



Disturbance intensity shapes the soil micro-food web compositions and energy fluxes during seven-year land use changes



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ABSTRACT

Soil micro-food webs play an important role in ecosystem functions through energy flow; they are strongly influenced by land use types. Previous studies have typically utilized the space-for-time substitution or single-time sampling method to reflect the land-use change effects by comparing differences among existing land-use types. These methods would increase random error. Research on how synchronized land-use change (starting at the same time and place) influences soil ecological processes and functions is urgently needed. Based on a controlled field experiment and seven years of observations, this study explored the effects of land-use change from natural shrubland to cropland (maize), forage land (tall-grass forage), and economic forest land (walnut plantation) on the community structure and energy dynamics of the soil micro-food webs. Cropland simplified the complexity of the soil food webs compared to the other three land-uses. Forage grassland maintained the highest biomasses of soil total microbes, fungi, and arbuscular mycorrhizal fungi. In addition, economic forest land improved the flow uniformity of the micro-food web by increasing energy transfer from resources to bacterivores, fungivores, and herbivores while decreasing herbivore energy flow to omnivores-predators. Omnivore abundance and nematode diversity were important predictors of total energy flux and flow uniformity of the soil micro-food webs, respectively. In addition, omnivores maintained the complexity of soil micro-food webs by promoting interactions among trophic groups through top-down control. Soil organisms are sensitive to the response of agricultural management and planting time, and it may take several years or more to reach a dynamic equilibrium. Different types and levels of ecosystem disturbance (e.g., tillage and no-tillage, fertilizer rates, aboveground biomass removal intensity) may be the major drivers of soil community during land use change. Our findings highlight the importance of conservation agriculture in maintaining soil food web structure and energy flow for future sustainable land uses, and that promoting omnivore abundance is essential for food web complexity and stability.

1. Introduction

As one of the drivers of global change, land use exerts a profound influence on biodiversity and ecosystem functions on a global scale (Sala et al., 2000; Maxwell et al., 2016). In particular, the transition from forest ecosystems to agricultural ecosystems and their continuous intensive use have led to the loss of ecosystem services and the diminution of human well-being through changing above ground vegetation

and frequent re-shaping of underground communities (Gossner et al., 2016; Le Provost et al., 2021), impacting soil physico-chemical properties (Biro et al., 2013; Emadi et al., 2008; Trabaquini et al., 2015), and altering nutrient cycling processes (Kaye et al., 2005; McLauchlan et al., 2007; Wang et al., 2015).

Karst landscape covers about 15–22% of the global land area (Larsen, 2011; Wang et al., 2019). The humid subtropical and tropical karst area in southwest China is one of the largest continuous karsts in the

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world (Wang et al., 2019). Due to human pressure and the fragility of the topsoil, the karst region faces severe ecological degradation. The enormous population pressure and food shortage have compelled farmers to extend cropland from valleys and lowlands to slopes, transforming forests or shrublands into agricultural land (Liao et al., 2018). Typical agricultural land use types include cropland, pasture, and economic forest plantation (e.g., walnut) in this region. In general, cropland can provide food security for basic living, pasture protects soil health and is good for the economic, and economic forest also provides good benefits. However, many previous studies reported that land use change from natural or semi-nature land use types to agricultural land use types have decreased the soil ecological functions and resulted in soil degradation (Hu et al., 2020; Lal, 2015; Baude et al., 2019; Raiesi and Salek-Gilani, 2020). Those studies commonly used space instead of time approach (i.e. space-for-time substitution) and/or single-time sampling method to evaluate the ecosystem services or health status of different land uses (Green et al., 2019; Guan et al., 2021; Rodríguez-León et al., 2021). Few studies of land use change effects are based on preplanned experimental designs that began at the same time and were monitored over time. Therefore, researches with a sound experimental design, continuous treatment, and long-term monitoring are required to accurately assess the land use change effects.

Soil biota, including bacteria, fungi, and animals, have a central role in all aspects of global biogeochemistry, affecting soil fertility and exchange of gases such as carbon dioxide with the atmosphere (Paul, 2014). The evaluation of interactions among the entire soil biological groups is challenging due to the extensive diversity of soil organisms and the intricate relationships among trophic groups (Wardle et al., 1998; Jiao et al., 2022). It is very useful to have nematodes as a proxy for the whole system. Nematodes are the most abundant soil faunas on the earth (Van Den Hoogen et al., 2019). Owing to different life history strategies and feeding habits, they occupy various trophic levels in food webs (Bongers and Ferris, 1999) and provide valuable information on ecosystem status through functional shifts (Ferris et al., 2001). With their very limited mobility they could indicate conditions in the soil horizon that they inhabit (Bongers and Ferris, 1999). In addition, nematode feeding types and life history strategies are well documented at genus or family levels (Yeates et al., 1993; Bongers and Bongers, 1998). Hence, they can serve as excellent ecological indicators. Soil micro-food web is mainly composed of soil bacteria, fungi, protozoa, algae, and nematodes (Coleman and Wall, 2015). It is the foundation of the soil food web containing several trophic levels. Through trophic interaction and energy flow, the soil micro-food web drives many ecosystem functions such as controlling pest, shaping plant performance (Wilschut and Geisen, 2021), and facilitating nutrient cycling (Crowther et al., 2019; Delgado-Baquerizo et al., 2020; Bardgett and van der Putten, 2014; Evans et al., 1993). Moreover, the soil micro-food web is sensitive to the intensity of land use (Tsiafouli et al., 2015). Changes in the diversity or abundance of one group within the soil food web may affect another group through bottom-up or top-down control (Gessner et al., 2010), thereby influencing food web structure, diversity, or stability (Neutel et al., 2002). For instance, the transition from grassland to cropland decreased the abundance of soil nematodes, microarthropods, and earthworms (Postma-Blaauw et al., 2010). The conversion of grassland to winter wheat cropland reduced the complexity of the soil food web (Tsiafouli et al., 2015). Cropland abandonment for eight years benefited the soil food web, especially in terms of abundance and diversity (Guan et al., 2021). Therefore, shifts in the composition and structure of soil food webs, as well as associated soil biogeochemical processes, are important aspects of land use transitions.

Assessments of energy flux through food webs show promise for reflecting ecosystem multifunctionality (Barnes et al., 2018; Wang et al., 2024). As noted above, soil nematodes have advantages as excellent indicators of soil food webs. Patterns of nematode trophic compositions and metabolic carbon consumptions can be utilized as a proxy for energy flux and energy distribution (i.e., flow uniformity) (George and Lindo,

2015; Potapov et al., 2021). In addition, the nematode functional guild was defined based on the trophic behaviors (bacterivores, fungivores, herbivores, predators or omnivores) and its ecological life strategy as a colonizer-persister values (*cp* 1–5) (Bongers, 1990; Ferris et al., 2001). Generally, opportunistic microbivores (bacterivores and fungivores) are more common in *cp* 1–2 categories and respond faster to exogenous carbon supply than herbivores and omnivores in *cp* 3–5 categories (Turnbull et al., 2014; Zhang et al., 2017). The energy flux through decomposers is typically associated with C sequestration (Pollierer et al., 2012), litter decomposition (Wall et al., 2008), and nutrient cycling (de Ruiter et al., 1994). The energy flow from plants to herbivores relates to plant productivity and pest control (McNaughton et al., 1989; Barnes et al., 2020). Previous studies have reported that land use types significantly affected the energy fluxes through soil food webs (Potapov et al., 2019; Wan et al., 2022a). For examples, the total carbon flux through the soil micro-food webs was higher in the cropland than that in the grass-shrubland (Zheng et al., 2023). Transitions from tropical rainforests to plantations decreased the energy flux of predators (Potapov et al., 2019).

