



Dominant mycorrhizal association of trees determines soil nitrogen availability in subtropical forests

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ABSTRACT

Trees and their associated arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi drive carbon (C) and nitrogen (N) cycling patterns. However, the mechanisms underpinning this relationship and the degree to which mycorrhiza mediate the effects of forest tree composition on soil N cycling outside of the temperate zone remain unclear. Here, we conducted field surveys to establish a natural gradient with increasing ECM tree dominance in subtropical forests, and explored the effects of tree mycorrhizal associations on soil N cycling. Across this mycorrhizal gradient, we quantified soil available N, microbial biomass N, net N transformation rates, as well as N-acquiring enzyme activities, litterfall biomass and quality, and soil pH during the one-year growing season. We found that with increasing ECM tree dominance, the dissolved organic N and nitrate N decreased, while the microbial biomass N increased linearly. Soils dominated by AM trees had 1.8–2.3 times larger mineral N contents, net N mineralization rate, and net nitrification rate than ECM-dominated stands, suggesting a rapid N cycling in AM-dominated stands. ECM trees and their associated fungi reduce the net N mineralization rate in topsoil mainly by producing recalcitrant litterfall (i.e., higher C:N) and by secreting β -N-acetylglucosaminidase to deplete N directly from soil organic matter, which together increased N limitation for free-living decomposers. The low pH and high C:N ratio in ECM-dominated soils inhibit the proliferation of ammonia-oxidizers and thus decrease the net nitrification rate. Our results demonstrate that the increasing ECM tree dominance increase soil N-acquiring enzyme activity and C:N ratio but decrease pH value, all of them critically mediating soil N availability. Consequently, by altering the relative abundances of tree mycorrhizal associations shifts in forest composition under global changes and plantation establishment can be expected to result in altered soil N cycling.

1. Introduction

Soil nitrogen (N) availability is closely related to forest carbon (C) storage and ecosystem productivity, as well as nitrous oxide emissions and nitrate (NO_3^-) leaching (LeBauer and Treseder, 2008; Wolf et al., 2011). The plant available N largely depends on soil N transformation processes, which can be affected in turn by numerous factors such as the microbial diversity and community composition, the quality and quantity of soil organic matter (SOM), and pH (Wang et al., 2016; Xiao et al., 2018). All of these factors can be affected by tree species composition

because of species-specifics in tree growth rates, quantity and quality of litterfall and rhizodeposition, and interactions with soil microorganisms (Chapman et al., 2006; Kaiser et al., 2011; Prescott and Grayston, 2013; Henneron et al., 2020). Globally, forests are currently undergoing a large-scale shift in tree species composition due to anthropogenic and natural causes such as climate change, atmospheric N deposition, alterations in disturbance, conversion to plantations, and exotic species invasion (Dale et al., 2001; Vilà et al., 2011; Fei et al., 2017; Jo et al., 2019; Wang et al., 2021). Therefore, understanding how shifting forest tree composition can influence soil N cycling is crucial for estimating

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potential ecosystem-level consequences.

The roots of nearly all tree species form symbiotic associations with either arbuscular (AM) or ectomycorrhizal (ECM) fungi to gain access to water and nutrients (Smith and Read, 2008; van der Heijden et al., 2015; Brundrett and Tedersoo, 2018). Compared with AM trees having nutrient-acquisitive traits, ECM trees usually possess nutrient-conservative traits such as lower relative growth rates and poorer leaf litter quality (Read, 1991; Lin et al., 2018; Averill et al., 2019). Meanwhile, many ECM fungi can directly mine organic N from SOM through secreting oxidative and hydrolytic enzymes, while AM fungi have limited capabilities in producing these enzymes (Talbot et al., 2008). The direct organic N uptake implies ECM fungi limit the amount of N available for free-living microbes, which subsequently reduce SOM decomposition rates and soil N availability (Gadgil and Gadgil, 1971; Wurzbarger and Brookshire, 2017). Recently, a mycorrhizal-associated nutrient economy (MANE) framework has been developed in recognition of these distinct trait-mediated patterns in biogeochemical cycling (Phillips et al., 2013). The MANE framework predicts that AM forests utilize an inorganic nutrient economy, while the economy of ECM forests is passed on organic nutrients. The MANE framework is further verified through a global meta-analysis (Lin et al., 2017), which illustrates that ECM-dominated forests exhibit more “closed” N cycling with small pools of soil mineral N and lower nitrification transformation rates relative to AM-dominated forests.

Current understanding of mycorrhizal association effects on soil N cycling is predominantly from studies carried out in temperate forests, and thus it remains unknown whether the MANE framework holds for tropical or subtropical forests, which notably contain co-occurring AM and ECM tree species of high ecological importance (Brundrett and Tedersoo, 2018). Available evidences indicate that uptake of organic N mediated by ECM fungi is negligible in tropical forests, as i) tropical forests are characterized by faster organic N mineralization rates due to their higher temperature and larger presence and higher activity of hydrolytic enzymes (Andersen et al., 2017), ii) the $\delta^{15}\text{N}$ signal was found similar or even higher in ECM trees than in the AM trees in a tropical forest (Tedersoo et al., 2012; Mayor et al., 2015). These results suggest that N cycling in tropical forests should generally be open and rapid, regardless of mycorrhizal types (Kuyper, 2012; Andersen et al., 2017). However, a recent study in tropical montane forests showed that the dominant ECM tree species, *Oreomunnea mexicana*, depleted N directly from SOM, which increased N limitation for co-occurring AM trees and heterotrophic soil microbes (Corrales et al., 2016). Thus, the applicability of MANE framework to non-temperate forest ecosystems needs further verification.

