Relationships between soil nematode communities and soil multifunctionality as affected by land-use type

zhi li¹, Xiaomei Chen¹, Dejun Li², Jiangnan Li², Xionghui Liao², Xunyang He², Wei Zhang², and Jie Zhao²

¹Guangzhou University ²Institute of Subtropical Agriculture Chinese Academy of Sciences

June 23, 2022

Abstract

Researchers have used both soil nematode data and soil multifunctionality data as indicators of soil quality. However, the relationship between soil nematodes and soil multifunctionality is poorly understood. This study explored the relationship between soil nematode properties and soil multifunctionality in different land-use types in a subtropical karst region of Southwest China. We selected the following five typical land-use types that differ in the degree of soil disturbance: cropland (maize-soybean), sugarcane, mulberry, forage grass, and forest. Soil multifunctionality was calculated based on bulk density (BD), soil pH, the ratio of soil organic carbon to total nitrogen (C: N), the contents of soil water (SWC), soil total nitrogen (TN), soil organic carbon content (SOC), calcium (Ca), magnesium (Mg), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), ammonium nitrogen (AN), and nitrate nitrogen (NN). We found that the abundance, Simpson dominance index, and metabolic footprint of soil nematodes were highest in the forest, followed by sugarcane, cropland (maize-soybean) and forage grass, and mulberry. Soil multifunctionality was significantly higher in the forest than in the other land-use types. Soil multifunctionality was positively correlated with the abundance of total nematodes and all nematode trophic groups except omnivores. A random forest model revealed that the dominant nematode genera (i.e., *Coomansus* and *Acrobeloides*) and the rare genera (i.e., *Wilsonema* and *Heterocephalobus*) were closely associated with soil multifunctionality. Our results suggest that the soil nematodes (especially keystone genera) may mediate the effects of ecosystem disturbance on soil multifunctionality.

Type of contribution: research paper

Date of preparation: June 22, 2022

Number of text pages: 42

Number of tables: 2

Number of figures: 6

Title:Relationships between soil nematode communities and soil

multifunctionality as affected by land-use type

Zhilei Li $^{\rm a,\ b},$ Xiaomei Chen $^{\rm a},$ Dejun Li $^{\rm b,\ d,e}$, Jiangnan Li $^{\rm b,\ c},$ Xionghui Liao $^{\rm b,\ c},$ Xunyang He $^{\rm b,\ d,\ e}$, Wei Zhang $^{\rm b,\ d,\ e},$ Jie Zhao $^{\rm b,\ d,\ e,\ f}*$

^a School of Geography and Remote Sensing, Guangzhou University, Guangzhou 510006, China

^b Key Laboratory of Agro-ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Changsha 410125, PR China

^c College of Resources and Environment, Hunan Agricultural University, Changsha 410128, China

^d Huanjiang Observation and Research Station for Karst Ecosystems, Chinese Academy of Sciences, Huanjiang547100, PR China

^e Guangxi Industrial Technology Research Institute for Karst Rocky Desertification Control, Nanning, Guangxi 530012, China

^f Guangxi Key Laboratory of Karst Ecological Processes and Services, Huanjiang, Guangxi, 547100, China

* Corresponding author and reprint request: Dr. Jie Zhao

Email: jzhao@isa.ac.cn

Tel.: +86-20-37252631

Fax: +86-20-37252615

ABSTRACT

Researchers have used both soil nematode data and soil multifunctionality data as indicators of soil quality. However, the relationship between soil nematodes and soil multifunctionality is poorly understood. This study explored the relationship between soil nematode properties and soil multifunctionality in different land-use types in a subtropical karst region of Southwest China. We selected the following five typical land-use types that differ in the degree of soil disturbance: cropland (maize-soybean), sugarcane, mulberry, forage grass, and forest. Soil multifunctionality was calculated based on bulk density (BD), soil pH, the ratio of soil organic carbon to total nitrogen (C: N), the contents of soil water (SWC), soil total nitrogen (TN), soil organic carbon content (SOC), calcium (Ca), magnesium (Mg), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), ammonium nitrogen (AN), and nitrate nitrogen (NN). We found that the abundance, Simpson dominance index, and metabolic footprint of soil nematodes were highest in the forest, followed by sugarcane, cropland (maize-soybean) and forage grass, and mulberry. Soil multifunctionality was significantly higher in the forest than in the other land-use types. Soil multifunctionality was positively correlated with the abundance of total nematodes and all nematode trophic groups except omnivores. A random forest model revealed that the dominant nematode genera (i.e., *Coomansus* and *Acrobeloides*) and the rare genera (i.e., Wilsonema and Heterocephalobus) were closely associated with soil multifunctionality. Our results suggest that the soil nematodes (especially keystone genera) may mediate the effects of ecosystem disturbance on soil multifunctionality. These findings increase our understanding of the relationships between soil organisms and soil multifunctionality.

Keywords:

Soil nematodes, land use, soil quality, soil multifunctionality,karst region

1. Introduction

Although adequate soil quality is essential for food production and the functioning of global ecosystems, soil quality is threatened by the growth of human populations, urbanization, and extensive and irrational management of available cultivable land (Paz-Ferreiro and Fu, 2013; Bünemann et al., 2018). Soil quality assessment provides a basic means to evaluate the sustainability of human-managed land systems (Doran and Parkin, 1996). At present, soil quality is commonly assessed based on its physical structure, chemical nutrient levels, and biological indicators (Paz-Ferreiro and Fu, 2013; Jing et al., 2015; Delgado-Baquerizo et al., 2016; Liu et al., 2017). The biological indicators include soil nematodes, which are a main component of the soil fauna (Bardgett and van der Putten, 2014) and which occupy multiple niches in soil detrital food webs (Bongers and Ferris, 1999; Ferris et al., 2001). They are sensitive to environmental disturbances, which makes them excellent ecological indicators, especially for evaluating the effects of environmental change and agricultural management (Bongers, 1990; Yeates and Bongers, 1999; Neher, 2001). Although a number of studies have used nematodes as indicators of the quality of soil or the health of different ecosystem types and land-use types (Yeates, 1979; Porazinska et al., 1999; Berkelmans et al., 2003; Neher et al., 2005), few

studies have comprehensively analyzed whether the information indicated by soil nematodes is related to data on other soil properties such as soil nutrients, physical properties, and microorganisms. Therefore, the relationships between soil nematodes and soil physical, chemical, and microbial properties require further study.

