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Research

Contrasting effects of ectomycorrhizal and arbuscular mycorrhizal tropical tree species on soil nitrogen cycling: the potential mechanisms and corresponding adaptive strategies

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While it is increasingly recognized that ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) tree species vary in their effects on soil nitrogen (N) cycling, little is known about the mechanisms causing and how ECM and AM trees adapt to this variation. Using monoculture plots of six ECM and eight AM tropical trees planted in a common garden, we examined whether the contrasting effects of ECM and AM trees on soil N cycling could be explained by their differences in plant traits. Furthermore, rhizosphere effects on soil N transformations and soil exploration by fine roots were also measured to assess whether ECM and AM trees differed in N acquisition capacities. Results showed that soil NH_4^+-N concentration, net N mineralization and net nitrification rates were markedly lower, but soil C:N ratio was significantly higher beneath ECM trees than beneath AM trees. This more closed N cycling caused by ECM trees was attributed to their resource-conservative traits, especially the poorer leaf litter decomposability compared with AM trees. To adapt to their induced lower soil N availability, ECM trees were found to have greater rhizosphere effects on NO_3^--N concentration, net N mineralization and net nitrification rates to mine N, and higher soil exploration in terms of root length density to scavenge N from soils, indicating that these two strategies work in synergy to meet N demand of ECM trees. These findings suggest that ECM and AM trees have contrasting effects on soil N cycling owing to their differences in leaf litter decomposability and correspondingly possess different N acquisition capacities.

Introduction

Understanding how tree species influence soil nitrogen (N) cycling is critical in predicting potential ecosystem consequences of changes in tree species composition resulting from invasion and global change (Eviner and Chapin 2003, Hobbie 2015).

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Recently, it has been increasingly recognized that ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) tree species systematically differ in their effects on soil N cycling (Phillips et al. 2013, Lin et al. 2017a). Compared with AM trees, ECM trees and their associated mycorrhizal fungi are suggested to possess an integrated suite of traits contributing to more closed N cycling characterized by lower soil inorganic N concentrations and slower N cycling rates (Read 1991, Phillips et al. 2013). These contrasting modes of N cycling induced by AM and ECM trees have been widely used to explain their distinct response to global change factors (Thomas et al. 2010, Lankau et al. 2015, Terrer et al. 2016) and the monodominant patches of some ECM trees in high-diversity tropical forests (Corrales et al. 2016). However, the mechanisms underlying the differential effects of ECM and AM trees on soil N cycling and how they adapt to their induced differences in soil N availability are still largely unknown.

The distinct effects of AM and ECM trees on soil N cycling have been mainly attributed to their variations in associated mycorrhizal fungal traits (Read and Perez-Moreno 2003, Averill 2016, Corrales et al. 2016). Specifically, ECM fungi can produce extracellular enzymes accessing organic N directly from soil organic matter (SOM), while AM fungi lack these enzymatic capabilities (Read and Perez-Moreno 2003, Talbot et al. 2008). This direct N uptake implies the N competition between ECM fungi and saprotrophs, which subsequently reduces SOM decomposition rates and soil N availability (Corrales et al. 2016, Wurzburger and Brookshire 2017). Apart from mycorrhizal fungal traits, intrinsic differences in plant traits between ECM and AM trees may also contribute to their varying effects on soil N cycling (Cheeke et al. 2017, Lin et al. 2017a). Indeed, previous studies have shown differences between ECM and AM trees in leaf litter quality (Midgley et al. 2015, Taylor et al. 2016, Lin et al. 2017a). Although leaf litter quality has been suggested to be useful in explaining tree species-specific effects on soil N dynamics (Scott and Binkley 1997), few studies have directly tested whether the distinct effects of AM and ECM trees on soil N dynamics are due to their intrinsic differences in leaf litter quality (Midgley et al. 2015, Cheeke et al. 2017). Additionally, leaf and root traits are not necessarily correlated with each other across tree species (Jackson et al. 2013, Weemstra et al. 2016). Previous studies have shown little correlations between leaf and root litters in chemical traits and decomposition rates (Hobbie et al. 2010, Taylor et al. 2016). Therefore, considering their significant roles in ecosystem processes, root traits should also be considered to fully understand plant functions (Bardgett et al. 2014). However, whether AM and ECM trees systemically differ in root traits and how these differences contribute to mycorrhizal associated soil N dynamics have not been thoroughly evaluated.

