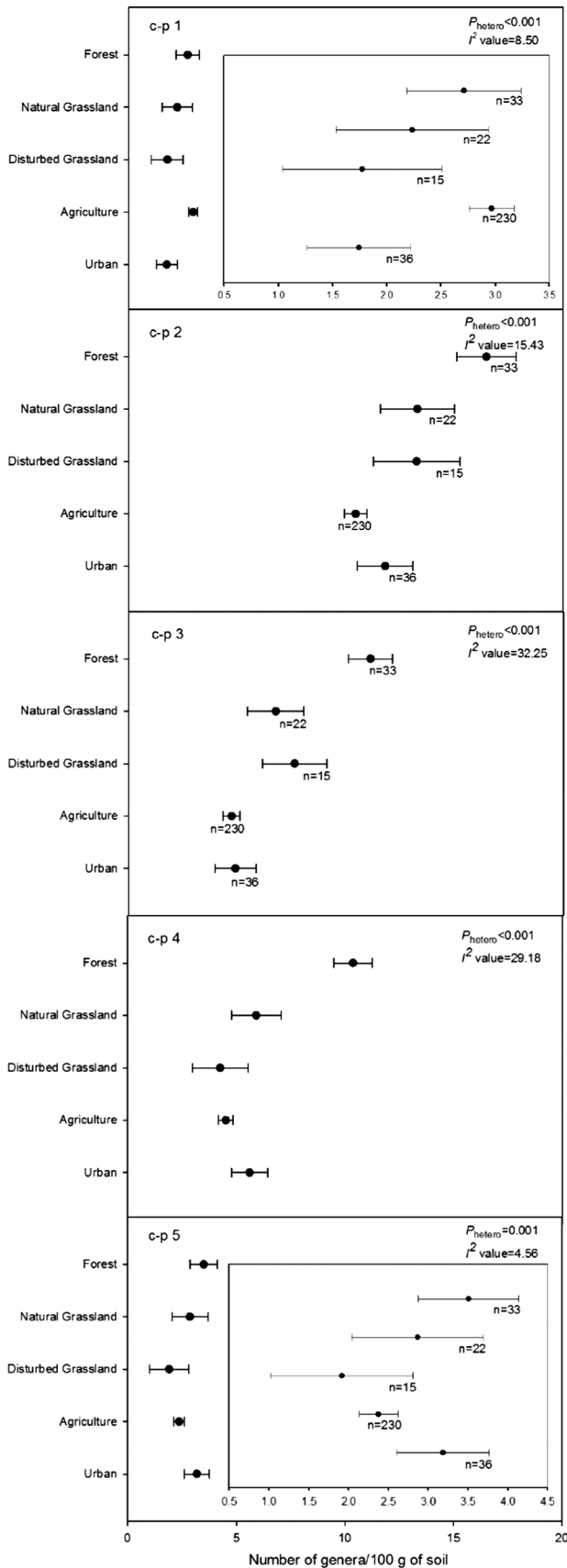


Figure 3: Effect of ecosystem on genus-level nematode richness of each c-p guild. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing richness of nematodes at c-p guilds 1 to 5 per 100 g of soil in different ecosystems. Letter *n* is the number of studies reporting data at each ecosystem. $P_{hetero} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels. The inset in c-p 1 and c-p 5 forest plots is the enlarged view of the respective forest plots.

Materials and methods

Data collection

The Web of Science core database was systematically searched for relevant publications on October 7, 2016, with the following combination of search terms: ('nematode communities' or 'soil nematodes' or 'nematode diversity' or 'nematode abundance' or 'nematode biodiversity') and ('grassland' or 'forest' or 'agriculture' or 'prairie' or 'urban'), which resulted in 1,613 articles. Criteria for including an article in the analysis were: studies were conducted in forest, grassland, urban, or agriculture ecosystems; studies identified nematodes to family or genus level; studies reported mean abundance or richness expressed per grams or cm^3 of soil; soil samples were collected from natural conditions; and studies reported sample size. Criteria for excluding an article were: studies conducted in controlled conditions like microcosms, mesocosms, pots, or greenhouses; studies expressing abundance of nematodes as relative abundance instead of absolute abundance; and studies reporting data for total free-living nematodes instead of each trophic group. Among the 1,613 articles, 598 relevant articles that contained data on richness and abundance of nematodes in different ecosystems were selected by examining titles and abstracts. Among the 598 articles, 111 articles (Supplementary Material) met the inclusion criteria and were selected for data extraction. Among the 111 articles, 91 expressed data in grams and 20 expressed data in cm^3 . The first 200 articles from a Google Scholar search were examined using the above search terms, which did not produce additional articles. A spreadsheet was constructed by extracting data from each article on authors, title,