Other key questions about the MANE framework remain. The specific effects of AM and ECM trees on soil N cycling have been commonly observed by comparing AM-dominated and ECM-dominated plots (Lin et al., 2017), but have not covered a gradient in ECM relative to AM tree dominance. Simple comparisons of the two forests with differential mycorrhizal type may not well explain the mycorrhiza-mediated effects, as various environmental factors, edaphic conditions, together with mycorrhizal tree abundance, are different between the two forest types. Additionally, it is necessary to look beyond “ECM-dominated” and “AM-dominated” systems, as most plots in natural forests contain the mixtures of AM and ECM tree species rather than AM dominated or ECM dominated (Phillips et al., 2013; Craig et al., 2018). Further study should also observe soil N cycling at a higher resolution (i.e., different depths and pools). Therefore, “mycorrhizal gradients” (denoted as graphs of the relative abundances of AM versus ECM trees in a forest ecosystem) can serve as appropriate suitable experimental “proving ground” for assessing the effects of mycorrhizal associations on biogeochemical processes (Cheeke et al., 2017; Jo et al., 2019).

To further evaluate the linkages between tree mycorrhizal associations and soil N cycling, we quantified N-cycling variables in the organic horizon and mineral topsoil along a natural mycorrhizal gradient in subtropical forests. Subtropical secondary forests are rich in tree species

diversity and play an important role in buffering the rising CO_2 levels and driving biogeochemical cycles in the subtropics (Xiang et al., 2013; Ouyang et al., 2021). However, subtropical forests are threatened by high levels of forest conversion (e.g., deforestation for plantations) (Wang et al., 2021) and chronically elevated N deposition rates (Jia et al., 2013), which can strongly influence forest mycorrhizal associations. This study aimed to test (i) whether the mycorrhizal associations of locally dominant tree species explain the within-site variation in soil N availability; (ii) if and how soil N cycling relates to forest mycorrhizal type. We hypothesized that soil N availability would decrease with the increasing ECM tree dominance and that soil N cycling rate would be slower in ECM-dominated stands than in AM-dominated stands.

2. Materials and methods

2.1. Site description and experiment design

We conducted this study in the Dashanchong Forest Park (28°23'58"-28°24'58"N, 113°17'46"-113°19'08"E), Changsha County, Hunan Province, China. The forest park is located in a humid mid-subtropical monsoon climate region and is a mountainous area with an elevation of 55–260 m a.s.l. The mean annual precipitation and temperature of this area are 1416 mm and 17.3 °C, respectively. Soils in this site are well-drained red clay-rich loam developed on shale and slate rock, and are grouped as an Alliti-Udic Ferrosols according to the World Reference Base for Soil Resource (IUSS Working Group WRB, 2015). The climatic vegetation in this region is evergreen broadleaf forest. The park has no primary forest due to ancient human disturbances, and possesses a range of secondary forests which developed from the natural restoration of the destructed forests since the late 1950 s (Xiang et al., 2013). These secondary forests are suitable for assessing the impact of the dominant mycorrhizal tree associations on soil processes, as they develop under similar soil parent material, climate, and topography (Ouyang et al., 2016; Chen et al., 2019).

In October 2019, we established forty-five plots (10 m × 10 m) to reflect a natural mycorrhizal gradient in these secondary forests. In each plot, we identified trees to species, recorded their diameter at breast height (DBH), and determined their mycorrhizal association (Wang and Qiu, 2006; van der Heijden et al., 2015). We sited plots to capture the complete gradient of mycorrhizal tree dominance as determined by basal area (BA) of tree species associated with either AM or ECM fungi. This mycorrhizal gradient was established randomly and that there were no other natural gradients visible. Plots across the gradients were identified as ECM-dominated ($n = 15$, ECM tree contained $\geq 70\%$ of the total BA of the plot), mixed ($n = 15$, ECM or AM trees constituted 30–70% of the total BA), and AM-dominated plots ($n = 15$, $\geq 70\%$ AM tree by BA) (Fig. S1 and Table S1). Dominant ECM trees in these forest plots include *Pinus massoniana* Lamb., *Lithocarpus glaber*, *Cyclobalanopsis glauca* (Thunberg) Oersted, *Quercus fabri*. The dominant AM-associated tree species were *Choerospondias axillaris*, *Cunninghamia lanceolata*, *Elaeocarpus japonicus*, *Cinnamomum camphora*, *Phyllostachys pubescens*. The understory was composed mainly of *Cleyera japonica*, *Loropetalum chinense*, *Lophatherum gracile*, *Carex filicina*, *Dicranopteris linearis*, *Pteridium aquilinum* var. *latiusculum*.

2.2. Sample collection

We collected litterfall every month from December 2019 to November 2020, using a trap (1.0 m × 1.0 m) installed in the middle of each plot. Samples from the trap were kept in plastic bags, delivered to the laboratory, dried at 60 °C, and weighed. Annual litter biomass was the sum of the 12-months' litterfall, and the litterfall quality (litterfall C: N ratio) was determined using an elemental analyzer (EA3000, Euro-Vector, Italy).

Soil samples from plots of the mycorrhizal gradient were collected on February, July, and November 2020, respectively, using 5-cm-diameter

