

Article

Divergent Effects of Forest Canopy Opening on Soil Fauna and Microbes: A Global Meta-Analysis

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Abstract

Forest canopy opening can significantly affect understory environment and thus further influence the communities of soil biota, but this has not been well quantified in the literature. Here, using meta-analysis method, we evaluated the effects of forest canopy opening on soil fauna density and diversity as well as microbial biomass using 4056 paired observations. We found that (1) as a whole, forest canopy opening showed positive effects on soil fauna communities, significantly increasing the density of total soil fauna by 70.5%, and the total richness, Margalef index, and fungi abundance by 33.1, 30.0, and 64.1%, respectively; (2) canopy opening significantly decreased the Pielou index, bacteria abundance, and soil microbial biomass phosphorus concentration by 16.0, 20.9, and 21.0%, respectively, but did not affect microbial biomass carbon or nitrogen concentration; and (3) forest canopy opening effects on soil biota were regulated by latitude, elevation, climate, canopy opening size, and soil pH, with canopy opening size being the most important factor. Overall, our results demonstrate significantly positive impacts of forest canopy opening on soil fauna and fungi abundance but negative influences on other microbes, which will help us to better understand and predict the responses of soil biota to environmental changes and provide theoretical references for forest management and biodiversity conservation under future environmental change scenarios.

Keywords: soil fauna; microbial biomass; density; richness; canopy opening size



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1. Introduction

Forests play a key role in terrestrial ecosystems, sustaining biodiversity and performing ecosystem functions [1,2]. Due to frequent climate change and human activities, the structure of global forest ecosystems has profound changes [3]. Forest canopy opening is mainly caused by global or local extreme droughts, pests, strong storms, and/or human logging activities. This not only affects the canopy structure but significantly alters many functional processes of the forest ecosystems [4–6]. Some studies have reported that forest canopy opening has led to a decline in the integrity and continuity of forest ecosystems worldwide [7,8]. Forest canopy opening effectively increases light intensity and regulates

soil temperature and moisture conditions. Therefore, a unique microclimate that is different from closed canopy is formed in these conditions [9]. The formation of microclimate affects the physical and chemical properties of forest soil and further brings a series of subsequent effects on soil biota [10]. However, until now, we lack a quantitative evaluation on the effects and driving factors of forest canopy opening on soil biota on a regional scale.

Soil fauna and microbes play essential roles in biogeochemical cycles in forest ecosystems, promoting the decomposition of organic matter, nutrient fixation, and release [11,12]. Forest canopy opening can directly or indirectly regulate soil fauna and microbes through some ecological processes such as light radiation, water evaporation, plant transpiration, and organic matter input [13]. Human activities such as thinning and felling have resulted in the formation of many gaps of varying sizes in plantations [14]. This changes the understory microenvironment and further affects the colonization and distribution of soil fauna. For example, in *Pinus massoniana* plantations, canopy opening increases soil temperature and moisture, creating favorable conditions for soil fauna, thereby enhancing their diversity [15]. Furthermore, studies have shown that the canopy opening of natural forests affects the concentrations of microbial biomass carbon (MBC) and microbial biomass phosphorus (MBP) and can also affect microbial activities by adjusting soil temperature and the abundance of fungivorous nematodes [16,17]. These findings suggest that forest canopy opening may have positive impacts on soil fauna and microbes by regulating soil microenvironment conditions such as improving soil temperature, humidity, and aeration [18–20].

Although the positive effects of forest canopy opening on soil fauna and microbes were found in previous studies, it may also have negative effects [21–23]. Previous studies have shown that smaller gaps can enhance microbial biomass and soil enzyme activity, while as gap size increases, soil microbial biomass and soil respiration rate gradually decrease [17,24]. This may be because larger canopy openings substantially alter solar radiation, soil moisture, and nutrient availability, making it more challenging for soil fauna and microbes to adapt [25,26]. In addition, canopy opening regulates soil physical environment, and soil nutrient cycling by changing rainfall distribution and litter input, ultimately affecting the activity and population dynamics of microbial communities [26–28].