In recent years, many studies have used soil multifunctionality as an indicator of soil quality (Bunemann et al., 2018). Early research mainly focused on the relationship between species diversity and individual ecosystem functions, such as the effect of plant species richness on net primary productivity and nitrogen accumulation (Hector et al., 1999; Hooper et al., 2005; Cardinale, 2011). Using a single ecosystem function in place of a holistic ecosystem function can be highly misleading, however, because it may underestimate the effects of biodiversity loss on soil functions (Gamfeldt et al., 2008). In other words, the assessment of multiple functions is more useful than the assessment of a single function for understanding soil quality and ecosystem processes (Zavaleta et al., 2010; Delgado-Baquerizo et al., 2020). Over time, research on ecosystem multifunctionality has gradually expanded from terrestrial plants (Gamfeldt et al., 2008) to aquatic plants (Cardinale, 2011) and to soil microorganisms (Chen et al., 2020; Delgado-Baquerizo et al., 2020). At present, researchers generally agree that ecosystem functionality is related to aboveground biodiversity. However, the relationship between soil nematodes and ecosystem multifunctionality is poorly understood.

Karst ecosystems are widely distributed in the world (Wang et al., 2019). They are fragile and are currently experiencing extreme degradation in many regions. Karst rocky desertification has been identified as the most severe ecological problem in Southwest China (Wang et al., 2019). The long-term extensive reclamation of cropland (especially corn) is considered the main cause of the rocky desertification (Zhao et al., 2014b; Wang et al., 2019). Land planted with corn is being reclaimed in Southwest China because the economic benefits of corn cultivation are too low to alleviate poverty. Therefore, many farmlands have been protected to form forests, and some farmlands have been transformed for the cultivation of sugarcane (*Saccharum officinarum L.*), mulberry (*Morus alba L.*), and forage grass (Li et al., 2018a; Li et al., 2018b).

Different land-use types experience different disturbances and management practices resulting in changes in soil quality or soil multifunctionality. How the land-use changes described in the previous paragraph affect soil quality is not well known in the karst areas of Southwest China. The purpose of our study was to assess the composition of soil nematode communities of different land-use types and determine the relationship between soil nematode properties and soil multifunctionality. We tested two hypotheses: 1) the intensity of agricultural disturbance (e.g., tillage and replanting frequency) is negatively correlated with soil nematode abundance, diversity, and community maturity; and 2) there is a positive relationship between the properties of soil nematode communities and ecosystem multifunctionality.

2. Materials and Methods

2.1 Study region and experimental design

The study was conducted in Huan jiang County (107deg51'-108deg43'E, 24deg44'-25deg33'N), Guangxi Province, China (Fig. 1). The region has a subtropical monsoon climate, with a mean annual air temperature ranging from 17.8 to 21.1degC, and a mean annual precipitation ranging from 1346 to 1498 mm. The region has two seasons: a wet season (from April to August) and a dry season (September to March of the following year). The region is interwoven with karst and non-karst areas and is characterized by flat valleys surrounded by hills. The karst areas have calcareous lithosols (Wen et al., 2016; Li et al., 2017).

The study had a randomized complete block design with five blocks (about 9 km² each) distributed over a karst region. The distance between any two blocks ranged from 4 to 20 km. In each block, the following four agricultural land-use types were randomly distributed: cropland (maize-soybean), sugarcane field, mulberry field, and forage grass. The latter three land-use types were transformed from maize-soybean field and had been managed continuously for about 15 years. All plots were located in valleys or on lower slopes. A representative field was selected for each land-use type in each block. In each field, one plot (> 400 m² each) was designated for soil sampling. In addition, five nearby mature forest sites (>50 years old and located in the Mulun National Nature Reserve; 107deg53'-108deg05'E, 25deg06'-25deg12'N) were selected

for comparison. Detailed information on the study and study sites was provided by Li et al. (2018b).

2.2. Field sampling and analyses

Soil sampling was carried out in October 2016. Ten soil cores were randomly collected from the mineral horizon (0-10 cm) of each plot. The soil cores were thoroughly mixed to form one composite sample per plot. Bulk density (BD) was measured with metal rings. Soil water content (SWC) was determined after drying about 10 g soils at 105degC for 24 h. Soil microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were measured with the chloroform fumigation-extraction method (Carter and Gregorich, 2006). Nitrate nitrogen (NN) and ammonium nitrogen (AN) concentrations were analyzed with an autoanalyzer (FIAstar 5000, FOSS, Sweden). For the determination of soil pH, soil was mixed with water (1:2.5 soil/water ratio) and assayed using a pH meter (FE20K, Mettler-Toledo, Switzerland). The dichromate redox colorimetric method was used to determine soil organic carbon (SOC) content after wet oxidation of soil. Soil total nitrogen (TN) was measured with an elemental analyzer (EA 300; Euro Vector, Italy). To determine exchangeable magnesium (Mg) and calcium (Ca), soils were extracted with 1 M ammonium acetate and assayed by inductively coupled plasma atomic emission spectroscopy.

2.3. Nematode extraction and index calculations

2.31. Nematode extraction and identification

Nematodes were extracted from 100 g of fresh soil using the Baermann funnel method (Barker, 1985). Turbid nematode suspensions were cleaned by repeated settling at 4 degC (Zhao and Wang, 2021). After fixation in a 4% formalin solution, nematodes were counted and identified to genus with the aid of a differential interference contrast microscope (ECLIPSE 80i, Nikon, Japan) at 400–1000x magnification. The functional guild was determined based on the known trophic behavior (bacterivore, fungivore, herbivore, predator, or omnivore) and cp value of the genus (Yeates et al., 1993; Bongers and Bongers, 1998).