Here, a long-term field experiment was conducted to investigate the effects of land use changes from natural shrubland to forage grassland, economic forest land, and cropland on soil micro-food web structure and energy flux. We hypothesized that the transition from natural shrubland to monocultured artificial ecosystems would simplify the structure and complexity of soil food webs. We further hypothesized that transforming natural shrubland into monocultured artificial ecosystems would reduce the energy flux and flow uniformity of the soil micro-food webs. Specifically, we expected that this land use changes would reduce energy allocation to herbivores and omnivores rather than microbivores, and that the disproportional energy allocation among trophic groups would reduce the flow uniformity of energy through the soil micro-food webs.

2. Materials and methods

2.1. Study site description and experiment design

The long-term field experiment was established at the Huanjiang Observation and Research Station for Karst Ecosystems (107°51'–108°43' E, 24°44'–25°33' N), Chinese Academy of Sciences (CAS), Guangxi Province, China. The climate of this region is influenced by subtropical mountain monsoon which is defined as wet (from April to August) seasons and dry (from September to March) seasons, with an average annual temperature and precipitation of 18.5 °C and 1234 mm, respectively. The soil in the area is calcareous, which developed from a dolostone base (Zhao et al., 2015a; Xiao et al., 2020). The main vegetation type is shrub, and there are patches of secondary forest distribution in places with high ratio of bare rock (Fu et al., 2015). The vegetation has gradually recovered after human population relocation and land abandonment in the 1980s. The dominant species in the naturally recovered shrubland were *Cipadessa cinerasce* ns (Pell.) Hand.-Mazz, *Rosa laevigata* Michx, *Imperata cylindrica* (L.) Beauv, and *Bidens pilosa* L.

In early 2013, twelve experimental plots were set up and arranged side-by-side on a 23.5°hill slope, each with a projected area of 20 × 5 m. The present study represented a randomized block design with the 12 plots divided into three blocks (replicates). To prevent water, litter, and rhizosphere exchange between plots, 1 m wide edge trenches (extending to the depth of unweathered bedrock) were excavated on the left, right, and upper sides of each plot. These side ditches were then thoroughly grouted and sealed using cement mortar to form a comprehensive surrounding concrete wall (Liu et al., 2023). The plot establishment was finished in late 2013 and the experiment began in 2014.

Four land use types were randomly implemented on the four plots in each of the three blocks. The four land use types include natural shrubland (NS), cropland (CL), forage grassland (FG) and economic forest land (EL). The natural shrubland is the original vegetation on this

hill slope and considered as control. The cropland, forage grassland, and economic forest land were transformed from the shrubland which were clear cut and replanted with maize, hybrid napiergrass, and walnut trees, respectively. From 2014, corn seeds (*Zea mays* L.) were sown in March, soil was tilled before planting, and all aboveground biomass of corn was harvested in July every year in the cropland. During each growing season, weeds were controlled artificially, and compound fertilizers were applied at rates of 160 kg N ha⁻¹ yr⁻¹, 90 kg P ha⁻¹ yr⁻¹ and 90 kg K ha⁻¹ yr⁻¹ to the cropland. The hybrid napiergrass (Guimu-1 cultivar) (a hybrid of *Pennisetum americanum* (L.) × *P. purpureum* Schumach) was planted in forage grassland in 2014 and mowed 4 times a year. The hybrid napiergrass is a perennial C4 tall grass that is predominantly clonally propagated (Zhao et al., 2014). It can withstand repeated cuttings, no more replanting was carried out during the experiment. Compound fertilizer was applied yearly at a rate of 300 kg ha⁻¹ (N:P₂O₅:K₂O = 15:15:15). Specifically, 50 kg ha⁻¹ of urea (CO (NH₂)₂), 50 kg ha⁻¹ of potassium fertilizer, and 15 kg ha⁻¹ of phosphate fertilizer were applied after each mowing. In 2014, ten walnut trees (*Juglans regia* L.) with a height of 50–80 cm were planted in each plot of the economic forest land. The walnut plots were weeded in early March each year. In the first four years, 0.16 kg nitrogen fertilizer, 0.09 kg phosphate fertilizer, and 0.09 kg K fertilizer were applied annually to each walnut tree every growing season, and no fertilizer had been applied since 2018. In this study, the corn seeds were bought from Agricultural Mechanization Technology Promotion Center of Huanjiang Maonan Autonomous County. The hybrid napiergrass (Guimu-1 cultivar) was provided by the Huanjiang Observation and Research Station for Karst Ecosystems, Chinese Academy of Sciences, Guangxi Province, and walnut trees were distributed by the Huanjiang County Government in Hechi City, Guangxi Province.

2.2. Soil sampling

Soil was sampled in July (wet seasons) and January (dry seasons) from 2015 to 2020 except for January 2018. Soil samples were randomly collected by taking five soil cores (diameter 5 cm, depth 10 cm), which were mixed to generate one sample per plot. Before soil cores were collected, the surface litter was meticulously cleared. In total, there were 12 composite soil samples collected at every sampling event. After roots and stones were removed and the soil was gently mixed, each soil sample was separated into two parts. One half was kept at -80 °C for phospholipid fatty acid (PLFA) assessment. The other half was maintained fresh for soil nematode extraction and analysis of soil water content (SWC).

2.3. Soil analysis

The composition of soil microbial communities was determined by the analysis of phospholipid fatty acids (PLFAs) according to Bossio and Scow (1998). Lipids were extracted from 8 g freeze-dried soil. Concentrations of each PLFA were expressed as PLFAs nmol/g dry soil against an internal standard (19:0). PLFAs 15:0, i15:0, a15:0, i16:0, 16:1 ω 7c, 17:0, a17:0, cy17:0, i17:0, and cy19:0 were used as indicators of bacterial biomass, PLFA 18:2 ω 6,9c was used as an indicator of fungal biomass, PLFA 16:1ω5c was used as an indicator of arbuscular mycorrhizal fungi (AMF) biomass, PLFAs 10 Me 16:0, 10 Me 17:0, 10 Me 18:0, were used as indicators of actinomycetes biomass, PLFAs 20:0:0 and 20:4ω6,9,12,15c were used as indicators of protozoa biomass, and PLFAs 18:1ω9c was used as an indicator of green algae biomass (Frostegård and Bååth, 1996; Frostegård et al., 2011; Zhao et al., 2015b).

A total of 100 g of fresh soil was used to extract soil nematodes using the Baermann funnel method. Turbid nematode suspensions were cleaned using the method of repeated settling at 4 °C (Zhao and Wang, 2022), and then counted using an inverted microscope (Eclipse Ts100, Nikon) after being fixed in a 4% formalin solution. The first 200 individuals encountered were identified to genus using differential

interference contrast (DIC) microscope (ECLIPSE 80i, Nikon). Nematode genera were assigned to five trophic groups (Yeates et al., 1993) and colonizer-persister guilds (Bongers and Bongers, 1998) according to feeding habits and ecological life strategy. The five trophic group include bacterivores (BF), fungivores (FF), plant parasites (PP) or herbivores (He), omnivores (Om), and predators (Pr). The functional guild is defined by the nematode's trophic behavior and its ecological life strategy as a colonizer or persister (cp scale/class) (Gao et al., 2020).

The diversity of nematode community was separately evaluated in the genus, family, or functional (cp) guild level. It was estimated by the Shannon-Wiener diversity index (H') and richness index (SR) (Neher and Darby, 2009) as follows:

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

$$SR = \frac{S - 1}{\ln N} \quad (2)$$

Where P_i is the relative abundance of i th genus, family or cp guild of the sample, S is the total number of nematode genera, family, or cp guild in the community, and N is the number of total nematodes in the community.

2.4. Energy fluxes of nematode communities

The energy flux of nematode community was calculated based on six main steps as follows.

Step 1, the fresh biomass of each nematode individual was extracted from the published papers (Zhao et al., 2015a). If some taxon are not found in the paper, the publicly available data (<https://nemaplex.ucdavis.edu/Ecology/>) was used.