In addition to ECM fungi having greater capacity to acquire organic N as mentioned above (Talbot et al. 2008), it is still unclear whether ECM trees also possess other N acquisition strategies from the 'phytocentric' perspective. Under N limitation, plants optimize their growth by allocating more carbon (C) to roots to scavenge N via expanding the exploited soil volume or mine N from SOM via releasing root exudates (Phillips and Fahey 2006, Bae et al. 2015). For the 'scavenging strategy', previous studies have proposed that fine-root length (root length density, RLD) or surface area per soil area (root area index, RAI) can represent the capacities of plant species to acquire soil nutrients (Jackson et al. 2008, Fort et al. 2014). Therefore, to adapt to their induced N-limited soils, ECM trees should maintain higher RLD or RAI than AM trees (Jackson et al. 2008). For the 'mining strategy', it has been shown that plants release ca 3–5% of their fixed C in photosynthesis to soils as root exudates, which can stimulate saprotrophs to produce extracellular enzymes and then increase N availability in the rhizosphere relative to that in bulk soils (i.e. rhizosphere effect, Jones et al. 2004, Finzi et al. 2015). Rhizosphere effects on N transformations vary widely among plant species and largely depend on soil N availability (Phillips and Fahey 2008, Finzi et al. 2015). Considering a greater proportion of N in organic forms in soils beneath ECM trees, they are proposed to have higher root exudation rates and greater rhizosphere effects (Phillips et al. 2013). Indeed, this proposition has been demonstrated by previous studies (Phillips and Fahey 2006, Yin et al. 2014, Brzostek et al. 2015). However, it remains unknown whether the 'scavenging strategy' and 'mining strategy' act in synergy or tradeoff for ECM trees to adapt to their induced N-limited soils.

It should be noted that current understanding of the differential effects of ECM and AM trees on soil N cycling is mainly based on studies conducted in temperate forests. In contrast with the general pattern shown in temperate forests, inconsistent results were exhibited in limited studies conducted in tropics with ECM trees showing a more closed N cycling in some studies (Corrales et al. 2016, Waring et al. 2016) but not in others (Tedersoo et al. 2012, Mayor et al. 2015). Therefore, much more evidence is needed for tropical forests, which differ from temperate forests in plant lineages of ECM trees and biogeochemical cycles (Vitousek et al. 2010, Wurzburger et al. 2017). Specifically, several plant orders in which ECM trees occur mostly exist in tropics (e.g. Malvales), which is different from the ECM lineages dominated in temperate forests (Fagales and Pinales, Wurzburger et al. 2017). Moreover, N limitation is generally stronger in temperate forests, whereas phosphorus (P) is generally more limiting in tropics owing to higher P loss rates (Vitousek et al. 2010).

In this study, we established monoculture plots of six ECM and eight AM tropical tree species to assess the extent to which mycorrhizal type affected soil N dynamics. Since these tree species were planted in a common garden for more than 23 years under the same soil and climate conditions, the potential variations in soil N dynamics should be attributed to tree species-specific rather than environmental effects (Zhang et al. 2015). Based on the mycorrhizal-associated nutrient economy model proposed by Phillips et al. (2013), we hypothesized that a more closed soil N cycling characterized by lower inorganic N concentrations and

slower N transformation rates would be beneath ECM trees than beneath AM trees. To explore the mechanisms underlying mycorrhizal type associated soil N dynamics from the 'phytocentric' perspective, we measured leaf and root morphological traits, and leaf litter decomposability of these 14 tree species. We hypothesized that ECM trees would have resource-conservative traits (e.g. higher leaf and root tissue density, and poorer leaf litter decomposability) relative to resource-exploitive traits of AM trees, which may contribute to their differential effects on soil N cycling. Additionally, soil exploration by fine roots and rhizosphere effects on N transformations were also measured to analyze whether ECM and AM trees differed in N acquisition capacities. We hypothesized that ECM trees would have higher soil exploration (e.g. higher RLD and RAI) and greater rhizosphere effects to adapt to their induced lower soil N availability.

Material and methods

Study site and target tree species

This study was conducted at Xishuangbanna Tropical Botanical Garden (XTBG, 21°41′N, 101°25′E, 570 m a.s.l.) of the Chinese Academy of Sciences located in Mengla County, Yunnan Province, southwest China. This study site has a typical tropical monsoon climate with a rainy season from May to October and a dry season from November to April. Mean annual temperature is 21.6°C and mean annual precipitation is 1476.4 mm (more than 80% occurring in the rainy season). Soil of this study site is classified as Ferralic Cambisol (FAO Soil Taxonomy) developed from alluvial deposits, with the following properties: organic C of 15.97 g kg^{-1}, total N of 1.27 g kg^{-1}, total P of 0.30 g kg^{-1}, and pH of 5.08 (soil:water ratio 1:2.5) in the surface soil layer (0–10 cm).

Thousands of tree species have been planted in the Arboretum of XTBG since 1959. In 2014, 14 tree species were selected according to the following criteria: tree species were planted in an identical soil, on the same topography, with the same planting density and in monoculture; the planted area of each tree species was larger than 400 m^2; the age of tree species was larger than 20 years old. These 14 tree species belong to nine families, with six from Dipterocarpaceae and eight from other families (Table 1). At the time of sampling, the selected tree species were 23–54 years old. Each tree species was planted in unreplicated plot, thus there were a total of 14 plots (plot sizes ranging from 400 to 1000 m^2). These plots are distributed in three neighboring sites with the distance between site 1 (seven plots) and site 2 (six plots) being ca 500 m, and the distance between site 1 and site 3 (one plot) being ca 2 km (Fig. 1). These studied plots are on fairly flat ground with a slope of less than 2°. The planting density of each plot is about 1100 trees per hectare. There is almost no understory development owing to the fairly closed canopy.