2.3.2 Index calculation

The nematode data were used to calculate the enrichment index (EI), structure index (SI), channel index (NCR), Shannon-Wiener diversity index (H'), Margalef richness index (SR), Simpson dominance index (λ), maturity index (MI), plant parasite index (PPI), and channel index (NCR) for each sample (Bongers, 1990; Ferris et al., 2001). The formulas for these indices were as follows:

 $EI = 100 \times (e/(e+b)) (1)$

 $\mathrm{SI}=100$ \times (s/ (s+b)) (2)

NCR = Ba/(Ba + Fu) (3)

 $\mathbf{H}' = \sum_{i=1}^{n} \operatorname{Pi} \times \ln \operatorname{Pi} (4)$

 $\lambda = [?] Pi^2$ (5)

 $SR = (S-1) / \ln N (6)$

MI or PPI = $\sum_{i=1}^{n} v(i) \times f(i)$ (7)

For EI and SI, where e represents the enrichment component (Ba₁, Fu₂), and b and s represent basal (Ba₂ and Fu₂) and structure (Ba₃Ba₅, Fu₃-Fu₄, Om₄-Om₅, and Pr₃-Pr₅) components, respectively. All components of b and s were calculated by [?] $k_b \times n_b$ and [?] $k_s x n_s$, respectively, where k_b and k_s are the weightings assigned to nematode functional guilds, and n_b and n_s are the nematode abundances of those guilds, and For NCR, Ba and Fu represent the abundance of bacterivores and fungivores, respectively, in each sample; For H' and λ , Pi represents the relative abundance of taxon i of the sample; For MI and PPI, v(i) represents the colonizer-persister (cp) value assigned to taxon i of nematodes other than herbivores, f(i) represents the frequency of taxon i in the sample, and n represents the number of free-living nematodes and plant-parasitic nematodes in a sample for calculations of MI and PPI, respectively.

2.4 Data analysis

The effects of land-use type on soil physicochemical properties and nematode variables were determined using one-way ANOVAs. Statistical significance was determined at p < 0.05. Pearson correlation analysis was used to analyze the correlation between nematode variables and other biotic and abiotic variables. One-way ANOVAs and Pearson's correlation analysis were performed using IBM SPSS version 26.0 software (IBM, USA). The network of nematode genera compositions in different land-use types were analyzed using Gephi software. The network was constructed based on a Spearman rank correlation matrix of nematode biomass data of each trophic group. The relationship between nematode biodiversity and soil multifunctionality was evaluated by Spearman correlation analysis. The average approach was used to evaluate ecosystem multifunctionality using the standardized average of 12 variables (Hooper and Vitousek, 1998). Z-score transformation (overall mean of 0 and standard deviation of 1) was used to standardize the data for the soil nematode community and ecosystem functions (Maestre et al., 2012; Bradford et al., 2014a). Z score data were analyzed using SPSS 26 statistical software (SPSS Inc., Chicago, IL, USA). Statistical significance was determined at p < 0.05. A random forest model was used to identify major nematode predictors of soil multifunctionality. The model was analyzed using R software with the "Random Forest" package. A total of 10 nematode genera were selected for random forest modelling.

3. Results

3.1 Soil nematode community

3.1.1 Total number of soil nematodes and trophic groups

A total of 56 genera of nematodes were identified in the soil samples. Coomansus was the dominant genus. The abundances of total nematodes and of each trophic group were higher in the forest plots than in the other four land-use plots (Fig. 2). The order of total nematode abundance was forest > sugarcane > forage grass > cropland > mulberry (Fig. 2a). Bacterivore was the most abundant trophic group (Fig. 2b), and bacterivore abundance and fungivore abundance were significantly higher in the forest plots than in the other land-use plots. Herbivore, predator, and omnivore highest in the forest plots, lowest in the mulberry plots, and intermediate in the other plots (Fig. 2d, e, and f).

3.1.2 Ecological index and metabolic footprint of the soil nematode communities

The nematode structure and maturity index were significantly lower in the mulberry plots than in the other land-use plots. The footprint of soil nematodes and omnivores-predators were significantly higher in forest and sugarcane plots than in forage grass, mulberry, or cropland plots (Table 1). The metabolic footprints of herbivores, bacterivores, and fungivores did not significantly differ among land-use types. Whether in forest or in agricultural plots, the sizes of the metabolic footprints of nematodes were in the following order: predator and omnivore > herbivore > bacterivore > fungivore (Fig. S1). The nematode network pattern was more complex in the forest plots than in the of agricultural plots (Fig. 3).

3.1.3 Relationship between soil nematode communities and soil physicochemical properties

Nematode trophic group structure and ecological indices were correlated with soil physicochemical properties (Table 2). Total soil nematode abundances were negatively correlated with BD and positively correlated with SOC, C: N, and Mg. Fungivore and herbivore abundances were positively correlated with TN and SWC. Nematode EI was negatively correlated with pH and Ca. The abundances of *Coomansus* (the dominant genus) and *Plectus*(a common genus) were positively correlated with most soil physicochemical properties, while the abundance of *Acrobeloides* (a common genus) was negatively correlated with most soil properties (Fig. S2).

3. 2 Relationship between nematode properties and ecosystem multifunctionality

Soil multifunctionality was significantly higher in the forests than in the four agricultural land-use types, and did not significantly differ among the agricultural land-use types (Fig. 4). The ordinary least-squares (OLS)

regression models revealed a positive linear correlation between ecosystem multifunctionality and the abundances of total nematodes and all nematode trophic groups except omnivores for total nematode abundance ($\mathbb{R}^2 = 0.297$, p < 0.01), bacterivore ($\mathbb{R}^2 = 0.16$, p < 0.05), fungivores ($\mathbb{R}^2 = 0.272$, p < 0.01), herbivores ($\mathbb{R}^2 = 0.218$, p < 0.05), and predator ($\mathbb{R}^2 = 0.175$, p < 0.05) (Fig. 5). A total of 10 genera were incorporated in the random forest model. The results showed that the most important nematodes associated with ecosystem multifunctionality were predators and especially the following bacterivores: *Coomansus* (Spearman, p < 0.01), *Acrobeloide* (Spearman, p < 0.01), *Wilsonema* (Spearman, p < 0.01), and *Heterocephalobus* (Spearman, p < 0.05) (Fig. 6).

