



## Energy flows through nematode food webs depending on the soil carbon and nitrogen contents after forest conversion

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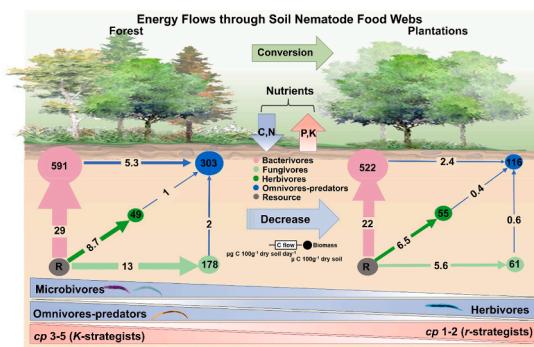
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### HIGHLIGHTS

- Forest conversion reduced the abundance, maturity, diversity and stability of soil nematodes.
- Conversion increased *r*-strategy nematodes but decreased the *K*-strategists.
- Energy flows and uniformity via the nematode food web declined after conversion.
- Soil food web structure and energy flows were related to soil C and N contents.

### GRAPHICAL ABSTRACT



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### ABSTRACT

The swift proliferation of forests converted into monoculture plantations has profound impacts on soil nutrients, microbial communities, and many ecological processes and functions. Nematodes are soil microfauna that play a pivotal role in biogeochemical cycling and in soil food web, whereas the response of soil nematode communities and energy flows to forest conversion remains unknown. Here, we assessed the community composition and the energy flows of the nematode food webs as a function of soil chemistry after conversion from natural forests (Forest) to four plantations (8-year-old): *Amygdalus persica* (Peach), *Myrica rubra* (Berry), *Camellia oleifera* (Oil), and *Cunninghamia lanceolata* (Fir). After forest conversion, soil organic carbon (SOC) and total nitrogen (TN) contents decreased by 65 % and 55 %, respectively. Forest conversion strongly reduced the abundance (particularly large-bodied omnivorous-predatory nematodes), diversity, maturity, and stability of the soil nematode community. The shifts in composition and structure of nematode communities after forest conversion are

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reflected in changes in the abundance of predominant genera and trophic taxa, especially bacterivorous, fungivorous, and omnivorous-predatory nematodes. *Acrobeloides* notably increased, whereas *Plectus*, *Prismatolaimus*, *Tylencholaimus*, and *Tripyla* decreased. Accordingly, the abundances of *r*-strategy nematodes (*cp* value = 1–2) increased, but that of the *K*-strategists (*cp* value = 3–5) declined. Additionally, the energy flow across the soil nematode food web was reduced by 36 % and flow uniformity declined by 24 % after forest conversion. These changes in nematode diversity and abundance were triggered by diminishing soil C and N contents, thereby affecting the energy flows via the nematode food webs. Thus, forest conversion affects soil biotas and multifunctions from the perspective of nematode food web structure and energy flows, and underlines the interconnections between ecosystem and energy dynamics across multi-trophic levels, which is crucial for sustainable forest management.

## 1. Introduction

Natural forests are known for abundant biodiversity and a wide variety of crucial ecological functions and services (Wang et al., 2021b; Feng et al., 2022), such as carbon (C) sequestration, conservations of soil water and biodiversity, but are undergoing continuous degradation and large-scale conversion to monoculture plantations (Wang et al., 2017; Liu et al., 2020). During the last two decades, with the increasing demand for wood products and food, >60 % of primary and natural secondary forest areas in subtropical regions have shrunk with the rapid deforestation and conversion to plantations (Jin et al., 2019). This conversion gives rise to biodiversity loss, soil erosion, and fertility decline, which in turn leads to dramatic degradation of ecosystem services (Guillaume et al., 2018; Liu et al., 2022). Changes in plant species and diversity, litter quality and quantity, and silvicultural management practices caused by forest conversion affect soil texture, organic matter content and composition, and nutrients stoichiometric ratios, which are critical for maintaining biological productivity and supporting the growth of soil biome (Wang et al., 2021b). Nevertheless, there are still uncertainties about the variation in soil macronutrients and their impacts on soil biota after forest-to-plantation conversion in the subtropics. Therefore, quantifying and clarifying the effects of natural forest conversion on soil biota is necessary to evaluate soil biodiversity and multifunctionality.

As a primary component of soil metazoan and detritus food webs, nematodes perform a pivotal role in regulating nutrient dynamics and microbial communities, facilitating biogeochemical cycling in the soil biosphere (Fitter et al., 2005; Van den Hoogen et al., 2019). From an ecological perspective, the roles of nematodes are usually inferred by their trophic position, and are categorized into several trophic groups according to feeding types, encompassing herbivores, microbivores (bacterivores and fungivores), omnivores and predators. According to the colonizer persister (*cp*) scale, the life strategy of soil nematodes classified as *cp* 1–2 is *r*-strategy (opportunistic and fast-growing), while those of *cp* 4–5 are *K*-strategists (low fecundity, long generation times, struggle to recover after suffering detrimental effects) (Bongers, 1990). The structure, functional diversity and life strategy of soil nematodes respond rapidly to biotic (e.g., plant diversity and microbial activity) and abiotic (e.g., resource quality, and soil habitats) factors (Kitagami et al., 2020; Karuri, 2021). Many previous studies have confirmed that soil C and nitrogen (N) contents dropped sharply after natural forests were converted to plantations, which was mainly due to site reclamation, increased soil erosion and reduced plant diversity during the conversion process (Guillaume et al., 2015; Guillaume et al., 2018; Liu et al., 2020). The dramatic reduction of macronutrients will reduce the mineralization and turnover of soil C and N, resulting in the loss of microbial biomass and changes in soil microhabitat (Wang et al., 2021b; Liu et al., 2022). Ultimately, this leads to a decrease in food resources for microbivorous nematodes and a simplification of the omnivore-predators community structure thereafter (Karuri, 2021). However, compared to soil properties or microbial communities, studies on the diversity, functional groups, and life strategies of soil nematode communities after forest conversion remain rare and largely unclear in subtropical areas (Zhang et al., 2023).

In addition, nematodes are considered an ideal microfauna model for quantifying multitrophic energy flows because of their extensive niche width in lifestyle and living habitat, since they cover multiple trophic levels within soil food webs (Potapov et al., 2019; Liao et al., 2023). The distribution and allocation of energy through various trophic guilds of nematodes affect the complexity, stability and multifunctionality of the soil food web directly (Potapov, 2022). Energy flow across the food webs indicates the ability of nematodes to process C and is usually represented by C fluxes, which describe the energy consumption and structure of multiple trophic groups (Barnes et al., 2014; Wan et al., 2024). The nematode-based indices developed by Ferris and Barnes have greatly contributed to understanding it (Ferris, 2010; Barnes et al., 2014). Based on nematode biomass, the energy flow through the nematode food web can be estimated by calculating the total metabolic rate of nematode respiration and production (Van den Hoogen et al., 2019; Wan et al., 2024; Wang et al., 2024). In general, the complexity of soil food web structure and ecosystem status can be assessed through multiple indicators based on abundance, feeding types, energy flows, ecological indices, and functional traits of nematode (Du Preez et al., 2022; Hou et al., 2023). However, studies on how changes in soil nutrients, plant biomass, litter quality and quantity, and management practices during forest conversion affect the assemblage pattern, ecological performance, and energy flows of the nematodes, thereby altering the stability and multifunctionality of soil food webs, are currently lacking. Therefore, disentangling the impacts and proximate drivers of forest conversion on soil nematodes and energy flows is vital to assess the consequences faced by soil food webs and guide sustainable fauna-based forestry management after conversion.

