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Canopy gap impacts on soil organic carbon and nutrient dynamic: a meta-analysis

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Abstract

Key message The forest canopy gaps, formed by natural or anthropogenic factors, have been found to reduce soil carbon content and increase nutrient availability. The magnitudes of these effects have been observed to increase with gap age and size, and are largely influenced by changes in temperature, precipitation, and solar radiation.

Context Local studies have illustrated the influence of canopy gaps on the spatial heterogeneity of soil carbon and nutrients, playing a pivotal role in driving forest regeneration and succession. Nevertheless, it remains largely unknown whether the response of soil carbon and nutrient content to gap formation is consistent across forest ecosystems at global scale.

Aims The aim of this paper is to assess the homogeneity of the observed responses of soil carbon and nutrients following gap formation among a wide array of forest ecosystems and climatic regions.

Methods We performed a meta-analysis synthesizing 2127 pairwise observations from 52 published articles to quantify the changes in in soil physical, chemical, and microbial variables resulting from gap creation in natural forests and plantations spanning tropical to boreal regions.

Results Canopy gaps resulted in significant decrease of soil organic carbon (C_{org}) and microbial carbon (C_{mic}). The concentrations of ammonium (NH_4^+), nitrate (NO_3^-), and available phosphorus (available P) increased following gap creation. These changes mainly occurred in the growing season and in the mineral soil layer, becoming more pronounced with increasing gap age and size. The change in C_{org} was negatively regulated by mean annual precipitation, and was associated with the changes in N_t and N_{mic}. The change in NH_4^+ was positively regulated by mean annual temperature, and was associated with the changes in available P and oxidoreductases (Ox-EEAs). The model explaining the change in soil carbon content exhibited a higher explanatory power than the one accounting for changes in soil nutrient availability.

Conclusion The results indicated that forest canopy gaps resulted in a reduction in soil carbon content and an increase in nutrient availability. These findings contribute to a better understanding of the role of small-scale disturbances as drivers of forest ecosystem succession.

Keywords Canopy gaps, Soil organic matter, Nutrient cycling, Topsoil properties, Climate effects, Forest ecosystems

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1 Introduction

Canopy gaps widely occur in forest communities and are mainly formed by natural treefalls or as a consequence of selective logging (Pollmann 2002). The heterogeneity of environmental resources caused by the occurrence of canopy gaps drives plant community succession (Fahey and Puettmann 2008; Kelemen et al. 2012; McNab et al. 2021). Numerous studies have shown that canopy gap dynamics, along with the resulting variations in light, temperature, and soil moisture regimes (Gray et al. 2002; Ritter et al. 2005; Galhidy et al. 2006), generally promote forest regeneration and succession (Yamamoto 2000; Dechnik-Vazquez et al. 2016; Zhu et al. 2021; Lu et al. 2023). For instance, a global meta-analysis demonstrated that canopy gaps enhanced woody plant regeneration and that the effects were influenced by gap characteristics, such as gap age and size, and environmental factors (Zhu et al. 2014). Meanwhile, recent local studies have reported that the plant community succession and microclimatic change following canopy gap creation exert certain impacts on the soil carbon flow and nutrient cycling (Gough et al. 2021; Griffiths et al. 2021).

Forest regrowth following disturbances plays a crucial role in facilitating the terrestrial biosphere's noticeable absorption of anthropogenic CO2 emissions (Pugh et al. 2019; Jayakrishnan et al. 2022). Nevertheless, the impacts of creating canopy gaps on soil carbon fractions have shown ambiguity, with reports of both positive and negative effects, as well as instances where no impact was observed (dos Santos et al. 2016; Amolikondori et al. 2022). To a considerable extent, this disparity can be accounted for by the reality that canopy gaps modify the decomposition patterns of soil organic matter, thereby impacting the storage of carbon in the soil. Simultaneously, canopy gaps elevate environmental heterogeneity, giving rise to distinct microbial community structures and vegetation compositions. This, in turn, influences the input of exogenous organic carbon into the soil.

Mounting evidence suggests that soil nutrient availability stands out as a primary limiting factor for forest primary productivity, co-regulated by plant diversity and species turnover throughout the stages of forest succession (Long et al. 2018; Liu et al. 2021; Joshi and Garkoti 2023). Typically, canopy gaps play a role in expediting soil nutrient cycling within forest successional processes, encompassing nutrient release, migration, and transformation (Muscolo et al. 2014). In addition, canopy gap characteristics, including size, spatial pattern, locations, and frequency, can influence light and water distribution as well as rates of litterfall decomposition, potentially leading to changes in nutrient availability (Zhang and Zak 1995; Eysenrode et al. 2002; Prescott 2002; Mataji and Vahedi 2021). Hence, it is imperative to investigate the alterations in soil nutrient availability following gap creation, aiming to discern the potential ramifications on forest regeneration and succession within forest ecosystems.

The heightened levels of light, temperature, and rainfall, coupled with diminished plant nutrient uptake, may collectively govern soil carbon and nutrient dynamics following gap formation. The impacts of canopy gap creation on forest regeneration and succession are closely associated with climate conditions at larger spatial scales (Ackerly 2003; Zhu et al. 2014; Pope et al. 2023). Furthermore, there is a well-established correlation between the characteristics of canopy gaps and the composition as well as dynamics of forest stands (Kneeshaw and Bergeron 1998; Ren et al. 2021). Therefore, future climate condition changes would greatly increase the uncertainty of the impacts of canopy gap creation on soil carbon and nutrient availability across various forest types.

The objectives of this paper are: (1) to investigate the effects of canopy gaps on carbon content and available nutrients; (2) to identify when and where canopy gaps may significantly impact soil carbon content and available nutrients; (3) to assess whether climate conditions would promote or constrain the effects of canopy gaps on soil carbon sink and fertility. Our findings will not only broaden the understanding of the response of the soil carbon pool and nutrient availability to small-scale disturbances but also aid in exploring the potential mechanisms of canopy gap effects on forest regeneration and succession.

2 Materials and methods

2.1 Data collection

We compiled our dataset by collecting articles published before September 2021 from the Web of Science and China National Knowledge Infrastructure (CNKI). The keyword combinations used for retrieval were (("canopy gap" *OR* "treefall gap" *OR* "forest gap") *AND* ("soil" *OR* "microbial" *OR* "soil enzyme") *AND* ("carbon" *OR* "nitrogen" *OR* "phosphorus" *OR* "nutrient" *OR* "stoichiometry"). To avoid unintentional biases, we developed the following criteria to select pooled articles: (i) the article had to be a field survey conducted in forest areas; (ii) both canopy gaps and forest understory control treatments were reported; (iii) canopy gaps underwent strict natural recovery processes without artificial nutrient input or tree planting; (iv) if the study contains samples from multiple time points, the data applied to analyze the canopy gap effects for the growing season and non-growing season was extracted from the middle of the growth season and the end of non-growing season, respectively; (v) information on the sample size and the means of control and treatment groups were explicitly reported (Fig. 10 in Appendix). In total, 2127 paired observations were extracted from 52 articles that met the abovementioned criteria (Text 1 in Appendix), and the dataset was made publicly available in the Figshare repository (Tong et al. 2023). The geographic distribution of the canopy gap experiments in the meta-analysis is shown in Fig. 1.

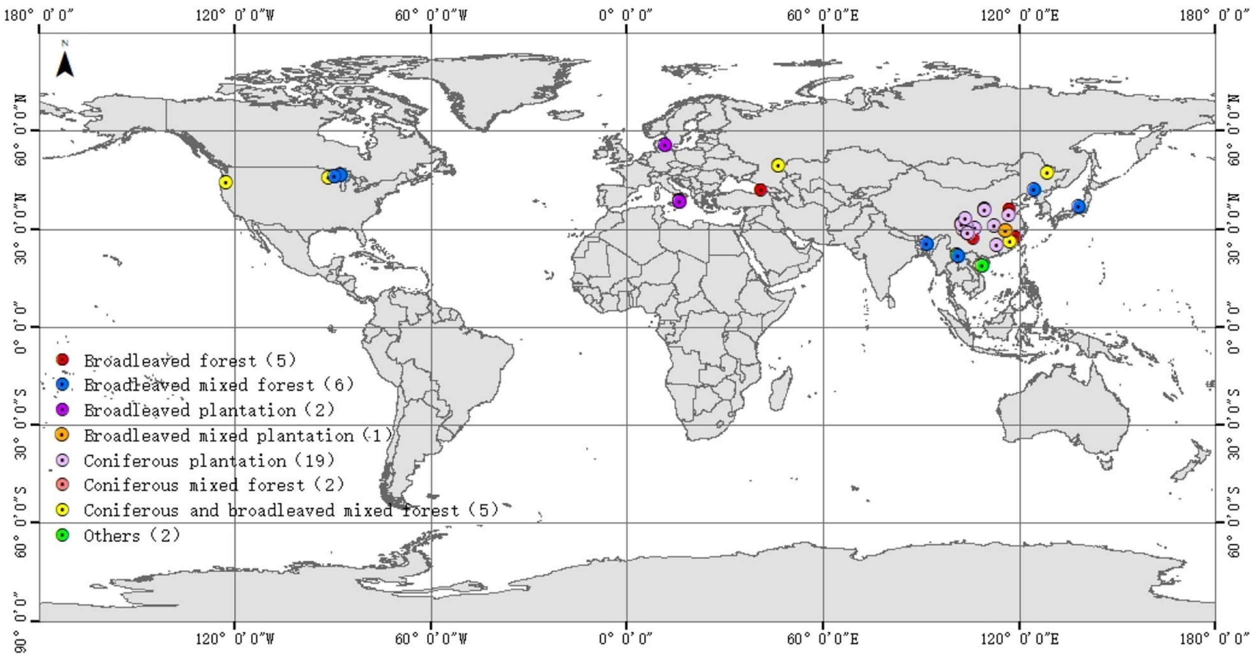

Fig. 1 Distribution of study sites included in this meta-analysis. The forest types are shown as colored dots