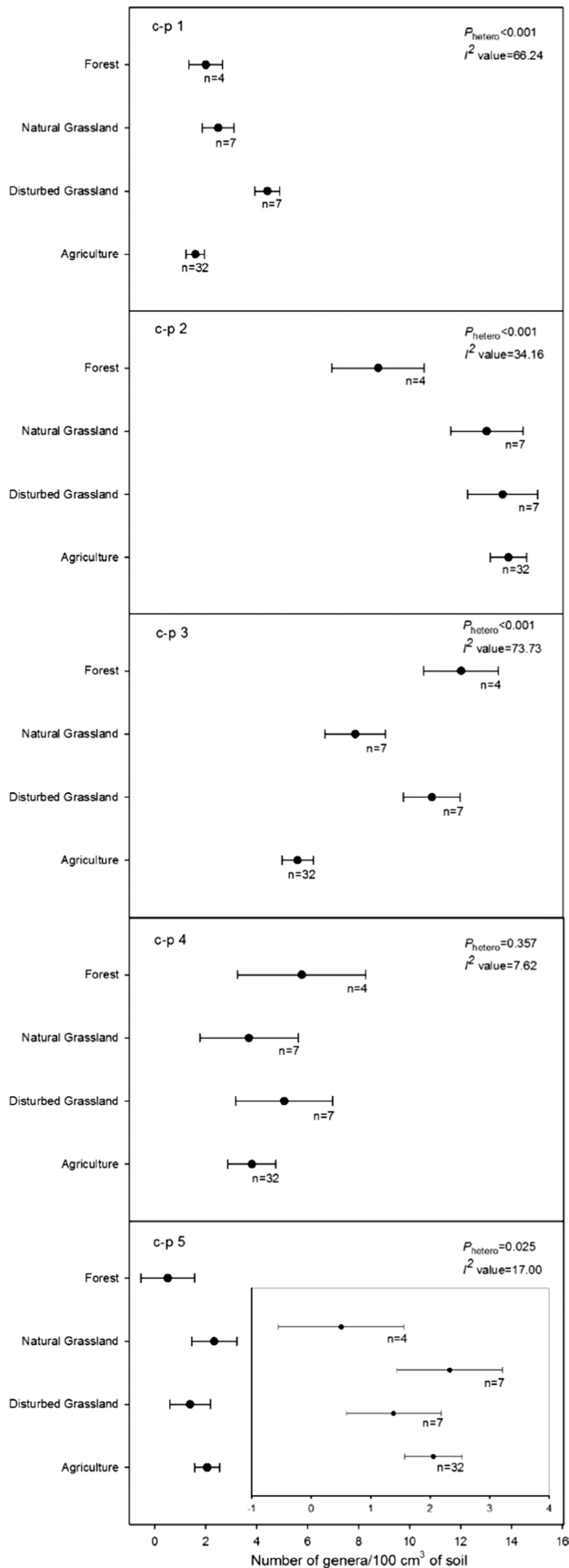


Figure 4: Effect of ecosystem on genus-level nematode richness of each c-p guild. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing richness of nematodes at c-p guilds 1 to 5 per 100 cm³ of soil in different ecosystems. Letter *n* is the number of studies reporting data at each ecosystem. $P_{hetero} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels. The inset in c-p 5 forest plot is the enlarged view of the respective forest plot.

year of publication, unit of soil, richness and abundance of nematodes of each trophic group and each c-p guild, overall richness and overall abundance of nematodes, treatment, sample size, and type of ecosystem. Overall richness and overall abundance of nematodes were calculated by adding the number of genera/families and abundance of nematodes of either all trophic groups or all c-p guilds, respectively. Richness and abundance of nematodes under each trophic group and each c-p guild were calculated by adding the number of genera/families and abundance of nematodes corresponding to each guild and each trophic group, respectively. If there was more than one treatment in an article, they were considered as distinct studies in the meta-analysis. For example, there were two treatments, conventional-conservation tillage and organic-conservation tillage in Sánchez-Moreno et al. (2009), these two treatments were considered as two distinct studies. Based on these criteria, a total of 667 studies were subjected for meta-analysis of which 449 studies conducted in agriculture, 28 conducted in DGL, 74 conducted in forest, 36 conducted in NGL, and 80 conducted in urban ecosystems. Soil units in nematode studies are typically expressed as grams (Briar et al., 2007) or in cm³ (Wang et al., 2006). Therefore, the richness and abundance of nematodes expressed per 100g of soil and 100cm³ of soil were analyzed separately. Richness and abundance of nematodes per 100g of soil were compared across all five ecosystems. However, the data expressed per 100cm³ of soil were compared across only four ecosystems as no urban ecosystem studies using 100cm³ were available. Abundance of nematodes that was not expressed per 100g or cm³ of soil was converted to 100g or cm³ of soil. However, richness of nematodes was not converted because increase in richness cannot be assessed with increase in the quantity of soil.

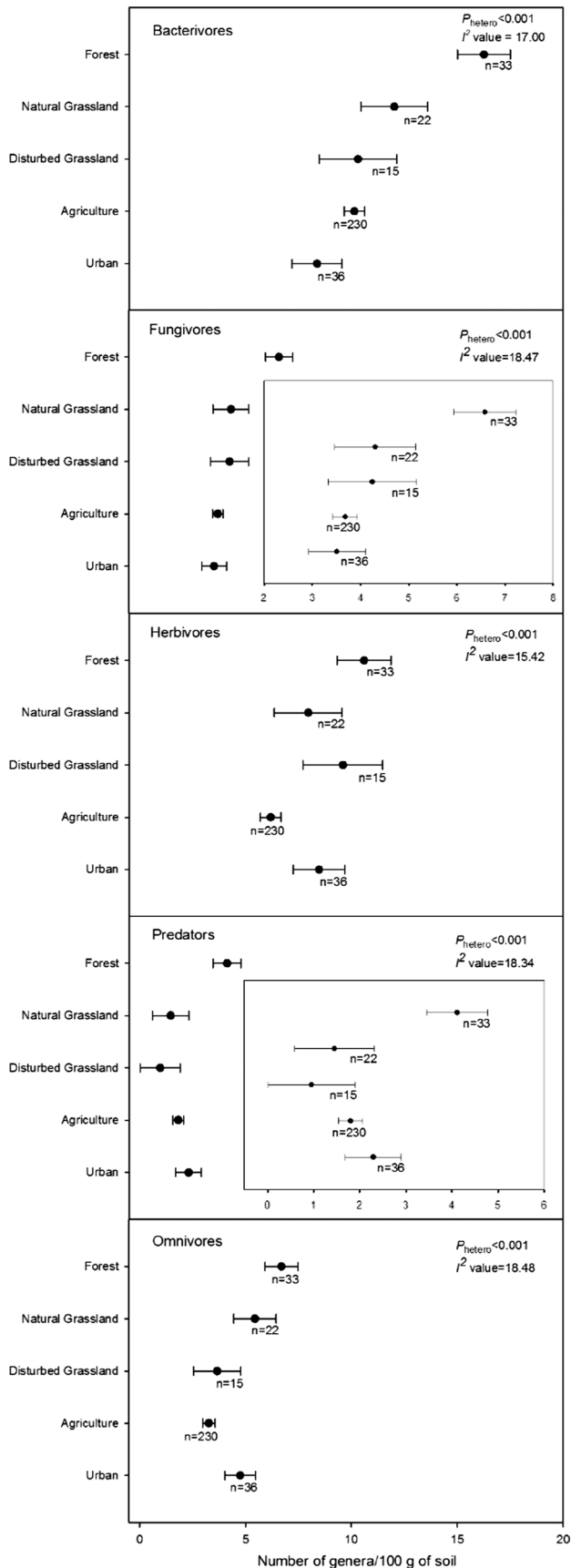


Figure 5: Effect of ecosystem on genus-level nematode richness of each trophic group. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing richness of nematodes of each trophic group per 100 g of soil in different ecosystems. Letter n is the number of studies reporting data at each ecosystem. $P_{hetero} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels. The inset in fungivores and predators forest plots is the enlarged view of the respective forest plots.