This work seeks to examine the nematode community structure, composition, diversity, and energy flows depending on macronutrients in the soil after the conversion from forest to four monoculture plantations in subtropics. The purposes are: (1) to evaluate the alternations in soil macronutrients levels along conversion, including C, N, P and K contents; (2) to analyze changes and reactions in the composition, life strategy and diversity of soil nematodes, and to quantify the energy flow and food web structure after conversion; and (3) to clarify the linkages among soil nutrients, nematodes and energy flows. We hypothesize that forest conversion reduces nematode abundance and diversity by reducing soil C and N contents, thus inhibiting energy flow from resources (prey) to consumers (predators).

## 2. Materials and methods

### 2.1. Site description

The study area was located in the Lutou National Station for Scientific Observation and Research of Forest Ecosystems, Hunan Province, China (E113°51', N28°38'). The area has a sub-tropical monsoon climate, with an altitude of 124 m–1270 m, an average annual precipitation of 1420 mm, an average annual temperature of 15.8–9.6 °C, and an average air humidity of 82 %. Most of the soils within the region are Ferric and Orthic Acrisols. The natural secondary forests in the region are dominated by evergreen broad-leaved vegetation, hereafter referred to as “Forest”, and is mainly composed of *Pinus massoniana*,

*Cinnamomum camphora*, *Schima superba*, *Cyclobalanopsis glauca* and *Liquidambar formosana*.

In 2013, a great portion of the natural forests was deforested and cultivated. The following monoculture plantations were established: *Amygdalus persica* (Peach), *Myrica rubra* (Berry), *Camellia oleifera* (Oil), and *Cunninghamia lanceolata* (Fir). These four tree species are commonly found in subtropical timber forests and fruit tree plantations, which have certain commercial values and are suitable for planting in southern hilly areas. The original natural forest (Forest) in this area that has not been disturbed by human activities was selected as a control. In the Peach plantation, manure ( $4360 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) and mineral fertilizer (N: P: K ratios = 1:1:2,  $545 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) were applied every July and October. In the Berry plantation, manure ( $4360 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) was also distributed per October. Within the Oil, a total of  $163 \text{ kg ha}^{-1} \text{ yr}^{-1}$  of mineral fertilizer was received in May per year. Each tree was fertilized around 0.3 m under the base of the stem. Besides, site reclamation, weeding, herbicides and pesticides were carried out on the three plantations mentioned above. No management practice was performed on the Fir plantation.

## 2.2. Experimental design and soil sampling

In November 2018, a total of 20 plots ( $20 \times 20 \text{ m}^2$ ) were established using a completely randomized design in one natural forest and four monoculture plantations, with four replicates for each forest type, 20 m apart. In June 2021, five topsoil (0–20 cm) underneath the litter layer were taken from each plot by a five-point sampling method and mixed into one sample. A total of 20 bulk soil samples (5 treatments  $\times$  4 replicates) were collected, homogenized, and sieved using a 2 mm screen to remove roots and rocks to improve the nematode extraction efficiency (Schulz et al., 2018; Cesarz et al., 2019), and quickly carried back to the lab by ice box. Each sample was divided into three parts: the first part was stored at  $4^\circ\text{C}$  for nematode extraction (fresh soils), the second part was determined for the dissolved organic carbon and nitrogen content and microbial biomass (fresh soils), and the other was air-dried for chemical property analysis.

## 2.3. Soil chemical property analysis

Soil pH was assessed in mixtures with a soil-to-water proportion of 1:2.5. Soil organic carbon (SOC) was measured using a TOC analyzer (Shimadzu Corporation, Kyoto, Japan). Contents of microbial biomass carbon (MBC) and nitrogen (MBN), dissolved organic carbon (DOC) and nitrogen (DON) were assayed by the chloroform fumigation-extraction method using TOC and TN analyzers, respectively. Total nitrogen (TN) content was quantified by a continuous-flow analyzer (AA3, Bran + Luebbe, Germany). Alkali-hydrolyzable nitrogen (Available N) content was assayed by the semi-micro Kjeldahl method. Soil total phosphorus (TP) and available phosphorus (Available P) were determined by the molybdenum antimony anti-colorimetric method. Total potassium (TK) and available potassium (Available K) contents were measured using an atomic absorption spectrophotometer. Each sample was measured triplicate in parallel to minimize experimental errors.

## 2.4. Nematode extraction, identification and index calculations

Firstly, we extracted nematodes from each moist soil (100 g) by the Baermann funnel method (Barker et al., 1985; Cesarz et al., 2019), and then purified them through the frequent settling method at  $4^\circ\text{C}$  to clarify the turbid nematode suspensions. After preservation in 4% formaldehyde solution, all soil nematodes were counted and identified the first 200 individuals in each sample at the genus level using an inverted compound microscope and a differential interference contrast compound microscope, respectively. When the number of nematodes in the soil sample was below 200, all nematodes were identified. To ensure extraction efficiency and data reliability, we inserted a blank (without

soil samples) into each patch of 20 samples and performed a parallel measurement on each sample. The nematodes were divided into four trophic groups, including bacterivores, fungivores, herbivores, and omnivores-predators (Bongers, 1990). Furthermore, the functional guilds were determined based on the trophic behavior of nematodes and their ecological life strategies as colonizers or persisters (Bongers, 1990).

Nematode diversity was assessed using indices of the Shannon-Wiener ( $H'$ ), Pielou's evenness ( $J$ ) and Simpson's dominance ( $\lambda$ ) as follows (Gao et al., 2020) (Eqs. (1)–(3)):

$$H' = - \sum_{i=1}^S P_i \times \ln P_i \quad (1)$$

$$J = \frac{H'}{\ln S} \quad (2)$$

$$\lambda = \sum P_i^2 \quad (3)$$

In those equations,  $P_i$  represents the proportional abundance of taxon  $i$  in a soil sample, and  $S$  represents the total number of nematode genera.

The nematode data were additionally employed for the computation of the maturity index (MI) (Bongers, 1990). It was determined based on a colonizer-persister ( $cp$ ) scale, which ranges from a colonizer ( $cp$  value = 1–2,  $r$ -strategy) to a persister ( $cp$  value = 3–5,  $K$ -strategy). Low and high scores of MI indicate relative severely disrupted and stable soil environments, respectively. The calculation of MI was proceeded as follows (Eq. (4)):

$$MI = \sum_{i=1}^n v(i) \times f(i) \quad (4)$$

In this equation,  $v(i)$  is the taxonomic  $cp$ -value of a specific nematode genus, and  $f(i)$  is the frequency of this genus to the total density of free-living nematodes in soil samples. The nematode  $cp$  1–5 groups are all involved in this calculation.

Besides, the enrichment (EI) and structure (SI) indices of each soil sample were computed as follows (Ferris et al., 2001) (Eqs. (5)–(6)):

$$EI = e/(e + b) \times 100 \quad (5)$$

$$SI = s/(s + b) \times 100 \quad (6)$$

In the equation, the components are represented as follows:  $e$  represents the enrichment element (Ba1 and Fu2),  $b$  represents the fundamental food web element (Ba2 and Fu2), and  $s$  corresponds to the structure element (Ba3-Ba5, Fu3-Fu5, Om3-Om5, and Pr2-Pr5). The trophic groups are denoted as Ba for bacterivores, Fu for fungivores, Pr for predators, and Om for omnivores, respectively. Specific numbers associated with these groups represent particular  $cp$  values. The enrichment index (EI) indicates the equivalent level of food availability (available labile organic carbon) and nutrient enrichment, with values typically ranging from low to high (0–100). The structure index (SI) is commonly used to quantify the structure and complexity of soil food webs and disturbances caused by environmental or anthropogenic factors. Higher SI values indicate a more stable soil food web structure, while lower values indicate disturbed food webs (Du Preez et al., 2022). Faunal analysis involves the graphical representation of EI and SI values against one another, producing a four-quadrant diagram (Fig. S1). This diagram provides a visual representation of key characteristics that describe the stability of the soil food web and the amount of available resources (Ferris et al., 2001). The fresh weight of nematodes was calculated by abundance  $\times$  fresh body mass. The body mass was obtained from published papers and an openly accessible database (<http://Nemaplex.ucdavis.edu>).