Soil sampling and analysis

Soil was sampled from the upper 10 cm of mineral soil using a 10-cm diameter stainless steel corer in August 2014. Five to eight replicate soil cores were gathered from each plot to ensure sufficient mass of rhizosphere soils (more than 30 g). Large aggregates of soil cores were gently broken apart. After that, fine roots (the first two orders) were picked out using fine forceps and then shaken gently to separate rhizosphere soils (soils adhering to fine roots) from bulk soils (non-adhering soils, Phillips and Fahey 2006). In the present study, rhizosphere soils were defined as soils adhering to the first two order-roots owing to these roots having higher metabolic activities and exudation rates than higher order-roots within root branching system (McCormack et al. 2015, Lin and Zeng 2017). Rhizosphere soils were carefully removed from fine roots by gently brushing. Bulk and rhizosphere soil samples were pooled by plot and then sieved to pass a 2 mm mesh. Rhizosphere soils and one subsample of bulk soils were stored at 4°C before measuring NH_4^+-N and NO_3^--N concentrations, and net N mineralization and

Table 1. Abbreviation, family, mycorrhizal type, age, DBH and height of the 14 tree species. ECM, ectomycorrhizal; AM, arbuscular mycorrhizal; DBH, diameter at breast height (1.3 m).

Species	Abbreviation	Family	Mycorrhizal type	Age (years)	DBH (cm)	Height (m)
Dipterocarpus alatus	DA	Dipterocarpaceae	ECM	33	42.6	32.1
Dipterocarpus retusus	DR	Dipterocarpaceae	ECM	27	26.4	23.5
Hopea hainanensis	HH	Dipterocarpaceae	ECM	26	21.7	19.5
Parashorea chinensis	PC	Dipterocarpaceae	ECM	29	18.2	24.2
Vatica mangachapoi	VM	Dipterocarpaceae	ECM	25	13.5	12.5
Vatica xishuangbannaensis	VX	Dipterocarpaceae	ECM	29	19.8	19.6
Anogeissus acuminata	AA	Combretaceae	AM	26	21.1	30.4
Artocarpus heterophyllus	AH	Moraceae	AM	24	25.6	13.2
Hevea brasiliensis	HB	Euphorbiaceae	AM	54	41.1	24.3
Mesua ferrea	MF	Calophyllaceae	AM	25	19.7	16.1
Metadina trichotoma	MT	Rubiaceae	AM	32	20.6	18.4
Pachira macrocarpa	PM	Malvaceae	AM	23	15.3	9.7
Phoebe puwenensis	PP	Lauraceae	AM	26	34.6	16.3
Tectona grandis	TG	Lamiaceae	AM	52	31.2	25.7

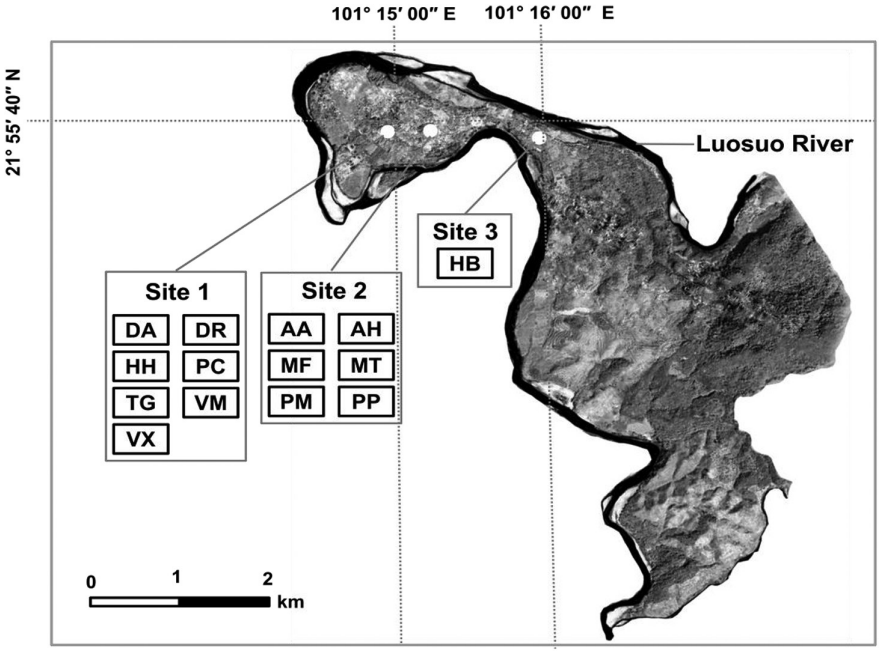

Figure 1. Map showing locations of the 14 studied plots in Xishuangbanna Tropical Botanical Garden. Abbreviations of tree species are shown in Table 1.

net nitrification rates, which were processed within three days of sampling. The other bulk soils were air-dried and milled (pass a 0.25 mm mesh) to determine total organic C and total N concentrations.