Step 2, the total carbon budget (in ug per day) for each nematode was then calculated. This involved the addition of the carbon amounts utilized in respiration and production, as given by the formula:

$$C_{total} = \frac{n^t \cdot 0.104 W_t}{12cp_t} + 0.0159(W_t)^{0.75} \quad (3)$$

where n^t , W_t , and cp_t are the number of individuals, the fresh biomass, and the cp class of taxon t , respectively (Ferris, 2010; Van Den Hoogen et al., 2019).

Step 3, a five-node food web topology was constructed and the feeding preferences of omnivores-predators on other trophic groups were assumed according to abundance of the nematodes community (Barnes et al., 2018; Wan et al., 2022b).

Step 4, the metabolism of each node was the summation of metabolism of all individuals in the corresponding trophic group.

Step 5, assimilation efficiencies (e_a) were used as follows: 0.25 for herbivores, 0.60 for bacterivores, 0.38 for fungivores and 0.5 for omnivores-predators according to Barnes et al. (2014) and De Ruiter et al. (1993).

Step 6, energy fluxes between nodes were calculated as follows:

$$F_i = (F + L)/e_a \quad (4)$$

where F_i was the energy flux through nematode trophic groups i , F was the energy metabolism of nematode community for respiration and growth, L was the energy loss to higher trophic levels, and e_a is the assimilation efficiency of a given nematode trophic group (Barnes et al., 2018). We assume that omnivore-predator have the same feeding preference for lower trophic groups (bacterivore, fungivore, and herbivore), and that this preference depends on the relative abundance of the nematodes community (Barnes et al., 2018). The energy flux through omnivore-predator in the soil micro-food webs is then calculated first, since the energy loss of predation is assumed to be zero. Next, we

proceeded downwards to the lower trophic groups of nematodes. The predation loss of low trophic groups was equal to the energy flux of omnivore-predator. For example, for the bacterivore, the energy losses (L) can be calculated following $L = D_{BO} \times F_0$, where D_{BO} represents the feeding preference of omnivore-predator for bacterivore, F_0 was the energy flux through omnivore-predator (Wan et al., 2022b). However, it is important to note that omnivorous-predators nematodes are not the top predators in the soil food web, they are also preyed on by higher predators, including protozoa, some micro-arthropods and others (Moore et al., 1988; Hyvonen and Persson, 1996). In addition, lower trophic groups of nematodes may also be preyed by other higher predators, or may be killed by pathogenic bacteria and decomposed by other bacteria and fungi (Niu et al., 2010). Therefore, the direction of energy loss in the nematode community is diverse and not as simple as just five nodes mentioned above. Nevertheless, nematodes are being used as an indicator proxy for the more complex nature on interactions and trophic exchanges occurring in the soil (Ferris and Tuomisto, 2015).

2.5. Statistical analysis

Prior to the statistical analysis, all data were $\log_{10}(x+1)$ transformed to improve normality and homogeneity of variance. Due to great season effects, the data of soil biota in the wet season and dry season were separately analyzed. Repeated-measures ANOVA (RMANOVA) followed by the least significant differences (LSD) post hoc test (significance at $p < 0.05$) was used to determine the effects of land use type, sampling time, and their interaction on the abundances and energy fluxes of nematode and microbial PLFAs in the wet or dry season. The RMANOVAs were performed using IBM SPSS version 26.0 software (IBM, USA), and all data were visualized by GraphPad Prism software, version 8.0.2.263. Furthermore, the effects of the land use type on soil micro-food web structures were explored using Spearman's rank correlation matrix based on biomass data of microorganisms and nematode abundance which were depicted through network analysis using Gephi software (WebAtlas, Paris., FRA, version 0.10.1). Specifically, each network was created by computing the co-occurrence across 30 replicates. A valid co-occurrence was defined as a statistically significant connection between species with Spearman's coefficients (significance at $p < 0.05$) (Jiang et al., 2017). Spearman correlation matrices were computed using the R package psych (Revelle, 2017). The numbers of nodes and edges, positive and negative correlations, graph density, and modularity (M) of each network were calculated. Network complexity was measured using the number of nodes and edges, as well as graph density, with higher values indicating a more complicated network (Yuan et al., 2021; Guseva et al., 2022). Random forest regression analysis was employed to predict the importance of various biological traits (including soil microbial biomass, microbial diversity, soil nematode abundance, nematode diversity and richness) to total energy flux and flow uniformity of the soil micro-food webs. Before analysis, all biological traits were standardized using the 0–1 transformation (Delgado-Baquerizo et al., 2020). The importance of accuracy was calculated for each tree and averaged across the forest (5000 trees). The relevance of these biological variables was estimated using the percentage increase in the mean square error (MSE). A high MSE% value represents the biological trait is an important driver of energetic structure of soil micro-food web. These analyses were carried out using the R package random forest (Liaw and Wiener, 2002). R package A3 was used to assess the significance of the models and cross-validated R^2 values. The R package rfPermute was used to determine the importance of each predictor on the response variables (Archer, 2016).

3. Results

3.1. Compositions and structures of soil micro-food webs

There were significant time effects on the total microbial, bacterial,

fungal, and AMF biomasses during the experiment in the wet or dry season (Fig. 1). In the dry season, the total microbial, fungal, and AMF biomasses were significantly different among the four land use types. Specifically, the biomass of total microbial, fungi, and AMF were the highest in forage grassland, followed by economic forest land, natural shrubland, and cropland, of which were significantly higher in forage grassland than those in cropland (Fig. 1a–e, g, and Table S1). In addition, there were significant interaction effects of sampling time and land use type on fungal biomass in the dry season (Fig. 1e). Furthermore, the microbial biomass showed strong seasonal differences in forage grassland, with the dry season being higher than the wet season (Table S1).

There were significant sampling time effects on the total nematode abundance and abundances of bacterivores and omnivores-predators during the experiment in the dry season (Fig. 2a–c, and i), and abundances of fungivores and herbivore in the wet season (Fig. 2f and h). The total nematode abundance and the abundances of bacterivores and herbivores were significantly lower in cropland, forage grassland, and economic forest land than those of natural shrubland in the dry season (Fig. 2a–c, g, and Table S2). In addition, natural shrubland had the highest abundance of omnivore-predators, which was significantly higher than that of cropland and forage grassland (Fig. 2i and Table S2). Besides, there were significant interaction effects of sampling time and land use type on the abundance of bacterivores in the dry season (Fig. 1c). The abundances of total nematodes and fungivores had significant seasonal dynamic differences in forage grassland and natural shrubland (Table S2). The abundance of bacterivores was higher in the dry season than in the wet season, regardless of land use type (Table S2).

Co-occurrence network analysis showed that the network of cropland had the lowest values for the number of edges (932) and the graph density (0.155) (Fig. 3). The natural shrubland had the highest number of edges (1018), and forage grassland had the highest graph density (0.198) (Fig. 3). The simplified network analysis further showed that the network structure of forage grassland was most complex compared with the other three land use types (Fig. S1). In addition, the abundance of omnivores was positively correlated with the fungal biomass and abundances of bacterivores, fungivores and herbivores (Table 1). However, there was no significant correlation between fungal biomass and abundance of fungivores (Table 1).