2.2 Data compilation

The variables extracted from the included studies were classified into five main groups: (i) basic soil characteristics (i.e., pH, soil moisture, and soil temperature), (ii) soil organic carbon and total nutrients (i.e., soil organic carbon [C_{org}], total nitrogen [N_t], total phosphorus [P_t], and ratio of soil organic carbon to total nitrogen [$C{:}N$]), (iii) soil available nutrients (i.e., ammonium [NH_4^+], nitrate [NO_3^-], and available phosphorus [available P]), (iv) the activities of extracellular enzymes (i.e., hydrolases [Hy-EEAs] and oxidoreductases [Ox-EEAs]), and (v) soil microbial biomass carbon and nutrients (i.e., microbial biomass carbon [C_{mic}], microbial biomass nitrogen [N_{mic}], microbial biomass phosphorus [P_{mic}], and the ratio of microbial biomass carbon to microbial biomass nitrogen [$C_{mic}{:}N_{mic}$]). For each observation, we also recorded the other parameters, such as the latitude and longitude of the experimental locations, climate patterns encompassing the mean annual temperature (MAT) and mean annual precipitation (MAP), forest type (natural forest and plantation), and other information (canopy gap age and size, sampling time and location). We also extracted each sampling site's mean UV radiation data from a global dataset (http://www.ufz.de/gluv) (Beckmann et al. 2014). The correlation between geographical and climatic variables is shown in Table 1 in Appendix. The mean ($\overline{X}$), sample size (n), and standard deviation (SD) of all variables were extracted from the original articles. If the study used standard error (SE) rather than SD, we used $\mathrm{SD} = \mathrm{SE} \times \sqrt{n}$ to calculate SD. When some studies did not report the SD or SE (n = 283), we multiplied the reported mean by the average coefficient of variance of the complete dataset to calculate the missing SD (Weir et al. 2018). Data were directly obtained from the table or text, and those in digitized graphs were extracted with Getdata Graph Digitizer (version 2.22, Moscow, Russia).

We subdivided the potential categorical variables influencing changes in soil carbon content and available nutrients following gap creation. These variables encompassed sampling time (growing season and non-growing season), sampling location (gap center and gap edge), sampling layer (mineral layer (0–30 cm) and organic layer), gap origins (natural and artificial), gap age (≤ 3, 4–10, and > 10 years), and gap size (≤ 100, 101–400, and > 400 m^2). We established these thresholds for potential categories primarily by referencing previous meta-analyses (e.g., Zhu et al. (2014)), determining general breakpoints from manipulative canopy gap experiments within our dataset, and analyzing the data distribution of numerical variables related to canopy gap characteristics (Fig. 12 in Appendix). In addition, the canopy gap age ranged from 1 to 40 years, and the gap size ranged from 14 to 1600 m^2.

2.3 Statistical analyses

The effects of canopy gap creation on soil carbon content and available nutrients were calculated by the natural log-transformed response ratio (lnRR) according to Hedges et al. (1999):

$$\mathrm{lnRR} = \ln(\overline{Y_t}/\overline{Y_c}) = \ln\overline{Y_t} - ln\overline{Y_c}$$

where $\overline{Y_t}$ and $\overline{Y_c}$ are the means of variables in the canopy gap treatment group and forest understory control group, respectively. The variance (v) of each lnRR was calculated as follows:

$$v = \frac{s_t^2}{n_t \overline{Y_t}^2} + \frac{s_c^2}{n_c \overline{Y_c}^2}$$

where s_t and s_c are the SDs of variables in the canopy gap treatment group and forest understory control group, respectively; n_t and n_c are the sample sizes for the canopy gap treatment group and forest understory control group, respectively.

The meta-analysis was performed using OpenMEE software (Wallace et al. 2017), which took the "study" as a random factor to determine the mean effect size of each variable. Confidence intervals (CI) of effect size were calculated using the maximum likelihood (ML) random-effect model. An effect of canopy gap treatment was considered significant if the 95% CI did not overlap zero. The overall effects of canopy gap creation on soil carbon content and available nutrients were identified first. Subsequently, subgroup analysis was conducted to evaluate the response of soil carbon content and available nutrients to canopy gap creation among different categorical comparisons (sampling time, sampling location, or gap characteristics). Higgins I^2 statistics and the Q test were used to quantify the heterogeneity degree (Q_m) among different studies. The random-effects model was used for highly heterogeneous studies ($I^2 > 50\%$ and $p < 0.05$) rather than a fixed-effect model because it had the characteristics of close weights among studies and extensive applicability.

OpenMEE software offered the standard tools for exploring publication bias, including 'fail-safe N' (Rosenberg 2005) and funnel plots (Egger et al. 1997). If the fail-safe number was higher than 5n + 10 (n represented the number of paired observations in the analysis), it could be concluded that the current result was robust and believable. Funnel plots should be funnel-shaped and symmetrically centered around the summary effect estimate of the analysis in the absence of bias and heterogeneity. In this study, it was suggested that no publication biases were detected from our results, except for C_{mic}:N_{mic} (Table 2 and Fig. 11 in Appendix). We used the forest plot to show the results of this meta-analysis, and its generation was performed using GraphPad Prism version 9.0.0 for Windows.

We utilized network visualization in Gephi software to demonstrate significant correlations (Chen et al. 2019). In this approach, variables in the dataset were represented by network nodes, and pairwise conditional associations between variables were depicted by edges. Moreover, all network edges connected nodes that exceeded a predefined significant threshold calculated through Pearson correlation (p-value < 0.05).

The random-forest method was employed to identify the primary predictors of the response ratios for carbon content and nutrient availability. Concurrently, predicted partial least squares path modeling (PLS-PM) was utilized to analyze the impacts of biotic and abiotic factors on changes in carbon content and nutrient availability resulting from gap opening. All the aforementioned data analyses were conducted using R 4.0.2 (R Core Team, 2020).

3 Results

3.1 Mean canopy gap effects

Overall, canopy gaps increased soil moisture and soil temperature but did not affect soil pH (Fig. 2). Canopy gaps had a negative effect on C_{org} and N_t but a positive effect on P_t. For available nutrients, canopy gaps enhanced NH_4^+, NO_3^-, and available P by 19.4%, 13.5%, and 17.3%, respectively. Canopy gaps reduced the Ox-EEAs while having no significant effect on the Hy-EEAs. Furthermore, canopy gaps exhibited significant negative effects on C_{mic}, N_{mic}, and P_{mic}, but a positive effect on C_{mic}:N_{mic}.

3.2 Factors influencing the changes induced by canopy gaps

We employed the subgroup analysis method to evaluate the factors influencing canopy gap effects, as illustrated in Figs. 3 and 4. During the non-growing season, canopy gaps exhibited a negative impact on soil pH. Throughout both the growing and non-growing seasons, canopy gaps led to increased soil moisture and soil temperature. In the non-growing season, canopy gaps negatively affected C_{org} and N_t, whereas no effects were observed during the growing season. In the growing season, the P_t, available P, NH_4^+, and NO_3^- were enhanced following gap creation. Canopy gaps significantly reduced Ox-EEAs in both the growing and non-growing seasons, with no significant effect observed on Hy-EEAs. In the growing season, canopy gaps resulted in decreased C_{mic} and N_{mic}, and in the non-growing season, there were reductions in N_{mic} and P_{mic}. (Fig. 3a).

Canopy gaps exerted a negative impact on soil pH in the organic layer, while showing no effect in the mineral layer. Canopy gaps increased the soil moisture by 7.6% and 15.9% in the mineral and organic layers, respectively, and only increased soil temperature by 5.1% in the mineral layer. The C_{org} and N_t decreased while P_t increased in the mineral layer due to gap opening. Canopy gaps notably enhanced available P, NH_4^+, and NO_3^- in the mineral layer but were statistically insignificant in the organic layer. The Ox-EEAs decreased in the mineral layer, and Hy-EEAs increased in the organic layer following gap creation (Fig. 3b).

Canopy gaps had a negative effect on soil pH at the gap edge but not at the gap center. The soil moisture

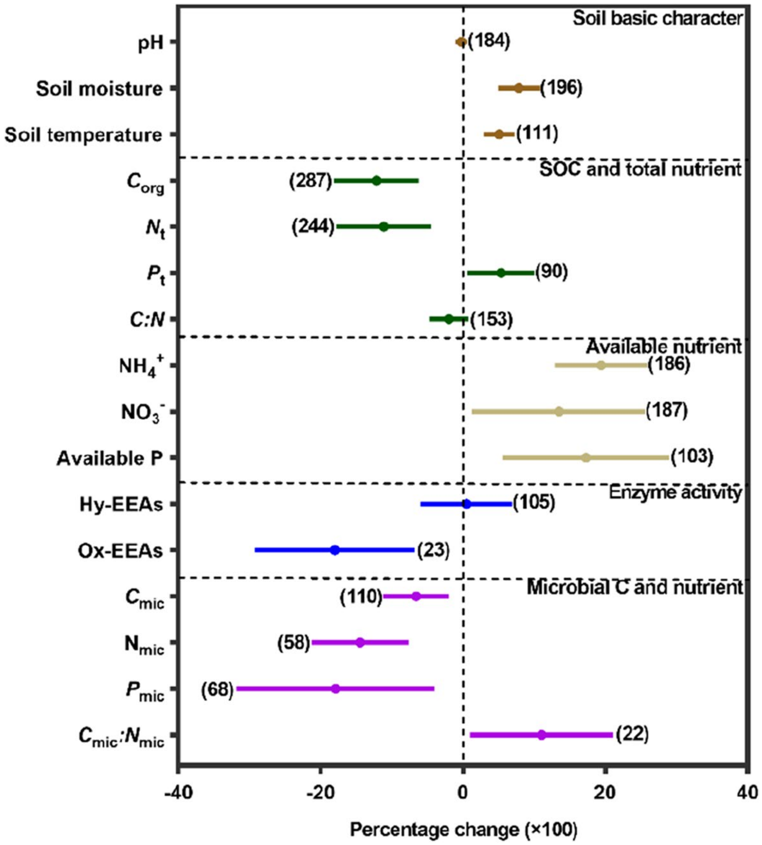

Fig. 2 Overall effects of canopy gaps on the SOC content and nutrient availability. Values are mean effect size (× 100%) ± 95% confidence intervals (CI). The vertical line is drawn at lnRR = 0. The number of observations is within the parentheses. C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; *C:N*, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus; C_{mic}:N_{mic}, the ratio of microbial biomass carbon to microbial biomass nitrogen

and temperature were enhanced at both the gap center and edge following gap creation. Canopy gaps reduced C_{org} and N_t at both the gap center and gap edge while only enhanced P_t at the gap center. The NH_4^+ and NO_3^- increased at the gap center, and the available P and NH_4^+ increased at the gap edge following gap creation (Fig. 3c).