In fact, the effects of canopy opening on soil fauna and microbes can be regulated by multiple factors. In addition to canopy opening size, factors such as soil fauna taxonomic group, forest stand age, climate, and soil properties should also be taken into consideration. Due to the unique survival strategies and environmental tolerance among different soil fauna taxonomic groups, their responses to forest canopy opening often differ. Therefore, the taxonomic group may thus be an important moderator variable influencing the relationship between soil fauna and canopy opening [26]. Forest stand age would be another significant regulating variable, because as the stand age increases, the accumulation and decomposition rates of litter and root biomass increase simultaneously, thereby affecting the feeding strategies of different fauna groups [29]. Climatic factors would also be critical, because canopy opening increases soil water content, helping to mitigate the negative effects of drought on soil biota [30]. However, our knowledge on how these moderator variables may regulate forest canopy opening effects on soil fauna and microbes at regional scales remains limited.

To fill this knowledge gap, we conducted a meta-analysis with 4056 paired observations collected from 59 publications to quantify the effects of forest canopy opening on soil fauna density, richness, diversity indices, microbial biomass carbon, nitrogen, and phosphorus as well as the abundance of bacteria, fungi, and actinomycete. We also evaluated how different soil fauna taxonomic groups, ecosystem types (natural forests and tree plantations), climate, latitude, elevation, forest stand age, canopy opening size, soil temperature,

and soil pH may influence the effects of forest canopy opening. We hypothesized that (1) forest canopy opening may have overall positive effects on soil fauna (density and diversity) and microbial biomass, but its effects would vary along with canopy opening size; and (2) latitude, elevation, forest stand age, climate, soil temperature, and pH can significantly influence the effects of forest canopy opening on soil fauna and microbial communities.

2. Methods and Materials

2.1. Data

According to the PRISMA method [31], we conducted a search of peer-reviewed papers, book chapters, and academic theses published before April 2024 on platforms such as Web of Science, Google Scholar, and China National Knowledge Infrastructure (CNKI). The search terms used were (“microclimate*” OR “forest gap*” OR “canopy gap*” OR “canopy open*” OR “canopy thin*” OR “canopy destroy”) AND (“soil fauna” OR “soil invertebrate” OR “macrofauna” OR “mesofauna” OR “microfauna” OR “soil biota” OR “soil organism” OR “soil microbe” OR “bacteria” OR “fungi” OR “actinomycete”). To be included in our study, the primary studies should comply with the following criteria: (1) data must be derived from field-based manipulative experiments (comparing natural canopy vs. canopy opening); data obtained through remote sensing or model simulation studies were excluded; (2) at least one of the variables of interest [i.e., the density of total soil fauna ($Density_{total}$), the richness of total soil fauna ($Richness_{total}$), the density of meso- and micro soil fauna ($Density_{meso+micro}$), the richness of meso- and micro soil fauna ($Richness_{meso+micro}$), Shannon–Wiener index, Pielou index, Simpson index, Margalef index, microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), microbial biomass phosphorus (MBP), Bacteria abundance, Fungi abundance, and Actinomycete abundance] was reported; (3) the measurements for soil fauna density, diversity, and microbial biomass in the control and treatment groups were carried out at the same spatiotemporal scales; (4) the level of taxonomic groups for soil fauna was clearly reported; and (5) the means and sample sizes of the tested variables were clearly reported or could be estimated according to the provided data in the primary study.