3.2. Energy fluxes of soil micro-food webs

Sampling time significantly affected the energy fluxes of total nematodes and omnivore-predators and the flow uniformity of soil micro-food web during the experiment in dry the season (Fig. 4a and i), and significantly affected the energy fluxes of total nematodes, bacterivores, and fungivores in the wet season (Fig. 4b–d, and f). In the dry season, land use change from natural shrubland to cropland and forage grassland significantly reduced the energy fluxes through total nematodes, bacterivores and omnivore-predators (Fig. 4a–c, i, and Table S3). Land use change from natural shrubland to cropland, forage grassland, and economic forest land apparently reduced the energy fluxes from resources to herbivores in the dry season (Fig. 4g and Table S3). In addition, land use type and its interaction with sampling time have significant effects on flow uniformity of soil micro-food web in the wet season (Fig. 4l). Specifically, economic forest land had a higher flow uniformity compared to natural shrubland (Fig. 4l and Table S3). The energy fluxes of bacterivores in the forage grassland, economic forest land, and natural shrubland were higher in the dry season than in the wet season (Table S3). The energy fluxes of herbivores in cropland and forage grassland were higher in the wet season than in the dry season (Table S3). Besides, the flow uniformity in the wet season was higher than that in the dry season in forage grassland (Table S3).

Among the four land use types, omnivore-predators exhibited the highest biomass compared to other trophic groups (Fig. 5). During the dry season, cropland and forage grassland had lower biomass of omnivores-predators and herbivores compared to natural shrubland and

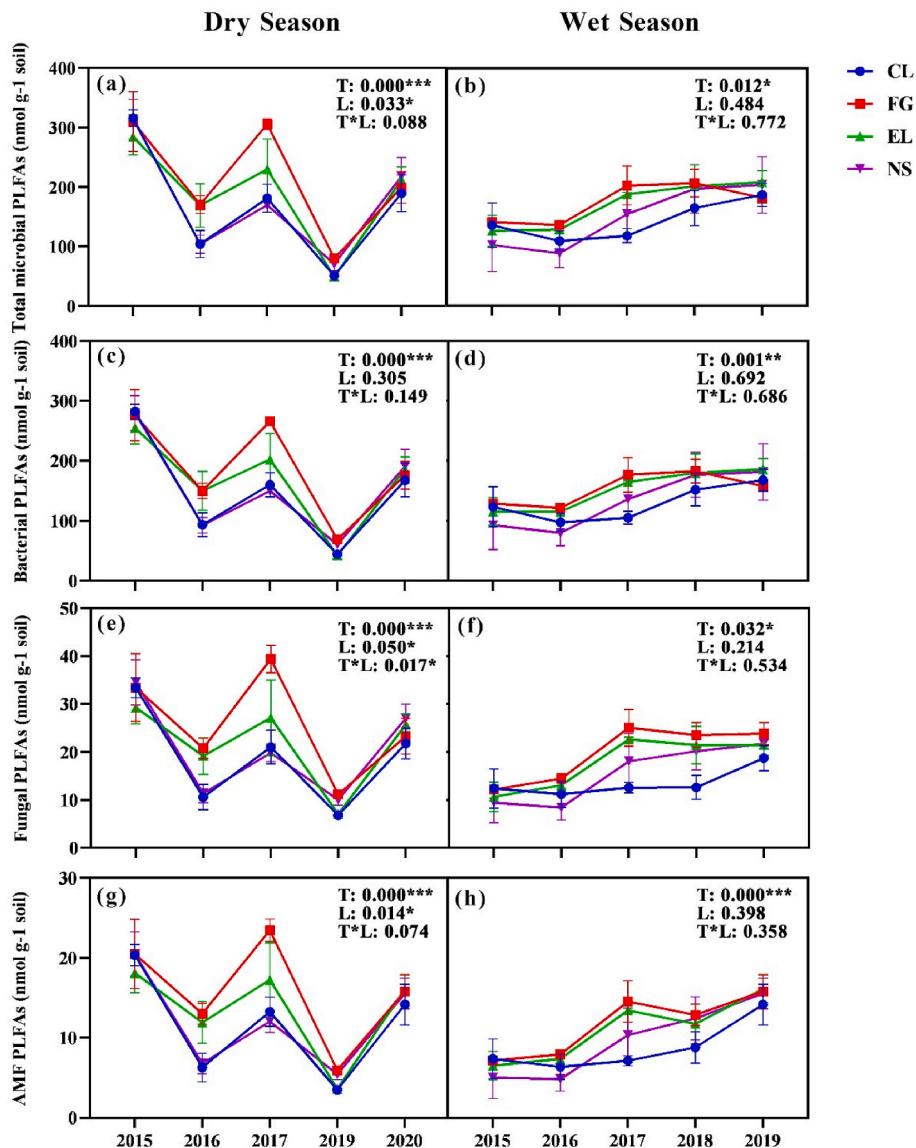


Fig. 1. The total microbial biomasses (a and b), bacterial biomasses (c and d), fungal biomasses (e and f), and AMF biomasses (g and h) as affected by four land-use types in the dry and wet seasons from 2015 to 2020. *p* values are the results of repeated-measures ANOVA. T, L, and T*L refer to the effects of sampling time, land use type, and their interactions, respectively. Significance levels at * *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001. CL, cropland; FG, forage grassland; EL, economic forest land; NS, natural shrubland.

economic forest (Fig. 5). In the wet season, however, the biomasses of omnivore-predators and herbivores were significantly higher in cropland compared to the other three land use types (Fig. 5). In the dry season, land use change from natural shrubland to economic forest enhanced the energy fluxes from resources to bacterivores, fungivores, and herbivores (Fig. 5). Additionally, economic forest had the highest flow uniformity of soil micro-food webs energetic structure, regardless of seasons (Fig. 5).

3.3. The relationships between soil biological traits and the energetic structures of soil micro-food webs

The abundance of omnivores and nematode taxonomic diversity were the most important biological traits associated with the total energy flux through soil micro-food web (Fig. 6a). Other organisms (e.g., Gram+/Gram-, abundances of predator and fungivore) were also contributing to the energy fluxes (Fig. 6a). The random forest regression model further highlighted that the diversity and richness of nematodes, both taxonomically and functionally, are crucial in predicting the flow

uniformity of energetic structure of soil micro-food webs (Fig. 6b).

4. Discussion

In alignment with our first hypothesis, land transition from natural shrubland to cropland and economic forest land reduced the complexity of co-occurrence network of soil biota. Specifically, the soil micro-food web complexity of cropland was the most simplified, with the fewest edges, lowest graph density, and the lowest modularity. This result can be attributed to changes in management frequency and disturbance intensity (e.g., tillage frequency, fertilization rate, aboveground biomass removal intensity, and trampling intensity). The cropland experienced periodical and strong disturbances, which resulted in severe environmental changes and subsequently suppressed the soil biota. In addition, land use changes from natural shrubland to agricultural ecosystems significantly reduced the soil nematode abundance. On the one hand, agricultural lands typically undergo frequent fertilization, weed control, aboveground biomass removal, and/or tillage, which may result in lower plant diversity than natural shrubland and increase soil water