4. Discussion

4..1 Effects of land-use type on soil nematode communities

In the current study, nematode abundance, diversity, and footprint were highest in the forest and sugarcane plots, intermediate in the forage grass and cropland plots, and lowest in the mulberry plots. These results were partially consistent with our first hypothesis, which was that these nematode properties would be negatively correlated with the degree of agricultural disturbance. In previous studies, soil nematode abundance or diversity was generally higher in less disturbed than in more disturbed ecosystems (Neher and Campbell, 1994; Ou et al., 2005; Li et al., 2007). With less disturbance and a relatively stable input of leaf litter and rhizodeposition, forests may support a relatively complex nematode community structure and network (Wardle, 1995). Natural forest ecosystems, like those in the current study, generally support more abundant and diverse soil nematode communities than agricultural ecosystems (Gao et al., 2020), probably because soil nematodes depend mostly on the distribution of soil organic matter (Ou et al., 2005; Quist et al., 2016). In agricultural soils, nematode abundance was found to be higher with no-tillage than with conventional tillage (Fu et al. (2000). In the current study, however, the abundance and diversity of nematodes were higher in the sugarcane plots than in the forage grass plots, probably because almost all of the leaves are left on the soil surface when the sugarcane is harvested, eventually providing a substantial input of organic matter to support soil food webs. Tillage is often found to be the main cause of organic carbon depletion in agricultural soil (Baker et al., 2007). Therefore, frequent tillage leading to lower organic carbon levels may partly account for the lower abundance and diversity of soil nematodes in the maize-soybean plots. Nematode abundance and diversity were the lowest in mulberry plots, which may be related to the frequent disturbances and harvesting of leaves and branches of mulberry plants. In the studied area, the mulberry leaves are manually harvested every 20 days from April to November, and all of the aboveground stems and branches are cut and removed at the end of the growing season in July and December (personal communication with local farmers) (Li et al., 2018b). In addition, compound fertilizer (N: P_2O_5 : $K_2O = 15:15:15$) was applied to the mulberry plots in March and July at a rate of about $1,100 \text{ kg ha}^{-1}$ each time, and weed control was conducted every month (Li et al., 2018b; Zhang et al., 2021).

Nematodes in the genus *Filenchus* were previously reported to be more likely to occur in soils with abundant organic matter (Okada and Kadota, 2003). Consistent with the latter report, we found that the nematodes in the genus *Filenchus* were especially abundant in forest and sugarcane plots (Table S2), which had high soil organic carbon contents (Table S1). The changes of soil nematodes in Fu₂ and Pr₄ functional guilds might account for such changes of soil nematode communities between the five land use types.

The abundances of soil nematodes were significantly related to SOC, C: N, and Mg contents in the current study. Previous studies reported that abiotic factors (e.g., soil physicochemical properties) had substantial effects on soil biota (Viketoft, 2013; Zhao et al., 2014a). Yeates (1978) found a positive correlation between nematode abundance and SOC content. In another study, the abundances of total nematodes, herbivores, and omnivores were positively correlated with SOM content (Wall et al., 2002). That is reasonable because the abundance of soil nematodes and the size of the entire food web are ultimately determined by the availability of SOM (van den Hoogen et al., 2019).

We found that soil Mg content was correlated with nematode abundance and diversity, which is reasonable because the stability of SOM in the karst region depends on organic matter complexes formed with Ca^{2+}

and Mg^{2+} (Wen et al., 2016; Yang et al., 2016). Total nitrogen and the C/N ratio are also important factors affecting nematode communities (Li et al., 2007). Change in soil carbon and nitrogen resources can affect the microbial community and plant growth, and therefore change the food resources for different nematode trophic groups (Ingham et al., 1985; Zhang et al., 2016), ultimately affecting the number, community composition, and ecological indices of soil nematodes (Guan et al., 2018). Moreover, the plots in the current study were located in the karst area in Southwest China, where pH is strongly influenced by land-use type (Table S1). Consistent with our results, previous studies reported that soil pH was an important factor affecting soil nematode communities in various ecosystems in different regions (Röty and Huhta, 2003; Zhao and Neher, 2014).

4.2 Relationship between nematodes and soil multifunctionality

Soil multifunctionality was significantly higher in the forest plots than in the other types of land-use plots, indicating that the forest soil had stronger functions than the other four soils. In addition, there was no significant difference in soil multifunctionality among the other land-use types although soil multifunctionality tended to be higher in the forage grass plots than in the cropland, sugarcane, and mulberry plots. Although soil disturbance tended to gradually decrease from cropland plots to sugarcane and then to mulberry plots, nematode community properties and ecosystem multifunctionality did not gradually increase with these differences in land use. However, previous studies have found that land-use intensity (Allan et al., 2015). farming method (Zhang et al., 2019), and farmland management method (Luo et al., 2019) could directly or indirectly affect ecosystem multifunctionality. Perhaps the determination of soil multifunctionality depends on which indicators assessed. There is no uniform approach to the selection of indicators for quantifying ecosystem multifunctionality (Hansen and Pauleit, 2014; Jing and He, 2021). For example, Zhang et al. (2019) focused on C and N cycling to compare the resistance and resilience to dry-wet cycles under notillage and ridge tillage. Delgado-Baquerizo et al. (2020) explored the role of soil biodiversity in regulating multiple ecosystem functions; their multifunctionality index included nutrient cycling, decomposition, plant production, and reduced potential for pathogenicity and belowground biological warfare. It follows that the methods used for assessing ecosystem multifunctionality vary among studies. As a result, it is difficult to compare multifunctionality values among studies (Bradford et al., 2014b; Dooley et al., 2015).

In line with our second hypothesis, there was a significant positive relationship between soil nematode abundance and soil multifunctionality. In agreement with this finding, a synthetic study of worldwide data reported that ecosystem multifunctionality was positively correlated with the diversity of soil nematodes and other soil organisms (Delgado-Baquerizo et al., 2020). An increasing number of studies have demonstrated that microbial communities help determine belowground ecosystem multifunctionality (Bradford et al., 2014a; Delgado-Baquerizo et al., 2016). The current study shows that nematode abundance also helps determine ecosystem multifunctionality.