After extraction and organization, a total of 4056 paired observations (control vs. treatment; 235 for $Density_{total}$, 231 for $Richness_{total}$, 169 for $Density_{meso+micro}$, 169 for $Richness_{meso+micro}$, 124 for Shannon index, 124 for Pielou index, 122 for Simpson index, 120 for Margalef index, 1136 for MBC, 971 for MBN, 281 for MBP, 125 for Bacteria abundance, 124 for Fungi abundance, and 125 for Actinomycete abundance) were included in our database (Figure 1). In most of the primary studies, soil fauna density was reported for different taxonomic groups and diversity indexes were calculated based on different taxonomic levels (e.g., order, family, or genus). We first treated the data from different taxonomic groups or levels as individual observations and then assessed if the effects of forest canopy opening on soil fauna communities varied among taxonomic levels [26]. To explore the influence of moderator variables on canopy opening effects, we also recorded data of ecosystem type (natural forests and tree plantations), latitude, elevation, forest stand age, mean annual temperature (MAT), mean annual precipitation (MAP), canopy opening size, soil temperature, and soil pH in our database, where available. Data were directly extracted from the text, tables, figures, and/or appendices of the publications, or digitized from figures using GetData Graph Digitizer (version 2.26; <http://www.getdata-graph-digitizer.com> (accessed on 10 April 2024)).

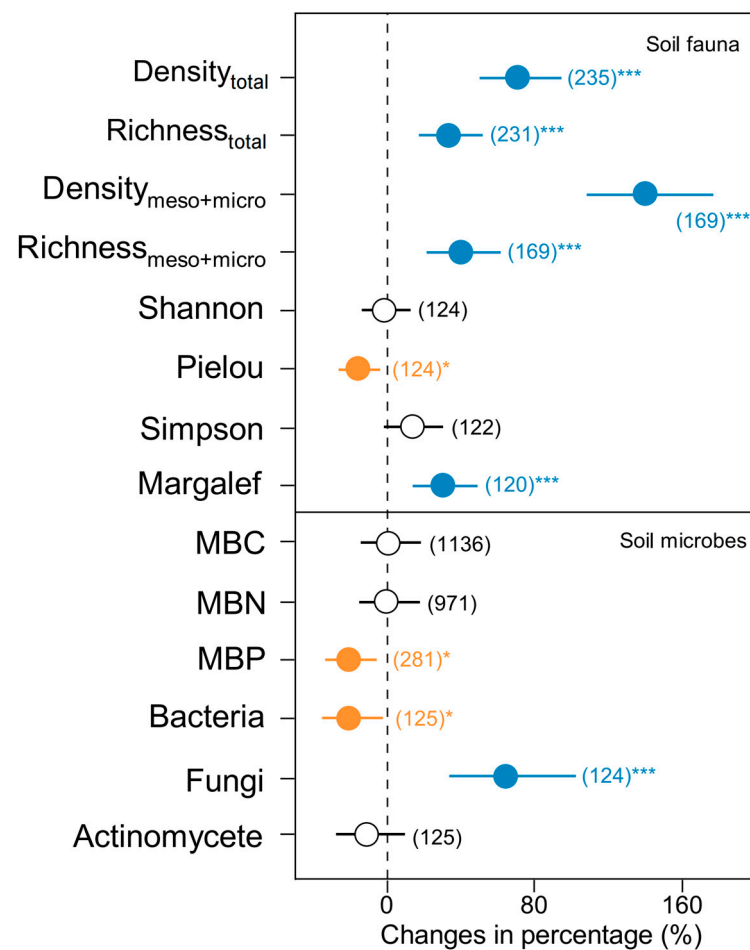


Figure 1. Overall effects of forest canopy opening on soil biota. Values are means $\pm$ 95% confidence intervals; number of paired observations is shown in parentheses; blue and orange represent positive and negative effects, respectively, at * $p < 0.05$, *** $p < 0.001$. The units of microbial biomass carbon, nitrogen, and phosphorus are expressed as concentrations. Bacteria: Bacteria abundance; Fungi: Fungi abundance; Actinomycete: Actinomycete abundance.