## 2.5. Energy (carbon) flows through soil nematode communities

The energy (carbon) flow through soil nematodes was calculated by summing the parts of production and respiration (Andrássy, 1956; Ferris, 2010) (Eq. (7)):

$$F = \sum \left( \left( \frac{0.1W_i}{12cp_i} + 0.0159W_i^{0.75} \right) \times N_i \right) \quad (7)$$

where  $F$  refers to the total metabolic rate ( $\mu\text{g C } 100 \text{ g}^{-1} \text{ dry soil day}^{-1}$ ),  $N_i$  refers to the count of individuals of taxon  $i$ ,  $W_i$  and  $cp_i$  refer to the fresh body mass and  $cp$  value of taxon  $i$ , respectively.

In addition, we estimated C flow to each node by accounting for energy loss ( $D_{i0} \times F_0$ ) and assimilation efficiency ( $e_a$ ) at higher trophic levels. Bacterivores had an absorption efficiency of 0.60, fungivores of 0.38, herbivores of 0.25, and omnivores of predators of 0.50 (Barnes et al., 2014). First, the energy flows across the omnivores-predators were calculated. This computation of energy metabolism was mainly intended to evaluate the energy demands of nematodes without taking into account energy losses at higher trophic groups ( $F_0$ ). Second, it is assumed that omnivores-predators have similar dietary preferences and the abundance of community members will affect their feeding preferences for other trophic groups (Barnes et al., 2018; Liao et al., 2023; Wang et al., 2024). Finally, the energy loss from herbivorous, bacterivorous, and fungivorous to omnivorous-predatory nematodes is represented by  $D_{i0} \times F_0$  (Eq. (8)).

$$F_i = \frac{F + (D_{i0} \times F_0)}{e_a} \quad (8)$$

where  $F_i$  represents the potential C flow computed from nematode biomass of trophic group  $i$ .  $D_{i0}$  represents the omnivore-predators abundance-dependent feeding preference for trophic level  $i$ ,  $F_0$  represents the energetic demand of omnivore-predators, and  $e_a$  represents the assimilation efficiency. In addition, the uniformity of energy flow in the nematode food web was assessed by the proportion of the average energy flows across various channels to the standard deviation of these average values (Buzhdyan et al., 2020).

## 2.6. Data and statistical analysis

All data and statistical analysis and visualization were implemented in R (version 3.6.0) (Goslee and Urban, 2007; Villanueva and Chen, 2019). To ensure compliance with the normality and variance homogeneity, variables related to the nematode community were subjected to a  $\log_{10}(x+1)$  transformation before analysis. Soil properties, nematode communities and energy flows under five forest types were evaluated using a one-way analysis of variance (ANOVA) with least significant difference (LSD) multiple comparison tests ( $p \leq 0.05$ ). Principal coordinate analysis (PCoA) was performed to determine the Beta ( $\beta$ )-diversity of the nematode community according to the Bray-Curtis distance. To reveal the inter-connections of nematodes, we constructed the co-occurrence networks of nematodes based on the Benjamini-Hochberg's approach with the Spearman correlations ( $r > 0.6$  and  $p \leq 0.05$ ), and visualized in the "Gephi" software (Benjamini and Hochberg, 1995; Bastian et al., 2009). Furthermore, a robustness test was subjected to evaluate the resistance of each co-occurrence network by the natural connectivity of attacking nodes or edges, and the larger changes observed in the same proportion indicate lower stability within nematode community networks (Wu et al., 2021). Pearson's correlation coefficient and redundancy analysis (RDA) allowed us to clarify the correlations between soil nematode indicators and chemical parameters. More analysis details of RDA are shown in Tables S3–S6. To display the energy flow structure, the "igraph" package in R was used to construct and visualize a model of the soil micro-food web (Gauzens et al., 2018). In addition, a partial least squares path model (PLS-PM) was used to elevate the underlying effects of soil carbon (SOC, DOC, MBC), nitrogen

(TN, available N, DON, MBN), phosphorus (TP, available P), potassium (TK, available K), abundance, diversity ( $H'$ ,  $J$ ), structure index (SI) and nematode community composition (principal coordinate analysis of community composition selected the first axis, PCoA1, Table S2) on the total energy flow and flow uniformity by using the "plspm" package in R. The scores of each observable variable in the outer models and details of the inner models are listed in Tables S7–S10.

## 3. Results

### 3.1. Soil properties

After conversion from forest to plantations, soil pH elevated in plantations (Fig. 1a). The SOC contents decreased by 65 % in plantations (Fig. 1b). The DOC contents declined in plantations except for the Berry, and the MBC contents were also reduced except for the Oil (Fig. 1c and d). An analogous downward pattern was observed of TN, available N, and DON contents, especially the contents of TN and available N in the plantation declined sharply, by 55 % and 49 %, respectively (Fig. 1e–g). The reductions of TP and available P content were also observed in Oil and Fir plantations (Fig. 1i and j). However, both TK and available K contents increased, especially in Peach plantations (Fig. 1k and l).

### 3.2. Nematode community composition and diversity

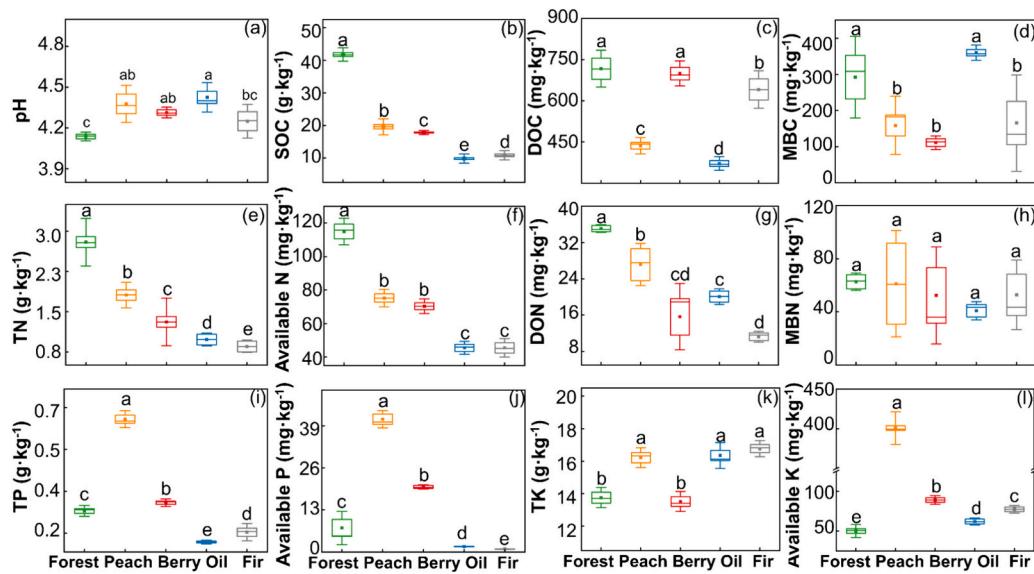
Morphological character identification of soil nematodes distinguished a total of 32 genera within the five forest types. The dominant genera were bacterivorous and fungivorous nematodes, including *Acrobeloides*, *Prismatolaimus*, *Plectus* and *Tylencholaimus* (Fig. 2; Table S1). Soil nematode communities presented clear separation along the forest conversion via PCoA analysis (Fig. 3l; Table S2). Compared with Forest plots, the bacterivorous nematode *Acrobeloides* increased by 50 %–975 %, while *Plectus* and *Prismatolaimus* decreased by 44 %–80 % and 31 %–90 % in plantations, respectively. Similarly, the fungivorous nematode *Tylencholaimus* declined by 100 %–968 %. Furthermore, notable changes in herbivores and omnivores-predators were primarily observed within the genera of *Helicotylenchus*, *Lelenchus* and *Tripyla*. Specifically, *Helicotylenchus* in the Berry plantation substantially enriched by 334 %, whereas *Lelenchus* and *Tripyla* in the four plantations declined by 21 %–95 % and 66 %–88 %, respectively (Fig. 2; Table S1).