Effect size

Effect size typically represents the strength of the relationship between two variables or two groups (treatment and control) but can also refer to the estimate of a single group or value such as richness or abundance of each study (Borenstein et al., 2009). Summary effect size is defined as weighted mean of richness or abundance of all studies in each ecosystem. Meta-analyses were conducted to compare the summary effect sizes of overall richness and overall abundance of nematodes and nematodes of each trophic group and each c-p guild per soil weight and volume basis among different ecosystems such as forest, NGL, DGL, agriculture, and urban ecosystems. Overall richness and overall abundance of nematodes per grams and per cm^3 of soil were considered as four main effect sizes; richness and abundance of nematodes per grams and per cm^3 of soil in each trophic group and each c-p guild were considered as subgroup effect sizes.

Moderator variable

The types of ecosystems, forest, NGL, DGL, agriculture, and urban, were considered as moderator levels. These five ecosystems were assumed to have different regimes of disturbance where forest and NGL are considered less disturbed, whereas agriculture and urban ecosystems are considered highly disturbed from continuous human intervention. The moderator was chosen to determine the influence of disturbance on soil health.

Meta-analysis

The procedures and terminology of Borenstein et al. (2009) were followed in this analysis. Comprehensive meta-analysis (CMA) software was used to estimate

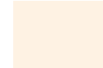
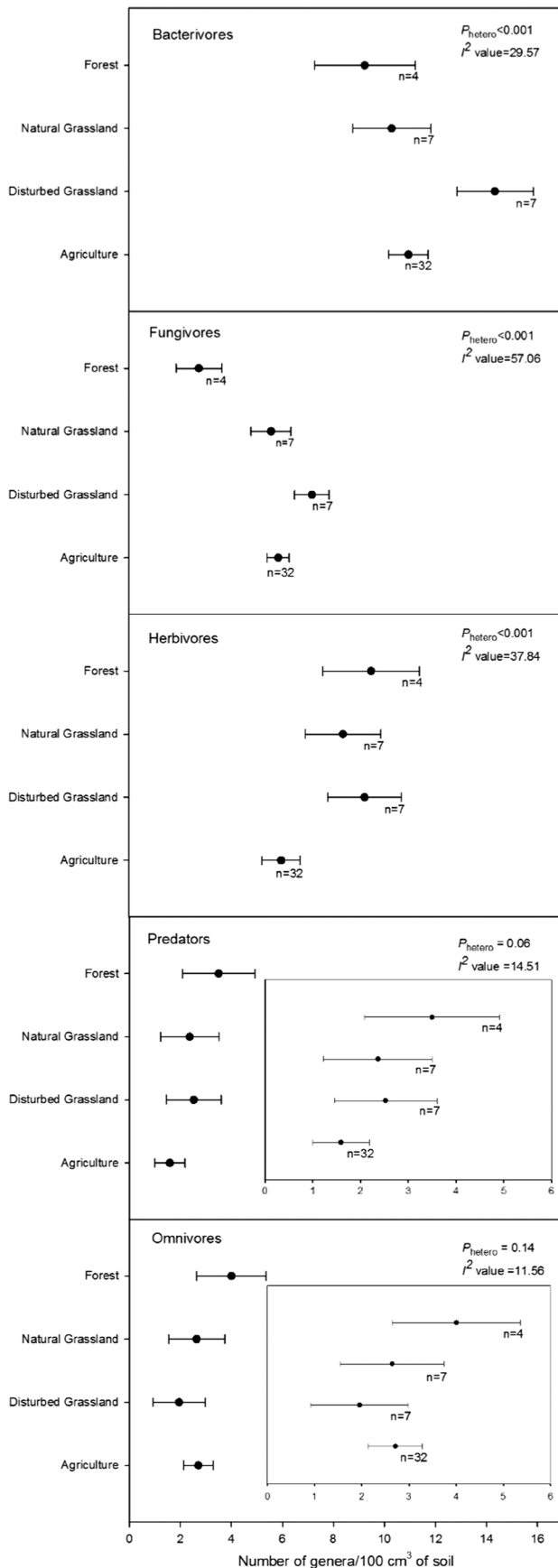


Figure 6: Effect of ecosystem on genus-level nematode richness of each trophic group. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing richness of nematodes of each trophic group per 100cm³ of soil in different ecosystems. Letter *n* is the number of studies reporting data at each ecosystem. $P_{hetero} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels. The inset in predators and omnivores forest plots is the enlarged view of the respective forest plots.

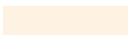
effects of different levels of moderator on nematodes based on their confidence intervals, P_{hetero} values, Q statistics, and I^2 values where Q is heterogeneity, and I^2 is a measure of inconsistency across the studies (Version 3, Biostat, Englewood, NJ, USA; 2014). Random effects model was used rather than fixed effects model for meta-analyses as it considers within-study variance along with between-studies variance. Each study was weighted by the inverse of non-parametric variance. Non-parametric variance was calculated using the formula $1/n$, where n is the sample size adjusted by using the following formula:

$$V = (1/n \times (1 + (t-1) \times 0.5)) \times (m/t)^{0.5},$$

where m is the number of studies in a paper; and t the number of time-points within a year (Borenstein et al., 2009, equation 24.6). Studies within a paper are generally considered as not independent (Mengersen et al., 2013), therefore, studies were down-weighted by a factor of $m^{0.5}$, (assuming 0.1 correlation among studies). After estimating different summary effects using CMA, the results were plotted in forest plots using SigmaPlot version 13.0 (Systat Software, San Jose, California). The summary effects along with their confidence intervals (CIs) from the meta-analyses were graphically depicted in forest plots.