For NO_3^--N and NH_4^+-N concentrations, four grams of soils were extracted with 40 ml of 2 mol l^{-1} KCl, shaken for 1 h, and then filtered. KCl extracts were analyzed by a continuous-flow autoanalyzer to determine NO_3^--N and NH_4^+-N concentrations. Net N mineralization and net nitrification rates were measured by quantifying changes in soil inorganic N (NO_3^--N + NH_4^+-N) and NO_3^--N concentrations before and after a 28-day aerobic incubation in the laboratory at 25°C, respectively. Total organic C concentration was analyzed using $K_2Cr_2O_7$–H_2SO_4 oxidation method. For total N concentration, soils were digested by the Kjeldhl method and then measured by the continuous-flow autoanalyzer.

Root sampling and analysis

Considering that roots were damaged during collecting rhizosphere soils, root sampling was conducted in September 2014 according to the method described by Guo et al. (2004). Three locations were chosen per plot and then one soil block (10 cm depth × 20 cm length × 20 cm width) per location was excavated using a shovel. These harvested soil blocks were placed into coolers and transported to the laboratory within several hours for subsequent processing.

In the laboratory, soil blocks were gently loosened to obtain large intact root branches. To accurately estimate root growth indices, remainders of soil blocks were sieved (0.5 mm) to collect broken root segments. These collected roots were washed with distilled water to remove adhering soils. Before dissection, we picked out and discarded dead roots which were more wrinkled, easier fragmented and darker in color than live roots. Live roots were dissected into absorptive (the first two orders) and transport (the third or higher orders) roots using fine forceps based on the time-saving functional classification method proposed by McCormack et al. (2015). Broken root segments were classified into different functional groups by comparing their diameters and tissues to the roots isolated from intact branching hierarchy whose functional groups were accurately identified.

Mycorrhizal type of each tree species was designated using a dissecting microscope (20× magnification), according to the morphological features of absorptive fine roots (e.g. branching pattern, color, and diameter) which can be modified by ECM but not by AM fungal infection (Smith and Read 2008). When root samples of tree species exhibited ectomycorrhizal morphological features, these tree species were considered as ECM types; otherwise, they were considered as AM types (Smith and Read 2008). Across the 14 tree species, the six Dipterocarpaceae tree species were ECM types with other eight tree species being AM types. Furthermore, we only measured morphological traits and growth indices of absorptive fine roots owing to their more significant roles in nutrient acquisition and ecosystem functions than transport roots (McCormack et al. 2015, Lin and Zeng 2017). Absorptive fine roots were scanned with a desktop scanner (400 dpi). Scanned images were analyzed by the WinRHIZO software (Regent Instr., QC, Canada) to measure average root diameter, and total root length, surface area and volume. After that, root samples were dried at 65°C until constant mass and weighed. Specific root length (SRL) and root tissue density (RTD) were calculated as total root length and

volume divided by root biomass, respectively. Root length density (RLD) and root area index (RAI) were defined as total root length and surface area per sampling area, respectively.

Leaf morphological traits and leaf litter decomposability

In August 2014, five individuals were sampled for each tree species, and for each individual, more than 30 current season, fully expanded, sun-exposed leaves were collected from the outer canopy of the sunny side. Once collected, half of the leaves were used to determine leaf dry matter content (LDMC, the oven-dry mass of leaves divided by their water-saturated fresh mass), according to the method described by Cornelissen et al. (2003). The remaining leaves were used to measure leaf thickness (LT), specific leaf area (SLA) and leaf tissue density (LTD). LT was measured between major leaf veins using digital calipers. After that, fresh leaves were scanned by a portable scanner to determine leaf area using the ImageJ software. The scanned leaves were then dried at 65°C until constant mass and weighed. SLA was calculated as the ratio of leaf area to oven-dried mass. LTD was then calculated as the inverse of SLA multiplied by LT.

Leaf litters of each tree species were collected using litter traps during peak litter fall (March to April, 2015). After removing petioles, leaf litters were cut into pieces (3 × 3 cm) and then dried at 65°C to constant mass. Leaf litter decomposability was determined using laboratory microcosms following the method described by Lin et al. (2013). A total of 42 microcosms (14 tree species × 3 replications × 1 sampling time) were constructed by plastic cylinders (5 cm in diameter and 10 cm in height) filled with 100 g field-moist soil. Soils used for incubation were mixtures of soil samples collected from 0–10 cm depth of each plot. This was done to avoid any potential effects of home-field advantage on litter decomposition (Ayres et al. 2009). Two grams of oven-dried leaf litters were placed on the soil surface of each microcosm. Distilled water was added to microcosms to achieve 65% of soil water-holding capacity. Microcosms were covered with perforated adherent films to reduce humidity loss but allow gaseous exchange. After that, weight of each microcosm was recorded. Microcosms were incubated in laboratory incubators under dark conditions with constant temperature (25°C) and relative humidity (80%). During incubation, soil moisture of microcosms was maintained at 65% of water-holding capacity by weighing microcosms weekly and adding distilled water if necessary. After one year decomposition, leaf litters were removed from microcosms, cleaned, dried to constant mass and then weighed. Leaf litter decomposability was calculated as percentage differences between initial and final weights.