According to several recent studies, multifunctionality may require high levels of biodiversity (Hector and Bagchi, 2007; Maestre et al., 2012). It is unclear, however, which taxa have more important roles in regulating ecosystem functions. Although common species are generally believed to determine the level of ecosystem multifunctionality (Lohbeck et al., 2016), recent studies have found that rare species can also be important. For example, Chen et al. (2020) found that bacterial and fungal taxa with a low relative abundance ($^{-1}-3\%$) were major contributors to multifunctionality. Regarding soil nematodes, almost all studies have focused on the dominant taxa and have commonly overlooked rare taxa. In the present study, both rare genera (e.g., *Wilsonema* and *Heterocephalobus*) and dominant genera (e.g., *Coomansus* and *Acrobeloide*) were found to be important contributors to soil multifunctionality. Many taxa often share similar functions, and rare taxa might not be necessary for maintaining those function. The functional importance of the rare taxa may be due to the 'insurance effects', i.e., rare taxa may perform functions when common taxa do not (Jousset et al., 2017). The rarity of taxa may be not permanent, and their abundance is influenced by both abiotic and biotic factors (Gaston, 2008; Gudelj et al., 2010). The ecological role of the rare nematode genera is poorly understood and warrants additional research.

5. Conclusions

Our soil nematode data indicate that soil quality was highest in the forest plots and lowest in the mulberry plots. The main factors determining the properties of soil nematode communities may the intensity of ecosystem disturbance and the quantity of resource input. The differences in soil multifunctionality among the five land-use types generally matched the differences in soil nematode properties. Finally, soil nematode properties were positively related with soil multifunctionality, which suggests that soil nematodes may greatly affect soil functions. In addition, both the rare and dominant nematode genera contributed to soil multifunctionality. These results increase our understanding of nematodes as ecological indicators and the relationship between soil nematodes and soil multifunctionality.

Acknowledgements

We thank Prof. Bruce Jaffee for his help in preparing the manuscript. This study was supported by the Joint Funds of the Natural Science Foundation of China (No.U21A20189), the Natural Science Foundation for Distinguished Young Scholars of Hunan Province (No.2021JJ10042), the Youth Innovation Promotion Association of Chinese Academy of Sciences (No.Y201969), and the Guangxi Bagui Scholarship Program given to Dejun Li. The authors declare that this research was conducted without any conflict of interest.

References

Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Bluethgen, N., Boehm, S., Grassein, F., Hoelzel, N., Klaus, V.H., Kleinebecker, T., Morris, E.K., Oelmann, Y., Prati, D., Renner, S.C., Rillig, M.C., Schaefer, M., Schloter, M., Schmitt, B., Schoening, I., Schrumpf, M., Solly, E., Sorkau, E., Steckel, J., Steffen-Dewenter, I., Stempfhuber, B., Tschapka, M., Weiner, C.N., Weisser, W.W., Werner, M., Westphal, C., Wilcke, W., Fischer, M., 2015. Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. Ecology Letters 18, 834-843.

Baker, J.M., Ochsner, T.E., Venterea, R.T., Griffis, T.J., 2007. Tillage and soil carbon sequestration - What do we really know? Agriculture Ecosystems & Environment 118, 1-5.

Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515, 505-511.

Barker, K.R., 1985. Nematode Extraction and Bioassays. An Advanced Treatise on Meloidogyne, 19-35.

Berkelmans, R., Ferris, H., Tenuta, M., van Bruggen, A.H.C., 2003. Effects of long-term crop management on nematode trophic levels other than plant feeders disappear after 1 year of disruptive soil management. Applied Soil Ecology 23, 223-235.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14-19.

Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Applied Soil Ecology 10, 239-251.

Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends in Ecology & Evolution 14, 224-228.

Bradford, M.A., Wood, S.A., Bardgett, R.D., Black, H.I., Bonkowski, M., Eggers, T., Grayston, S.J., Kandeler, E., Manning, P., Setala, H., Jones, T.H., 2014a. Discontinuity in the responses of ecosystem processes and multifunctionality to altered soil community composition. Proc Natl Acad Sci U S A 111, 14478-14483.

Bradford, M.A., Wood, S.A., Bardgett, R.D., Black, H.I., Bonkowski, M., Eggers, T., Grayston, S.J., Kandeler, E., Manning, P., Setala, H., Jones, T.H., 2014b. Reply to Byrnes et al.: Aggregation can obscure understanding of ecosystem multifunctionality. Proc Natl Acad Sci U S A 111, E5491.

Bünemann, E.K., Bongiorno, G., Bai, Z., Creamer, R.E., De Deyn, G., de Goede, R., Fleskens, L., Geissen, V., Kuyper, T.W., Mäder, P., Pulleman, M., Sukkel, W., van Groenigen, J.W., Brussaard, L., 2018. Soil quality – A critical review. Soil Biology and Biochemistry 120, 105-125.

Cardinale, B.J., 2011. Biodiversity improves water quality through niche partitioning. Nature 472, 86-89.

Carter, M., Gregorich, E., 2006. Soil sampling and methods of analysis. Lewis Publ. Boca Rat. FL, 481-483.

Chen, Q.-L., Ding, J., Zhu, D., Hu, H.-W., Delgado-Baquerizo, M., Ma, Y.-B., He, J.-Z., Zhu, Y.-G., 2020. Rare microbial taxa as the major drivers of ecosystem multifunctionality in long-term fertilized soils. Soil Biology and Biochemistry 141.

Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Jeffries, T.C., Gaitan, J.J., Encinar, D., Berdugo, M., Campbell, C.D., Singh, B.K., 2016. Microbial diversity drives multifunctionality in terrestrial ecosystems. Nat Commun 7, 10541.

Delgado-Baquerizo, M., Reich, P.B., Trivedi, C., Eldridge, D.J., Abades, S., Alfaro, F.D., Bastida, F., Berhe, A.A., Cutler, N.A., Gallardo, A., Garcia-Velazquez, L., Hart, S.C., Hayes, P.E., He, J.Z., Hseu, Z.Y., Hu, H.W., Kirchmair, M., Neuhauser, S., Perez, C.A., Reed, S.C., Santos, F., Sullivan, B.W., Trivedi, P., Wang, J.T., Weber-Grullon, L., Williams, M.A., Singh, B.K., 2020. Multiple elements of soil biodiversity drive ecosystem functions across biomes. Nat Ecol Evol 4, 210-220.

Dooley, Á., Isbell, F., Kirwan, L., Connolly, J., Finn, J.A., Brophy, C., Buckley, Y., 2015. Testing the effects of diversity on ecosystem multifunctionality using a multivariate model. Ecology Letters 18, 1242-1251.