2.2. Statistical Analysis

To quantify forest canopy opening effects, we utilized the natural log response ratio (lnRR) as the standard effect size [32]. The lnRR for each individual observation was calculated using the following Equation (1):

$$\ln RR = \ln \left(\frac{\bar{X}_t}{\bar{X}_c} \right) \quad (1)$$

where $\bar{X}_t$ and $\bar{X}_c$ are means of soil fauna or microbial variables in the treatment (canopy opening) and control (natural canopy) groups, respectively. We used the number of replicates associated with each observation [33] to calculate the weight (W_r) corresponding to each effect size, as a substitute for the standard deviation (SD) or standard error (SE) that were not reported in many of the primary studies, which was estimated using Equation (2):

$$W_r = \frac{N_c \times N_t}{N_c + N_t} \quad (2)$$

where W_r represents the weight assigned to each lnRR, and N_t and N_c correspond to the sample sizes of the treatment and control groups, respectively, for soil fauna or microbial variables.

Due to the unavailability of SD in our dataset, conventional methods for detecting publication bias, such as funnel plots or Egger’s regression, could not be applied. Instead, we reviewed the data distribution and observed normal distributions, which suggest that our dataset encompasses a comprehensive set of available studies in the literature (Figure S1). To calculate the weighted overall effect size ($\ln RR_{++}$), which reflects the impact of forest canopy opening on soil biota, we used the *lme4* package in R [34], fitting $\ln RR$ as the response variable and identifying the primary study as a random-effects factor. This random-effects factor was included to account for the potential non-independence of data points from the same study [34,35]. To evaluate the influence of moderator variables on forest canopy opening effects, we conducted linear mixed-effects meta-regression models by fitting each moderator variable (latitude, elevation, forest stand age, MAT, MAP, and canopy opening size) as continuous or categorizing variables (ecosystem type and taxonomic group). Because of the significant variation in the number of data points across different moderator variables, we focused on evaluating their interactions. Given the considerable variation in the number of data points across different moderator variables, assessing the interactions between them was not feasible. Therefore, we employed univariate models to separately evaluate the effects of each variable. For ease of explanation, $\ln RR_{++}$ and the associated 95% confidence intervals (CI) were back-transformed using the equation of $(e^{\ln RR_{++}} - 1) \times 100\%$. All statistical analyses were performed using R version 4.1.3 [36].

3. Results

Forest canopy opening showed general positive effects on soil fauna communities, increasing the density of total soil fauna and meso- and micro fauna by 70.5 and 139.7%, respectively (Figure 1). Forest canopy opening also significantly increased the richness of total soil fauna, richness of meso- and microfauna, the Margalef index, and fungi abundance by 33.1, 39.9, 30.0, and 64.1%, respectively. However, in contrast, forest canopy opening significantly decreased the Pielou index, soil MBP concentration, and bacteria abundance by 16.0, 21.0, and 20.9%, respectively, but did not affect MBC and MBN concentration.

When evaluated for different taxonomic groups, forest canopy opening showed positive impacts on the density of diptera larvae (106.9%), enchytraeidae (100.1%), entomobryidae (104.3%), onychiuridae (174.9%), and poduridae (417.3%), but did not affect the density of other taxonomic groups (Figure 2). Ecosystem type did not affect the effects of canopy opening either on soil fauna density/diversity or on microbial biomass (Figure 3). Forest canopy opening had no significant effect on the density and diversity of soil fauna communities among different taxonomic groups (Figure 4). Latitude, elevation, stand age, MAT, MAP, and canopy opening size showed positive impacts on the effects of canopy opening on the density of meso- and micro soil fauna (Table 1). The effects of canopy opening size on canopy opening effects were substantial; they were positive for total soil fauna density and richness, but negative for the concentrations of MBC and MBN. The effects of canopy opening on the Margalef index were significantly affected by latitude and MAP, while soil pH and stand age showed remarkably positive and negative impacts on the responses of the richness of meso- and micro soil fauna and the concentrations of MBP to canopy opening, respectively.