Total nematode abundance was greater in the Forest, Peach, Berry and Oil plantations than that in the Fir ( $p \leq 0.05$ ) (Fig. 3e). After forest conversion, a loss of bacterivore abundance was observed in the Fir plantations, the abundance of herbivores declined in the plantations except for the Berry, and the omnivore-predator declined except for the Oil (Fig. 3a, c and d,  $p \leq 0.05$ ). The value of EI was highest in the Peach among the five forest types (Figs. 3f and S1). Forest conversion resulted in an average decrease of 27 and 0.5 in the SI and MI values of the nematode community in the plantations, respectively (Fig. 3g and h,  $p \leq 0.05$ ). The values of  $H'$  in the Peach, Berry and Oil plantations declined, but the  $\lambda$  index increased (Fig. 3i and k,  $p \leq 0.05$ ).

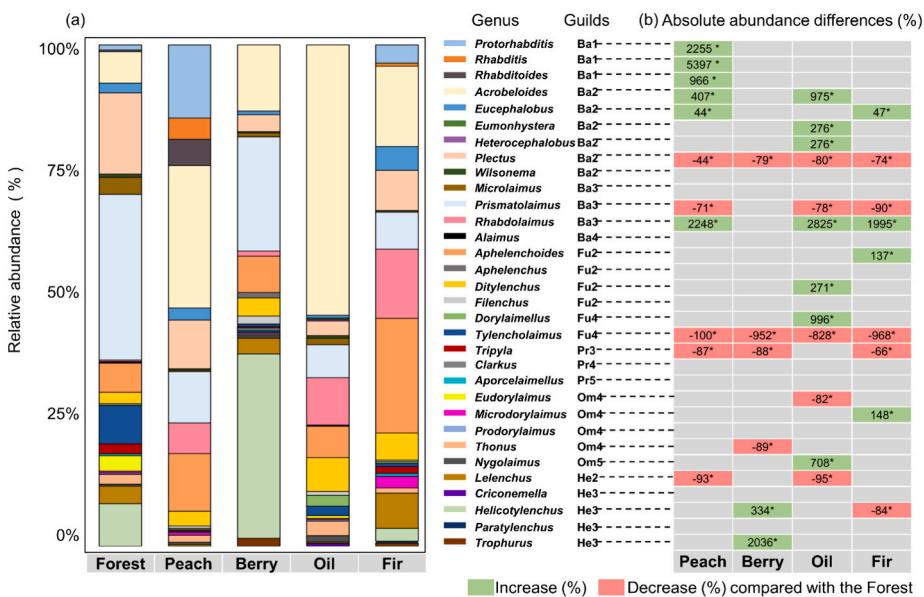
The soil nematode co-occurrence networks indicated that the average degree (connectivity) and link density (complexity) of nodes increased with forest conversion, especially for the Berry and Peach plantations (Fig. 4). Compared with the Forest, the degree and density of these two plantations increased by 29 % and 36 %, respectively. In contrast, the connectivity and complexity of the Fir and Oil networks remained stable or slightly declined with the conversion, notably in the Fir. These results were confirmed by the robustness test. Peach and Berry had steeper slopes of natural connectivity of networks, indicating lower resistance when eliminating an identical percentage of nodes or edges (Fig. 4).

### 3.3. Energy flows and uniformity through nematode food webs

Forest conversion resulted in a downward trend in the total energy



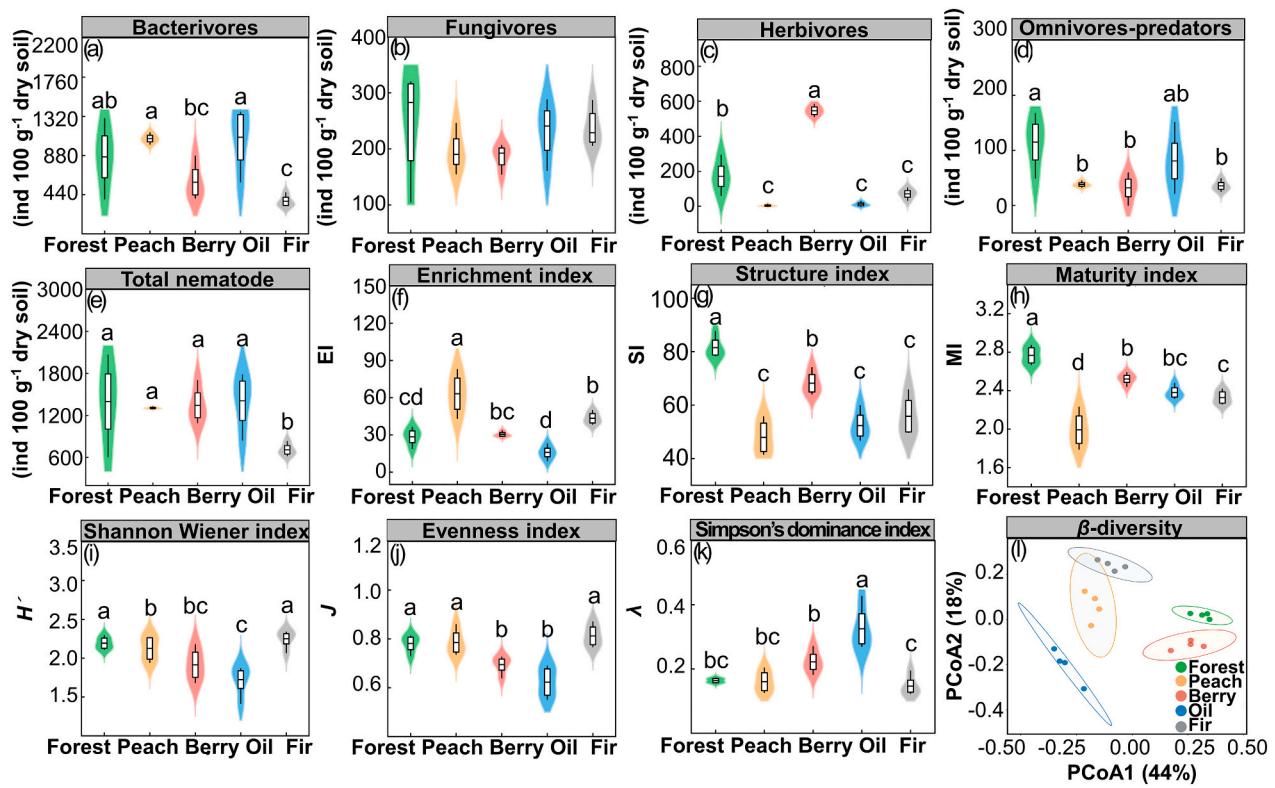
**Fig. 1.** Soil biochemical properties in the Forest, and monoculture plantations of Peach, Berry, Oil and Fir. pH: soil pH (a), SOC: soil organic carbon content (b), DOC: dissolved organic carbon (c), MBC: microbial biomass carbon (d), TN: total nitrogen content (e), Available N: alkali-hydrolysable nitrogen (f), DON: dissolved organic nitrogen (g), MBN: microbial biomass nitrogen (h), TP: total phosphorus (i), Available P: available phosphorus (j), TK: total potassium (k), Available K: available potassium (l). Boxes represent the interquartile ranges, and the median and mean values are represented by the lines and points, respectively. Significant differences are represented by lowercase letters ( $p \leq 0.05$ ) according to the LSD test.