Doran, J.W., Parkin, T.B., 1996. Quantitative indicators of soil quality, a minimum data set. SSSA Special Publication 49.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Applied Soil Ecology 18, 13-29.

Fu, S.L., Coleman, D.C., Hendrix, P.F., Crossley, D.A., 2000. Responses of trophic groups of soil nematodes to residue application under conventional tillage and no-till regimes. Soil Biology & Biochemistry 32, 1731-1741.

Gamfeldt, L., Hillebrand, H., Jonsson, P.R., 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. Ecology 89, 1223-1231.

Gao, D., Wang, F., Li, J., Yu, S., Li, Z., Zhao, J., 2020. Soil nematode communities as indicators of soil health in different land use types in tropical area. Nematology 22, 595-610.

Gaston, K.J., 2008. Bliodiversity and extinction: the importance of being common. Progress in Physical Geography-Earth and Environment 32, 73-79.

Guan, P., Zhang, X., Yu, J., Cheng, Y., Li, Q., Andriuzzi, W.S., Liang, W., 2018. Soil microbial food web channels associated with biological soil crusts in desertification restoration: The carbon flow from microbes to nematodes. Soil Biology and Biochemistry 116, 82-90.

Gudelj, I., Weitz, J.S., Ferenci, T., Claire Horner-Devine, M., Marx, C.J., Meyer, J.R., Forde, S.E., 2010. An integrative approach to understanding microbial diversity: from intracellular mechanisms to community structure. Ecol Lett 13, 1073-1084.

Hansen, R., Pauleit, S., 2014. From Multifunctionality to Multiple Ecosystem Services? A Conceptual Framework for Multifunctionality in Green Infrastructure Planning for Urban Areas. AMBIO 43, 516-529.

Hector, A., Bagchi, R., 2007. Biodiversity and ecosystem multifunctionality. Nature 448, 188-190.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. Science 286, 1123-1127. Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75, 3-35.

Hooper, D.U., Vitousek, P.M., 1998. EFFECTS OF PLANT COMPOSITION AND DIVERSITY ON NU-TRIENT CYCLING. Ecological Monographs 68, 121-149.

Ingham, R.E., Trofymow, J.A., Ingham, E.R., Coleman, D.C., 1985. INTERACTIONS OF BACTERIA, FUNGI, AND THEIR NEMATODE GRAZERS - EFFECTS ON NUTRIENT CYCLING AND PLANT-GROWTH. Ecological Monographs 55, 119-140.

Jing, X., He, J., 2021. Relationship between biodiversity, ecosystem multifunctionality and multiserviceability: literature overview and research advances. Chinese Journal of Plant Ecology, 1-18.

Jing, X., Sanders, N.J., Shi, Y., Chu, H., Classen, A.T., Zhao, K., Chen, L., Shi, Y., Jiang, Y., He, J.S., 2015. The links between ecosystem multifunctionality and above- and belowground biodiversity are mediated by climate. Nat Commun 6, 8159.

Jousset, A., Bienhold, C., Chatzinotas, A., Gallien, L., Gobet, A., Kurm, V., Kusel, K., Rillig, M.C., Rivett, D.W., Salles, J.F., van der Heijden, M.G., Youssef, N.H., Zhang, X., Wei, Z., Hol, W.H., 2017. Where less may be more: how the rare biosphere pulls ecosystems strings. ISME J 11, 853-862.

Li, D., Liu, J., Chen, H., Zheng, L., Wang, K., 2018a. Soil gross nitrogen transformations in responses to land use conversion in a subtropical karst region. J Environ Manage 212, 1-7.

Li, D., Liu, J., Chen, H., Zheng, L., Wang, K., 2018b. Soil microbial community responses to forage grass cultivation in degraded karst soils, Southwest China. Land Degradation & Development 29, 4262-4270.

Li, D.J., Wen, L., Yang, L.Q., Luo, P., Xiao, K.C., Chen, H., Zhang, W., He, X.Y., Chen, H.S., Wang, K.L., 2017. Dynamics of soil organic carbon and nitrogen following agricultural abandonment in a karst region. Journal of Geophysical Research-Biogeosciences 122, 230-242.

Li, Q., Liang, W., Ou. Wei, 2007. Response of nematode community to land use pattern in aquic brown soil. Biodiversity Science 15, 8.

Liu, Y.-R., Delgado-Baquerizo, M., Trivedi, P., He, J.-Z., Wang, J.-T., Singh, B.K., 2017. Identity of biocrust species and microbial communities drive the response of soil multifunctionality to simulated global change. Soil Biology and Biochemistry 107, 208-217.

Lohbeck, M., Bongers, F., Martinez-Ramos, M., Poorter, L., 2016. The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape. Ecology 97, 2772-2779.

Luo, G.W., Wang, T.T., Li, K.S., Li, L., Zhang, J.W., Guo, S.W., Ling, N., Shen, Q.R., 2019. Historical Nitrogen Deposition and Straw Addition Facilitate the Resistance of Soil Multifunctionality to Drying-Wetting Cycles. Applied and Environmental Microbiology 85.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., Garcia-Gomez, M., Bowker, M.A., Soliveres, S., Escolar, C., Garcia-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceicao, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitan, J., Gatica, M.G., Ghiloufi, W., Gomez-Gonzalez, S., Gutierrez, J.R., Hernandez, R.M., Huang, X.W., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramirez-Collantes, D.A., Romao, R., Tighe, M., Torres-Diaz, C., Val, J., Veiga, J.P., Wang, D.L., Zaady, E., 2012. Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. Science 335, 214-218.

Neher, D.A., 2001. Role of nematodes in soil health and their use as indicators. Journal of Nematology 33, 161-168.

Neher, D.A., Campbell, C.L., 1994. Nematode communities and microbial biomass in soils with annual and perennial crops. Applied Soil Ecology 1, 17-28.

Neher, D.A., Wu, J., Barbercheck, M.E., Anas, O., 2005. Ecosystem type affects interpretation of soil nematode community measures. Applied Soil Ecology 30, 47-64.

Okada, H., Kadota, I., 2003. Host status of 10 fungal isolates for two nematode species, Filenchus misellus and Aphelenchus avenae. Soil Biology and Biochemistry 35, 1601-1607.