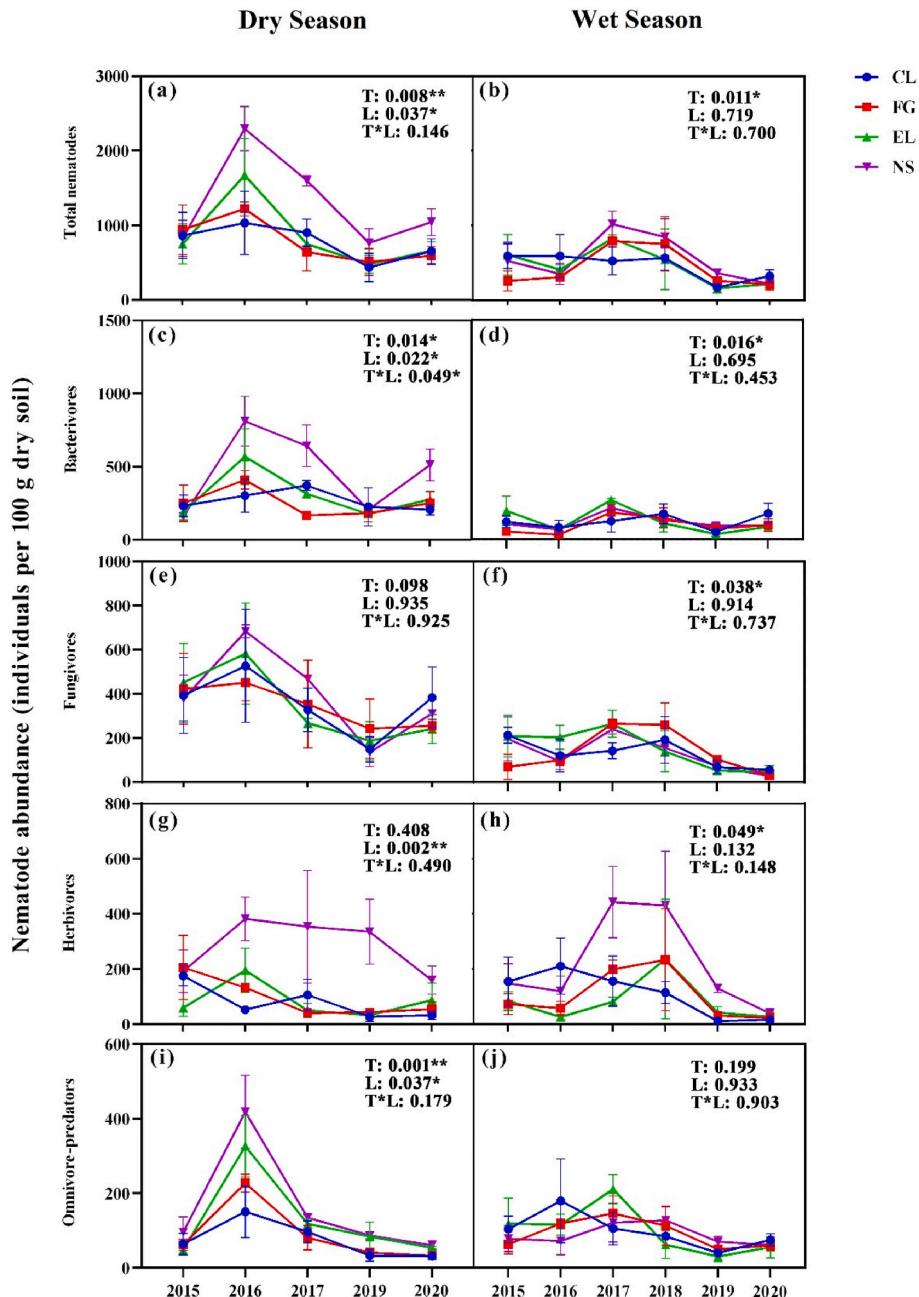


Fig. 2. The abundances (number of individuals 100 g^{-1} dry soil, mean \pm SE) of total nematodes (a and b), bacterivores (c and d), fungivores (e and f), herbivores (g and h), and omnivores-predators (i and j) as affected by four land-use types in the dry and wet seasons from 2015 to 2020. p values are the results of repeated-measures ANOVA. T, L, and T*L refer to the effects of sampling time, land use type, and their interactions, respectively. Significance levels at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. CL, cropland; FG, forage grassland; EL, economic forest land; NS, natural shrubland.

evaporation (Wang et al., 2009; Fischer et al., 2019), thereby proving disadvantageous for the colonization and reproduction of soil biota (Gao et al., 2021). On the other hand, the conversion of land use from natural to artificial ecosystems may increase the scarcity of decomposer community litter supplies, potentially restricting the ecological niche of soil nematodes and reducing nematode abundance in this study (Klerner et al., 2017; Krause et al., 2019). In contrast, the patterns of soil microbial biomass and micro-food web as affected by the land use change in this study differed from those of soil nematodes. Specifically, the forage grassland had the highest biomasses of total microbes, fungi, and AMF among the four land-use types and was significantly higher than cropland. In addition, the soil micro-food web of forage grassland was more complex than that of cropland, as indicated by greater number of

edges and higher graph density (Yuan et al., 2021; Guseva et al., 2022). There might be two factors contributing to these results. On the one hand, compared to forage grassland, cropland experience greater anthropogenic disturbance, such as more frequent tillage and trampling (Li et al., 2018). This may destroy the habitats of environmental-sensitive microbes, thereby reducing microbial biomass (Drenovsky et al., 2010). On the other hand, the well-developed fibrous roots in forage grassland may be rich in some recalcitrant cellulose and lignin, which may provide nutrients for certain fungi, promote their biomass, and thereby increase the total microbial biomass (Zhao et al., 2014). The increase in fungal biomass and the fungivore abundance were consistent with the increase in omnivore abundance. This suggests that the presence of abundant fungi in forage grassland