Growth rates of tree species

For each tree species, 15 average-sized individuals were sampled to measure diameter at breast height (1.3 m, DBH) and tree height using a diameter tape and a hypsometer, respectively. Given that there was no information on species-specific allometric regression equations, growth rates of tree species were evaluated by average rates of DBH growth and height growth, which were separately calculated by dividing DBH and height by tree age.

Statistical analysis

To test the hypothesis that a more closed soil N cycling would be beneath ECM trees than beneath AM trees, linear mixed models with residual maximum likelihood estimations were performed to assess mycorrhizal type effects on six variables (NO_3^--N concentration, NH_4^+-N concentration, net N mineralization rate, net nitrification rate, total N concentration and soil C:N ratio) related to bulk soil N cycling. All these models included mycorrhizal type as a fixed factor, and site as a random factor given the possible effects of landscape position and the nested nature of plots (Fig. 1). Furthermore, to visualize tree species-specific effects on bulk soil N cycling, these six variables were analyzed by principal component analysis (PCA). Scores of tree species along the first PCA axis (PC1) were used as a combined index representing bulk soil N availability in subsequent analyses. Prior to PCA, these six variables were standardized using the zero-mean approach.

To test the hypothesis that ECM trees would have resource-conservative traits relative to resource-exploitive traits of AM trees, linear mixed models as described above were performed to analyze whether there were significant differences between AM and ECM trees in five leaf traits (LDMC, LT, LTD, SLA and leaf litter decomposability) and three root traits (RD, SRL and RTD). To test the hypothesis that variations in plant traits between AM and ECM trees would account for their differential effects on soil N cycling, Pearson correlations were conducted to analyze relationships between these plant traits and the combined index representing bulk soil N availability. Furthermore, owing to the multicollinearity among plant traits (Supplementary material Appendix 1 Table A1), multivariate analyses were conducted to identify which plant traits, if any, were statistically significant in explaining variations in bulk soil N cycling. Given that the longest gradient was less than three according to detrended correspondence analysis (DCA), a partial redundancy analysis (RDA) using standardized data was performed to indentify statistically significant plant traits by a forward selection with a Monte Carlo permutation test (Šmilauer and Lepš 2014). Application of the forward selection meant that one plant trait would be excluded if it co-varied with other plant traits and did not have unique contribution in explaining data variability, although this trait could have a significant effect based on correlation analyses (Šmilauer and Lepš 2014). To assess the relative importance of leaf traits versus root traits in explaining variations in bulk soil N cycling, a variation partitioning analysis was conducted (Šmilauer and Lepš 2014).

To test the hypothesis that ECM trees would have higher N acquisition capacities, linear mixed models as described above were performed to test whether ECM trees had significantly higher fine root biomass, root length density, root area index and rhizosphere effects. Rhizosphere

effects were calculated as percentage differences between paired bulk and rhizosphere soils across 14 tree species for four variables (NO_3^--N concentration, NH_4^+-N concentration, net N mineralization and net nitrification rates) related to soil N cycling (Phillips and Fahey 2006). One-sample *t*-tests were used to analyze whether rhizosphere effects of these four variables were statistically different from zero. Significantly positive and negative rhizosphere effects meant more and less pools or fluxes of N cycling in rhizosphere relative to bulk soils, respectively. PCA was conducted on rhizosphere effects for these four variables to obtain a combined index representing rhizosphere effects. This combined index was obtained from ordination scores of tree species along the PC1, which explained 63.75% of the variation (Supplementary material Appendix 1 Fig. A1). Linear regressions were used to estimate whether PC1 of bulk soil N cycling was significantly related to PC1 of rhizosphere effects, fine root biomass, root length density and root area index.

Linear mixed models were carried out using NLME package in R (Pinheiro et al. 2017). PCA, DCA and the partial RDA were carried out using Canoco 5.0 software (Microcomputer Power, NY, USA). Analyses of *t*-test, Pearson correlation and linear regression were carried out using SPSS 16.0 (SPSS Inc.). Significant level of all analyses was set at $\alpha = 0.05$.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.2811b> (Lin et al. 2017b).

Results

Mycorrhizal type effects on bulk soil N cycling

Linear mixed models showed that AM and ECM trees had significantly different effects on five of the six variables related to bulk soil N cycling (Table 2). Specifically, NH_4^+-N ($F = 13.90$, $p < 0.01$) and NO_3^--N concentrations ($F = 18.54$, $p < 0.01$), and net N mineralization ($F = 7.57$, $p = 0.02$) and net nitrification rates ($F = 7.53$, $p = 0.02$) were significantly lower beneath ECM trees than beneath AM trees. Soil C:N ratio was significantly higher beneath ECM trees than beneath AM trees ($F = 6.19$, $p = 0.03$). Furthermore, no significant differences were found between ECM and AM trees in soil N concentrations (Table 2).