Short and medium-term canopy gaps increased soil moisture and soil temperature, whereas long-term canopy gaps exhibited diverse effects on them. Medium-term and long-term canopy gaps reduced C_{org} and N_t, and the short-term canopy gaps had no effect. Short-term canopy gaps increased P_t. Short-term and long-term canopy gaps increased available P and NO_3^-. Short-term, medium-term, and long-term canopy gaps enhanced NH_4^+ by 16.0%, 10.5%, and 66.9%, respectively. Medium-term and long-term canopy gaps reduced C_{mic} and N_{mic}, and long-term canopy gaps had a negative effect on P_{mic} (Fig. 4a).

Small and medium gaps decreased and increased the soil pH, respectively, whereas large gaps had no effect. Soil moisture and temperature notably increased while C_{org} decreased in each gap size class. Small and large gaps reduced N_t by 16.9% and 8.5%, respectively, and medium gaps showed a positive effect on P_t. The NH_4^+ was enhanced in each gap size class. The NO_3^- and available P were enhanced in medium and small gaps, respectively. The Ox-EEAs significantly reduced in small and medium gaps but increased in large gaps. The C_{mic} decreased in large gaps, and N_{mic} decreased in each gap size class (Fig. 4b).

3.3 Correlations between the changes in soil carbon content and nutrient availability

The result of network analysis showed that changes in soil moisture, C_{org}, N_t, NO_3^- and C_{mic} were the critical indicators closely associated with most of the other soil physical, chemical, and microbial properties (Fig. 5). Specifically, the change in soil moisture was significantly and positively related to the changes in C_{org}, N_t, available P, and NO_3^-, and was negatively associated with the changes in NH_4^+ and the Ox-EEAs. The change in C_{org} was significantly and positively related to the changes in N_t, P_t, *C:N*, available P,

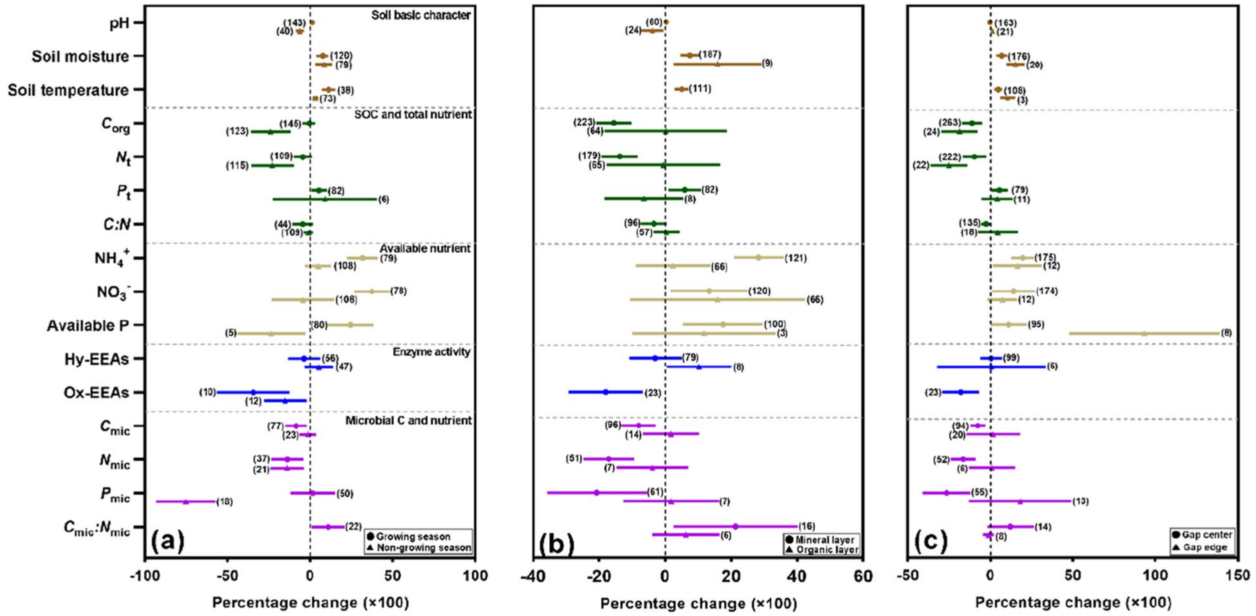

Fig. 3 Response of SOC content and nutrient availability to canopy gap creation for two categorical variables, including sampling time, sampling layer, and sampling location. Values are mean effect size (×100%) ± 95% confidence intervals (CI). The vertical line is drawn at lnRR=0. The number of observations is within the parentheses. C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; $C{:}N$, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus; $C_{mic}{:}N_{mic}$, the ratio of microbial biomass carbon to microbial biomass nitrogen

and N_{mic}, and the most pronounced correlation was found between changes in C_{org} and N_t. The changes in N_t and N_{mic} were positively correlated. The change in NO_3^- was negatively correlated with the change in N_t and NH_4^+. The change in P_t was negatively correlated with the change in Hy-EEAs. The changes in Hy-EEAs and Ox-EEAs were positively correlated. The change in C_{mic} was significantly and positively correlated with the changes in P_{mic} and $C_{mic}{:}N_{mic}$.

3.4 Correlations between climatic variables and the changes in soil properties

The changes in $NH_4^{\ +}$, Hy-EEAs, Ox-EEAs, and C_{mic} showed a positive correlation with MAT (Fig. 6a, c-e). The change in available P decreased with increasing MAT (Fig. 6). The changes in C_{org}, available P, and P_{mic} decreased with increasing MAP (Fig. 6f-h). The changes in soil temperature, C_{org}, N_t, and Ox-EEAs increased with increasing UV radiation (Fig. 6i-k, m). The change in available P, P_{mic}, and $C_{mic}{:}N_{mic}$ decreased with increasing UV radiation (Fig. 6l, n, o). The correlations between climatic variables and the changes in soil carbon content and nutrient availability are detailed in Figs. 13–15 in Appendix.

3.5 Key factors that regulate the changes in soil carbon content and nutrient availability in canopy gaps

The random forest analysis suggested that the most important factors associated with the change in C_{org} were the changes in N_t and N_{mic}. The changes in C_{mic}, available P, and Ox-EEAs were dominant factors regulating the change in NH_4^+. The changes in N_{mic}, available P, and pH were the dominant factors regulating the change in NO_3^-. However, the importance of the changes in influencing factors for C_{mic} and available P was relatively low (Fig. 7).

The explanation of PLS-PM for the variance in the response of soil carbon content was at the medium level (GoF = 0.42). The PLS-PM showed that no correlation was detected between climate (including mean annual temperature (MAT) and UV radiation) and the change in carbon content (including C_{org}). Climate negatively affects the change in basic soil characteristics (including soil moisture; path coefficient = -0.22, $p < 0.05$), while positively affecting the change in total nutrients (including N_t; path coefficient = 0.15, $p < 0.05$) and the change in microbial characteristics (including Hy-EEAs and Ox-EEAs; path coefficient = 0.23, $p < 0.05$). The change in basic soil characteristics had no association with the change in carbon content (path coefficient = 0.02, $p > 0.05$) but positively affected the change in total nutrients (path coefficient = 0.21, $p < 0.05$). The change in total nutrients positively affected the change in carbon content (path coefficient = 0.85, $p < 0.05$). The variance in the change in carbon content was explained by 74% with climate and changes in basic soil characteristics, total nutrients, and microbial characteristics (Fig. 8a).

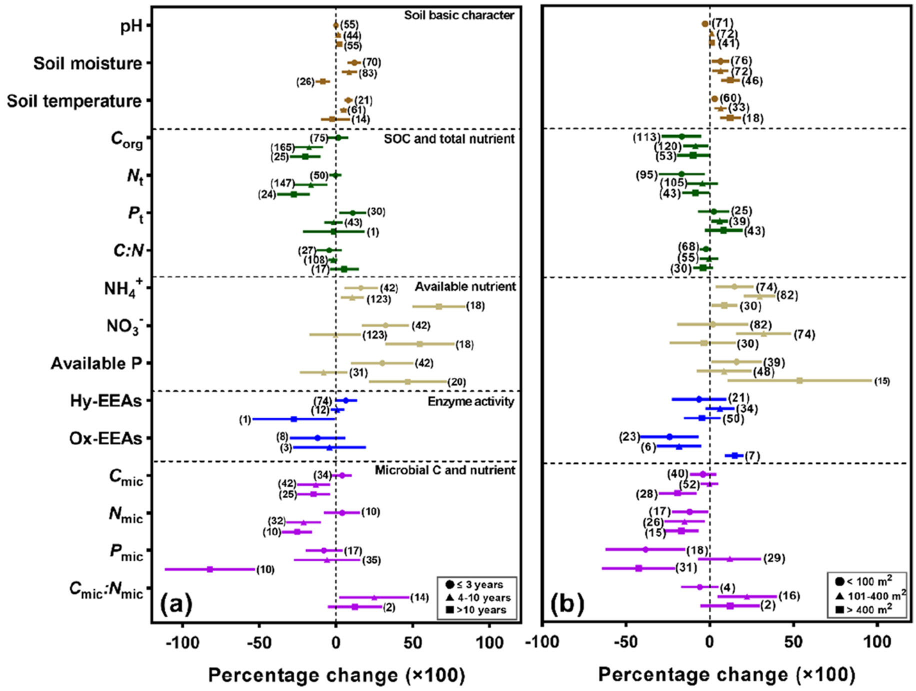

Fig. 4 Response of SOC content and nutrient availability to canopy gap creation for three categorical variables, including gap age and size. Values are mean effect size (×100%) ± 95% confidence intervals (CI). The vertical line is drawn at lnRR=0. The number of observations is within the parentheses. C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; *C:N*, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus; $C_{mic}:N_{mic}$, the ratio of microbial biomass carbon to microbial biomass nitrogen

Otherwise, the explanation of PLS-PM for the variance in the response of soil nutrient availability was at a relatively low level (GoF = 0.17). No correlations were detected between climate (including MAT and UV radiation) and the changes in nutrient availability (including NH_4^+ and NO_3^-), soil basic characteristics (including soil temperature), and total nutrients (including *C:N*). Climate negatively affected the change in microbial characteristics (including P_{mic} and Hy-EEAs; path coefficient = -0.14, $p < 0.05$). The change in total nutrients negatively affected the changes in microbial characteristics (path coefficient = -0.18, $p < 0.05$) and nutrient availability (path coefficient = -0.21, $p < 0.05$). The variance in the change in nutrient availability was explained by just 7% with climate and changes in basic soil characteristics, total nutrients, and microbial characteristics (Fig. 8b).