Heterogeneity

Q is a weighted squared deviation used to evaluate heterogeneity, defined here as real differences among summary effect sizes. It separates observed variation from true variation. Total variation ($Q\ddagger$) consists of Q_w (expected variation, within-study variation, or



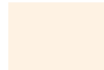
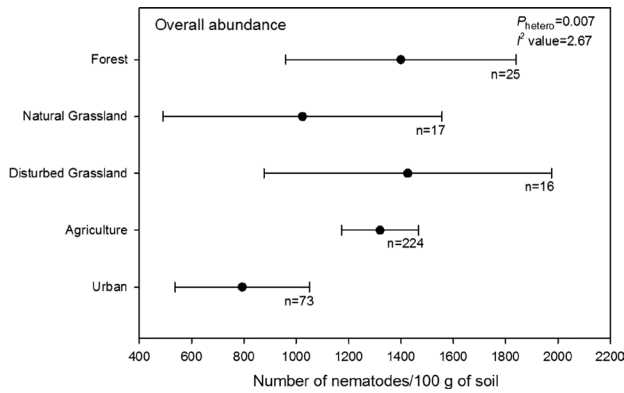


Figure 7: Effect of ecosystem on genus-level nematode abundance. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing overall abundance of nematodes per 100 g of soil in different ecosystems. Letter n is the number of studies reporting data at each ecosystem. $P_{\text{hetero}} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels.

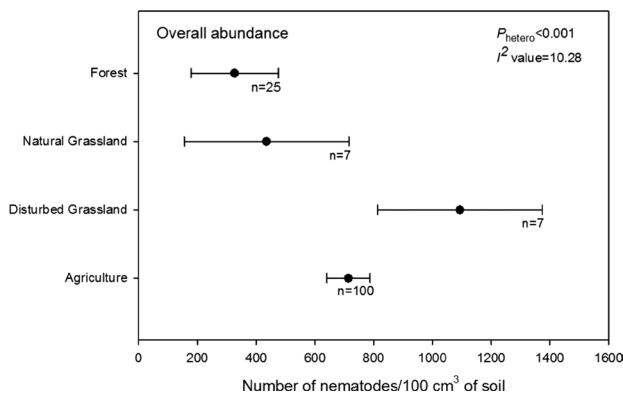


Figure 8: Effect of ecosystem on genus-level nematode abundance. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing overall abundance of nematodes per 100 cm³ in different ecosystems. Letter n is the number of studies reporting data at each ecosystem. $P_{\text{hetero}} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels.

sampling error) and Qm (excess variation, between-study variation) (Borenstein et al., 2009). I^2 is an estimate of the ratio of heterogeneity to total variation across the observed effect sizes (Higgins and Thompson, 2002; Huedo-Medina et al., 2006). It is the proportion of total variation due to heterogeneity in true effect size. I^2 is computed as $100 \times (Qt - df) / Qt$ %, where degrees of freedom (df) measures within-study variation and $Qt - df$ is true heterogeneity or between-study variation. I^2 reflects the percentage of variation due to real differences in outcomes among studies (Borenstein et al., 2009). I^2 values of 25, 50, and 75% may be considered as low, moderate, and high, respectively (Higgins et al., 2003). In meta-analysis, a significant heterogeneity P value (P_{hetero} value < 0.05) or positive I^2 indicates that there were real differences among studies; however, the converse is not true. A non-significant P -value (P_{hetero} value > 0.05) does not indicate that there were no real differences among studies because the non-significance could be due to low statistical power and/or large real dispersion of effect sizes and/or large within-study variance (Borenstein et al., 2009).

Sensitivity analysis and publication bias

A sensitivity analysis was conducted to assess the stability and consistency of the summary effects. The summary effect was recalculated by removing one study at a time. This measures how sensitive the results are to any one study. The potential presence of publication bias was tested using the Begg and Mazumdar rank (Kendall) correlation test and graphically by examining summary effect sizes vs their standard errors in funnel plots (Begg and Mazumdar, 1994; Borenstein et al., 2009).

Results

Heterogeneity test

A total of 44 summary effect sizes were tested in the meta-analysis performed, of which 40 summary effect sizes were significantly heterogeneous ($P_{\text{hetero}} < 0.05$) and all summary effects had positive I^2 values (Table 1). The five summary effect sizes that were not significantly heterogeneous included overall richness, c-p 4 richness and abundance, predator richness and omnivore richness from 100 cm³ soil samples ($P_{\text{hetero}} > 0.05$) (Table 1).

Sensitivity analysis and publication bias

Sensitivity analysis indicates the contribution of each study to the summary effect, which is measured by

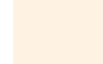
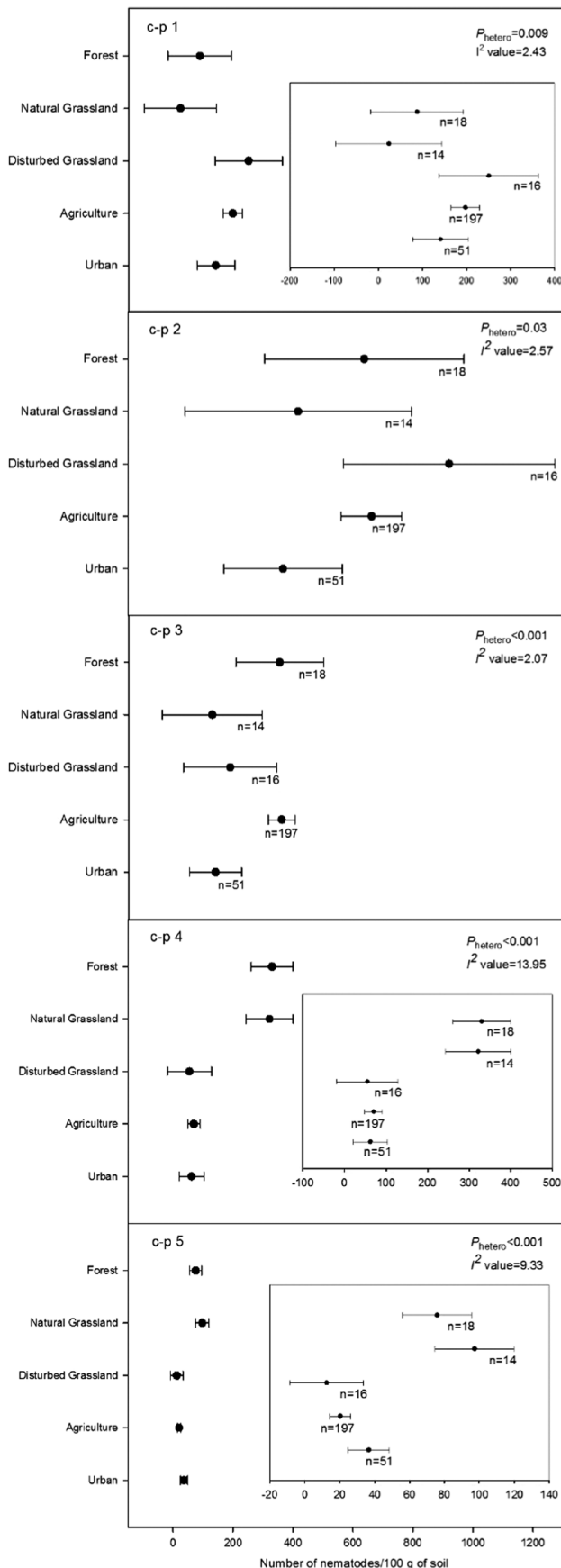