PCA showed clear variations among the studied 14 tree species in their effects on these six variables related to bulk soil N cycling (Fig. 2). The first two PCA axes explained 81.67% of variation in these six variables with 71.66% explained by the first axis (PC1) and 10.02% explained by the second axis. Along the PC1, soil C:N ratio showed a negative loading with the other five variables showing positive loadings. Linear mixed model conducted on tree species scores along PC1 showed that ECM and AM trees were significantly discriminated by PC1, with a continuum from ECM trees at the negative end to AM trees at the positive end ($p < 0.01$; Fig. 2).

Linkages between plant traits and bulk soil N cycling

For five leaf traits, linear mixed models showed that ECM trees had significantly lower leaf litter decomposability

Table 2. Differences between ECM ($n = 6$) and AM ($n = 8$) trees in variables related to bulk soil N cycling, plant traits and N acquisition capacities. F- and p-values are obtained from linear mixed models. ECM, ectomycorrhizal; AM, arbuscular mycorrhizal; SE, standard error.

		ECM trees	AM trees		
Variable subsets	Variables (abbreviation, unit)	Mean (SE)	Mean (SE)	F-values	p-values
Bulk soil N cycling	NH_4^+-N concentration (Soil NH, mg kg^{-1})	0.76 (0.10)	3.74 (0.68)	13.90	< 0.01
	NO_3^--N concentration (Soil NO, mg kg^{-1})	10.90 (1.61)	17.33 (3.05)	18.54	< 0.01
	Soil N concentration (Soil N, g kg^{-1})	1.15 (0.07)	1.36 (0.10)	3.47	0.09
	Soil C:N ratio (Soil C:N)	13.43 (0.38)	11.94 (0.41)	6.19	0.03
	Net N mineralization rate (Net N min, mg kg^{-1} d^{-1})	1.22 (0.45)	3.82 (0.72)	7.57	0.02
	Net nitrification rate (Net nitri, mg kg^{-1} d^{-1})	–0.34 (0.28)	1.77 (0.62)	7.53	0.02
Plant trait	Leaf litter decomposability (LDecom, %)	22.83 (1.57)	42.22 (3.78)	27.80	< 0.01
	Leaf thickness (LT, mm)	0.19 (0.01)	0.21 (0.03)	0.51	0.49
	Specific leaf area (SLA, cm^2 g^{-1})	125.61 (15.04)	161.28 (22.70)	14.31	< 0.01
	Leaf tissue density (LTD, g cm^{-3})	0.46 (0.04)	0.37 (0.06)	3.15	0.11
	Leaf dry matter content (LDMC, %)	46.89 (2.50)	38.68 (4.39)	12.20	< 0.01
	Root diameter (RD, mm)	0.28 (0.01)	0.41 (0.05)	2.37	0.15
	Specific root length (SRL, m g^{-1})	29.25 (2.19)	23.47 (2.39)	2.50	0.14
	Root tissue density (RTD, g cm^{-3})	0.56 (0.05)	0.38 (0.04)	7.44	0.02
N acquisition capacity	Rhizosphere effect of NH_4^+-N concentration (ReNH, %)	132.57 (32.14)	52.27 (26.96)	3.70	0.08
	Rhizosphere effect of NO_3^--N concentration (ReNO, %)	39.88 (9.82)	2.82 (9.63)	6.99	0.02
	Rhizosphere effect of net N mineralization rate (ReNM, %)	140.49 (27.04)	–50.64 (38.07)	14.58	< 0.01
	Rhizosphere effect of net nitrification rate (ReNN, %)	97.59 (36.18)	–42.14 (41.17)	6.05	0.03
	Fine root biomass (RBio, g m^{-2})	18.32 (2.31)	15.28 (3.01)	0.68	0.43
	Fine root length density (RLD, m m^{-2})	516.76 (47.05)	325.60 (44.51)	8.48	0.02
	Fine root area index (RAI, m^2 m^{-2})	0.46 (0.05)	0.41 (0.06)	0.43	0.53