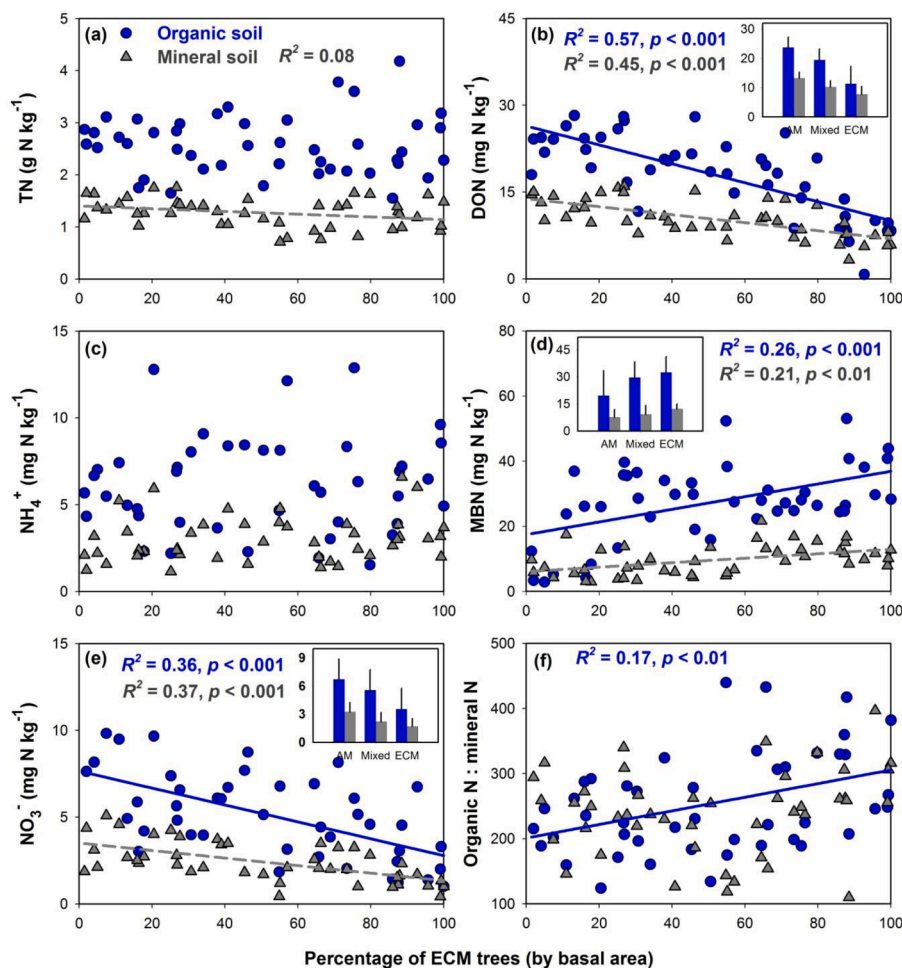


Fig. 1. The relationships between ectomycorrhizal (ECM) tree dominance and soil total N (TN, a), dissolved organic N (DON, b), ammonia N (NH_4^+ , c), microbial biomass N (MBN, d), nitrate N (NO_3^- , e) and organic N to mineral N ratio (f) in Dashanchong Forest Park, southern China. Only significant regressions are presented ($p < 0.05$). Bar graphs in the insets show the mean value of the corresponding N content in arbuscular mycorrhizal (AM) dominated plots, mixed plots, and ECM dominated plots. Each point represents the seasonal averages (February, July and November 2020) in each plot ($n = 45$ plots).

stainless steel soil corer. In each plot, organic horizon (c. 0–5 cm) and the topmost mineral soil (depth 15 cm) were taken at 5 points (1 point at the center and 4 points equidistant from the center to the plot corners). Soil samples from the same horizon collected at each time-point were pooled by plot and sieved with a 2-mm mesh to get rid of any debris. Therefore, 270 samples (45 plots \times 2 soil horizons \times 3 seasons) were obtained. Freshly-collected soil samples were stored in iced polyethylene bags and delivered to the laboratory. For each sample, 500 g fresh soils were air-dried and sieved before physicochemical analysis, and 200 g fresh soils were kept at 4 °C for testing microbial biomass and enzyme activities within 2 weeks.

2.3. Analytical measurement

We determined soil moisture after the soil samples were oven dried at 105 °C for 24 h. We measured soil pH using a pH meter (FE20K, Mettler-Toledo, Switzerland) with a soil: water ratio of 1:2.5. After grinding the air-dried soil samples, we determined soil organic carbon (SOC) and total N (TN) contents using the $\text{K}_2\text{Cr}_2\text{O}_7\text{-H}_2\text{SO}_4$ oxidation method and Kjeldahl method, respectively. Total phosphorus (TP) and available phosphorus (e.g., Olsen-P) were quantified by the Mo-Sb colorimetric method.

For mineral N, 15 g fresh soils were added to 50 mL K_2SO_4 (0.5 M) solution and shaken for 1 h. A flow injection analyzer (FIA star 5000, FOSS, Sweden) was used to measure NH_4^+ and NO_3^- contents in the filtrate. Dissolved organic N (DON) and NH_4^+ were converted to NO_3^- through persulfate oxidation, and total dissolved N (TDN) was measured (Xiao et al., 2018). DON content was quantified by comparing the difference between TDN and total mineral N (i.e., the sum of NH_4^+ and

NO_3^-). The rates of net mineralization and nitrification were calculated according to the differences in total inorganic N and NO_3^- , respectively, pre- and post-incubation for 24 h. The mineral N contents and the transformation rates were presented as units per gram of soil and units per milligram N, respectively.

We determined microbial biomass C (MBC) and N (MBN) by the chloroform fumigation extraction method (Vance et al., 1987). The potential activity of soil β -N-acetylglucosaminidase (NAGase), responsible for the depolymerization of organic N, was determined by using the fluorogenic methylumbelliferone-based (MUB) substrates in a fluorometric 96-well microplate (Saiya-Cork et al., 2002).

2.4. Statistical analysis

We generated yearly averages (mean value of February, July and November) of all parameters for each plot to reduce the impacts of seasonal variations and missing data prior to statistical tests. Changes of N cycling variables across the mycorrhizal gradient were evaluated using linear regression with the proportion of ECM trees as the predictive factor and the N cycling variables as response variables. The N cycling variables including available-N contents, net N transformation rates, etc. Differences in soil N and other variables among the plots dominated by AM trees, mixed and ECM trees were examined using one-way ANOVA with Tukey's HSD test.

To account for the effects of tree species richness, total basal area and other edaphic properties, we assessed the relationships between ECM tree dominance and soil available N contents by the ordinary least squares (OLS) multiple regression. Standardization of the variables (mean = 0 and standard deviation = 1) was performed using the "scale"