4 Discussion

4.1 Canopy gaps reduced soil carbon content

Effectively mitigating climate change may be achieved through the enhancement of forest carbon stocks resulting from sustainable forest management (Huang et al. 2023). Nevertheless, our results underscored a consistent reduction in both C_{org} and C_{mic} following gap creation, indicating a potential decline in the soil carbon stock (Ni et al. 2016; Amolikondori et al. 2020). In general, heightened levels of irradiance and soil temperature resulting from gap creation or forest thinning accelerated soil microbial activity, leading to increased soil respiration and, consequently, enhanced mineralization of soil organic matter and elevated surface carbon efflux (Scharenbroch and Bockheim 2008) (Fig. 9). Therefore, the distinct effects of gap formation and forest thinning on soil carbon stock might be attributed to the reduced initial carbon input, which could be potentially caused by tree mortality during natural gap formation and litter removal after selective logging. Nevertheless, it is worth noting that the increased plant diversity resulting from gap creation is likely to enhance soil carbon storage over the long term (Degen et al. 2005; Lange et al. 2015; Chen et al. 2018; Jia et al. 2021).

C_{org} is an integral component of the forest carbon pool, and its active organic carbon fraction not only plays a crucial role in the soil carbon turnover process but also serves as a sensitive indicator of changes in climate conditions (Zhu et al. 2020; Pravalie et al. 2021). C_{mic} plays a vital role in ecosystem functioning by serving as the supply and inventory of effective soil nutrient resources (Singh and Gupta 2018; Li et al. 2019). Our results showed that C_{org} and C_{mic} declined significantly following gap creation, which might be

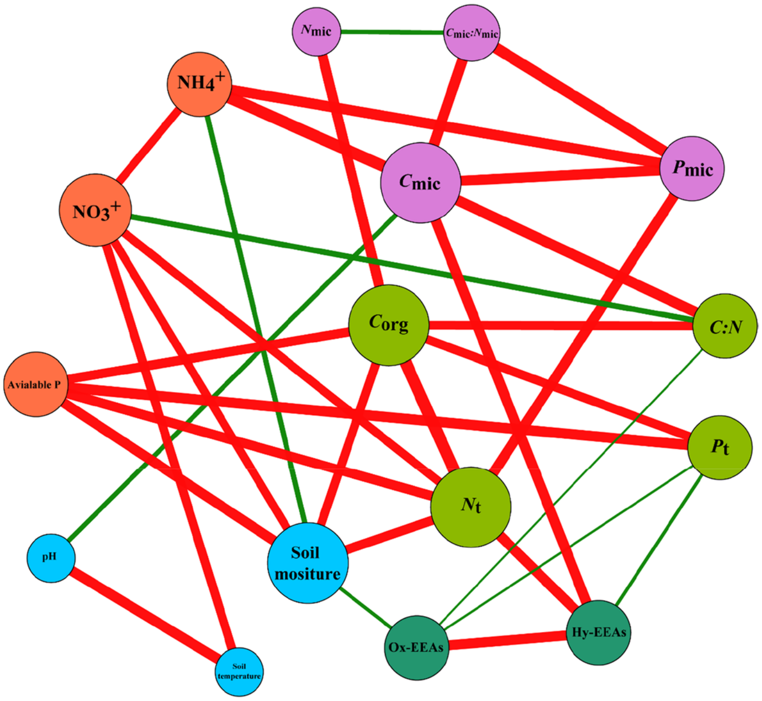

Fig. 5 Network analysis for the correlation between soil physical, chemical, and microbial properties. Node colors are communities obtained from the pre-classification; each community in the network is represented by the same node color. Node sizes are obtained from the ranking degree, and wider nodes are the parentheses having more correlations with other parentheses. Red and green edge lines represent positive and negative correlations, respectively. The edge thickness represents the strength of the correlation. C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; *C:N*, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus; C_{mic}:N_{mic}, the ratio of microbial biomass carbon to microbial biomass nitrogen

attributed to the heightened mineralization of soil organic matter mineralization brought by increasing soil microbial activity. Furthermore, the diminished input of readily available carbon sources, such as root exudates, might result in microbial carbon limitation, which was substantiated by our discovery that C_{mic}:N_{mic} decreased significantly following gap creation (Panchal et al. 2022). Nevertheless, despite the absence of a significant correlation between the response of C_{org} and C_{mic} to canopy gap disturbance, and the relatively modest reduction in C_{mic} compared to C_{org}, several potential factors may explain these observations. On the one hand, the inadequate input of plant and microbial residues led to a notable reduction in the Corg pool, thereby limiting the favorable impact of warming on soil microbial respiration in the warmed-up plots. On the other hand, microorganisms adapted to the rising temperature in external environment by producing enzymes with heightened thermal adaptation, ultimately contributing to the gradual stabilization of the microbial biomass pool.

Furthermore, we evaluated the effects of canopy gap attributes and spatiotemporal factors on the response of soil carbon content to canopy gap disturbance. C_{org} and C_{mic} displayed consistent responses to canopy gap creation. For instance, the results showed a remarkable reduction in C_{org} and C_{mic} in medium-term (4–10 years) and long-term (> 10 years) canopy gaps and no significant change in short-term (≤ 3 years) canopy gaps. These differences might arise from large amount of readily available carbon released from the remaining litterfall induced by increased light and temperature during the early stage of gap formation (Wang et al. 2015, 2021). Notably, significant decreases in C_{org} and C_{mic} occurred in the non-growing and growing seasons, respectively. This result might be attributed to the lower supplementation of root exudates during the non-growing season. In contrast, soil microbial respiration maintained a higher level in the growing season. Overall, the downward trend in soil carbon stock following gap creation might be attributed to variations in initial carbon input between canopy gaps and forest understory sites.

4.2 Canopy gaps enhanced soil nutrient availability

The efficient recycling of nutrients plays a crucial role in determining availability of nutrients in forest ecosystems. Typically, natural disturbances or partial harvesting practices that expedite nutrient recycling through the creation of canopy gaps also tend to enhance the spatial variability

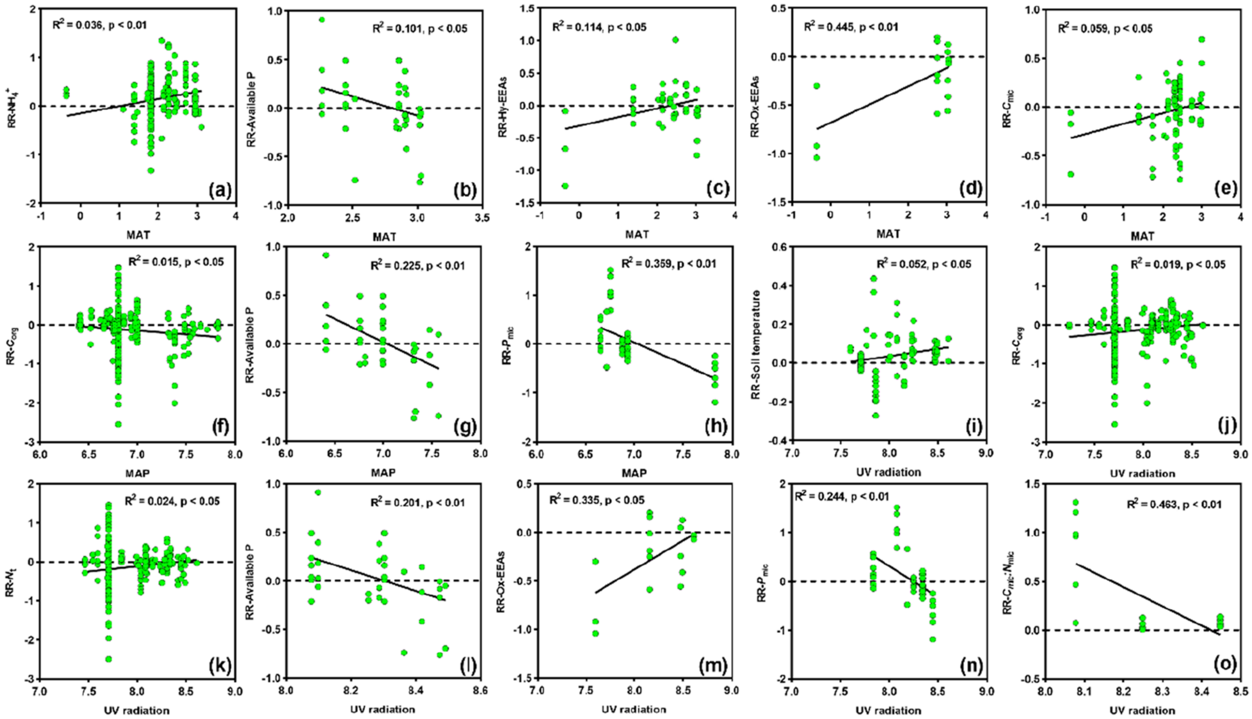

Fig. 6 Relationships of mean annual temperature (MAT, **a-e**), mean annual precipitation (MAP, **f–h**), and mean ultraviolet radiation (UV radiation, **i-o**) with response ratios (RR) of SOC content and nutrient availability. Fitted regressions and corresponding levels of significance are presented. C_{org}, soil organic carbon; N_t, total nitrogen; NH_4^+, ammonium; available P, available phosphorus; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; C_{mic}:N_{mic}, the ratio of microbial biomass carbon to microbial biomass nitrogen

in soil nutrient availability (Prescott 2002; Thiel and Perakis 2009; Xu et al. 2016). In the present study, there was a notable improvement in soil nitrogen availability following gap creation, as evidenced by a significant enhancement in NH_4^+ and NO_3^- concentrations, consistent with the findings from similar previous studies (Thiel and Perakis 2009; Kucera et al. 2020). This result could be primarily attributed to the reduction in nutrient uptake by vegetation, as well as a decrease in carbon inputs from litter and root exudation, which induced a decrease in nitrogen assimilation by soil microbial biomass. Meanwhile, the increase in soil microbial activity facilitated nitrogen mineralization from soil microbial biomass, predominantly during the growing season and in the mineral layer.