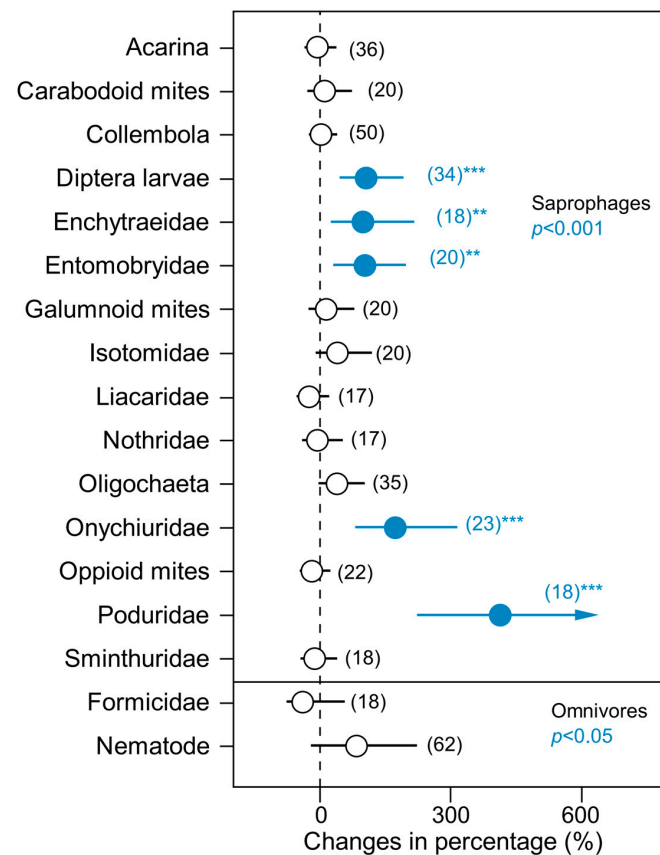


Figure 2. Effects of forest canopy opening on the density of soil fauna within different taxonomic groups. Values are means $\pm$ 95% confidence intervals; number of paired observations is shown in parentheses; blue represent positive effects at ** $p < 0.01$, *** $p < 0.001$.

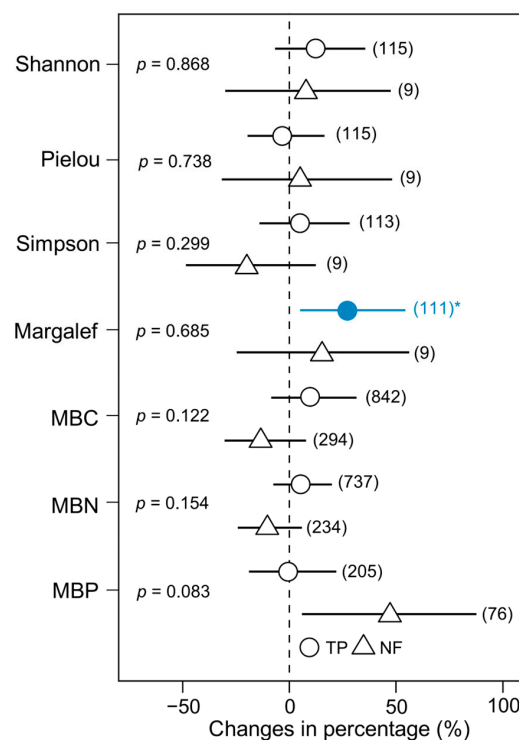


Figure 3. Effects of ecosystem type on the impact of forest canopy opening on soil fauna community indices and microbes. Values are means $\pm$ 95% confidence intervals; p values for the effect of ecosystem type are shown. The numbers of paired observations are shown in brackets; blue and red represent positive and negative effects, respectively. NF: natural forests; TP: tree plantations. * $p < 0.05$.