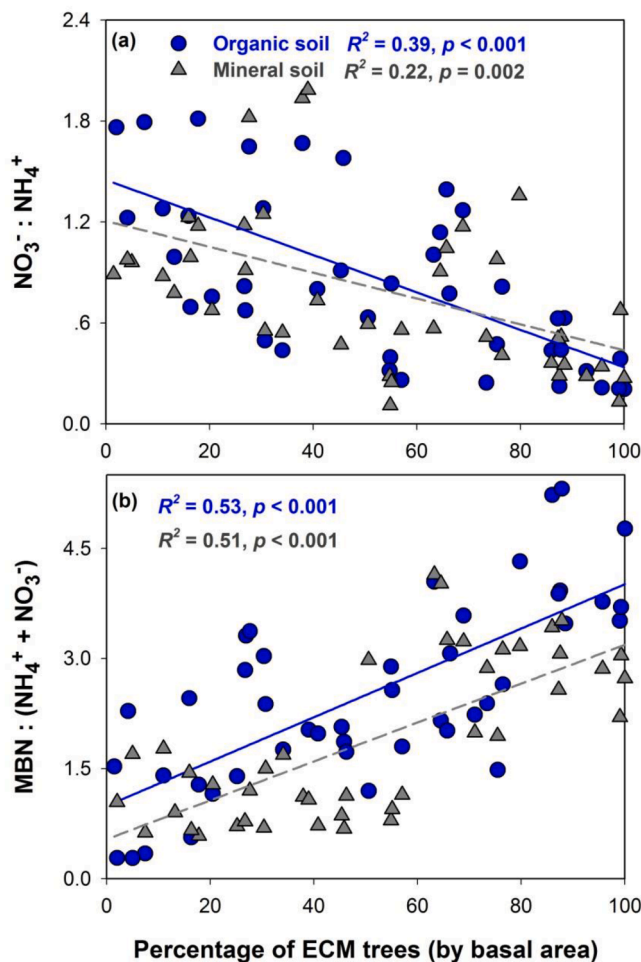


Fig. 2. Changes in the ratios of (a) $\text{NO}_3^- : \text{NH}_4^+$ and (b) $\text{MBN} : (\text{NH}_4^+ + \text{NO}_3^-)$ across the gradient of ectomycorrhizal (ECM) tree dominance in Dashanchong Forest Park, southern China. The ratios: $\text{NO}_3^- : \text{NH}_4^+$ and $\text{MBN} : (\text{NH}_4^+ + \text{NO}_3^-)$ represent the mean NO_3^- divided by NH_4^+ and MBN divided by the total mineral N, respectively, across all three dates sampled in February, July and November 2020 ($n = 45$ plots).

function. The best OLS model was identified by Akaike's information criterion (AIC) using the R package "MASS". The variance inflation factor (VIF) was determined using the R package "CAR", and $\text{VIF} < 3$ was used to identify appropriate variables in the model for eliminating strongly multicollinearity.

Finally, structural equation models (SEMs) were used to identify the direct and indirect effects of the ECM tree dominance on soil N availability. We expected that ECM tree abundance affects litterfall C:N ratio, pH and the soil C:N ratio, and these factors would in turn affect soil N transformation rate and subsequently available-N content. The "SEM" package in R was used for path analysis (Byrnes et al., 2016) and a path diagram was constructed after eliminating insignificant relationships. Requirements for an acceptable model included an insignificant chi-square test with $p > 0.05$, goodness-of-fit index > 0.95 and root mean square error of approximation < 0.05 (Schermelleh-Engel et al., 2003). The total effect was measured by summing all direct and indirect paths between the regulatory variables and soil available N content. All the data statistical analyses were performed in R 3.6.1 (R Core Team, 2019).

3. Results

3.1. Soil N changes across the mycorrhizal gradient

Across all plots, the contents of all forms of soil N (TN, MBN, DON, NH_4^+ , and NO_3^-) were generally higher in the organic horizon than in the mineral topsoil (Fig. 1). There were no detectable differences in TN contents across the mycorrhizal gradient (Fig. 1a, but marginally negative effect in mineral soil). However, the DON (Fig. 1b) and NO_3^- (Fig. 1e) content decreased linearly across the mycorrhizal gradient for both soil horizons. Specifically, the DON and NO_3^- contents were nearly 2.2-times higher in AM-dominated stands than in ECM-dominated stands ($p < 0.05$). In contrast, MBN increased linearly across the increasing ECM trees dominance in both organic and mineral horizons (Fig. 1d). There were no detectable differences in NH_4^+ content across the mycorrhizal gradient (Fig. 1c). The organic N to mineral N ratio increases with the increase in ECM trees percentage ($p < 0.01$) only in the organic horizon (Fig. 1f).

The $\text{NO}_3^- : \text{NH}_4^+$ ratio decreased with the increase in ECM tree dominance both in the organic and mineral horizons (Fig. 2a). Moreover, this ratios in the AM-dominated stands were generally > 1 , while the ratios for ECM-dominated stands were most below 1. The trend of change with mycorrhizal gradient in the MBN: ($\text{NH}_4^+ + \text{NO}_3^-$) ratio was opposite that of $\text{NO}_3^- : \text{NH}_4^+$ ratio (Fig. 2b). This ratio was generally higher in the organic horizon than in the mineral horizon, and consistently increased with the increase in ECM tree dominance.

As the percentage of ECM trees increased, the net N mineralization rates decreased in the organic horizon but had no trend in the mineral topsoil (Fig. 3a). Net N nitrification rates decreased sharply with ECM tree dominance, but only in the organic horizon (Fig. 3c, $p = 0.001$). Total mineral N was increased with the net N mineralization rates in the organic horizon (Fig. 3b, $p = 0.005$), and NO_3^- content was tightly correlated ($p < 0.001$) to net nitrification rates in the organic horizon (Fig. 3d).

3.2. Factors driving the soil N availability

Multiple regression analysis indicated that the relative abundance (by basal area) of ECM trees (hereafter abbreviated as ECM trees R_{BA}) and soil properties were usually the best predictors of extractable N contents (Table S2). Soil DON content in the organic horizon were predicted by ECM trees R_{BA} , litter C:N and soil available P, which together explained 62 % of the variation. The DON content in the mineral horizon was dependent on ECM trees R_{BA} , MBC and TN (53 % explained variation). For NH_4^+ content, MBC, litter C:N, pH, and available P accumulatively explained 34 % of the variation in the organic horizon, while ECM trees R_{BA} , pH, and MBC explained 10 % of the variation in the mineral topsoil horizon. The SOC, litter C:N, ECM trees R_{BA} , pH, and soil moisture explained 69 % of the NO_3^- variation in the organic horizon, whereas SOC, soil moisture and pH were the main factors of NO_3^- content in the mineral topsoil horizon (57 % explained variation).