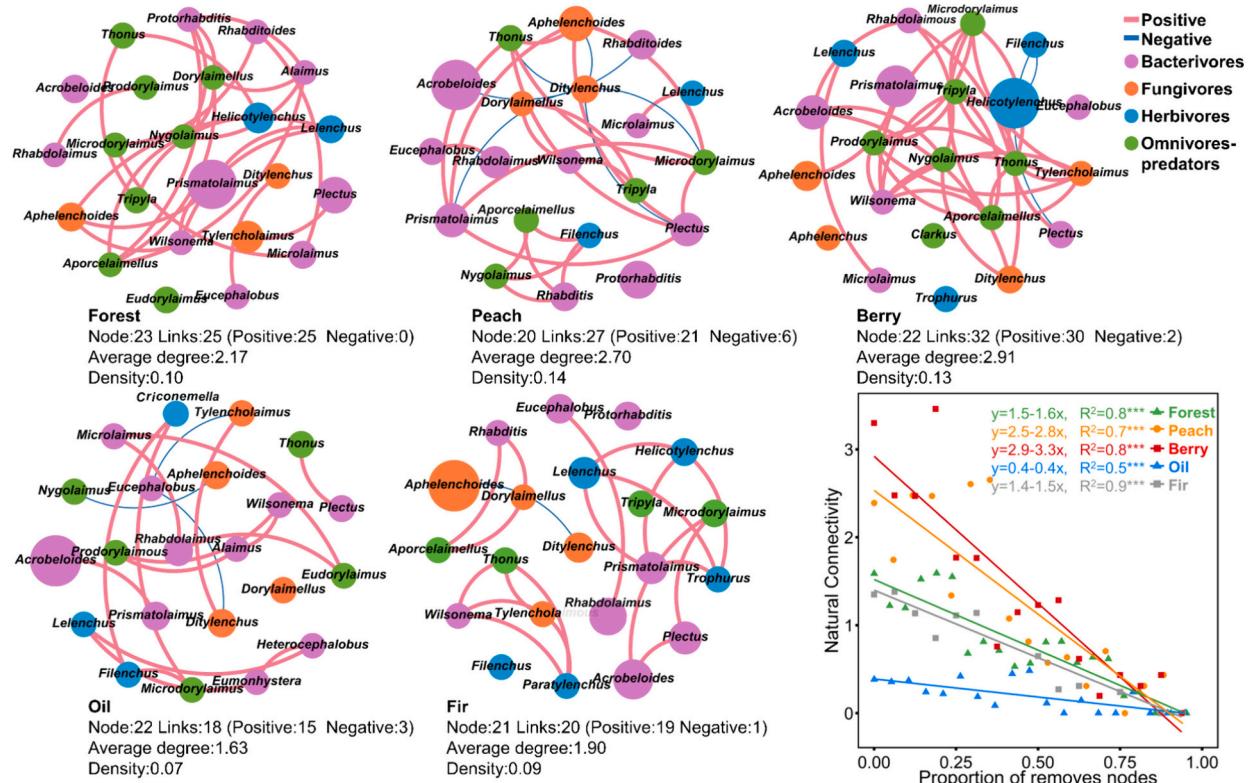
**Fig. 2.** Effects of forest conversion to monoculture plantations on soil nematode genera. (a) Stacked bar plot of the relative abundance of nematode genera for the Forest, Oil, Peach, Berry, and Fir. (b) Abundance differences in the four plantations compared to the Forest. The designation of nematode functional guild is a combination of trophic group and cp value: Ba, bacterivore; Fu, fungivore; Pr, predator; Om, omnivore; He, herbivore. The red grid indicates that the abundance in the plantation is fewer than that in the Forest, while the green grid indicates that the abundance in the plantation is greater than that in the Forest, the gray grid indicates that the genus is absent in the plantation, and \* indicates a significant difference ( $p \leq 0.05$ ).

flow and reduced sharply in Fir (Fig. 5a). The conversion process was associated with a remarkable drop in energy flow through each trophic level. Specifically, energy flows of fungivores depleted in four plantations, flows of herbivores declined in the Peach, Oil and Fir, and flows of omnivore-predators declined in Peach, Berry and Fir (Fig. 5c, d and e,  $p \leq 0.05$ ). Among the five types, the biomass of bacterivores was maximal than other trophic groups (Fig. 6). The conversion from forest to plantation caused a remarkable decrease in the biomass of fungivorous and omnivorous predatory nematodes. Therefore, the flow uniformity via the soil food web of the Forest was higher than that of the four

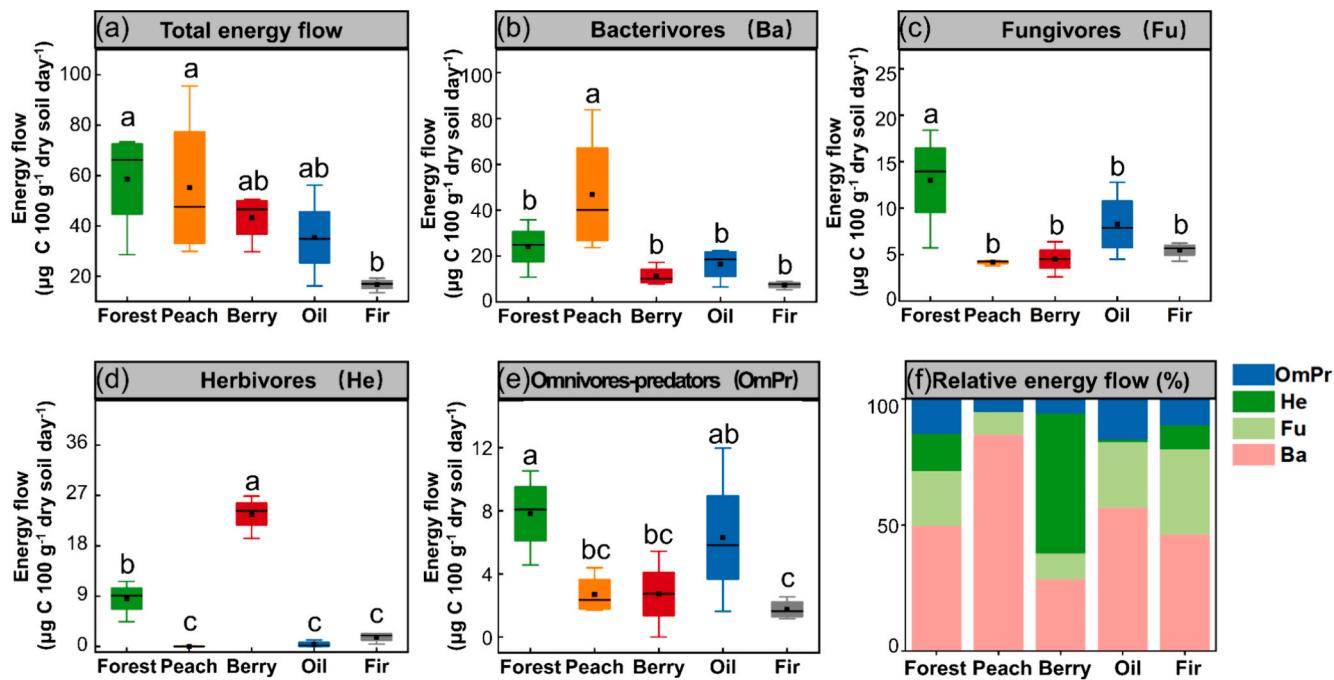
plantations. Compared to the Forest, the energy flows decreased from basic resources to fungivorous nematodes in four plantations, and flows to bacterivorous and herbivorous nematodes decreased except for the Peach and Berry, respectively. Consequently, the biomass of omnivore-predators and flows from these lower trophic groups to them declined after conversion (Fig. 6).