Figure 9: Effect of ecosystem on genus-level nematode abundance of each c-p guild. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing abundance of nematodes at c-p guilds 1 to 5 per 100g of soil in different ecosystems. Letter n is the number of studies reporting data at each ecosystem. $P_{hetero} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels. The inset in c-p 1, c-p 4, and c-p 5 forest plots is the enlarged view of the respective forest plots.

the change in the summary effect in its absence. The summary effect size of overall abundance per 100g of soil was most affected by the removal of treatment B4 at Bohemia in the study conducted by Čermák et al. (2011). This study reduced the summary effect size from 1,208.00 to 1,186.23 (Supplementary Material, Table 1). Similarly, the summary effect size of overall richness per 100g of soil was most influenced by the removal of Renčo and Baležentienė (2015), grassland (control) treatment, reducing the summary effect size from 27.35 to 27.21 (Supplementary Material, Table 2). The summary effect size of overall abundance per 100cm³ was most affected by the removal of the Bulluck et al. (2002), cotton-gin trash (harvest) treatment. This study reduced the summary effect size from 649.22 to 634.56 (Supplementary Material, Table 3). The summary effect size of overall richness per 100cm³ soil was most influenced by the removal of the control treatment from Kapagianni et al. (2010) from 28.97 to 28.70 (Supplementary Material, Table 4). These results indicated that no single study changed any of the summary effect sizes to any important degree. Funnel plots did not show any observable patterns between standard errors and point estimate values, indicating no publication bias in this meta-analysis. In addition, the Begg and Mazumdar rank correlation test gave absolute Kendall tau values for all four summary effect sizes of less than 0.22, suggesting no publication bias.

Overall nematode richness expressed per 100g soil was highest in forest compared to NGL, DGL, urban, and agriculture ($P_{hetero} < 0.05$) (Fig. 1). However, the overall richness expressed per 100cm³ of soil was not significantly heterogenous among ecosystems ($P_{hetero} > 0.05$) (Fig. 2). The nematode richness of c-p 2, c-p 3, and c-p 4 guilds per



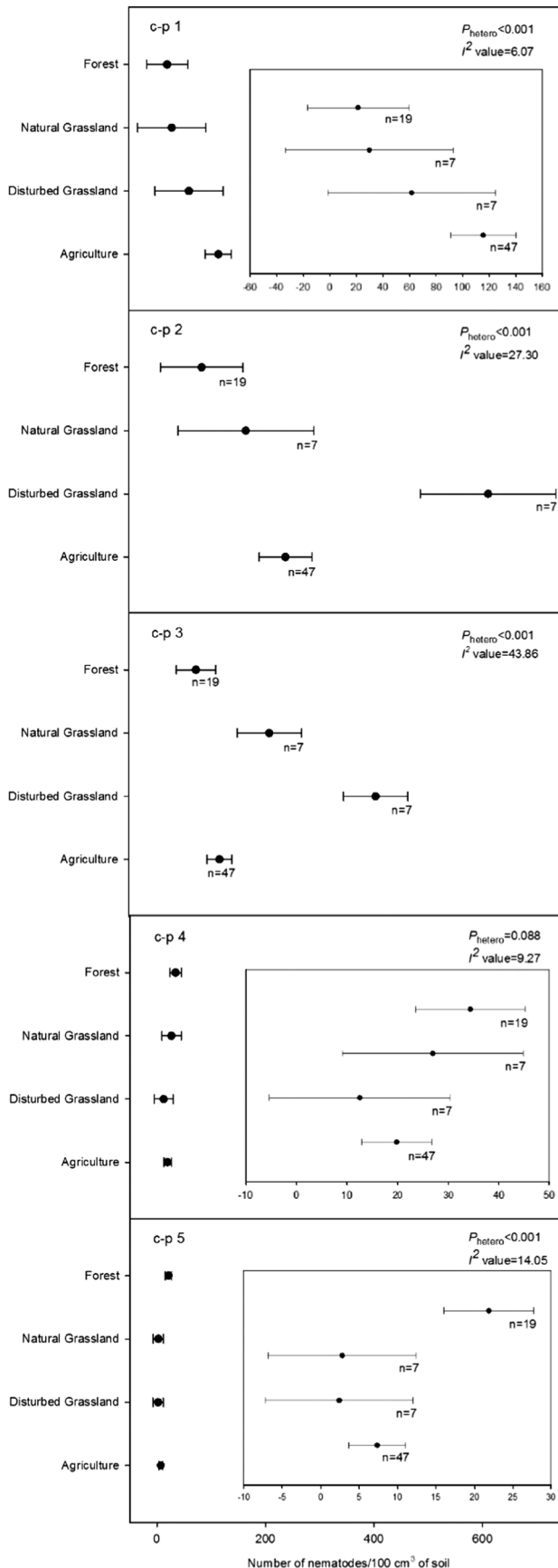


Figure 10: Effect of ecosystem on genus-level nematode abundance of each c-p guild. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing abundance of nematodes at c-p guilds 1 to 5 per 100 cm³ of soil in different ecosystems. Letter *n* is the number of studies reporting data at each ecosystem. $P_{hetero} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels. The inset in c-p 1, c-p 4, and c-p 5 forest plots is the enlarged view of the respective forest plots.