The SEM for the organic horizon indicated that the percentage of ECM trees affected soil N transformation rate and subsequently available N contents mainly by modifying litter C:N, soil C:N, pH, and soil moisture (Fig. 4). All these predictors together accounted for 82 % of the variation in soil NO_3^- content.

4. Discussion

4.1. Effects of mycorrhizal types on soil N cycling

Using a natural gradient of mycorrhizal associations in a subtropical forest where AM and ECM trees co-occur under the same soil and climate conditions, we explored the linkages between relative abundance of mycorrhizal trees and soil N cycling. Our findings clearly support the

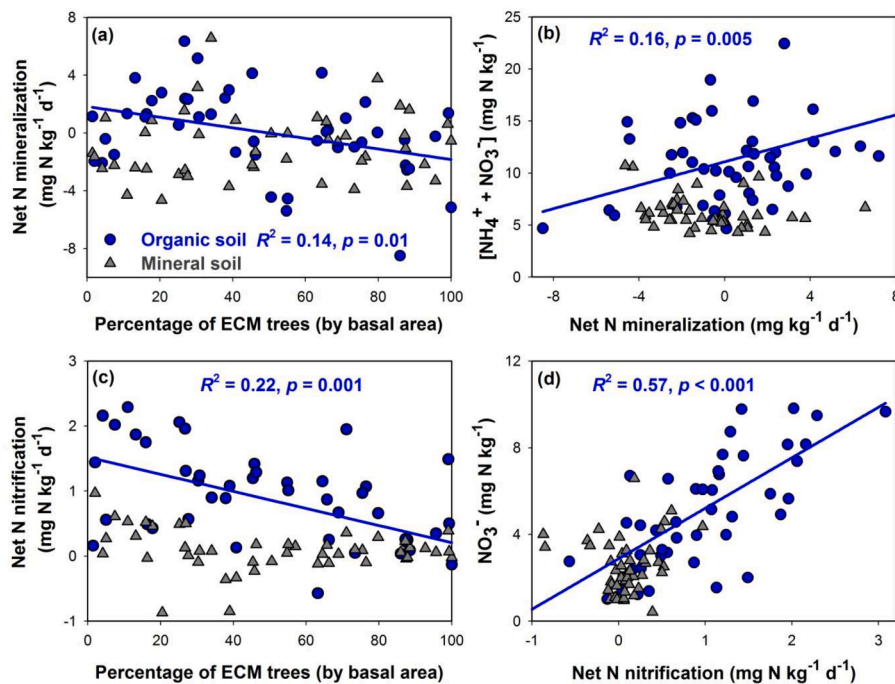


Fig. 3. Rates of (a) Net N mineralization and (c) net N nitrification across the gradient of ectomycorrhizal (ECM) tree dominance in Dashanchong Forest Park, southern China, and (b) the relationship between net N mineralization rate and total inorganic N, and (d) the relationship between net N nitrification rate and NO₃⁻. Each point represents the seasonal averages (February, July and November 2020) in each plot (*n* = 45 plots).

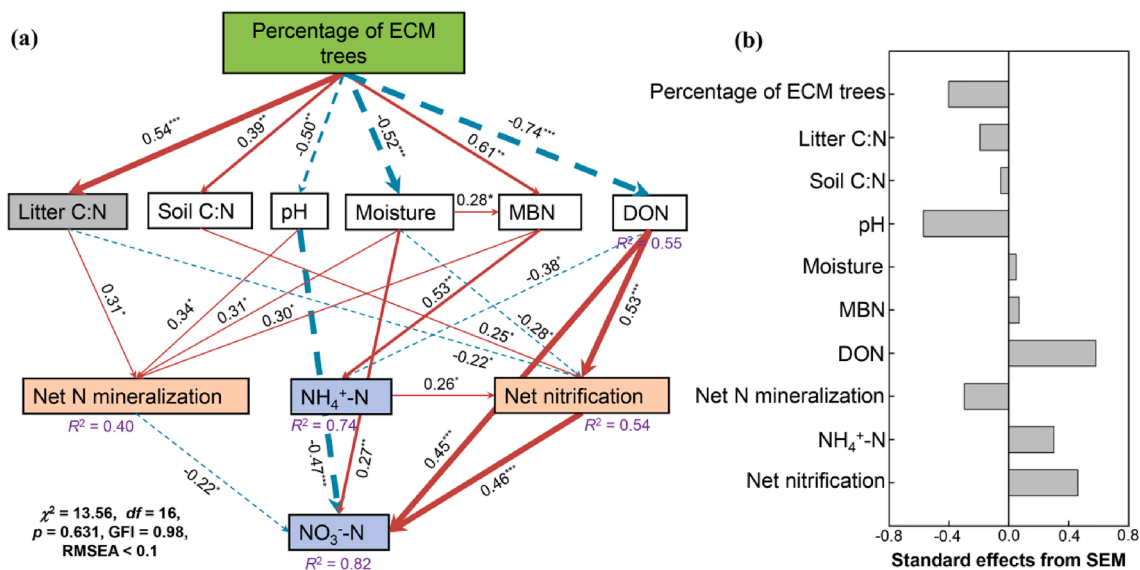


Fig. 4. Structural equation model (SEM) showing how ectomycorrhizal (ECM) tree dominance and edaphic factors regulate N availability in the organic horizon. In panel (a), arrows represent significant positive (solid red) and negative (dashed blue) pathways, respectively (*p* < 0.05). Numbers in the arrows indicate the standardized path coefficients, with the arrow thickness proportional to the strength of the path coefficients (**p* < 0.05, ***p* < 0.01, ****p* < 0.001). *R*² denotes the proportion of variance explained. In panel (b), the standardized total effect (direct plus indirect effects) of predictor variables on soil NO₃⁻ content. The chi-square test (χ^2), degree of freedom (*df*), goodness-of-fit index (GFI), and root-mean-square error of approximation (RMSEA) are listed on the model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hypothesis that more conservative N cycling is associated with ECM forests compared to AM forests. This was especially obvious for the organic horizon. Specifically, NO₃⁻ contents and net nitrification rates were decreased, and the organic N to mineral N ratio rose with increasing abundance of ECM trees (Fig. 1 and Fig. 3). These findings are consistent with the MANE framework, which was proven mainly in temperate forests (Midgley and Phillips, 2014; Brzostek et al., 2015; Cheeke et al., 2017).