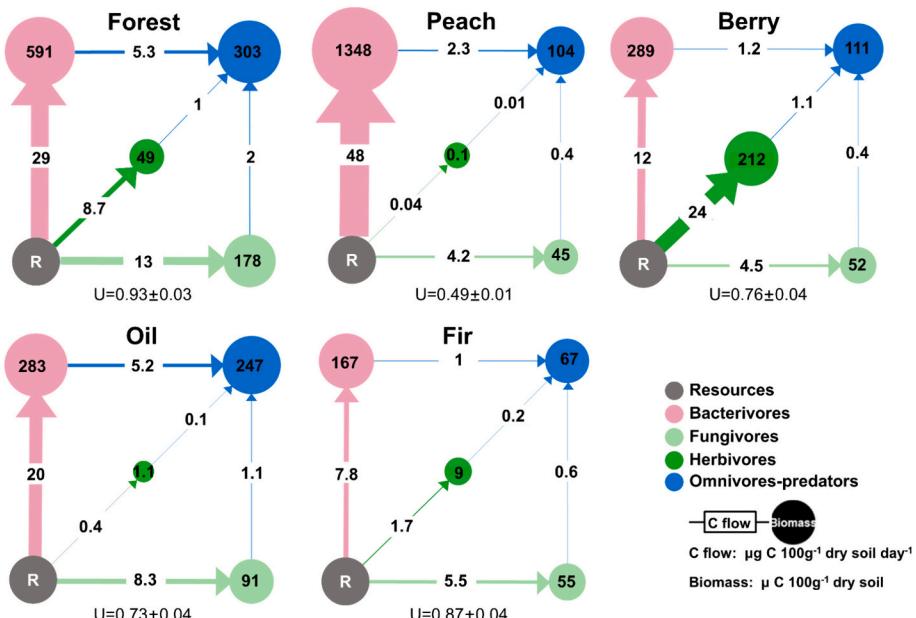
**Fig. 3.** Responses of soil nematode abundances (a-e), ecological indices (f-h) and diversities (i-l) to forest conversion to plantations. Boxes represent the interquartile ranges, and the mean values are represented by the lines, respectively. The colored clouds around the box represent the data distribution. Significant differences are represented by lowercase letters ( $p \leq 0.05$ ) according to the LSD test.



**Fig. 4.** Co-occurrence networks of nematode communities in the Forest and four plantations of Peach, Berry, Oil and Fir. Nodes in the network represent nematode genera. The size of each node is proportional to abundance. Pink and blue edges represent the positive and negative correlations, respectively. The width of the edge represents the strength of the correlation. Robustness analysis shows the relationships between nematode natural connectivity and the proportion of removed nodes.



**Fig. 5.** Energy flows through soil nematodes (a) and each trophic group (b–e), and the relative contributions of trophic groups (He, herbivores; Ba, bacterivores; Fu, fungivores; OmPr, omnivores-predators) to the whole community energy flow (f) in five forest types. Significant differences are represented by lowercase letters ( $p \leq 0.05$ ) according to the LSD test.



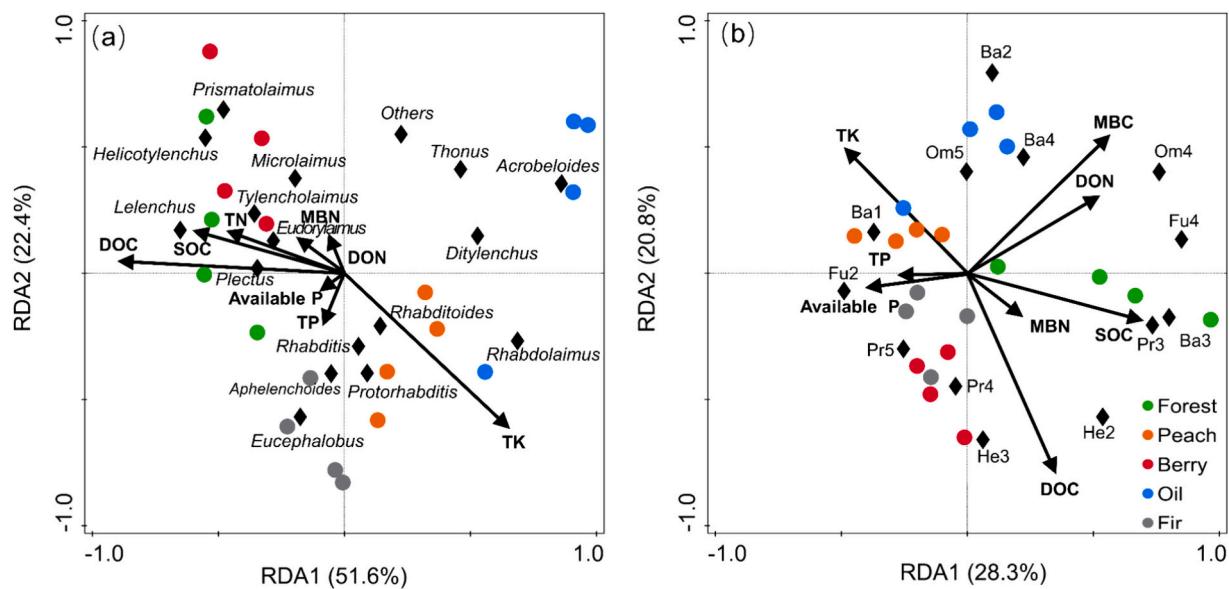
**Fig. 6.** Energy structure of soil nematode communities in the Forest, Peach, Berry, Oil and Fir plantations. For each forest type, a five-node food web is constructed with bacterivores (pink), fungivores (light green) and herbivores (green) receiving energy from basal resources (R, gray), and omnivores-predator (blue) receiving energy from other nodes. The numbers along the lines represent energy flow ( $\mu\text{g C } 100 \text{ g}^{-1} \text{ dry soil day}^{-1}$ ). The size of the nodes and their values correspond to the fresh biomass ( $\mu\text{g C } 100 \text{ g}^{-1} \text{ dry soil}$ ). U indicates the uniformity (mean  $\pm$  standard error) of soil nematode energy structure.