100 g of soil was higher in forest ecosystems than in other ecosystems but richness of c-p 1 nematodes per 100 g of soil was highest in agricultural ecosystems along with forest and NGL ecosystems ($P_{hetero} < 0.05$). The richness of c-p 5 nematodes per 100 g of soil was higher in forest ecosystems than in agriculture and DGL ecosystems ($P_{hetero} < 0.05$) (Fig. 3). On the other hand, the richness of c-p 1 ($P_{hetero} < 0.05$) nematodes per 100 cm³ of soil was higher in DGL ecosystems than in other ecosystems, whereas the richness of c-p 2 ($P_{hetero} < 0.05$) nematodes per 100 cm³ of soil was higher in NGL, DGL and agricultural ecosystems than in forest ecosystems. The richness of c-p 3 ($P_{hetero} < 0.05$) nematodes per 100 cm³ of soil was highest in DGL and forest ecosystems. However, richness of c-p 4 ($P_{hetero} > 0.05$) nematodes per 100 cm³ of soil was not significantly heterogenous among ecosystems. The richness of c-p 5 ($P_{hetero} < 0.05$) guild nematodes per 100 cm³ of soil was higher in agricultural ecosystems than in forest ecosystems (Fig. 4).

The richness of bacterivores, fungivores, and predators per 100 g of soil was higher in forest ecosystems than in the other ecosystems and the richness of omnivores per 100 g of soil was higher in forest ecosystems than in disturbed ecosystems. The richness of herbivores per 100 g of soil was higher in forest ecosystems than in agricultural ecosystems ($P_{hetero} < 0.05$) (Fig. 5). The richness of bacterivores ($P_{hetero} < 0.05$) and fungivores ($P_{hetero} < 0.05$) per 100 cm³ soil was higher in DGL ecosystems, whereas richness of herbivores per 100 cm³ soil was lower in agriculture than the other ecosystems ($P < 0.05$). Richness of predators and omnivores per 100 cm³ soil was not significantly heterogenous among ecosystems ($P_{hetero} > 0.05$) (Fig. 6).

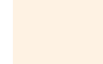
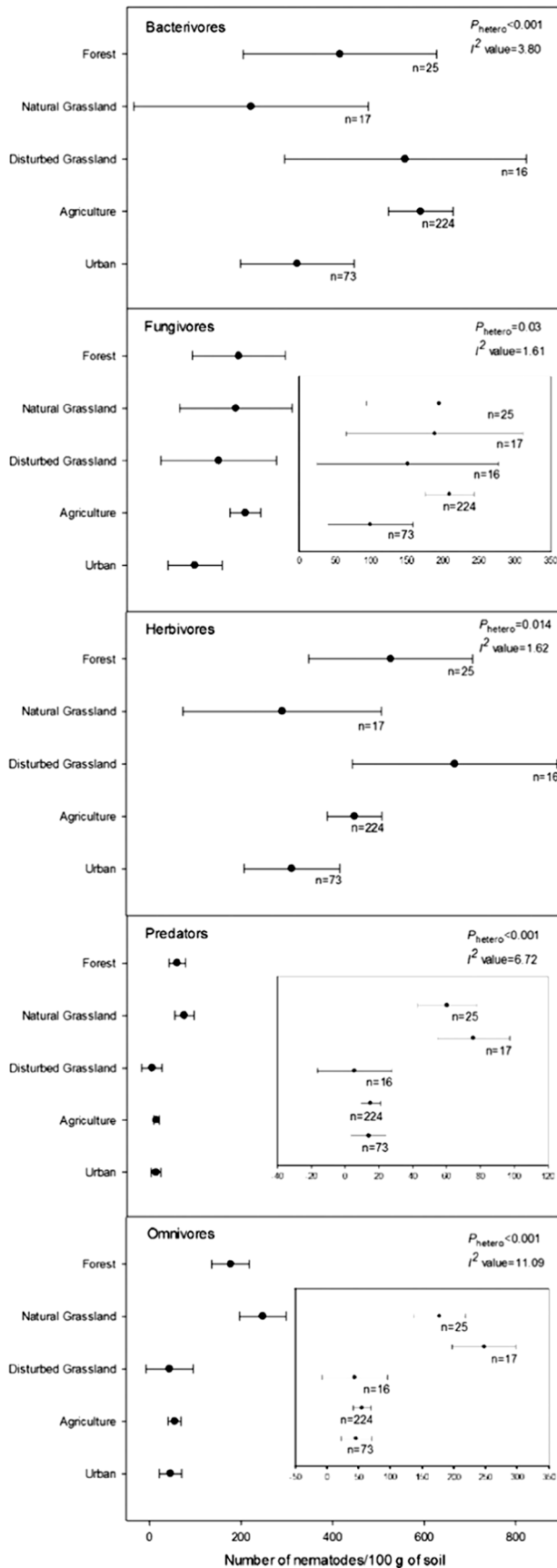
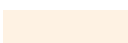


Figure 11: Effect of ecosystem on genus-level nematode abundance of each trophic group. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing abundance of nematodes of each trophic group per 100g of soil in different ecosystems. Letter n is the number of studies reporting data at each ecosystem. $P_{hetero} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels. The inset in fungivores, predators, and omnivores forest plots is the enlarged view of the respective forest plots.

The overall abundance of nematodes per 100g of soil was similar in forest, NGL, DGL, and agricultural ecosystems. However, overall abundance of nematodes per 100g of soil was higher in agricultural ecosystems than in urban ecosystems ($P_{hetero} < 0.05$) (Fig. 7). The overall abundance of nematodes per 100cm³ soil was highest in DGL ecosystems compared to other ecosystems, NGL and forest ($P_{hetero} < 0.05$) (Fig. 8).

The abundance of c-p 1 guild per 100g of soil was higher in agriculture ecosystems than in NGL ecosystems; abundance of c-p 2 guild per 100g of soil was higher in DGL and agriculture ecosystems than in urban ecosystems and abundance of c-p 3 guild per 100g of soil was higher in agriculture ecosystems than in NGL and urban ecosystems. In contrast, the abundance of c-p 4 and c-p 5 guilds per 100g of soil was higher in undisturbed ecosystems than disturbed ecosystems ($P_{hetero} < 0.05$) (Fig. 9). Likewise, the abundance of c-p 1 per 100cm³ soil was higher in agricultural ecosystems than in forest ecosystems. The abundance of c-p 2 and c-p 3 guilds per 100cm³ soil was higher in DGL ecosystems than the other ecosystems, while the abundance of c-p 5 guild per 100cm³ soil was higher in forest ecosystems, which are relatively undisturbed ($P_{hetero} < 0.05$). Abundance of c-p 4 nematodes per 100cm³ soil was not significantly different among ecosystems ($P_{hetero} > 0.05$) (Fig. 10).