Unlike temperate forests, the influences of mycorrhizal associations on soil N cycling in tropical or subtropical forests were inconsistent in previous plot-based studies. In a tropical forest, ECM-mediated organic N uptake was unimportant and showed an open and rapid N cycle (Tedersoo et al., 2012; Mayor et al., 2015). In contrast, our study and other studies (e.g., Corrales et al., 2016; Waring et al., 2016; Lin et al., 2018) conducted in tropical forests dominated by ECM trees showed a more closed N cycling. These studies suggest the mechanisms that lead

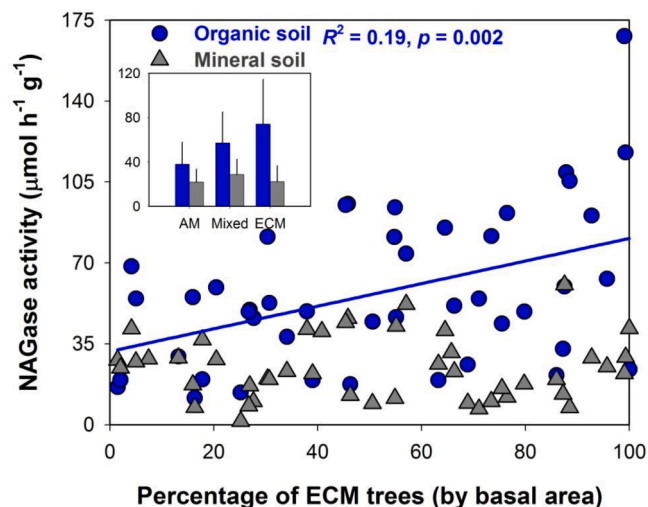


Fig. 5. Correlation of ectomycorrhizal (ECM) tree dominance with soil β -N-acetylglucosaminidase (NAGase) activity in Dashanchong Forest Park, southern China. Bar graph presented is the mean value of the NAGase activity in arbuscular mycorrhizal (AM)-dominated plots, mixed plots, and ECM-dominated plots. Each point represents the seasonal averages (February, July and November 2020) in each plot ($n = 45$ plots).

to the remarkable differences in soil N cycling between the two mycorrhizal types in temperate forests may be different or weakened in the tropics or subtropics, which are characterized by higher temperature, limitation of P and hyper-diverse biological communities. Anyway, the difference in soil N cycling between the AM and ECM forests can be reflected in soil N availability. Available N content depends on the balance between organic N mineralization, microbial N transformation and plant N uptake. In N poor ecosystems, NH_4^+ may be the most dominant form of mineral N due to an increasing competition between microorganisms and plants, which limits the amount of NH_4^+ supplied to nitrifier (Kuziakov and Xu, 2013). If NH_4^+ produced from SOM mineralization exceeds microbial and plant uptakes, a greater amount of NH_4^+ may be transformed to NO_3^- via nitrification (Schimel and Bennett, 2004). Therefore, the accumulation of NO_3^- exceeding NH_4^+ levels (i.e., $\text{NO}_3^- : \text{NH}_4^+ > 1$) for an ecosystem often indicates plentifully available N and relatively rapid N cycling (Davidson et al., 2007; Xiao et al., 2018; Xia et al., 2021). Our findings demonstrated that the $\text{NO}_3^- : \text{NH}_4^+$ ratio decreased across the mycorrhizal gradient (Fig. 2a), and this value in AM-dominated stands was commonly >1 , while was generally lower than 1 in ECM-dominated stands. This implies that soil N cycling is faster in AM forests than in ECM forests.

The MBN: ($\text{NH}_4^+ + \text{NO}_3^-$) ratio is another proxy of soil N cycling status. Microbial turnover (mineralization and immobilization) of N ensures a continuous storage of mineral N in the soil, and the relative strength of microbial N uptake and release are reflected by soil N availability (Xia et al., 2021). Due to an increase in organic N mineralization, the demands of both microorganisms and plants are gradually being fulfilled, which increases the supply of NH_4^+ to nitrifier (Templer et al., 2008). Hence, the release of mineral N by microorganisms is greater than their consumption. This is consistent with our findings, which shows that increasing ratios of MBN: ($\text{NH}_4^+ + \text{NO}_3^-$) across the mycorrhizal gradient as soil N availability decreased (Fig. 2b).

By sampling mycorrhizal gradients at a subtropical forest, we assessed the association between ECM dominance and soil N cycling with no confounding effects of climate or soil parent material. Although other factors (e.g., tree richness and productivity, or other soil properties) might co-vary with ECM dominance at the plot scale, the OLS multiple regressions analysis showed that the relative proportion of ECM trees had an exclusive effect on soil N availability (mainly DON and NO_3^-) after accounting for edaphic and tree effects. This provides strong