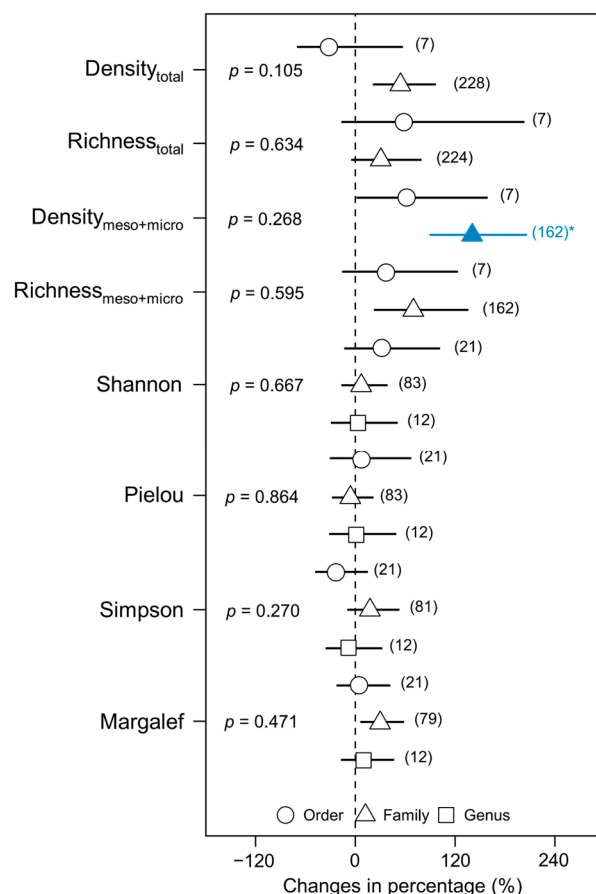


Figure 4. Effects of forest canopy opening on the diversity of soil fauna communities for different taxonomic groups. Values are means $\pm$ 95% confidence intervals. The numbers of paired observations are shown in brackets; blue represent positive significant effects, respectively. * $p < 0.05$.

Table 1. Impacts of predict variables on effect sizes (lnRR) of forest canopy opening on soil biota as assessed by linear mixed models. Estimate of the slope and number of observations (n) are given. Bold indicates significant effects, and empty indicates lack of data. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Predict Variables	Latitude (°)		Elevation (m)		Stand Age (yr)		MAT (°C)		MAP (mm)		Gap Size (m ²)		Soil Temp (°C)		Soil pH	
	Estimate	n	Estimate	n	Estimate	n	Estimate	n	Estimate	n	Estimate	n	Estimate	n	Estimate	n
Density _{total}	0.01	235	0.001	235	0.005	46	0.017	235	0.001	235	0.01 **	208				
Richness _{total}	0.01	231	0.001	231	0.01	42	0.017	231	0.001	231	0.001 ***	204				
Density _{meso+micro}	0.027 *	169	0.002 *	169	0.019 *	169	0.042 *	169	0.001 *	169	0.001 **	154			0.18	154
Richness _{meso+micro}	0.016	169	0.001	169	0.011	169	0.025	169	0.001	169	0.001	154			0.086 ***	154
Shannon	0.004	124	0.001	121	0.001	69	0.007	124	0.001	124	−0.001	116	0.021	9	0.024	55
Pielou	−0.001	124	0.001	121	0.001	69	−0.001	124	0.001	124	−0.001	116	0.011	9	−0.001	55
Simpson	0.001	122	−0.001	119	−0.002	69	0.002	122	−0.001	122	0.001	114	0.005	7	−0.001	55
Margalef	0.008 *	120	0.001	117	0.002	69	0.012	120	0.001 *	120	0.001	112	0.005	5	0.056	51
MBC (mg/kg)	−0.001	1136	0.001	1114	0.002	672	−0.003	1136	−0.001	1133	− 0.001 ***	754	0.001	150	−0.002	552
MBN (mg/kg)	0.001	971	0.001	967	−0.001	573	−0.005	971	−0.001	971	− 0.001 *	711	−0.002	147	0.001	554
MBP (mg/kg)	0.004	281	0.001	281	− 0.002 ***	127	0.009	281	0.001	281	0.001	196			0.02	98
Bacteria (CFU/g)	−0.019	125	−0.001	125	−0.004	92	−0.054	125	−0.001	125			−0.002	17	−0.014	17
Fungi (CFU/g)	0.031	124	0.001	124	−0.003	92	−0.005	124	0.001	124			0.066	17	−0.135	17
Actinomycete (CFU/g)	−0.001	125	−0.001	125	−0.003	92	−0.003	125	−0.001	125			−0.026	17	−0.036	17