The abundance of bacterivores per 100g of soil was higher in agriculture than in NGL and urban ecosystems; abundance of fungivores per 100g of soil was higher in agriculture than in urban ecosystems and abundance of herbivores per 100g of soil was higher in DGL ecosystems than in urban ecosystems. On the other hand, abundance of predators and omnivores per 100g of soil was higher in undisturbed ecosystems than in disturbed ecosystems ($P_{hetero} < 0.05$)



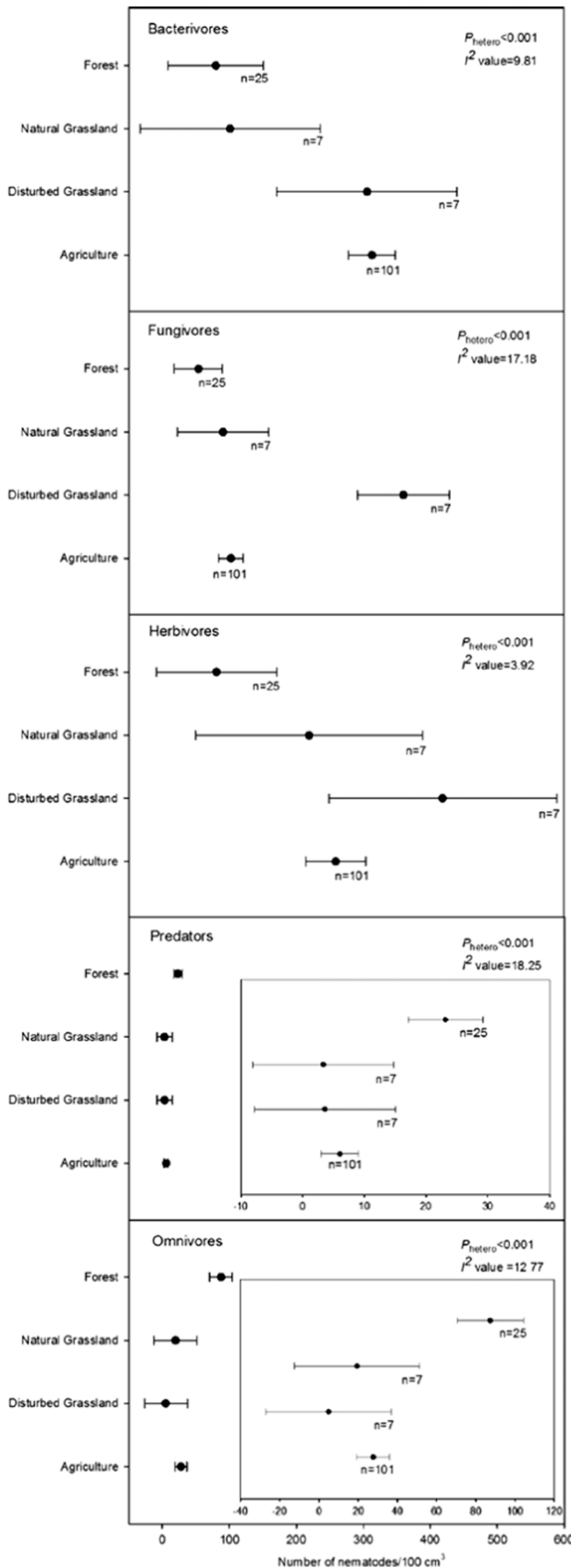


Figure 12: Effect of ecosystem on genus-level nematode abundance of each trophic group. Mean values are the weighted summary effect sizes and the bars represent standard error for comparing abundance of nematodes of each trophic group per 100 cm³ of soil in different ecosystems. Letter *n* is the number of studies reporting data at each ecosystem. $P_{hetero} < 0.05$ is evidence that ecosystem levels differed. I^2 is the percentage of true or real variation among ecosystem levels. The inset in predators and omnivores forest plots is the enlarged view of the respective forest plots.

(Fig. 11). The abundance of bacterivores per 100 cm³ of soil was higher in agriculture and DGL than in NGL and forest ecosystems; abundance of fungi-vores per 100 cm³ of soil was higher in DGL than in forest, NGL and agriculture ecosystems and abundance of herbivores per 100 cm³ of soil was higher in DGL and agriculture than in forest ecosystems. Conversely the abundance of predators and omnivores was higher in forest than other ecosystems ($P_{hetero} < 0.05$) (Fig. 12).

Discussion

Soil nematode assemblages can serve as ecological indicators since different nematode taxa vary in their sensitivity to disturbances in a terrestrial ecosystem (Bongers, 1990; Neher et al., 2005). Extensive research has been conducted on abundance and richness of nematode assemblages in different ecosystems but very few studies have been conducted to compare the impact of disturbances on nematode abundance and richness among two or more ecosystems (Neher et al., 2005; Briar et al., 2007; McSorley and Wang, 2009; Cardoso et al., 2015). Recently, meta-analysis was conducted using the literature published on soil nematodes to analyze soil energy pathways in different ecosystems (Zhao and Neher, 2014) and the effect of organic and inorganic fertilizers on soil nematodes in croplands (Liu et al., 2016). Meta-analysis was conducted to study the collective impact of anthropogenic disturbances on nematode assemblages by comparing five ecosystems with a gradient of human disturbance. Disturbances that are considered anthropogenic include physical disturbances such as burning, tillage, soil solarization, and harvesting; chemical disturbances such as addition of organic amendments

and inorganic fertilizers in agriculture ecosystems; heavy metal pollution; building and road construction in urban settings; and seeding, tillage, harvesting, fertilizer application, and grazing rate in DGL were considered as anthropogenic disturbances. Forests and NGL with little to no direct human intervention were considered as undisturbed ecosystems.

The results from data expressed per 100g of soil show that the overall richness of nematodes was highest in forest ecosystems compared to NGL, DGL, agriculture, and urban ecosystems. These results supported the hypothesis that the richness of nematodes is higher in undisturbed ecosystems than in human-disturbed ecosystems (Wasilewska, 1979; Bongers and Bongers, 1998; Briar et al., 2007; Darby et al., 2007). These results were congruent with the general statement that ecosystems with less or no disturbance support greater richness of soil biota (Hooper et al., 2005) consistent with the results of Hanel (1993), Ivezic et al. (2000), Neher et al. (2005), Brmež et al. (2007), Yeates (2007), Jiao et al. (2008), Cardoso et al. (2012, 2015). High richness in forest points to the stability of the ecosystem.