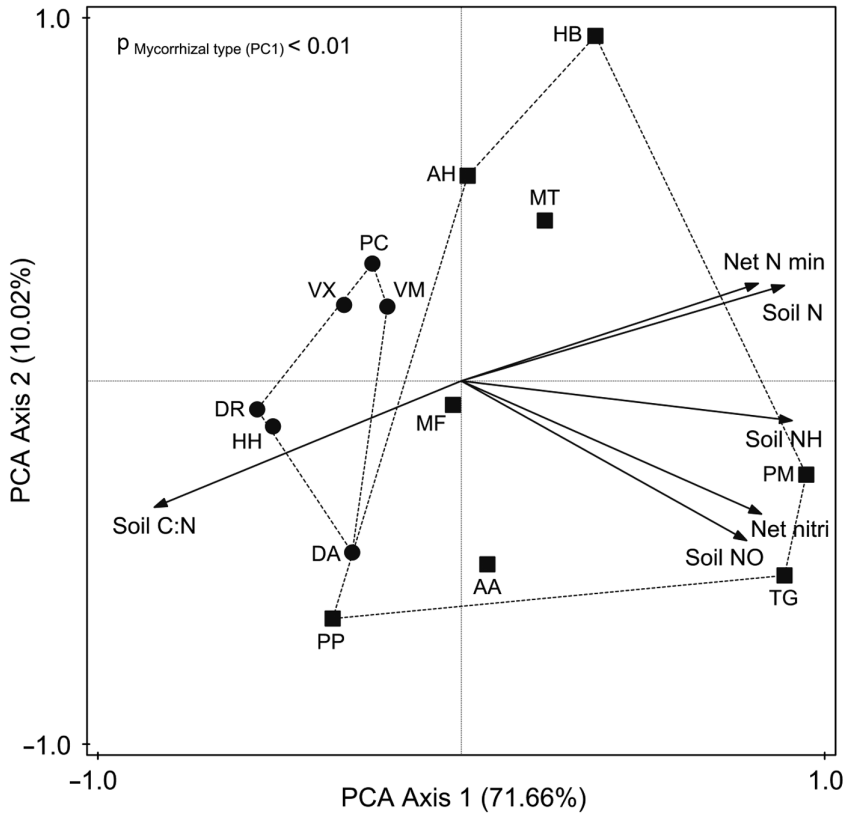

Figure 2. Biplot from principal component analysis (PCA) of six variables related to bulk soil N cycling across six ECM and eight AM tree species. Percentages of total variation explained by the first two PCA axes are given in parentheses. p-value is obtained from a linear mixed model analyzing effects of mycorrhizal type on species scores along the fist PCA axis (PC1). Circles and squares represent ECM and AM tree species, respectively. Abbreviations of tree species and variables related to bulk soil N cycling are shown in Table 1 and 2, respectively.

(F = 27.80, $p < 0.01$) and specific leaf area (F = 14.31, $p < 0.01$), and higher leaf dry matter content (F = 12.20, $p < 0.01$; Table 2). No significant differences were found between ECM and AM trees in leaf thickness and leaf tissue density. Furthermore, ECM trees had significantly higher root tissue density (F = 7.44, p = 0.02) than AM trees, with no significant differences in root diameter and specific root length (Table 2).

Pearson correlation revealed that species scores along PC1 as shown in Fig. 1, a combined index indicating bulk soil N availability, were significantly correlated with six of eight plant traits (Fig. 3). This combined index was significantly positively correlated with leaf litter decomposability ($r = 0.72$, $p < 0.01$), specific leaf area ($r = 0.61$, p = 0.02) and root diameter ($r = 0.64$, p = 0.01), and negatively correlated with leaf tissue density ($r = –0.55$, p = 0.04), leaf dry matter content ($r = –0.66$, p = 0.01) and root tissue density ($r = –0.61$, p = 0.02). To avoid multicollinearity among plant traits (Supplementary material Appendix 1 Table A1), a partial RDA analysis was conducted to select significant predictors in explaining variations of bulk soil N cycling. Leaf litter decomposability was the only significant plant trait after a forward selection with a Monte Carlo permutation test (pseudo-$F = 7.20$, $p < 0.01$; Fig. 4a). Variation partitioning analysis revealed that five leaf traits significantly explained 34.00% of the variation in bulk soil N cycling ($F = 2.60$, p = 0.04), while three root traits and their overlap with leaf traits had no significant effects (Fig. 4b).

Mycorrhizal type associated N acquisition capacities

Across the studied 14 tree species, NH_4^+-N and NO_3^--N concentrations were 86.69% and 18.70% higher in rhizosphere than in bulk soils, respectively (Fig. 5). Net N mineralization and net nitrification rates were 31.27% and 17.74% greater in rhizosphere relative to bulk soils, respectively (Fig. 5). One-sample *t*-tests showed that there were significant rhizosphere effects on NH_4^+-N ($t = 3.82$, $p < 0.01$) and NO_3^--N ($t = 2.23$, p = 0.04) concentrations, while no significant rhizosphere effects on net N mineralization ($t = 0.88$, p = 0.39) and net nitrification rates ($t = 0.53$, p = 0.60) were found (Fig. 5).