### 3.4. Pathways determining soil nematode composition, energy flows and uniformity

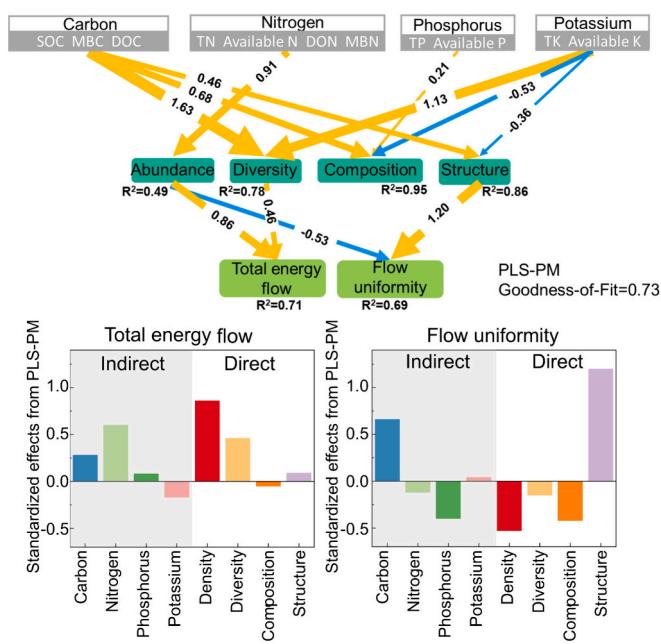
Following the RDA results, soil chemical properties explained 74 % and 49 % of the entire variation in the nematode composition and guilds, respectively (Fig. 7, Tables S3, S5). The soil nematode composition of the Forest had a closer relation to greater soil C and N contents, whereas the communities of the Peach and Fir were closer connected with P and

K contents (Fig. 7a; Table S4). The prevalence of prominent genera, including *Prismatolaimus*, *Microlaimus*, *Helicotylenchus*, *Tylencholaimus*, and *Eudorylaimus* increased with SOC, DOC, TN, MBN and DON contents ( $p \leq 0.05$ ) (Fig. 7a). Abundances of bacterivores, fungivores, and omnivores ( $cp$  values between 3 and 5) decreased with reduced SOC, MBC, and DON contents ( $p \leq 0.05$ ) (Figs. 7b and S2; Table S6).

The PLS-PM model explained 71 % of the total energy flow and 69 % of the uniformity of the nematode food web, respectively (Fig. 8; Table



**Fig. 7.** Redundancy analysis (RDA) between soil properties and (a) dominant nematode genera (abundance  $\geq 50\%$ , top 16), and (b) nematode cp-guilds. Black arrows and diamonds indicate soil properties and nematode genera or cp-guilds, respectively. Green, orange, red, blue and gray circles represent Forest, Peach, Berry, Oil and Fir, respectively.



**Fig. 8.** Partial least squares path model (PLS-PM) for energy flow and uniformity of soil nematode food webs. Standardized effects of soil carbon, nitrogen, phosphorus, and potassium, and nematode density, diversity, composition, and structure indices on the total energy flow and uniformity of nematodes after forest conversion. Yellow and blue arrows indicate positive and negative effects, respectively ( $p \leq 0.05$ ). Arrow thickness corresponds to the strength of standardized path coefficients (the numbers on the line). The  $R^2$ -values represent the proportion of variance explained.

S8). The community structure, composition, and diversity of the nematodes changed with decreasing C contents (SOC, DOC, MBC) (path coefficients were 0.46, 0.68 and 1.63, respectively,  $p \leq 0.05$ ) (Fig. 8; Table S9). Nematode abundance reduced with decreasing N contents (path coefficient = 0.91) (Table S9), whereas structure index (SI) and composition (PCoA1) changed with increasing potassium, respectively (path coefficients were -0.36 and -0.53, respectively) (Table S9). The

total energy flow was directly related to nematodes' abundance (path coefficient = 0.86) and diversity (path coefficient = 0.46), and indirectly related to soil C and N (Fig. 8; Table S10). Flow uniformity increased by raised structure (directly) index and C contents (indirectly) among all factors (Fig. 8; Table S10).

#### 4. Discussion

##### 4.1. Soil nematode composition and diversity impacted by forest conversion

The conversion from subtropical forests to monoculture plantations affected the abundances of dominant trophic groups of the nematode community. Particularly, the abundances of total nematodes and omnivores-predators reduced substantially in the plantations, but that of some bacterivores and fungivores enriched (Figs. 2 and 3). These findings align with variations in soil nematode communities after conversion from secondary forests to eucalyptus and litchi plantations (Gao et al., 2020), primarily owing to reductions of soil C, N contents and plant diversity, and shifts in management practices (Wang et al., 2021a). Firstly, a pronounced drop in soil C and N amounts contributed to a decline in the entire population of nematodes. The conversion caused this reduction in soil C and N content, leading to diminished food sources for soil organisms, thus exerting a bottom-up regulatory impact on nematode populations (Zhao et al., 2011). Besides, our previous study found that the soil C availability increased and the C:N ratio decreased after transformation, contributing to an increase in the abundance of *r*-strategic bacteria and fungi (Liu et al., 2022), thereby enriching the populations of *r*-strategic bacterivorous (e.g., *Acroboloides*) and fungivorous nematodes (e.g., *Ditylenchus*) (Xiao et al., 2014). Secondly, the loss of plant diversity in forest conversion to plantations, represented by a reduction in inputs such as litter, root biomass and rhizodeposition, had deleterious effects on food resources associated with microbial activity and viability (Soong et al., 2016; Krashevskaya et al., 2019; Da Silva et al., 2020). Consequently, as plant community diversity decreased within plantations, the populations of microbivores also decreased (Kitagami et al., 2020). Thirdly, soil disturbance caused by forestry management practices, including site reclamation, weeding, litter removal and fertilization, prompted different changes in the life strategies of nematodes, mainly increasing the abundance of *r*-strategists

(e.g., *Acrobeloides*) and decreasing in *K*-strategists (e.g., *Tylencholaimus*, *Tripyla*, *Thonus* and *Prodorylaimus*). The strong recovery of major *r*-strategy bacterivores (*Acrobeloides*) in the Peach and Oil plantations is attributed to the application of mineral fertilizers, as they are sensitive to N content (Zhao et al., 2014). However, it negatively affects *K*-strategy omnivore-predators (e.g., *Tripyla*) (Wang et al., 2022). Thus, the *K*-strategists at higher trophic levels of the nematodes' food web are less prevalent in disturbed plantation soils (Zhong et al., 2017).

After forest conversion, the structure, maturity and Shannon-Wiener indexes in plantations decreased, while the Simpson index increased. The enrichment index value of the Peach was greater than that of other forests (Fig. 3). In general, the structure index is used to assess alternations in soil micro-food web structure after disturbance (Ferris, 2010), and the maturity indicator is used for expressing the level of environmental disturbance (Du Preez et al., 2022). Lower values of these two nematode indices within plantations suggest degradation of the nematode community and a potential reduction in the stability of the soil micro-food web structure after conversion. Changes in the co-occurrence network and faunal analysis of weighted nematodes also confirmed these results (Figs. 4 and S2). The maturity and structure indices of nematodes decreased after conversion, mainly due to the reduced taxa at higher *cp* scales (Wang et al., 2021b). These groups, composed mainly of predators and omnivores, are thought to play a key role in regulating the stability of soil food webs (Bongers, 1990). In addition, management practices such as site reclamation, weed control, fertilization and habitat change after conversion may also lead to the disappearance of omnivorous-predatory nematodes that are difficult to recover after soil disturbance, thereby reducing maturity and structure index values (Xiao et al., 2014; Lu et al., 2016). Correspondingly, the reduction of these nematode groups causes a decline in predator-prey interactions, which can generate complex food webs to stabilize communities against disturbance and maintain ecosystem functions (Brose et al., 2019). Besides, the index of Shannon-Wiener places greater emphasis on rare taxa, while the Simpson attaches more importance to dominant taxa (Li et al., 2019). The decrease in Shannon-Wiener and the increase in Simpson values in monoculture plantations imply an increase in the homogeneity of the soil nematode community after forest conversion (Yan et al., 2018). This rise has been attributed to an increase in the dominant species *Acrobeloides* and a decrease in rare groups such as omnivores-predators along the conversion of the forest. Additionally, the higher enrichment index value of the Peach is possibly due to the application of organic and mineral fertilizers that enriched food resources and stimulated the proliferation of basal nematode groups (Liang et al., 2009).