The richness of nematodes of all c-p guilds was higher in forest ecosystems due to little or no disturbance but the richness of c-p 1 was higher in agricultural ecosystems along with forest and NGL ecosystems. Nematodes in the c-p 1 guild are considered enrichment opportunists as most are bacterial feeders, which are most active in the presence of abundant resources (De Goede et al., 1993). The high richness of c-p 1 taxa in agricultural ecosystems may be due to continuous addition and incorporation of fertilizers and organic matter. After addition of nutrients or organic matter incorporation into the soil, c-p 1 guild nematodes respond immediately and flourish in number due to increased microbial activity, resulting from the newly available nutrients (Ettema and Bongers, 1993). Richness of nematodes in c-p 3, c-p 4 and c-p 5 guilds, which are sensitive to disturbance, was higher in forest ecosystem due to little or no disturbance. Nematodes of higher c-p guilds were found to be sensitive to disturbances (Park et al., 2010; Cardoso et al., 2015). High richness of higher c-p guilds indicates a mature and stable ecosystem (Bongers, 1990, 1999).

The richness of nematodes of all trophic groups except herbivores was highest in forest ecosystems. This result is consistent with the reports of Briar et al. (2007), Jiao et al. (2008), and Kimenju et al. (2009). Forests typically support a greater richness of organisms including nematodes due to the absence of human intervention such as tillage, monocultures, cultivated lawns, and application of fertilizers and amendments. Nematode trophic groups in the higher

hierarchy of the soil food web such as omnivores and predators are particularly sensitive to disturbances (Korthals et al., 1996) and therefore are rich in undisturbed forest ecosystems. The presence of these nematodes maintains ecological balance by regulating nematode trophic groups in the lower hierarchy of the soil food web including plant feeding nematodes (Bilgrami and Brey, 2005).

Overall nematode abundance was similar in all ecosystems except urban ecosystems. Although high nematode abundance in an ecosystem represents high productivity of the ecosystem (Ritz and Trudgill, 1999), the high abundance in DGL and agriculture ecosystems was mostly attributed to high abundance of c-p 2, an indication of more stressful soil food web populated by recalcitrant bacterivores (Ferris et al., 2001). The higher abundance in forest and NGL ecosystems could be contributed by the higher abundance of predators and omnivores, most of which belong to c-p 4 and c-p 5 guilds.

The nematodes of c-p 1, c-p 2, and c-p 3 guilds were similar in all ecosystems, whereas the abundance of nematodes of c-p 4 and c-p 5 guilds was highest in forest and NGL ecosystems. The similar abundance of lower c-p guilds in disturbed ecosystems along with undisturbed ecosystems may be attributed to the incorporation of plant material and fertilizers, which favor microbial activity; thus, microbivorous colonizers with a high reproduction rate dominate these disturbed ecosystems (Bongers, 1990; Freckman and Ettema, 1993; Brmež et al., 2006; Brmež et al., 2007). Moreover, nematodes of lower c-p guilds are tolerant to disturbance (Bongers, 1990). On the other hand, the abundance of nematodes of higher c-p guilds, which are sensitive to disturbances, was highest in undisturbed ecosystems, which might be due to the absence of anthropogenic intervention such as tillage and fertilizer applications (Wasilewska, 1995; Grewal et al., 2011). High abundance of higher c-p guilds indicates mature soil food webs in an ecosystem (Neher, 1999; Yeates and Bongers, 1999).

The abundance of bacterivores, fungivores and herbivores was highest in DGL and agriculture ecosystems, whereas the abundance of predators and omnivores was highest in forest and NGL ecosystems. These results are consistent with the findings of Ivezic et al. (2000), Hanel (1993) and Háněl (2010). The abundance of nematode trophic groups in the lower hierarchy of soil food web is highest in disturbed ecosystems because bacterivores and fungivores with c-p 2 are tolerant and responding to more stressful soil environment (Bongers, 1990). High abundance of herbivores in disturbed ecosystems may be due to lack of omnivores

and predators that potentially feed on herbivores. On the other hand, the high abundance of predators and omnivores in forest and NGL ecosystems may be due to lack of human intervention (Ferris and Ferris, 1974; Wasilewska, 1979, 1995; Hanel, 1993; Cardoso et al., 2012). Perturbations in an ecosystem may increase the abundance of trophic groups in the lower hierarchy of soil food web (bacterivores, fungivores, and herbivores) but decrease the abundance of nematode trophic groups in the higher hierarchy of the soil food web (predators and omnivores), which play a crucial role in regulating the lower groups including herbivores. Therefore, losing these regulators may be detrimental to nutrient cycling dynamics and agricultural management.

Overall richness, overall abundance, and richness and abundance of each c-p guild and each trophic group per 100 cm³ of soil in all four ecosystems were analyzed as no urban ecosystem studies using 100 cm³ were available. Summary effect sizes of overall richness, richness and abundance of c-p 4, predator and omnivore richness were not significantly different (Table 1). The overall abundance, abundance of nematodes of all c-p guilds, and abundance of nematodes of all trophic groups expressed per 100 cm³ of soil followed a somewhat similar pattern as that of 100 g of soil. However, overall richness, richness of all c-p guilds, and richness of all trophic groups expressed per 100 cm³ differed from those for 100 g of soil. This ambiguity may be due to the lower numbers of studies that used abundance per 100 cm³ than that expressed in per g soil, low statistical power, or the variation in the quantity of soil depending on its compactness, bulk density, and soil moisture.

Comprehensive meta-analyses of distinct ecosystems with different schemes of human intervention from 111 publications, using random effects model and non-parametric variance, confirmed that nematode richness was higher in less disturbed ecosystems (forest and NGL) compared to more disturbed ecosystems (agriculture, DGL, and urban ecosystems), nematode abundance of trophic groups in the lower hierarchy of the soil food web was higher in more disturbed ecosystems and nematode abundance of trophic groups in the higher hierarchy of the soil food web was higher in less disturbed ecosystems, consistent with general findings from previous works in the field of nematode ecology.

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Appendix

The Supplementary Material for this article can be found online at: <https://drive.google.com/open?id=1wGcuYCzyUgUsNMucOjKOs-QAqXX-tvv>.