The elevation of soil moisture levels had both negative and positive effects on the subsequent increase in NH_4^+ and NO_3^- following gap creation. This indicated that maintaining an appropriate soil moisture level may accelerate soil nitrification (Chen et al. 2015; Osborne et al. 2016). Furthermore, our study revealed a significant enhancement in NO_3^- concentration following gap creation. This suggested that soil denitrification might decline and be primarily influenced by soil moisture, temperature, and *C:N* (Bremner and Shaw 1958; Elrys et al. 2021; Pan et al. 2022).

Our study detected a notable decrease in N_t and N_{mic} following gap creation, with this decline becoming more pronounced as gap age and size increased. This reduction might be attributed to the decrease in organic nitrogen, which severed as the primary nitrogen source of plants and microorganisms through litter nutrient return and root nutrient release. This, in turn, seemed to pose challenges in maintaining the soil nitrogen pool (Wu et al. 2022). Furthermore, our observations revealed a positive correlation between the changes in N_t and N_{mic}. This implied that microbial biomass, acting as a source of bioavailable nitrogen, played a pivotal role in predicting the spatiotemporal fluctuations within the soil nitrogen pool (Miltner et al. 2012; Daly et al. 2021).

The primary source of phosphorus in forest soil is derived from rock weathering (Kolowith and Berner 2002; Eger et al. 2018). We observed a noteworthy rise in P_t following gap creation, a trend in line with other forestry practices, such as thinning (Tian et al. 2019; Zhou et al. 2021). This increase might be attributed to the improved soil temperature and moisture levels resulting from gap creation, which in turn expedited the migration of phosphorus from the subsoil to the topsoil. Meanwhile, a notable positive correlation was observed

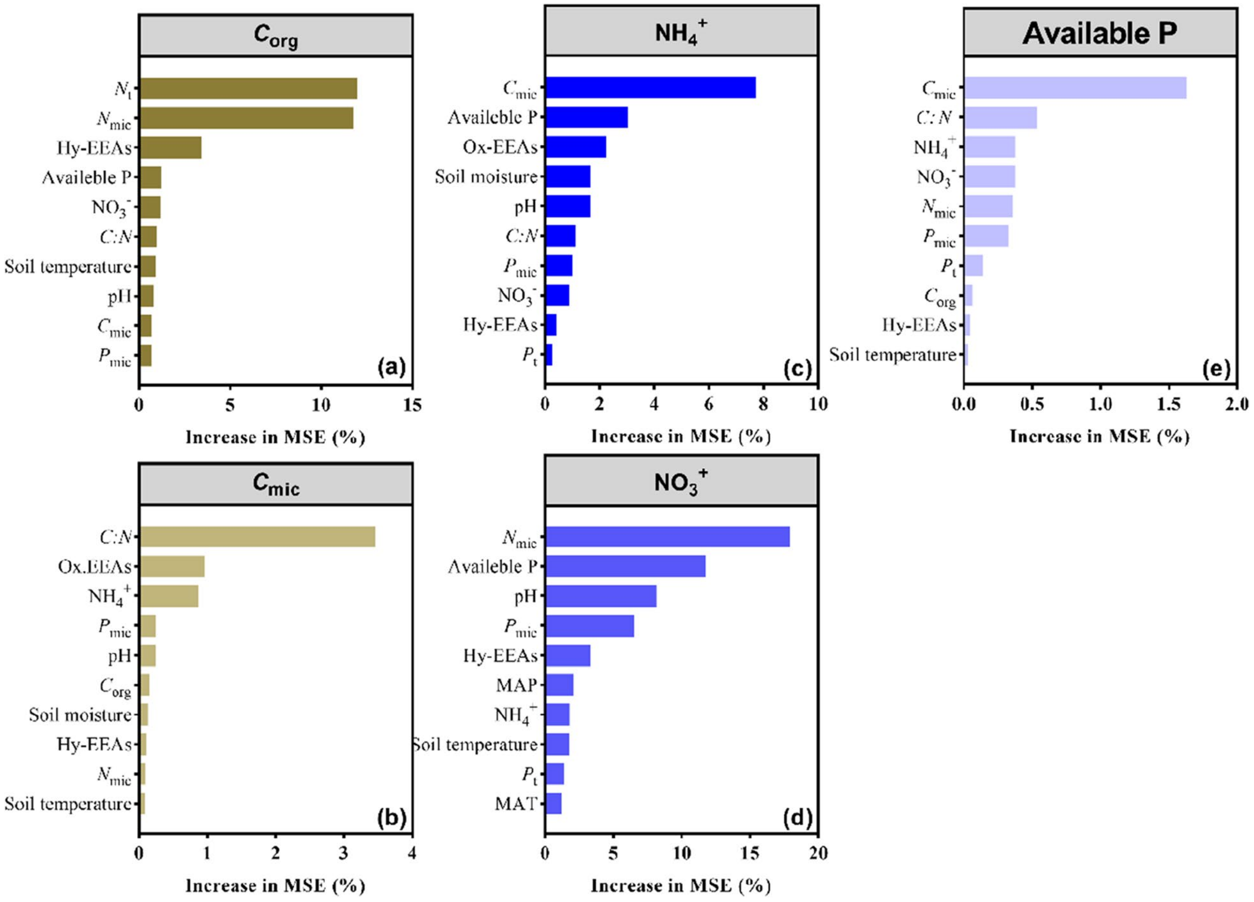

Fig. 7 The random-forest analysis to identify the main predictors of the response ratios of SOC content (**a**, **b**) and nutrient availability (**c**, **d**, **e**). The percent increase in mean squared errors (% IncMSE) represents the importance of main predictors, and negative values of % IncMSE, which indicate a lack of importance, are not shown. MAT, mean annual air temperature; MAP, mean annual precipitation; C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; *C:N*, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus

between enhancement of P_t and available P, indicating the crucial role of phosphorus migration in the soil phosphate supply. The microbial biomass could serve as a potential resource or reservoir of available plant nutrients under specific environmental conditions (Singh et al. 1989; Wardle et al. 2004; Sugito et al. 2010). This study observed a significant increase in available P and a simultaneous decrease in P_{mic} following gap creation. As mentioned earlier, the decrease in plant nutrient uptake might contribute to the rise in available P. Simultaneously, the insufficient substrate supply, resulting from reduced litter nutrient return and root nutrient release, could lead to a decline in microbial biomass. Additionally, the increased soil moisture might enhance phosphorus availability, likely achieved by promoting soil microbial activity (Gomoryova et al. 2006; Yang et al. 2023).

Enzyme activity serves as a crucial indicator of soil biological activity and nutrient cycling in forest ecosystems, with its alternation dependent on the initial soil nutrient and water status (Gomez et al. 2020; Levakov et al. 2021). This study observed a significant decline in Ox-EEAs following gap creation, potentially attributable to reduced soil nutrient supply. Furthermore, the decrease in Ox-EEAs exhibited a negative correlation with the increase in soil moisture, suggesting improved soil moisture conditions alleviated the reduction in soil enzyme activity. Overall, soil available nutrients were enhanced following gap creation, aligning with similar findings reported in the literature regarding the impact of global forest recovery on soil fertility (Zhou et al. 2022).

4.3 Effects of climate conditions on the changes in soil carbon content and nutrient availability

It is well-documented that changes in climate conditions have far-reaching impacts on carbon sink and nutrient cycling in forest ecosystems (Fung et al. 2005; Elrys et al.

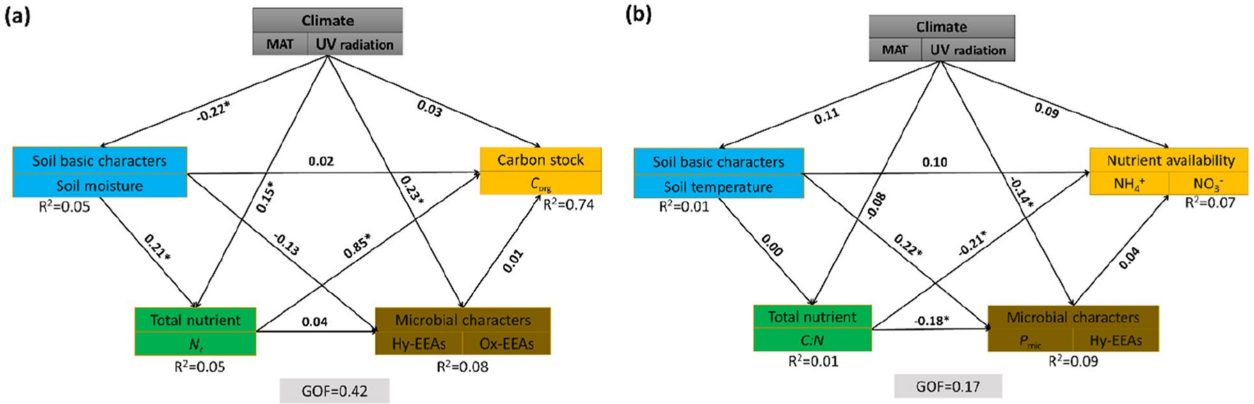

Fig. 8 Predicted partial least squares path modeling (PLS-PM) showing the effects of biotic and abiotic factors on the changes in SOC content (**a**) and nutrient availability (**b**). In the structural model, the lines indicated paths, and the values adjacent to the lines denote the magnitude of the path coefficients calculated by PLS regression. R^2 values are shown for all endogenous latent variables. Values in the measurement model represent the loadings between a latent variable and its indicators. The figure shows the final models after the model diagnosis processes. Specifically, some of the changes in the regulating factors were removed because of low loading (|loading|< 0.70). The * denote significant pathways ($p < 0.05$). The Pseudo Goodness-of-Fit (GoF) of model (**a**) and model (**b**) is 0.42 and 0.17, respectively. MAT, mean annual air temperature; MAP, mean annual precipitation; C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; *C:N*, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus

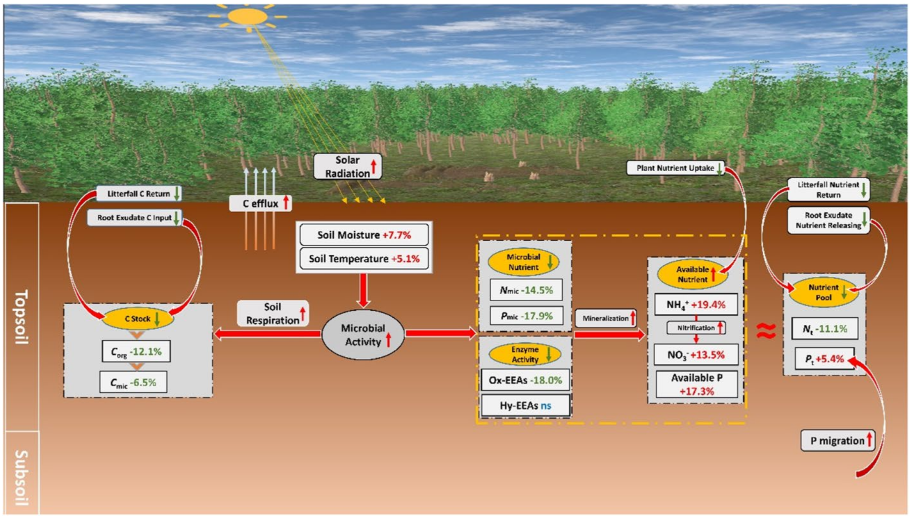

Fig. 9 Concept map of the potential mechanisms of SOC content and nutrient availability in response to canopy gap creation. C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; *C:N*, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus; C_{mic}:N_{mic}, the ratio of microbial biomass carbon to microbial biomass nitrogen

2021; Margalef et al. 2021). A recent study reported a global reduction in the forest recovery effect on soil carbon sink and soil fertility due to joint changes in temperature and rainfall (Zhou et al. 2022). In the present study, we examined the influence of climate condition changes on the dynamics of soil carbon content and available nutrients following gap creation (Figs. 13, 14 and 15 in Appendix). The results indicated that temperature generally attenuated the effects of canopy gaps on the soil carbon content and available nutrients. Conversely, precipitation enhanced the canopy gap effects, aligning partially with the findings of Zhou et al. (2022).

Specifically, our observations indicated that the elevated MAP mitigated the decline in C_{org} and P_{mic}, as well as the increase in available P (Fig. 14 in Appendix). These findings suggested that heavy precipitation might have constrained both soil microbial respiration and the transformation of P_{mic} into available P. The rise in MAT intensified the decrease in C_{mic} (Fig. 13 in Appendix). This phenomenon might be attributed to the carbon losses in the soil induced by warming, as explained by the mechanism of substrate depletion (Walker et al. 2018). In addition, the elevated MAT also amplified the increase in $\mathrm{NH_4}^+$, possibly due to the plant exhibiting heightened nutrient uptake at elevated temperatures.

Solar radiation is intricately linked to plant photosynthesis and nutrient stoichiometry, garnering heightened attention for its impact on biogeochemical cycling in recent studies (Epp et al. 2007; Ji et al. 2020; Barnes et al. 2023). In the current investigation, we evaluated the influence of UV radiation on the dynamics of both the physical and chemical properties of the soil following gap creation (Fig. 15 in Appendix). Previous studies have consistently demonstrated that the formation of canopy gaps significantly elevates soil temperature, primarily due to the increased solar radiation reaching the forest floor (Wang et al. 2022). Our study further observed a pronounced enhancement in soil temperature caused by UV radiation, potentially resulting in a more substantial impact on soil microbial respiration.

We observed that UV radiation enhanced the negative effects of canopy gaps on C_{org} and N_{t}, possibly due to an enhancement in soil microbial respiration. Likewise, our findings revealed that UV radiation facilitated a reduction in Ox-EEAs by instigating substantial losses in soil organic matter. In contrast, it was observed that UV radiation reduced the positive effects of canopy gaps on available P, as well as the negative effects on P_{mic}, suggesting that UV radiation might play a crucial role in regulating phosphorus cycling through the modulation of soil phosphorus-related enzyme activities, such as soil acid phosphatase. Meanwhile, we found that the increase in C_{mic}:N_{mic} was negatively associated with UV radiation, implying that high solar radiation could mitigate microbial nitrogen limitation to some extent.

4.4 Study limitations and management implications

While we have endeavored to offer a comprehensive understanding of the effects of canopy gaps on soil carbon content and nutrient availability through a global meta-analysis, there remain several potential limitations. Firstly, the sampled studies do not encompass the full spectrum of global forests, focusing primarily on eastern forests. Therefore, further research spanning a broader range of forest biomes, especially boreal and tropical forests, is imperative to ascertain the generality of our findings. Secondly, the analysis overlooks vital information regarding the surrounding gaps of trees. For example, tree height correlates with the angle of incoming solar radiation, and the crown radius is associated with gap edge effect. Thirdly, this study lacks direct evidence to elucidate potential mechanisms, particularly the responses of soil microorganisms after gap creation. Finally, previous research confirms the close association between biodiversity and soil nutrient availability. However, information regarding the variation in the gap-making species is not recorded in the present meta-analysis.

Our study has significant implications for sustainable forest management. Firstly, it highlights the pronounced effects of canopy gaps on the soil carbon sequestration, nutrient availability, and their interconnectedness with climate conditions. Consequently, integrating the canopy gap effect into spatially explicit models is crucial for achieving a comprehensive understanding of carbon sequestration and biodiversity conservation (O'Connor 2008; Forsius et al. 2021). Secondly, this study has significantly contributed to a comprehensive understanding of the effects of canopy gaps on soil carbon and nutrients. This, in turn, facilitates more accurate predictions of forest succession in the future. With the growing popularity of close-to-nature forest management, the implementation of small-scale harvests and artificial canopy gaps is poised to play crucial roles in restoration of low-quality secondary forests and monoculture plantations (Fig. 16 in Appendix). Thirdly, prior studies have emphasized the necessity of sustainable forest management for climate change adaptation (Canadell and Raupach 2008; Liu et al. 2013; Keenan 2015). Our study contributes valuable information regarding the impacts of changes in climate conditions on soil carbon content and nutrient availability after the creation of canopy gaps. This information is crucial for the implementation of artificial canopy gaps in forest management under current and future climate conditions.

5 Conclusions

The occurrence of canopy gaps was found to decrease soil carbon content while simultaneously increasing nutrient availability in the topsoil layer of forest ecosystems. These changes became more pronounced with the age and size of canopy gaps. The alteration in soil moisture level following gap creation might serve as a crucial driver of the response of soil carbon pool and nutrient availability. Precipitation and temperature played negative and positive roles, respectively, in influencing the soil carbon content and nutrient availability. Additionally, UV radiation exhibited a positive regulatory effect on the response of soil carbon and nitrogen components, while playing a negative regulatory role in the response of phosphorus components. In summary, this study sheds light on the significant roles played by canopy gaps in regulating carbon stock dynamics and nutrient biogeochemical cycles in forest ecosystems. The findings have noteworthy implications for ecological restoration and fine-scale regulation of forest structure.

6 Appendix

Text 1. List of the 52 papers from which the data were extracted for this meta-analysis.

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2. Jia, G., Xu, Q., Yang, H., Yang, Q., Li, Y., & Liu, W. (2020). soil methane flux of tropical mountain rainforest canopu gaps in Jianfengling, Hainan Island. Journal of Forest and Environment, 40(2), 126-132. (In Chinese)
3. Han, M., Tang, M., Shi, B., & Jin, G. (2020). Effect of canopy gap size on soil respiration in a mixed broadleaved-Korean pine forest: Evidence from biotic and abiotic factors. European Journal of Soil Biology, 99, 103194.
4. Liu, Y., Zhang, J., Yang, W., Wu, F., Xu, Z., Tan, B., Zhang, L., He, X., Guo, L. (2018). Canopy gaps accelerate soil organic carbon retention by soil microbial biomass in the organic horizon in a subalpine fir forest. Applied Soil Ecology, 125, 169-176.
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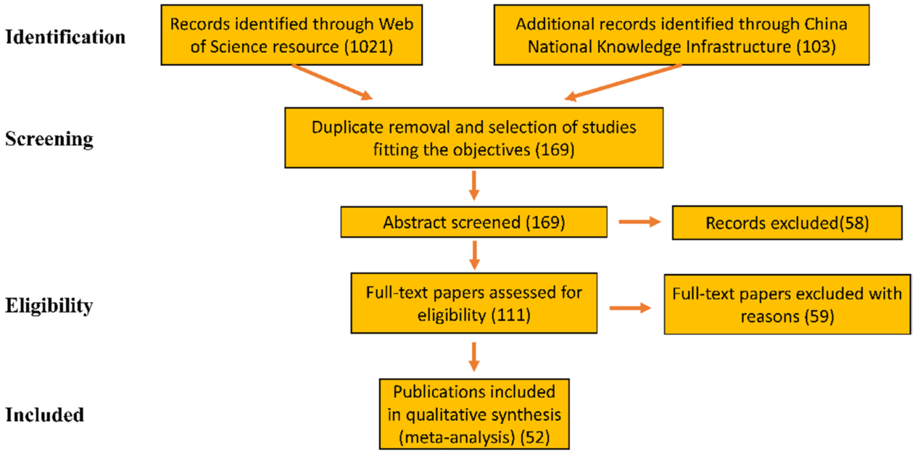