MAT: mean annual temperature; MAP: mean annual precipitation; Density_{total}: density of total soil fauna; Richness_{total}: richness of total soil fauna; Density_{meso+micro}: density of meso- and micro soil fauna; Richness_{meso+micro}: richness of meso- and micro soil fauna; MBC: microbial biomass carbon; MBN: microbial biomass nitrogen; MBP: microbial biomass phosphorus; Shannon: Shannon–Wiener index; Bacteria: Bacteria abundance; Fungi: Fungi abundance; Actinomycete: Actinomycete abundance; Gap Size: Canopy gap size; Soil Temp: Soil temperature.

4. Discussion

Partially consistent with the first hypothesis, our results clearly demonstrated that forest canopy opening significantly increased the density and diversity of soil fauna communities, which supports the results of a previous study [15]. The positive effects of forest

canopy opening may be mainly attributed to the adaptive response of soil fauna communities to the understory microclimate [37–39]. Canopy opening can effectively increase the light intensity received by the soil surface, thereby increasing soil temperature [15,19]. As temperature rises, the development and metabolic activity of soil fauna are enhanced, which will provide the possibility for an increase in the density and diversity of soil fauna communities, but excessive warming often brings drought [26,40]. Soil moisture significantly affects the metabolism and activities frequency of soil fauna [41,42]. Canopy opening effectively improves the distribution of rainfall on the ground, regulates soil moisture, and facilitates the growth of herbaceous plants [13,43]. This increases the food sources and living space for soil fauna [44,45].

Inconsistent with our hypothesis, we found that forest canopy opening significantly decreased the Pielou index, bacteria abundance, and MBP concentration, but did not affect MBC or MBN concentrations. These results suggest that the responses of soil biomes to canopy opening are multivariate. One possible explanation is that the surface soil at the center of canopy gaps lacks sufficient input from plant litter and root exudates, thereby reducing the microbial nutrient pool [16]. In addition, this may be due to changes in nutrient stoichiometry and environment heterogeneity caused by canopy opening. Forest canopy opening may accelerate carbon and nitrogen cycling, leading to soil C:P imbalance, which enhances the advantage of fungi in nutrient competition. Simultaneously, the higher humidity and intermittent anoxic environment within the canopy gaps inhibit bacterial activity [46].

Our results shows that canopy opening significantly increased the density of diptera larvae, enchytraeidae, entomobryidae, onychiuridae, and poduridae. This may be attributed to the fact that these different saprophages exhibit similar adaptive mechanisms in response to changes in the soil environment caused by canopy opening [47,48]. Canopy opening stimulates the growth of understory and pioneer plants, thereby increasing the input of litter and dead branches, which in turn provides abundant food resources for these saprophages [49]. Meanwhile, due to the removal of high-rise tree canopies, the coverage of understory vegetation will be significantly increased, which will help reduce water evaporation from the soil surface and increase soil moisture. Therefore, this more humid microenvironment is conducive to the growth and reproduction of saprophages [8,21].

Ecosystem type had no significant effect on the impact of forest canopy opening on soil fauna community indices and microbial biomass. This may be because forest canopy opening effect weakens the differences between these two ecosystem types, or it may be due to objective reasons such as differences in the data points [27]. In addition, canopy opening has similar effects on the microenvironment in different ecosystem types. These two may together mask the differences in the ecosystem types [26]. Similarly, forest canopy opening did not show significant effects on soil fauna communities at different taxonomic levels, which may be due to the limited data points, thus the statistical results were not significant.