#### 4.2. Predominate drivers of energy flows in nematode communities

As we hypothesized, forest conversion suppressed energy flows through soil nematodes, particularly the fungivores and omnivore-predators, due to the drastic reduction of soil C and N nutrients (Figs. 7, 8 and S2). The reasons are as follows: (1) high organic C content provides soil organisms with more substrates, facilitating more C transfer from bacteria and fungi to nematodes, thereby increasing the energy flow across nematodes (Wan et al., 2022). This was further confirmed by the higher MBC content and energy flow in the Forest (Fig. 1). And due to fungivores are relatively difficult to obtain resources compared to bacterivores, and the chemical resistance of fungal products to decomposition, which slows the degradation of microbial-derived organic matter in the fungal decomposition process. Thus, the reduction of C along conversion has a greater impact on the energy flows of fungivores than bacterivores, and results in energy reductions to omnivore-predators (Zhang et al., 2016). (2) Higher contents of soil N increase energy flow within the nematode communities. Because the high N content increases N mineralization, then increases N availability and microbial activity, which in turn, facilitates the feeding, motion, and propagation of nematodes (Zhang et al., 2021). (3) Soil C and N

resources alter energy flows by affecting the diversity and abundance of nematode groups, particularly omnivore-predators. High organic C and N contents can increase species diversity by regulating competition for dominant prey species, and stimulating greater energy flows and balanced energy allocation across the food web through trophic and functional complementarity (Potapov et al., 2019). For instance, larger-bodied predatory nematodes have been shown to facilitate coexistence and stimulate the diversification degree of prey species (Thakur and Geisen, 2019). This has been attributed to their capacity to enhance species interactions by hunting a wider range of prey sizes (Brose et al., 2019). This was supported by forest conversion reducing the omnivore-predators' abundance and causing a declined diversity of nematode communities.

According to the energy structure (Fig. 6), most of the energy flow within the plantation didn't transmit to predators, leading to a decoupling of the soil micro-food web, which reflects instability (Wan et al., 2022). However, compared to other plantations, the energy flows via bacterivorous and herbivorous nematodes were notably increased in the Peach and Berry, respectively. These results were attributed to the inputs of manure. Firstly, manure offers a large amount of microbes and labile C to bacterivores, which are more sensitive to resource acquisition than fungivores (Zhang et al., 2021). Thereby increasing more energy flow through these groups. Secondly, because manure increases the amount and diversity of organic substrates, accelerates the utilization rate of organic C in the micro-food web. Consequently, this contributed to a rise in nematode biomass and diversity, ultimately leading to a greater energy flow in those particular plantations (Wan et al., 2022). Thirdly, the application of manure raises the root growth of plants, which can provide more resources to herbivores and thus increase their abundances. Collectively, this indicated that the structure and energy flows of the nematode food web are regulated by the bottom-up effect, mediated by variations in soil C and N resources. However, forest conversion reduced those resources by decreasing the plant species richness aboveground (Sawada et al., 2023), thereby destroying soil food web structure and hindering energy flows (Potapov, 2022). The application of manure in plantations is conducive to the restorations of bacterivorous and herbivorous nematodes and increases energy flows across various trophic groups.

However, soil P and K contents adversely influenced soil nematode community structure and composition, eventually affecting energy flow and uniformity (Fig. 8; Table S9). The result is consistent with the impacts of P addition on the assemble patterns and composition of soil nematodes (Zhao et al., 2014). Since the addition of mineral P raised the nematode structural footprint index, which may dramatically decrease C utilization of soil nematode structural components (Zhao et al., 2014). Higher mineral P input even causes salt toxicity, which suppresses the growth of soil nematodes. Another explanation is that the drop in nematode abundance in plantations may be attributed to the inputs of mineral P, which increases the soil available P and leads to a reduction of resources from plants for soil organisms (Da Silva et al., 2020). As plants allocate resources (e.g., rhizodeposit) to soil microbes that are in charge of organic matter decomposition and P release, this P can be utilized by plants in low P availability environments. In high P content soils, however, plants can access P directly from the soil, leading to lessened P content for the soil biome, including nematodes and other micro-faunas (Xia et al., 2014). Krashevskaya et al. (2014) also observed that excessive P fertilizers have a detrimental influence on the diversity and density of soil biotas. Moreover, excessive K fertilization may adversely affect nematode maturity and food web stability Wang et al. (2013). This is in compliance with the decrease of structure and maturity index values of nematodes after the increases of TK and available K contents (Fig. S2). However, a limitation of this study is that it only assessed the nematode food web and did not compute empirically the identity, size and feeding pathways of protozoa and other microbivores. Since they are often viewed as bacterivores that control bacterial energy channels in soil food webs and playing a crucial role in the mineralization process (Hunt

et al., 1987). In addition, failure to consider the feeding preferences of various taxa may lead to overestimation or underestimation of the contributions of some faunal groups to energy flux and C cycling. But complex biological and feeding relationships have made it difficult to build energy flow models of food webs so far (Geisen, 2016). Therefore, future efforts should quantify the feeding efficiency and ecological functions of protozoa and other soil organisms, and then incorporate them into improved models to elucidate the structure, diversity, and energy flow of complex soil food webs.

## 5. Conclusions

The conversion from subtropical forests to plantations declined the abundance, maturity, diversity and structural stability of soil nematode communities. This conversion altered the composition of the dominant trophic groups within the nematode community. Particularly, the abundance of bacterivores (*Acrobeloides*) increased, but the abundance of bacterivores (*Plectus* and *Prismatolaimus*), fungivores (*Tylencholaimus*) and larger-sized omnivorous-predatory nematodes (*Tripyla*, *Thonus* and *Prodorylaimus*) decreased. According to the colonizer persistenter scale, forest conversion results in a boost for the abundances of the *r*-strategists (e.g., *Acrobeloides*) and a decrease in *K*-strategists (e.g., *Tylencholaimus*, *Tripyla*, *Thonus* and *Prodorylaimus*). This conversion therefore reduced the energy flow and uniformity of total nematodes and the most trophic taxa, especially the fungivores and omnivore-predators. Soil food web structure and energy flows are subjected to bottom-up control, which is related to reduced soil C and N contents due to the decrease of plant diversity, litter and rhizodeposition inputs. After forest conversion, the application of manure in plantations is beneficial to the recovery of *r*-strategy nematodes (such as *Acrobeloides*, *Protorhabditis*, *Rhabditis* and *Rhabditoides*). In summary, the natural forest conversion degraded nematode food web structure and energy flow, which are crucial for accurate predictions of soil biodiversity and the stability of terrestrial ecosystems. Therefore, the establishment and management of monoculture plantations should consider the protection and restoration of biodiversity and energy flows of soil micro-food web, including the diversity and structure of nematodes and microbial communities, to increase the stability and ecological functionality of plantation ecosystems.

## CRediT authorship contribution statement

**Jiachen Wang:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ting Liu:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Jie Zhao:** Writing – review & editing, Visualization, Methodology. **Chen Ning:** Writing – review & editing, Visualization, Methodology. **Shu Chen:** Writing – review & editing, Visualization, Methodology. **Xuyuan Zhang:** Writing – review & editing, Visualization, Methodology. **Gao-qiang Liu:** Writing – review & editing, Visualization, Methodology. **Yakov Kuzyakov:** Writing – review & editing, Visualization, Methodology. **Wende Yan:** Writing – review & editing, Supervision, Resources, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

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