Ou, W., Liang, W., Jiang, Y., Li, Q., Wen, D., 2005. Vertical distribution of soil nematodes under different land use types in an aquic brown soil. Pedobiologia 49, 139-148.

Paz-Ferreiro, J., Fu, S., 2013. Biological Indices for Soil Quality Evaluation: Perspectives and Limitations. Land Degradation & Development 27, 14-25.

Porazinska, D.L., Duncan, L.W., McSorley, R., Graham, J.H., 1999. Nematode communities as indicators of status and processes of a soil ecosystem influenced by agricultural management practices. Applied Soil Ecology 13, 69-86.

Quist, C.W., Schrama, M., de Haan, J.J., Smant, G., Bakker, J., van der Putten, W.H., Helder, J., 2016. Organic farming practices result in compositional shifts in nematode communities that exceed crop-related changes. Applied Soil Ecology 98, 254-260.

Roty, M., Huhta, V., 2003. Earthworms and pH affect communities of nematodes and enchytraeids in forest soil. Biology and Fertility of Soils 38, 52-58.

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S.R., Creamer, R., Mauro da Cunha Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutierrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q., Liang, W., Magilton, M., Marais, M., Martin, J.A.R., Matveeva, E., Mayad, E.H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K., Peneva, V., Pellissier, L., Carlos Pereira da Silva, J., Pitteloud, C., Powers, T.O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setala, H., Sushchuk, A., Tiunov, A.V., Trap, J., van der Putten, W., Vestergard, M., Villenave, C., Waeyenberge, L., Wall, D.H., Wilschut, R., Wright, D.G., Yang, J.I., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194-198.

Viketoft, M., 2013. Determinants of small-scale spatial patterns: Importance of space, plants and abiotics for soil nematodes. Soil Biology and Biochemistry 62, 92-98.

Wall, J., Skene, K., Neilson, R., 2002. Nematode community and trophic structure along a sand dune succession. Biology and Fertility of Soils 35, 293-301.

Wang, K.L., M, Y.Y., S, C.H., B, W.X., J, X., K, Q.X., W, Z., H, D., 2019. The comprehensive treatment of karst rocky desertification and its regional restoration effects. Acta Ecologica Sinica 39, 7432-7440.

Wardle, D.A., 1995. Impacts of Disturbance on Detritus Food Webs in Agro-Ecosystems of Contrasting Tillage and Weed Management Practices, Advances in Ecological Research Volume 26, pp. 105-185.

Wen, L., Li, D., Yang, L., Luo, P., Chen, H., Xiao, K., Song, T., Zhang, W., He, X., Chen, H., Wang, K., 2016. Rapid recuperation of soil nitrogen following agricultural abandonment in a karst area, southwest China. Biogeochemistry 129, 341-354.

Yang, L., Luo, P., Wen, L., Li, D., 2016. Soil organic carbon accumulation during post-agricultural succession in a karst area, southwest China. Sci Rep 6, 37118.

Yeates, G.W., 1978. Populations of nematode genera in soils under pasture. New Zealand Journal of Agricultural Research 21, 321-330.

Yeates, G.W., 1979. SOIL NEMATODES IN TERRESTRIAL ECOSYSTEMS. Journal of Nematology 11, 213-229.

Yeates, G.W., Bongers, T., 1999. Nematode diversity in agroecosystems. Agriculture, Ecosystems & Environment 74, 113-135.

Yeates, G.W., Bongers, T., , R.G., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera-an outline for soil ecologists. Journal of Nematology 25, 315-331.

Zavaleta, E.S., Pasari, J.R., Hulvey, K.B., Tilman, G.D., 2010. Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. Proc Natl Acad Sci U S A 107, 1443-1446.

Zhang, B., Liang, A.Z., Wei, Z.B., Ding, X.L., 2019. No-tillage leads to a higher resistance but a lower resilience of soil multifunctionality than ridge tillage in response to dry-wet disturbances. Soil & Tillage Research 195.

Zhang, C., Liu, G.B., Xue, S., Wang, G.L., 2016. Soil bacterial community dynamics reflect changes in plant community and soil properties during the secondary succession of abandoned farmland in the Loess Plateau. Soil Biology & Biochemistry 97, 40-49.

Zhang, Q., Li , S., Hu, S., Mao, L., Han, R., 2021. Discussion on Fertilization Techniques of Mulberry in Summer and Autumn. Agricultural Technology & Equipment, 135-136.

Zhao, J., Li, S., He, X., Liu, L., Wang, K., 2014a. The soil biota composition along a progressive succession of secondary vegetation in a karst area. PLoS One 9, e112436.

Zhao, J., Neher, D.A., 2014. Soil energy pathways of different ecosystems using nematode trophic group analysis: a meta analysis. Nematology 16, 379-385.

Zhao, J., Wang, K., 2021. Methods for cleaning turbid nematode suspensions collected from different landuse types and soil types. Soil Ecology Letters.

Zhao, J., Zhang, W., Wang, K., Song, T., Du, H., 2014b. Responses of the soil nematode community to management of hybrid napiergrass: The trade-off between positive and negative effects. Applied Soil Ecology 75, 134-144.

Table 1. Nematode community indices of five land-use types: cropland, sugarcane, mulberry, forage grass, and forest.