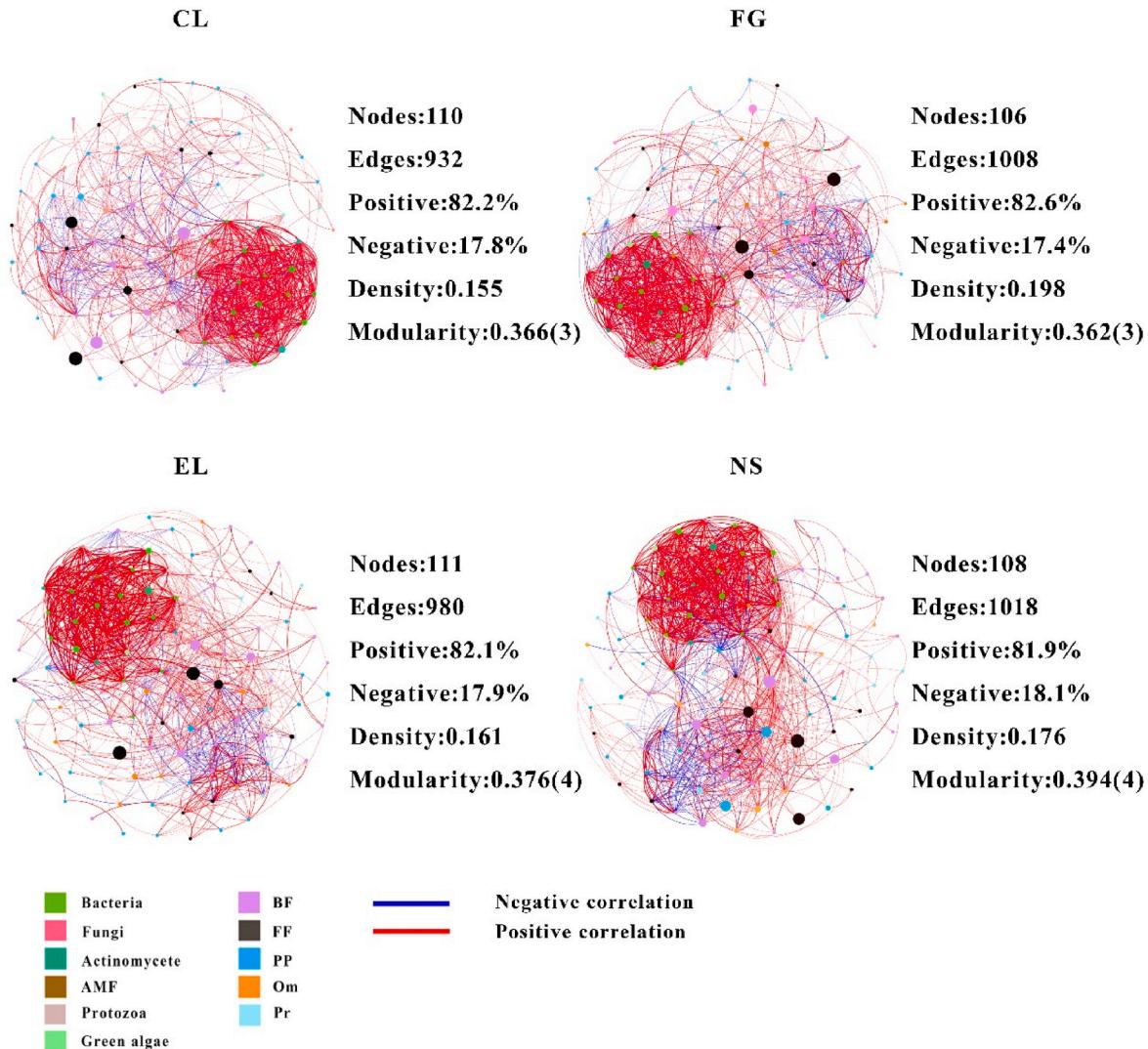


Fig. 3. Network visualization of the interaction strengths within soil micro-food webs. The size of the circle represents the amount of biomass or abundance, the thickness of each edge is proportional to the value of Spearman's correlation coefficients (significance at $p < 0.05$), red edges represent positive correlations, blue edges represent negative correlations, and the different filled colors represent different groups. BF, bacterivores; FF, fungivores; PP, plant parasites; Om, omnivores; Pr, predators. CL, cropland; FG, forage grassland; EL, economic forest land; NS, natural shrubland.

Table 1

Spearman's correlation coefficients between nematode abundance (individuals per 100 g dry soil) for various functional groups and microbes PLFA amounts (nmol g^{-1}). Ba, Fu, He, Om, and Pr represent bacterivores, fungivores, herbivore, omnivores, and predators, respectively. *, **, ***: correlation coefficient is significantly different to 0 at $p = 0.05$, 0.001 and 0.001, respectively. $n = 30$.

Guild	Ba	Fu	He	Om	Pr
Actinomycetes	-0.05	-0.194*	-0.189*	0.003	-0.109
Bacteria	-0.01	-0.163*	-0.133	0.036	-0.066
Fungi	0.101	-0.009	0.021	0.225*	0.039
AMF	0.018	-0.104	-0.133	0.019	-0.082
Green algae	-0.053	-0.185	-0.162	-0.003	-0.103
Protozoa	-0.108	-0.150	-0.092	0.106	-0.027
Ba	-	-	-	0.550***	0.434***
Fu	-	-	-	0.530***	0.536***
He	-	-	-	0.588***	0.522***

enhances the interactions among trophic groups and thus enhances the network complexity through bottom-up control (Leopold et al., 2017; Schuld et al., 2017). However, the pattern of fungal biomass as affected by land use changes did not correspond to the pattern of fungivore

abundance, possibly because the latter was controlled by predators or omnivore (Yeates et al., 1999). Top-down control by omnivore enhanced the interactions among trophic groups when fungal biomass was low (Crowther et al., 2013). Therefore, the results of this study highlight the critical role of omnivore in maintaining the complexity of soil micro-food webs. Notably, previous studies had suggested that the complexity of co-occurrence network of soil biota could reflect the stability of ecological communities and ecosystem functions; particularly, a more complex and interlinked co-occurrence network enhanced the stability of soil community (Krause et al., 2003; Harvey et al., 2017; Yuan et al., 2021) and maintained higher ecosystem functions (de Vries et al., 2018; Wu et al., 2021). Consequently, natural shrubland and conservation agriculture system increased the complexity of the soil micro-food web, which may result in increases in ecosystem multi-functionality and ecosystem sustainability.

Consistent with our second hypothesis, the transition from natural shrubland to monocultured artificial ecosystems reduced the energy flux through soil micro-food webs. Inconsistent with part of our second hypothesis, however, land use change did not reduce the flow uniformity of energy flux through soil nematodes. Previous studies have documented that monocultured artificial ecosystems have low root quality and

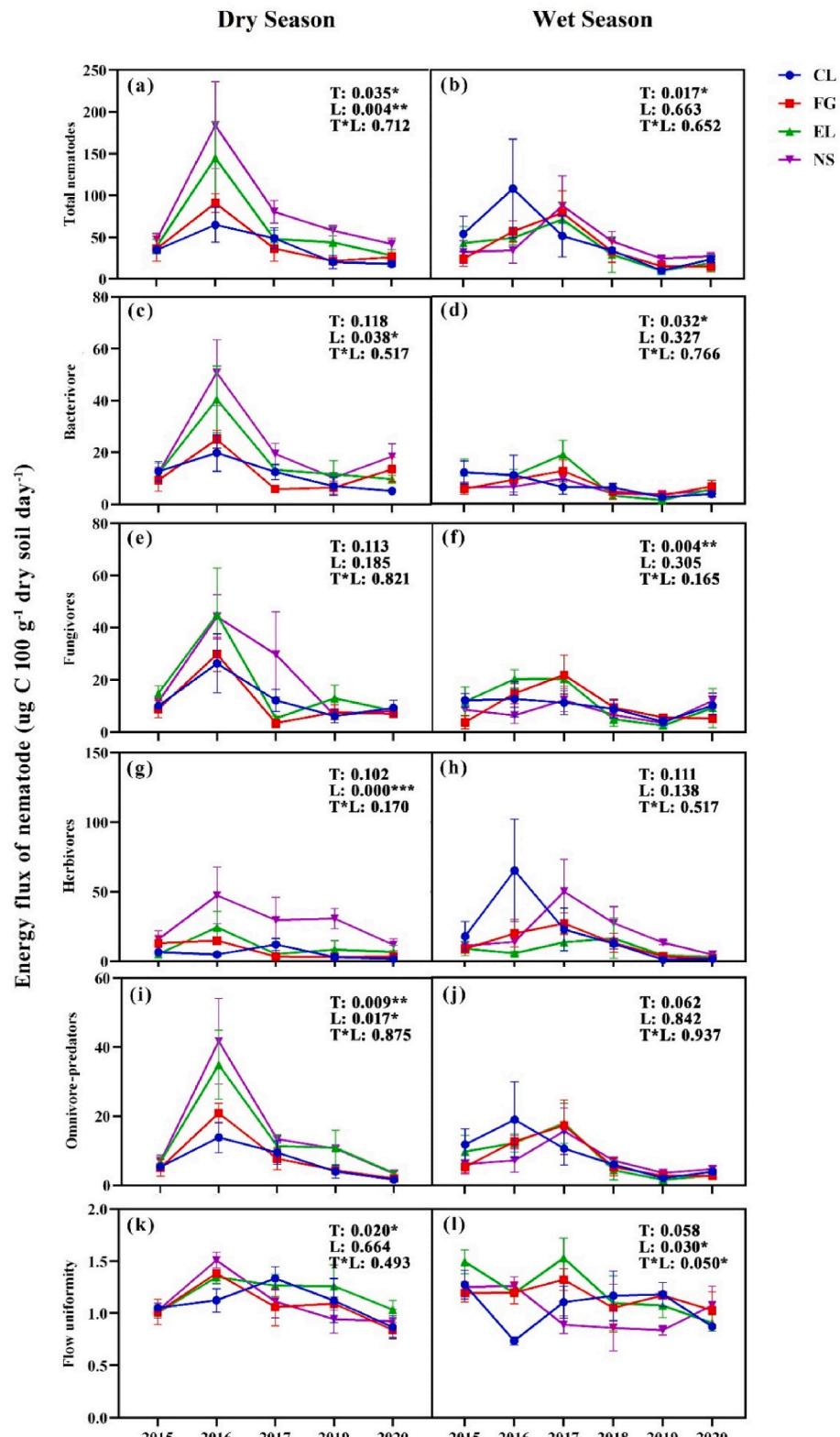


Fig. 4. The energy flux ($\text{ug C } 100 \text{ g}^{-1} \text{ dry soil per day}$, mean \pm SE) of total nematodes (a and b), bacterivores (c and d), fungivores (e and f), herbivores (g and h), omnivores-predators (i and j), and the energy uniformity (k and l) as affected by four land-use types in the dry and wet seasons from 2015 to 2020. p values are the results of repeated-measures ANOVA. T, L, and T*L refer to the effects of sampling time, land use type, and their interactions, respectively. Significance levels at * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. CL, cropland; FG, forage grassland; EL, economic forest land; NS, natural shrubland.