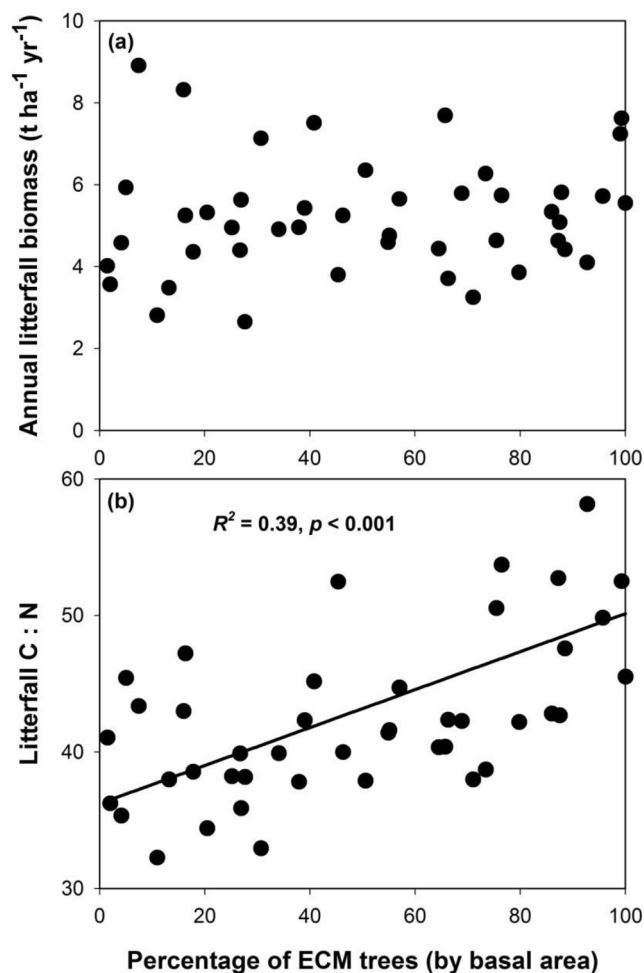


Fig. 6. (a) Annual litterfall biomass and (b) litterfall quality (i.e., C:N) across the gradient of ectomycorrhizal (ECM) tree dominance in Dashanchong Forest Park, southern China. Litterfall C:N is the seasonal averages from samples collected every month from December 2019 to November 2020 in each plot ($n = 45$ plots).

support for the hypothesis that there are varying effects of tree mycorrhizal types on soil N cycling in this subtropical secondary forest.

4.2. Mechanisms underlying mycorrhizal association effects on soil N cycling

Contrasting effects between AM- and ECM-dominated forests on soil N cycling have been suggested to be attributed to the differential access of mycorrhizal fungal guilds to organic and mineral N (Phillips et al., 2013). Specifically, ECM fungi can mine small organic N-bearing molecules (e.g., amino acids) directly from SOM via secretion of oxidative and hydrolytic enzymes (Chalot and Brun, 1998; Courty et al., 2010). In contrast, AM fungi scavenge only mineral N forms, leading to an increase in N mineralization by stimulating decomposers (Read and Perez Moreno, 2003; Talbot et al., 2008). Our findings demonstrated that the activity of NAGase rose linearly with increasing ECM tree abundance over the mycorrhizal gradient (Fig. 5). Previous work has shown that when C flow to roots was interrupted by girdling, a decrease in NAGase activity was observed in the rhizosphere of ECM trees but not in that of AM trees (Brzostek et al., 2015). However, we found that NAGase activity only increased across the ECM dominance gradient in the organic horizon, which might be due to the mycelium of ECM fungi mainly proliferating in the organic soil layers (Lindahl et al., 2007). The N acquisition strategies of these two forest mycorrhizal forms are

Effects of tree mycorrhizal type on soil N cycling

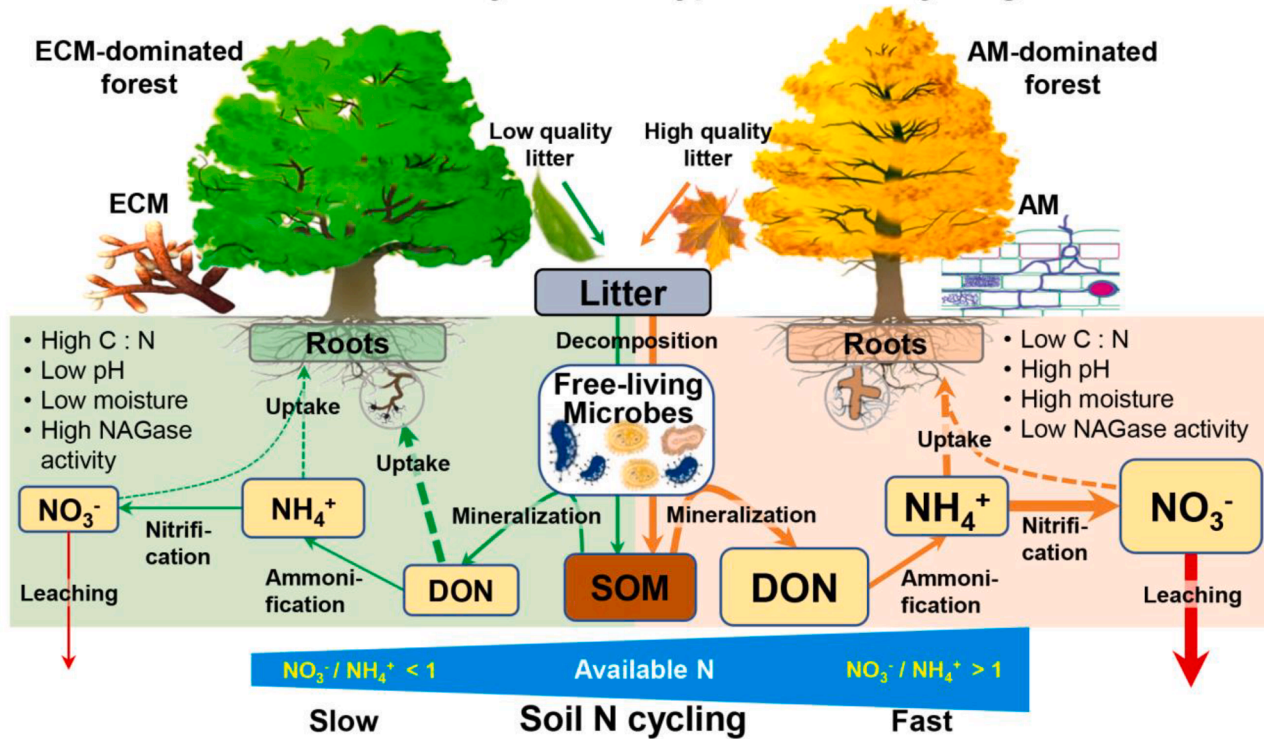


Fig. 7. Conceptual diagram illustrating the effects of tree mycorrhizal type on soil N cycling in subtropical forests. Green and yellow lines indicate the effects of ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM), respectively. Line width and pool size indicates the relative effect strength. Differences of soil N cycling processes are presented only for the organic horizon because the effects and mechanisms of ECM trees and associated fungi on soil N transformation were mainly reflected in topsoil. SOM and DON represent soil organic matter and dissolved organic N, respectively. NAGase, β -N-acetylglucosaminidase. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

remarkably different, leading to differences in SOM mineralization. By depleting N directly from SOM, ECM fungi are thought to limit the amount of N available for free-living saprotrophic decomposers, slowing down SOM decomposition by these microbes, which may be one of the mechanisms behind the “Gadgil effect” (Gadgil and Gadgil, 1971; Averill et al., 2014; Corrales et al., 2016; Wurzburger and Brookshire, 2017). Our results clearly showed that the net N mineralization rate in surface soil decreased across the mycorrhizal gradient (Fig. 3a), which implies that the microbial SOM decomposition for mineral N release is limited in ECM-dominated stands.