Fig. 10 The PICOS process of this meta-analysis

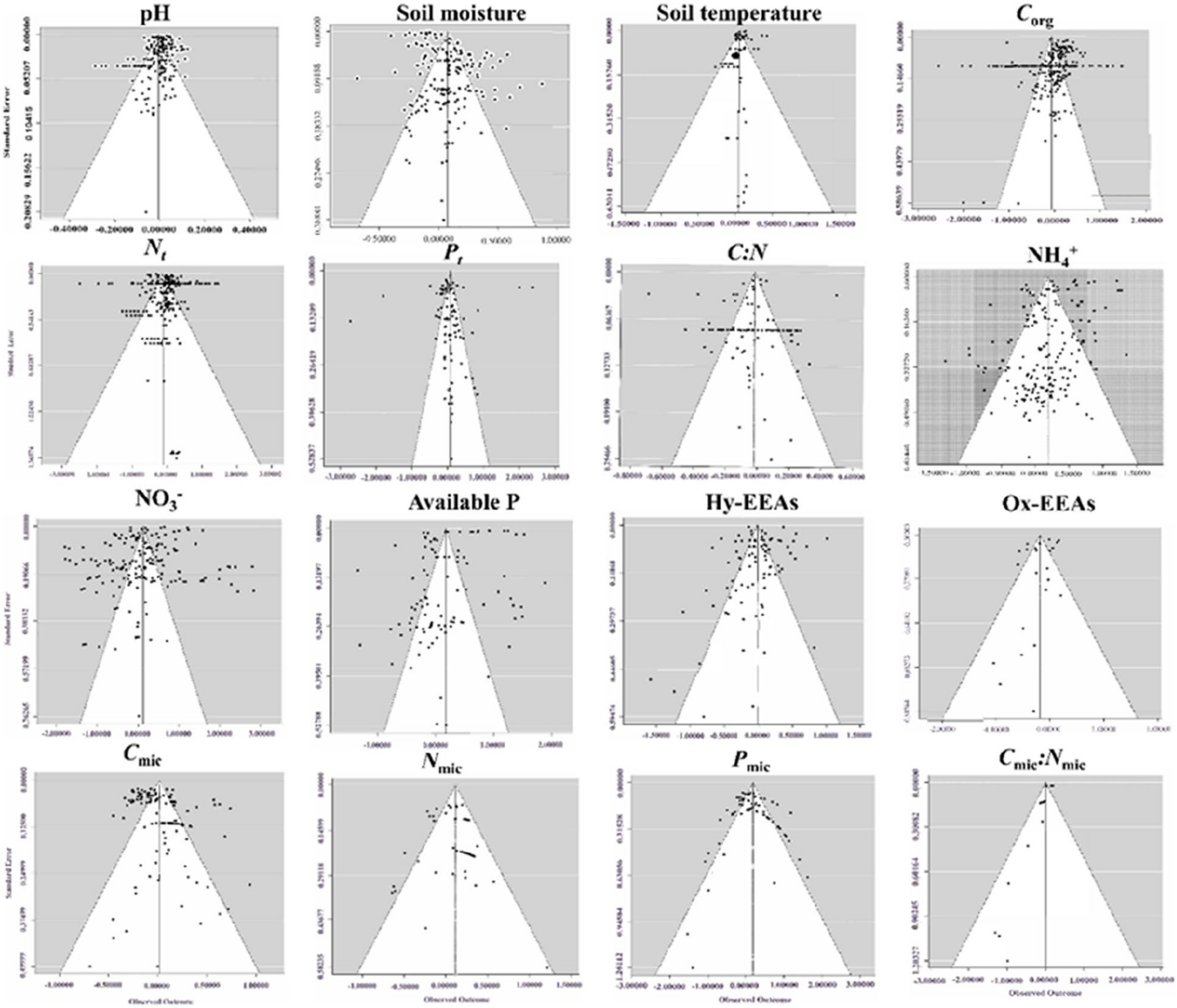

Fig. 11 Funnel plot for the 16 variables

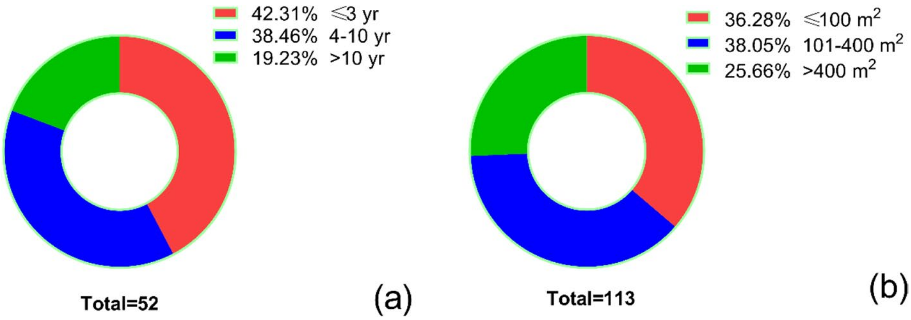

Fig. 12 Frequency of the division in gap age (**a**) and size (**b**)

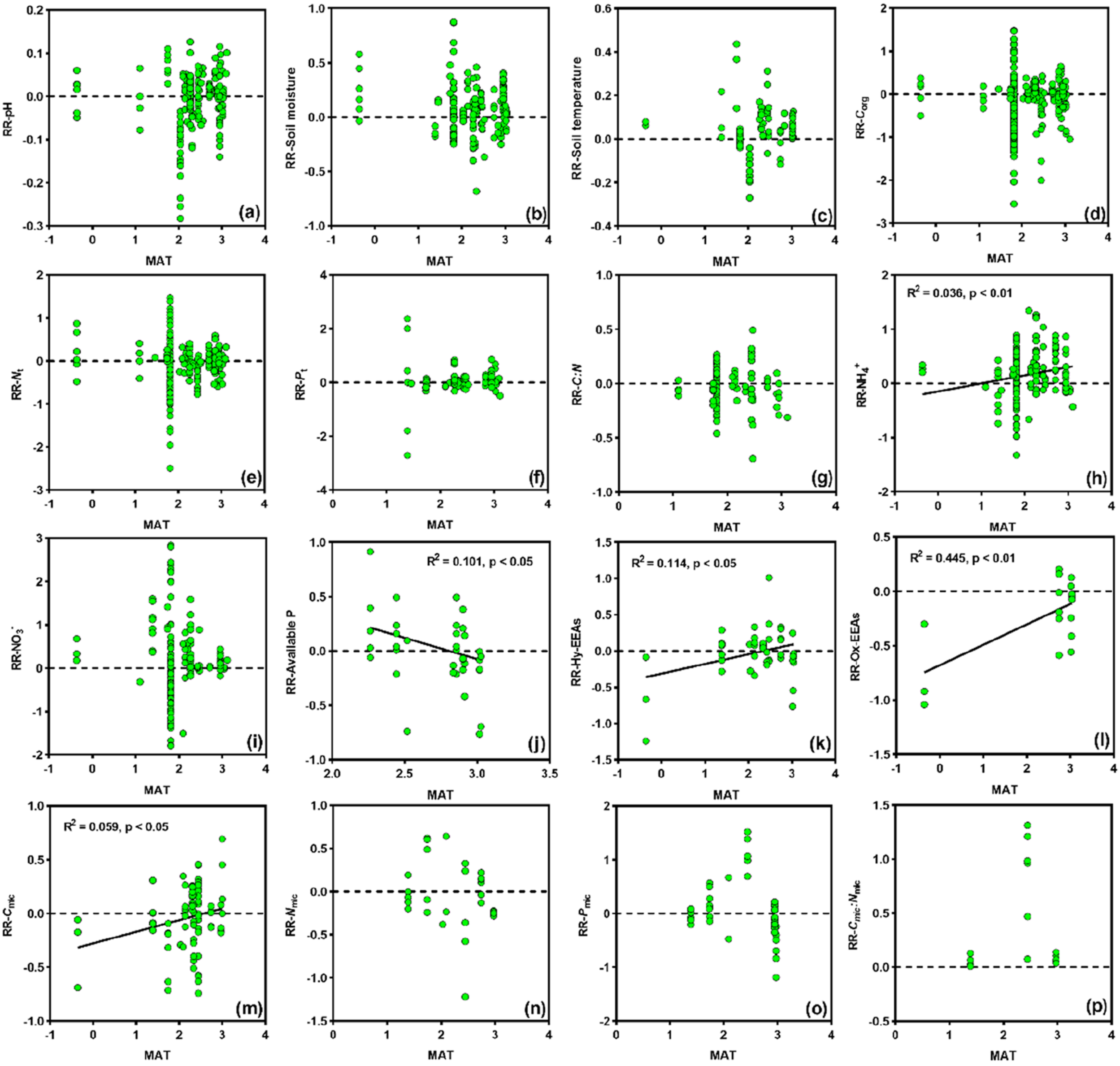

Fig. 13 Relationships of mean annual temperature (MAT, a-p) with response ratios (RR) of SOC content and nutrient availability. C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; *C:N*, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus; $C_{mic}:N_{mic}$, the ratio of microbial biomass carbon to microbial biomass nitrogen