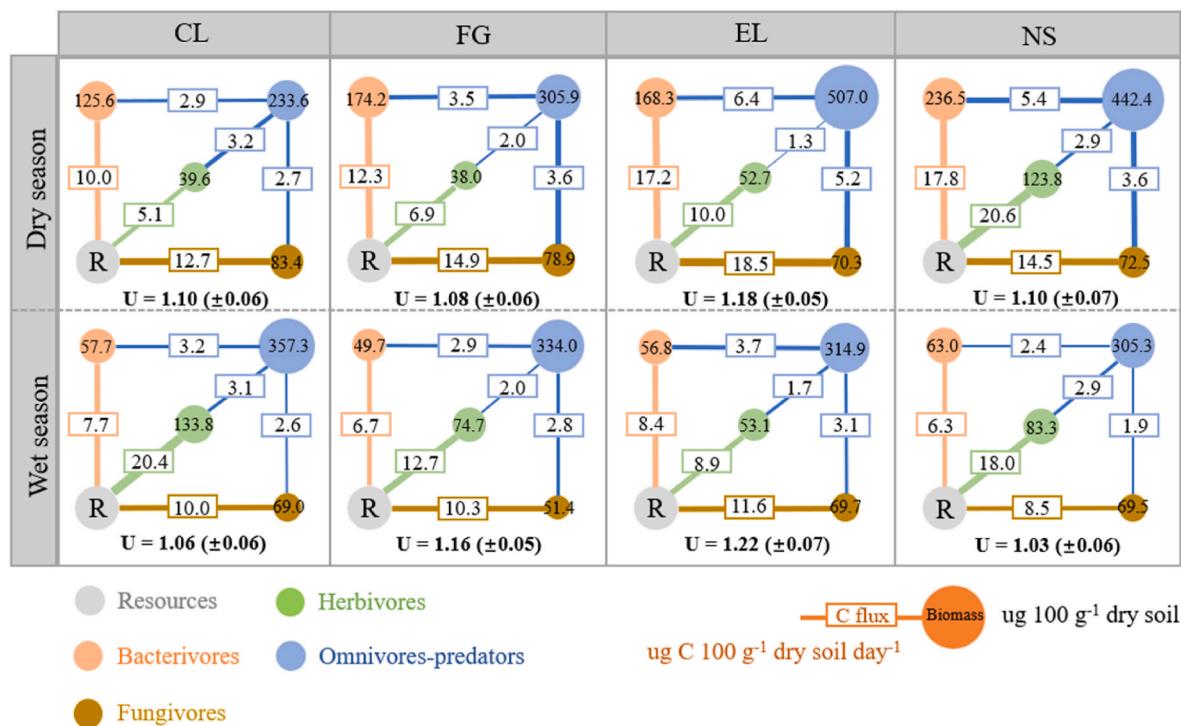


Fig. 5. Effects of land use type on the energetic structures of nematode communities in the dry and wet seasons. For each land use type, a five-node food web was constructed with bacterivores (orange), fungivores (yellow) and herbivores (green) receiving energy from basal resources (R), omnivores-predators (blue) receiving energy from other nodes. Numbers along the lines represented energy flux ($\mu\text{g C } 100 \text{ g}^{-1} \text{ dry soil day}^{-1}$). The size of nodes corresponds to the fresh biomass ($\mu\text{g } 100 \text{ g}^{-1} \text{ dry soil}$). Uniformity (U) of soil nematode energetic structure (unitless, mean \pm standard error) was calculated as the ratio of the mean of summed energy flux through each energy channel to the standard deviation of these mean values. CL, cropland; FG, forage grassland; EL, economic forest land; NS, natural shrubland.

quantity, which may limit the energy usage of soil communities that rely on both live and dead roots (Scharroba et al., 2012; Chen et al., 2020). In addition, agricultural practices often promote crop yield by employing chemical fertilization. Chemical fertilizers can cause carbon limitation and decrease substrate utilization efficiency of soil microbes, potentially driving some active microbial taxa to dormancy (Fontaine et al., 2003; Xiao et al., 2021). These changes may reduce the amount of carbon and energy transmitted from soil microbes to microbivores, which may be an alternative reason for the low energy flux through the soil micro-food webs within the three monocultured artificial ecosystems in the present study. However, land use change from natural shrubland to economic forest land increased the flow uniformity of energy flux through the soil micro-food webs. This result is likely due to the high nitrogen content of walnut bark and leaf (Ma et al., 2016), which increases nitrogen availability to the entire soil food web. Besides, the walnut plantation generally has greater aboveground biomass and litter amount compare to the natural shrubland. Therefore, high nitrogen content (resource quality) and litter amount (resource quantity) of walnut tree may exert a bottom-up control on soil decomposers and ultimately maintaining the abundance of omnivore-predators (Unsicker et al., 2006; Scherber et al., 2010). In addition, economic walnut plantation expedited the transfer of energy from resources to higher trophic levels (bacterivores, fungivores, and herbivores) and reduced the energy flow from herbivores to omnivore-predators, potentially enabling the balanced acquisition of resources across all trophic groups thereby increasing the flow uniformity of energy flux through soil micro-food webs (Buzhdyan et al., 2020). Furthermore, the energy fluxes through soil food web can be employed to comprehend how environmental change drives ecosystem multifunctionality and the stability of soil food webs (Wan et al., 2022a; Liao et al., 2023). Particularly, more energy fluxes channeling to lower trophic groups facilitate to meet top predators' energy demands and thus stabilize the entire soil community (Potapov, 2022), reduce the risk of function loss, and mitigate the

negative effects of species loss on ecosystem multifunctionality (Turnbull et al., 2014; Barnes et al., 2018). Therefore, the low energy flux of the soil micro-food webs in monocultured artificial ecosystems in the current study may indicate potential debilitation or loss of multiple ecosystem functions, as well as a weakening of ecosystem stability. These findings highlight the importance of preserving natural shrubland in karst area in southwest China. Moreover, agricultural land use and management may require to limit soil disturbances in order to sustain ecosystem multifunctionality by stabilizing the energy flux through soil micro-food web.

Seasonal effects are common and significant on the activities of soil biota, which is usually more active in the growing season (wet season) than in the non-growing season (dry season). Obviously, it is mainly caused by great differences in temperature, precipitation, resource amount, and other environmental factors between seasons (Hamel et al., 2006; Costa et al., 2013; Kotroczo et al., 2014). In the present study, significant seasonal effects were also detected on the soil microbial biomass, nematode abundance, and energy flux through soil micro-food web. Unlike the reports mentioned above, however, microbial biomass, nematode abundance, and energy fluxes of nematode were almost exclusively higher in the dry season than those in the wet season in this study. Two reasons may account for this phenomenon. First, plants may promote the growth of microorganisms in the dry season through rhizosphere inputs (e.g., root exudates) during the growing season and litter inputs during the non-growing season (Veen et al., 2019). Second, increases in litter input during the dry season may directly increase the abundance of some fungal taxa, because chemicals released by litter may have a strong selective effect on the fungi during decomposition (Zeng et al., 2018; Kang et al., 2019). This effect may need for a long time to reach high trophic levels (e.g., nematodes), because different soil biota are often involved in complex multitrophic interactions (De Vries and Wallenstein, 2017). In addition, the temporal dynamics of microorganisms are extremely unstable, which may take longer time to reach