The intrinsic difference in plant functional traits between AM and ECM trees is suggested to be another reason for their differential effects on soil N cycling (Lin et al., 2017; Keller and Phillips, 2018). The input and decomposition of litterfall is the main source of soil N in forest ecosystems, and decay rates dictate how quickly nutrients release from decaying litterfall become available (Hobbie, 2015). AM trees generate leaf litter with better decomposability and greater higher quality (i.e., lower C:N) compared to ECM trees (Read, 1991; Cornelissen et al., 2001; Hobbie et al., 2006; Vesterdal et al., 2013; Midgley et al., 2015; Taylor et al., 2016; Jacobs et al., 2018). However, a meta-analysis reported that the leaf litter decomposition rates are varied between AM and ECM trees in temperate forests but not in tropical forests (Keller and Phillips, 2019). In our study, the litterfall collected during one year showed that there was no difference in the annual litterfall biomass, but litterfall C:N ratio increased with increase of ECM tree percentage (Fig. 6). Moreover, the thick organic horizon was observed at the surface in ECM-dominated stands reflects the slower decay rate than their AM counterparts. Nonetheless, litter decomposition is also greatly affected by soil microclimate factors such as temperature and moisture (Cheeke et al., 2017; Joly et al., 2017).

Mycorrhizal trees and fungi also indirectly influence soil N cycling by

altering soil physico-chemical properties (Fig. 4). The ECM fungi may not assimilate C from SOM but selectively forage for N, leading to a high soil C:N ratio (Lindahl et al., 2007). Moreover, the recalcitrant leaf litter (high C:N ratio) and ample organic acid exudation results in relatively stronger soil acidification in ECM forests (Midgley and Phillips, 2016; Cheeke et al., 2017; Tedersoo and Bahram, 2019). Our results showed that C:N in the organic soil (but not mineral topsoil) increased across the mycorrhizal gradient (Fig. S2a). Moreover, a negative correlation between ECM tree percentage and soil pH (Fig. S2b). A decrease in soil pH can limit the activity of soil ammonia-oxidizers and thus reduce nitrification rates (Stempfhuber et al., 2015; Tatsumi et al., 2020). An excess acidification would reduce the abundance of bacteria and lead to deceleration of soil biochemical processes, which may also contribute to the Gadgil effect (Tedersoo and Bahram, 2019). We also found that soil moisture decreased with increase ECM tree dominance (Fig. S2c). These co-changing physicochemical properties are crucial for the microbial N transformations, and thus for soil N availability (Fig. 4). Given that plant input and ECM fungi mostly exert an influence near the soil surface, these mechanisms largely explain soil N dynamics in the organic horizon, but not for the mineral horizon in ECM-dominated plots. Nevertheless, there is compelling evidence that the two tree mycorrhizal associations have multiple above- and below-ground traits influencing soil N cycling in subtropical forest ecosystem (Fig. 7).

4.3. Implications

Our study shows that soil N availability scales linearly with increasing ECM tree abundances, thus strengthening evidence for the applicability of the MANE framework to subtropical forests. Our findings indicate that the ECM tree dominance can serve as an integrative proxy for soil N cycling in a forest stand or ecosystem. Differences along

the gradient indicate that N leaching is enhanced with increasing AM tree abundances, as AM soils tend to possess a large NO₃ pool. Accelerated nitrification and NO₃ leaching could lead to more N loss from forest ecosystems. By using forest inventory data or remote sensing (the relative abundances of AM and ECM trees are estimated based on the unique spectral signals their leaves, Fisher et al., 2016), our gradient results can be applied at a larger regional scale. Our finding should be helpful for land surface models, due to the complexity of biotic factors (Sulman et al., 2017). Our results, together with other studies supporting the MANE framework, demonstrate that evaluating the effect of mycorrhizal association is conducive to the incorporation of biotic factors in our prediction models for assessing soil N dynamics.

Forests dominated by AM and ECM trees respond differently to aspects of anthropogenic global environmental change such as long-term N deposition (Ma et al., 2021). ECM trees have an advantage in the ecosystems with organic N cycling dominance; however, as the N deposition is increased, ECM trees may have less advantageous compared to AM trees (Midgley and Phillips, 2014). It has been found that forest composition shifts from ECM to AM dominance in North America with increasing anthropogenic N pollution (Averill et al., 2019; Jo et al., 2019). Subtropical forests in China also received high levels of N deposition (Jia et al., 2014). This implies future changes in N deposition may favor AM trees at the expense of ECM trees and, consequently, will alter the capacity of the subtropical forest soil for C and N retention.

5. Conclusions

Soil N availability was examined across a natural mycorrhizal gradient within a subtropical forest site where AM and ECM trees co-occurred. The soil dissolved organic N, nitrate N, rates of net N mineralization and net nitrification declined linearly with increasing ECM tree dominance, especially obvious for the surface organic horizon. AM-dominated forest soils had markedly higher (1.8–2.3 times) available N contents and net nitrification rate than did ECM forests, indicating AM-dominated forests have fast N cycling rates, whereas ECM-dominated forests thrive in slow N cycling (Fig. 7). The NAGase involved in acquisition of organic N had higher activity in ECM forests compared with AM forests. Annual litterfall input was similar in the quantity, but the litter C:N ratio increased across the mycorrhizal gradient. The increasing ECM tree dominance increase soil C:N ratio, but decrease soil pH, all of them critically in mediating N availability. Collectively, mycorrhizal tree dominance can serve as important predictor of soil N cycling in subtropical forests, which represents a significant step for informing multiple ecosystem models.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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