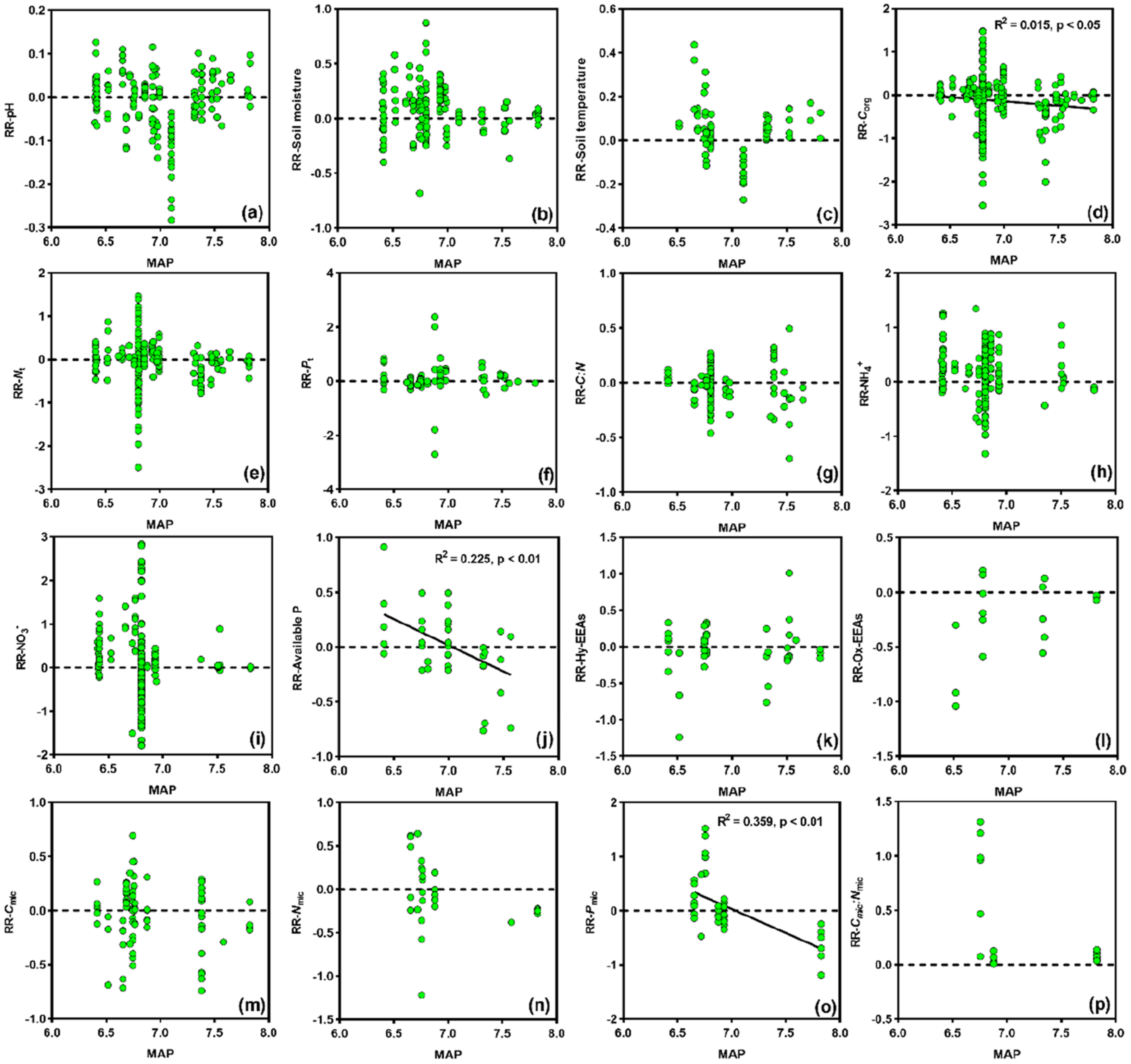

Fig. 14 Relationships of mean annual precipitation (MAP, a-p) with response ratios (RR) of SOC content and nutrient availability. C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; *C:N*, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus; C_{mic}:N_{mic}, the ratio of microbial biomass carbon to microbial biomass nitrogen

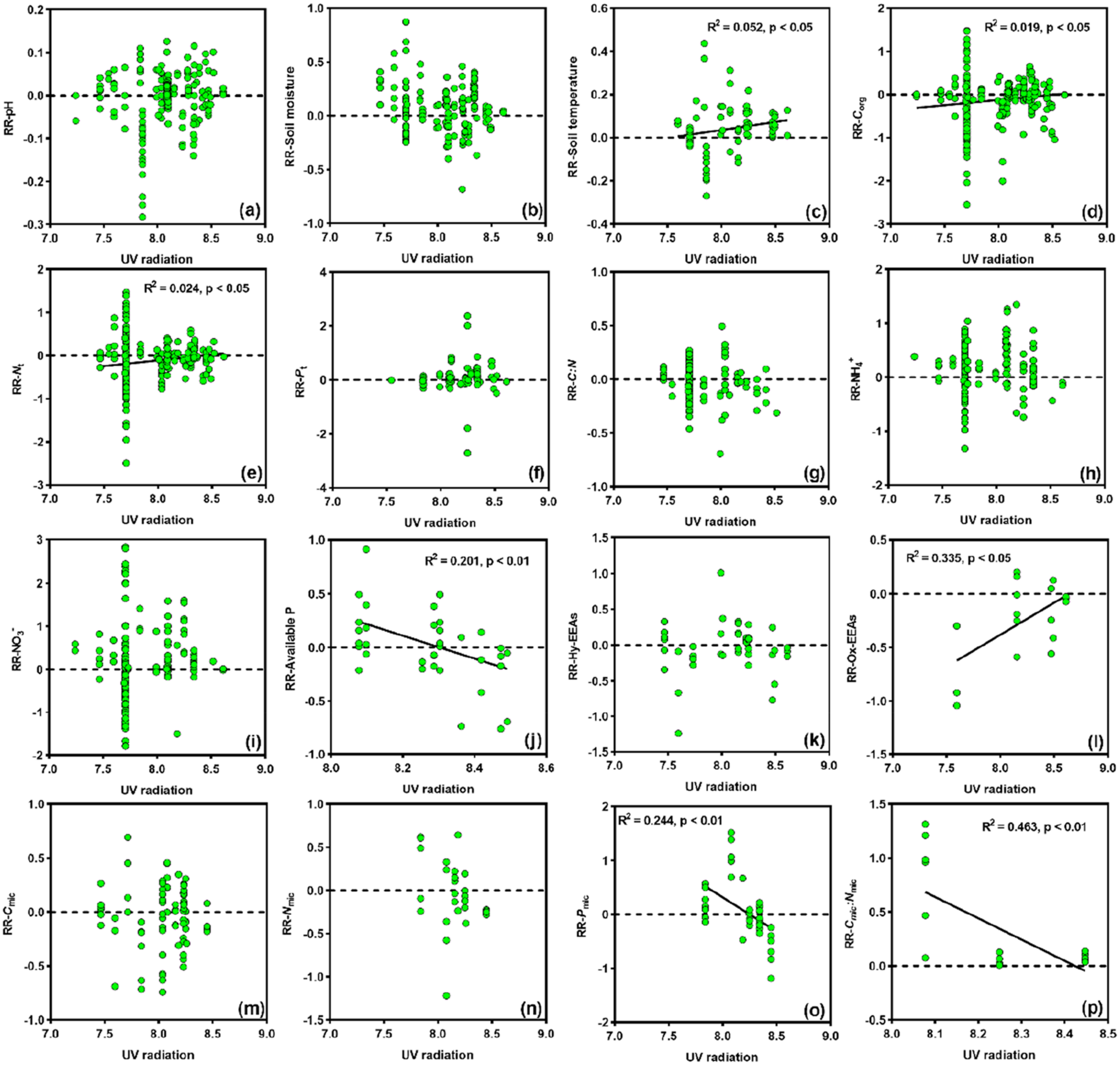

Fig. 15 Relationships of mean ultraviolet radiation (UV radiation, a-p) with response ratios (RR) of SOC content and nutrient availability. C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; *C:N*, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus; C_{mic}:N_{mic}, the ratio of microbial biomass carbon to microbial biomass nitrogen

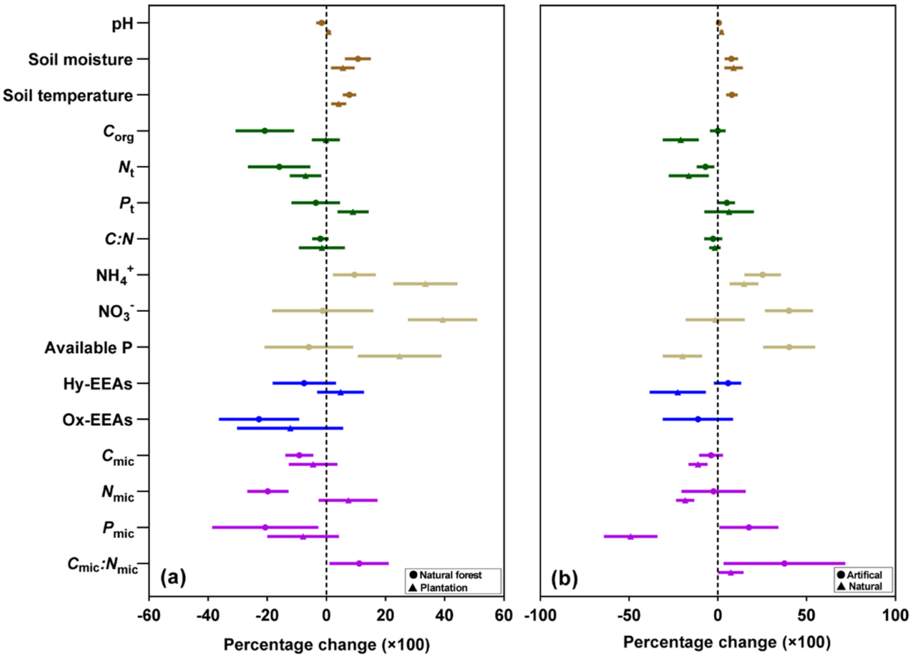

Fig. 16 Response of SOC content and nutrient availability to canopy gap creation for two categorical variables, including forest type and gap formation type. Values are mean effect size (× 100%) ± 95% confidence intervals (CI). The vertical line is drawn at lnRR = 0. The number of observations is within the parentheses. C_{org}, soil organic carbon; N_t, total nitrogen; P_t, total phosphorus; *C:N*, the ratio of soil organic carbon to total nitrogen; NH_4^+, ammonium; NO_3^-, nitrate; available phosphorus, available P; Hy-EEAs, hydrolases-extracellular enzymes activities; Ox-EEAs, oxidoreductases-extracellular enzymes activities; C_{mic}, microbial biomass carbon; N_{mic}, microbial biomass nitrogen; P_{mic} microbial biomass phosphorus; C_{mic}:N_{mic}, the ratio of microbial biomass carbon to microbial biomass nitrogen

Table 1 Correlation analysis of geographical and climatic variables. MAT, mean annual temperature; MAP, mean annual precipitation; UV radiation, ultraviolet radiation

	Latitude	Longitude	Elevation	MAT	MAP
Longitude	-0.313**	1			
Elevation	-	-	1		
MAT	-0.598**	-	-	1	
MAP	-0.418**	-	-	0.454**	1
UV radiation	-0.972**	0.328*	-	0.599**	0.403**

* $p < 0.05$; ** $p < 0.01$

Table 2 Description of the Fail-safe N for the 16 variables

	Sample size (n)	Fail-safe N		Sample size(n)	Fail-safe N
pH	192	2596	NO_3^-	178	233,147
Soil M	199	18,852	Available P	100	389,209
Soil T	117	35,450	Hy-EEAs	87	1992
C_{org}	303	5042	Ox-EEAs	23	427
N_t	238	23,171	C_{mic}	128	638
P_t	96	3052	N_{mic}	58	667
C:N	147	1553	P_{mic}	68	1590
NH_4^+	179	83,308	C_{mic}:N_{mic}	22	0*

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Code availability
Not applicable.

Authors' contributions
R T and TG W designed the study, provided the funding and revised the manuscript; R T, BY J, and GG W performed the experiments, data collection, and drafted the manuscript; CY L, C M performed data processing and statistics; NF Z and WW Y performed part of the experiment. All authors read and approved the final manuscript.

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Availability of data and materials
The datasets generated and/or analyzed during the current study are available in the Figshare repository at https://doi.org/10.6084/m9.figshare.24038883.v3.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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