The effects of forest canopy opening on the density of meso- and micro soil fauna were significantly affected by latitude, elevation, stand age, MAT, MAP, and canopy opening size. This result is partially consistent with our second hypothesis. Previous studies have revealed that latitude, MAT, and MAP are significant variables affecting environmental climate conditions and play a key role in adjusting soil fauna communities [50,51]. The reason may be that the improvement of temperature and moisture conditions accelerate the release and turnover of organic matter, nutrients, and elements in the understory soil, providing energy sources for soil microbes. Forest canopy opening may regulate the density of soil fauna communities by adjusting interspecific relationships [52,53]. As a significant regulatory factor, forest stand age regulates the symbiotic relationship between microbes by affecting the release of root secretions during vegetation recovery. As the stand

age increases, the demand for soluble phosphorus by the roots of understory vegetation increases, leading to a gradual decrease in the available phosphorus content in the soil, thereby limiting the acquisition and utilization of phosphorus by microbes [54,55]. The effect of canopy opening on the richness of total soil fauna was significantly affected by canopy opening size. The expansion of canopy opening may affect soil fauna and microbes by changing the microclimate of forest floor and understory vegetation. A study showed that forest canopy opening was positively correlated with detritivore abundance and biomass, which supports our analysis. The reason may be that forest canopy opening increases the richness and diversity of soil fauna through trophic cascade effects [56]. Soil pH significantly affects microbial activity, litter decomposition, and soil organic matter [57], and its dynamic changes can further regulate soil physical and chemical properties to affect soil fauna communities [58,59].

5. Conclusions

Our comprehensive analysis clearly showed that forest canopy opening significantly increased the density and richness of soil fauna communities and fungi abundance, while MBP concentration and fungi abundance were significantly reduced. Forest canopy opening size, MAT, and MAP were significant moderator variables regulating the effects of forest canopy opening on soil fauna density and richness, as well as microbial biomass, but taxonomic group and ecosystem type showed limited impacts. Overall, our results reveal how soil biota responded to forest canopy opening under natural and human disturbances, which would help to better understand the responses of soil biota to environmental changes and provide theoretical references for forest management and biodiversity conservation under future environmental change scenarios. However, given the uneven distribution of study sites across the globe in this study, canopy opening effects on soil biota at a global scale still need to be further explored for a more robust conclusion.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/f16111749/s1>, Figure S1. Global map showing the distribution of study sites across the globe. Figure S2. Frequency of the distribution of the density of total soil fauna (Density_{total}), the richness of total soil fauna (Richness_{total}), the density of meso- and micro soil fauna (Density_{meso+micro}), the richness of meso- and micro soil fauna (Richness_{meso+micro}), Shannon-Wiener index, Pielou index, Simpson index, Margalef index, microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), microbial biomass phosphorus (MBP), Bacteria abundance, Fungi abundance, and Actinomycete abundance. The numbers of paired observations are shown. Table S1. Summary of the study area, publications, and number of observations in the dataset. Supplementary S1. A list of the 59 primary studies used in the meta-analysis.

Author Contributions: S.W.: writing—original draft, visualization, validation, data collection, analysis. F.W.: writing—review and editing, supervision, methodology, conceptualization. C.L.: writing—review and editing, conceptualization, data collection. Q.W.: writing—review and editing, methodology, conceptualization. K.Y.: review and editing, supervision, methodology, funding acquisition, conceptualization. P.H.: writing—review and editing, visualization, validation. D.C.: writing—review and editing, visualization, validation, data collection, analysis. N.A.: writing—review and editing, supervision, conceptualization. Y.P.: review and editing, supervision, project administration, funding acquisition, analysis, conceptualization. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: Raw data used in the study will be available on request.

Conflicts of 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.

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