	Cropland	Sugarcane	Mulberry	Forage grass	Forest
EI	44.75 ± 1.92	41.81 ± 7.6	$38.41 {\pm} 2.94$	$43.74{\pm}4.87$	41.71±1.94
SI	$85.05 \pm 5.14a$	$82.19{\pm}19.34\mathrm{ab}$	$60.71 \pm 15.27 \mathrm{b}$	$63.27 \pm 24.39 \text{ab}$	83.19 ± 10.54 ab
NCR	$0.58 {\pm} 0.10$	$0.57 {\pm} 0.11$	$0.7 {\pm} 0.09$	$0.53 {\pm} 0.08$	$0.51 {\pm} 0.05$
H'	$2.22 {\pm} 0.12$	$2.09{\pm}0.13$	$2.37{\pm}0.21$	$2.55{\pm}0.17$	$2.28{\pm}0.28$
\mathbf{SR}	$2.98{\pm}0.32$	$2.6 {\pm} 0.37$	$3.2 {\pm} 0.44$	$3.68{\pm}0.38$	$3.35 {\pm} 0.26$
λ	$0.16 {\pm} 0.02$	$0.2{\pm}0.03$	$0.15 {\pm} 0.04$	$0.14{\pm}0.03$	$0.24{\pm}0.08$
MI	$3.06{\pm}0.1{\rm ab}$	$3.15{\pm}0.27\mathrm{a}$	$2.49{\pm}0.1\mathrm{b}$	$2.65{\pm}0.23\mathrm{ab}$	$3.11{\pm}0.18a$
PPI	$3.53 {\pm} 0.26$	$2.66 {\pm} 0.35$	$3.56 {\pm} 0.20$	$3.33{\pm}0.38$	$3.25 {\pm} 0.41$
Footprint	$55.46{\pm}11.57{\rm b}$	$101.52{\pm}33.28\mathrm{ab}$	$35.71{\pm}10.01\mathrm{b}$	$60.94{\pm}15.22\mathrm{b}$	$163.87 \pm 33.15a$

EI, enrichment index; SI, the structure index; NCR, nematode channel ratio; H', Shannon diversity index; SR, Margalef richness index; λ , Simpson dominance index; MI, maturity index; PPI, plant parasites index; Footprint, total nematode metabolic footprint. Values are means \pm SE. Different letters in the same row indicate significant differences at p < 0.05 level.

Table 2. Pearson's correlation coefficients between soil physicochemical properties and soil nematode varia-

	BD^b	SWC	SOC	TN	C: N	pН	Ca	Mg	AN	NN
Total ^a	-0.480*	0.299	0.579**	0.496*	0.615**	0.394	0.22	0.710**	-0.175	0.379
Ba	-0.364	0.26	0.430^{*}	0.366	0.470^{*}	0.193	0.144	0.487^{*}	0.013	0.213
Fu	-0.523**	0.408*	0.596^{**}	0.521^{**}	0.623^{**}	0.189	0.089	0.680^{**}	-0.309	0.500^{*}
He	-0.573**	0.439^{*}	0.492^{*}	0.483^{*}	0.460^{*}	0.319	0.261	0.530^{**}	-0.281	0.328
\Pr	-0.332	0.165	0.435^{*}	0.364	0.467^{*}	0.384	0.196	0.570^{**}	-0.152	0.29
Om	-0.219	0.125	0.246	0.23	0.266	0.3	0.172	0.298	0.121	0.024
EI	0.109	-0.161	-0.188	-0.252	-0.167	-0.509**	-0.577**	-0.101	-0.046	0.201
SI	-0.052	-0.055	0.123	0.025	0.178	0.265	-0.081	0.269	0.062	0.027
NCR	0.142	-0.181	-0.082	-0.038	-0.061	0.273	0.322	-0.123	0.218	-0.305
\mathbf{H}'	-0.019	0.159	-0.049	-0.033	-0.064	-0.098	-0.015	-0.188	-0.106	-0.023
\mathbf{SR}	-0.147	0.232	0.049	0.05	0.023	-0.093	-0.06	-0.013	-0.135	0.031
λ	-0.262	0.077	0.303	0.279	0.308	0.256	0.165	0.442^{*}	-0.005	0.183
MI	-0.121	-0.017	0.163	0.073	0.221	0.359	0.017	0.297	0.064	0.017
PPI	0.108	0.077	-0.094	-0.101	-0.11	-0.143	-0.084	-0.146	0.1	-0.192

^a Total, Total nematode abundance; Ba, bacterivore; Fu, fungivore; Pr, predator; Om, omnivore; Pl, herbivore. Nematode community indices include EI, enrichment index; SI, the structure index; NCR, nematode channel ratio; H', Shannon diversity index; SR, Margalef richness index; λ , Simpson dominance index; MI, maturity index; PPI, plant parasites index.

^b Environmental factors: BD, bulk density; SWC, soil water content; TN, soil total nitrogen; SOC, soil organic carbon; C:N, ratio of soil organic carbon to total nitrogen; soil pH; Ca, calcium; Mg, magnesium; AN: ammonium nitrogen; NN, nitrate nitrogen.

* and ** indicate significance at p < 0.05 and < 0.01, respectively.

Figure legends:

Fig. 1. Map of the study area and locations of sample sites. The two maps on the left indicate China and Guangxi Province, and the map on the right indicates Huan jiang County. In the key, high/low indicates altitude (m a.s.l.). The black dot indicates the location of farmland sample site. The red dot indicates the location of forest sample site. In each sample site, five land-use types (cropland, sugarcane, mulberry, forage grass, and mature forest) were selected.

Fig. 2. Abundances of total nematodes and different nematode trophic groups in the cropland, sugarcane, mulberry, forage grass, and forest. (a) Total nematodes; (b) Bacterivores; (c) Fungivores; (d) Herbivores; (e) Predators; (f) Omnivores. Values are mean \pm SE. Within each panel, values with the same or no letters are not significantly different (p > 0.05) according to the LSD test.

Fig. 3. Network visualization of the interaction strengths within the soil nematode communities of cropland, sugarcane field, mulberry field, forage grass field, and mature forest. A connection stands for a strong (Spearman's p > 0.75) correlation. The size of each node is proportional to the biomass of the nematode trophic group, and the nodes filled in purple are bacterivores, in light green are fungivores, in dark green are herbivores, in blue are predators, and in orange are omnivores. The connecting lines are colored according to interaction types; positive correlations are red, and negative correlations are green.

Fig. 4. Effects of land-use type on ecosystem multifunctionality. Values are means \pm SE. Means with the same letter are not significantly different (p > 0.05) according to the LSD test.

Fig. 5. Relationships between ecosystem multifunctionality index and soil nematode properties. Solid blue line represents a significant linear regression according to an ordinary least squares (OLS) regression model.

The area shaded in light blue indicates the 95% confidence interval.

Fig. 6. Random forest regression model showing the main nematode genera associated with ecosystem multifunctionality. * and ** indicate that the genera were significantly associated with multifunctionality at p < 0.05 and < 0.01, respectively.



Fig. 1.



Fig. 2.



Fig. 3.



Fig. 4.







Fig. 6.