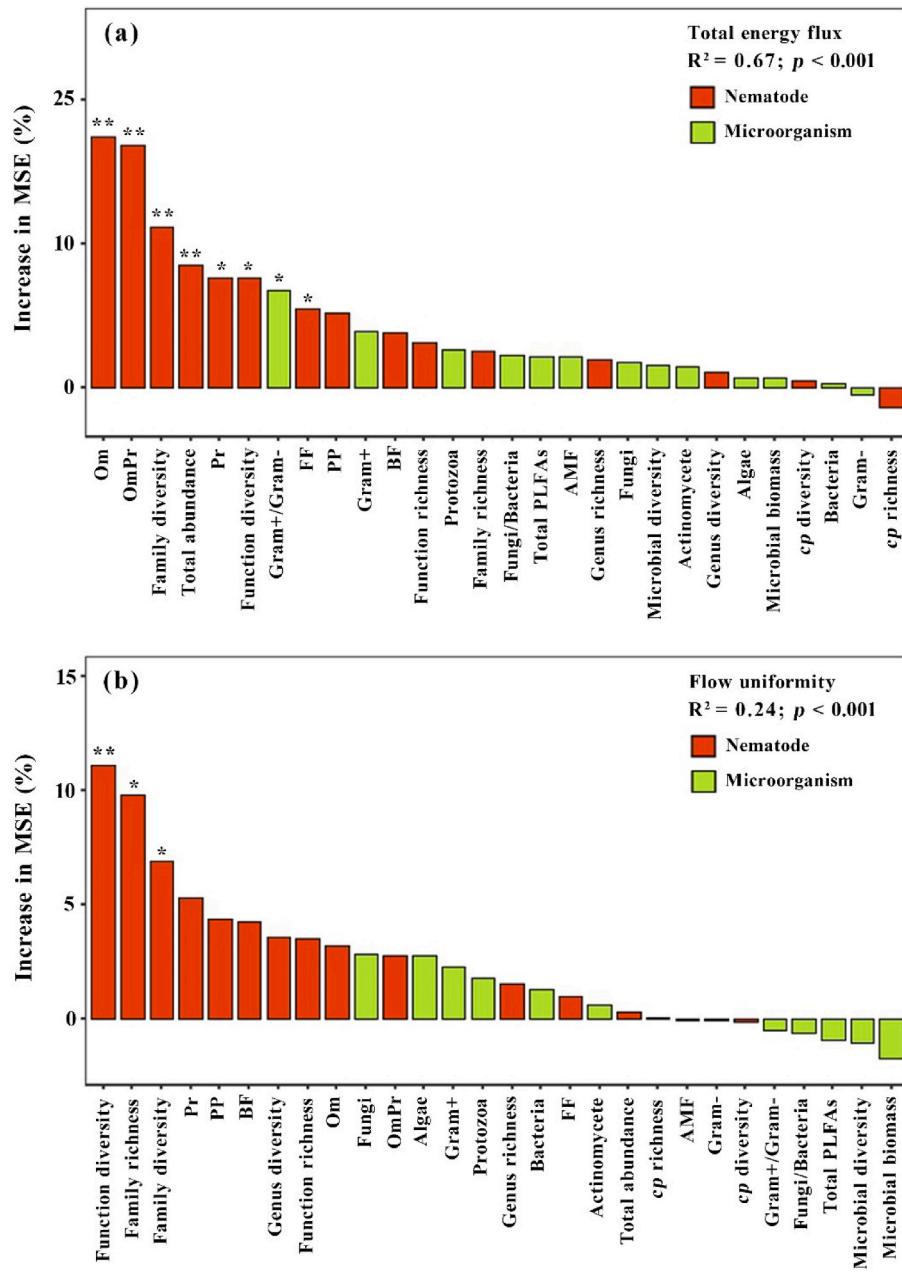


Fig. 6. The importance of soil microbial and nematode traits to total energy flux (a) and flow uniformity (b) of soil micro-food webs according to the results from random forest regression. The microbial and nematode traits include soil microbial biomass, microbial diversity, and soil nematode abundance and diversity. MSE is the mean square error. Significance levels at ** $p < 0.01$, * $p < 0.05$. BF, bacterivore; FF, fungivore; PP, plant parasites (herbivore); Om, omnivore; Pr, predator; OmPr, omnivore-predator; Gram+, gram-positive bacteria; Gram-, gram-negative bacteria; Gram+/Gram-, ratio of gram-positive bacteria biomass to gram-negative bacteria biomass. Fungi/Bacteria, ratio of fungal biomass to bacterial biomass.

dynamic equilibrium (Wardle et al., 1999b). However, soil nematode abundance reached its peak in the third year of the experiment, and then began to decline and gradually reached dynamic equilibrium, which is consistent with previous studies (Wardle et al., 1999a; Yeates et al., 1999). The findings of this study emphasize the necessity for conducting long-term monitoring experiments in order to gain a more comprehensive understanding of the true effects of agricultural practices on soil organisms.

Omnivore abundance and nematode diversity are positively correlated with total energy flux and flow uniformity, respectively. This finding is similar to previous studies that exploring the relationships between nematode diversity and energy flux (Jassey et al., 2023; Zheng et al., 2023). For instance, a positive correlation between energy flux

and nematode diversity was found in paddy fields and uplands in south China (Wan et al., 2022b). Soil invertebrate species loss clearly explained reduction in energy flux on the land transition from tropical rainforests to oil palm plantations (Barnes et al., 2014). In general, larger body-size individuals harbor greater energy flux (White et al., 2007). Thus, a greater abundance of omnivore-predators (i.e., large body-size nematodes) would support a higher energy flux. Besides, abundant soil invertebrates often harbor higher energy demands (Barnes et al., 2016), promoting a more even distribution of energy across the entire food web through increased trophic complementarity (Barnes et al., 2018). Furthermore, the positive correlation between nematode diversity and flow uniformity varies with land use types. For example, such positive correlations were only found in economic forest land and

natural shrubland in the present study. Therefore, the intensity of ecosystem disturbances may affect the relationship between soil nematode diversity and energy flow uniformity of the soil micro-food webs. Particularly, high intensity of disturbance may cause chaos in soil food web structures (both biodiversity-related structure and energetic structure).

5. Conclusions

Our study demonstrated that the transition from natural shrubland to monoculture artificial ecosystems significantly reduced soil nematode abundance and simplified soil micro-food web complexity in karst area in southwest China. Compared to conventional cropland, no-tillage forage grassland and walnut plantation had better soil biological conditions. This highlights the importance of accelerating the transition from traditional farmland to conservation farming in karst regions. Moreover, by taking a food-web energetics approach, land use change from natural shrubland to monocultured artificial ecosystems decreased the energy flux through soil micro-food webs, indicating potential decreases in ecosystem functioning and ecosystem stability in monocultured artificial ecosystems. Furthermore, nematode diversity is positively correlated with energy flux and flow uniformity, suggesting that high diversity or richness of nematodes would benefit ecosystems by promoting the magnitude and evenness of energy distribution across the entire soil micro-food web. In addition, omnivores play a key role in maintaining soil micro-food web complexity through top-down control, and increase the energy fluxes of soil micro-food webs due to their higher energy demands. Moreover, land use change had a substantial impact on the temporal patterns of soil organisms. It may take several years or even longer to reach dynamic equilibrium after disturbance. Long-term experiments are therefore necessary to accurately understand the true effects of agricultural practices on the compositions of soil biota and energetic structures of soil food webs.

CRediT authorship contribution statement

Xianwen Long: Writing – review & editing, Writing – original draft. **Jie Zhao:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Jiangnan Li:** Supervision. **Xionghui Liao:** Supervision. **Jiachen Wang:** Supervision. **Zhiyong Fu:** Funding acquisition. **Wei Zhang:** Funding acquisition. **Xiajiao Liu:** Investigation. **Kelin Wang:** Funding acquisition.

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

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2024.109424>.

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