When tree species were grouped by mycorrhizal association, linear mixed models showed that ECM trees had significantly greater rhizosphere effects on NO_3^--N concentration (F = 6.99, p = 0.02), net N mineralization (F = 14.58, $p < 0.01$) and net nitrification rates (F = 6.05, p = 0.03), but not on NH_4^+-N concentration compared to AM trees (F = 3.70, p = 0.08;

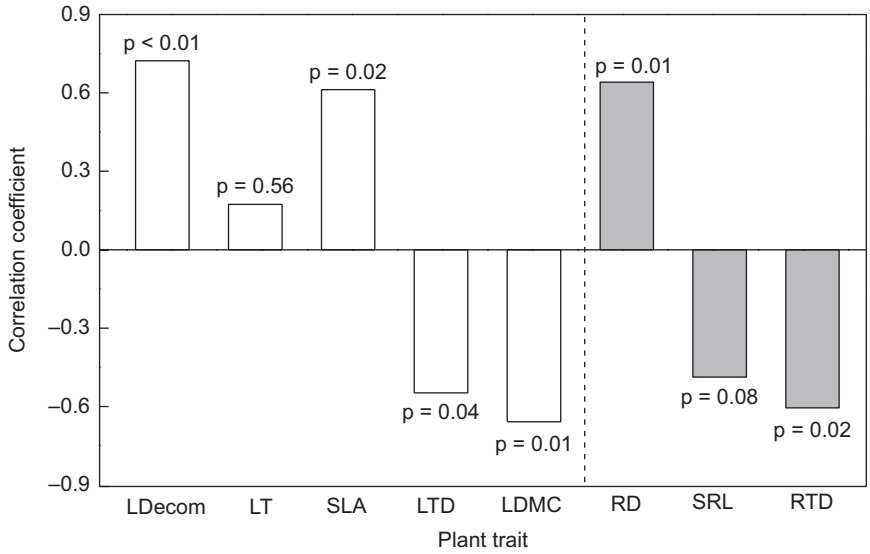

Figure 3. Correlation coefficients between plant traits and tree species scores along the first axis of principal component analysis (PC1) as shown in Fig. 2. Tree species scores along PC1 represent a combined index indicating bulk soil N availability. Open and gray bars represent leaf and root traits, respectively. Abbreviations of plant traits are shown in Table 2.

Table 2). Furthermore, ECM trees had significantly higher fine root length density relative to AM trees ($F=8.48$, $p=0.02$). No significant differences were found between ECM and AM trees in fine root biomass ($F=0.68$, $p=0.43$) and fine root area index ($F=0.43$, $p=0.53$; Table 2).

PC1 of rhizosphere effects, a combined index representing interspecific differences in rhizosphere effects (Supplementary material Appendix 1 Fig. A1), was negatively correlated with PC1 of bulk soil N cycling ($p < 0.01$; Fig. 6a). Regression analyses also showed that there was significantly negative linear relationship between fine root length density and PC1 of bulk soil N cycling ($p < 0.01$; Fig. 6c). Furthermore, no significant relationships were found between PC1 of bulk soil N cycling, and fine root biomass ($p=0.27$; Fig. 6b) and fine root area index ($p=0.22$; Fig. 6d).

Owing to wide variations in ages and sizes among the 14 tree species (Table 1), Pearson correlations were conducted to analyze whether there were significant relationships between growth rates of tree species and variables related to bulk soil N cycling and N acquisition capacities. Results showed that growth rate of DBH did not significantly correlate with any of these variables, except root area index (Supplementary material Appendix 1 Fig. A2). There were no significant relationships between growth rate of height and any variables related to bulk soil N cycling and N acquisition capacities (Supplementary material Appendix 1 Fig. A3).

Discussion

Using monoculture plots of six ECM and eight AM tropical tree species planted in a common garden, we examined the mechanisms underlying the contrasting effects of tree species with different mycorrhizal associations on soil N cycling. Moreover, we also analyzed the variations between ECM and AM trees in N acquisition capacities. Our results showed that soil N transformation rates were lower and soil C:N ratio was higher beneath ECM trees relative to those beneath AM trees (Table 2, Fig. 2). This more closed N cycling caused by ECM trees was mainly attributed to their significantly lower leaf litter decomposability relative to AM trees (Fig. 4). To adapt to soils with lower N availability, ECM trees were found to possess higher soil exploration in terms of fine root length density and greater rhizosphere effects on N transformations (Fig. 6). These results indicate that ECM and AM trees have distinct effects on soil N cycling owing to their variations in plant traits and possess correspondingly different N acquisition capacities.

Mycorrhizal type effects on soil N cycling

In general, our results supported the initial hypothesis that ECM trees would induce a more closed soil N cycling relative to AM trees. Specifically, soil NH_4^+-N concentration, net N mineralization and net nitrification rates were lower, and soil C:N ratio was higher beneath ECM trees than beneath AM trees (Table 2). Furthermore, the six Dipterocarp ECM trees were clearly separated from the eight AM trees by the first axis of PCA conducted on six variables related to soil N cycling (Fig. 2). These findings are consistent with mycorrhizal-associated nutrient economy model, which predicts that ECM trees possess an organic and closed N cycling whereas AM trees have an inorganic and open N cycling (Phillips et al. 2013). This conceptual model has been extensively demonstrated by many studies conducted in temperate forests (Midgley and Phillips 2014, Brzostek et al. 2015, Cheeke et al. 2017).

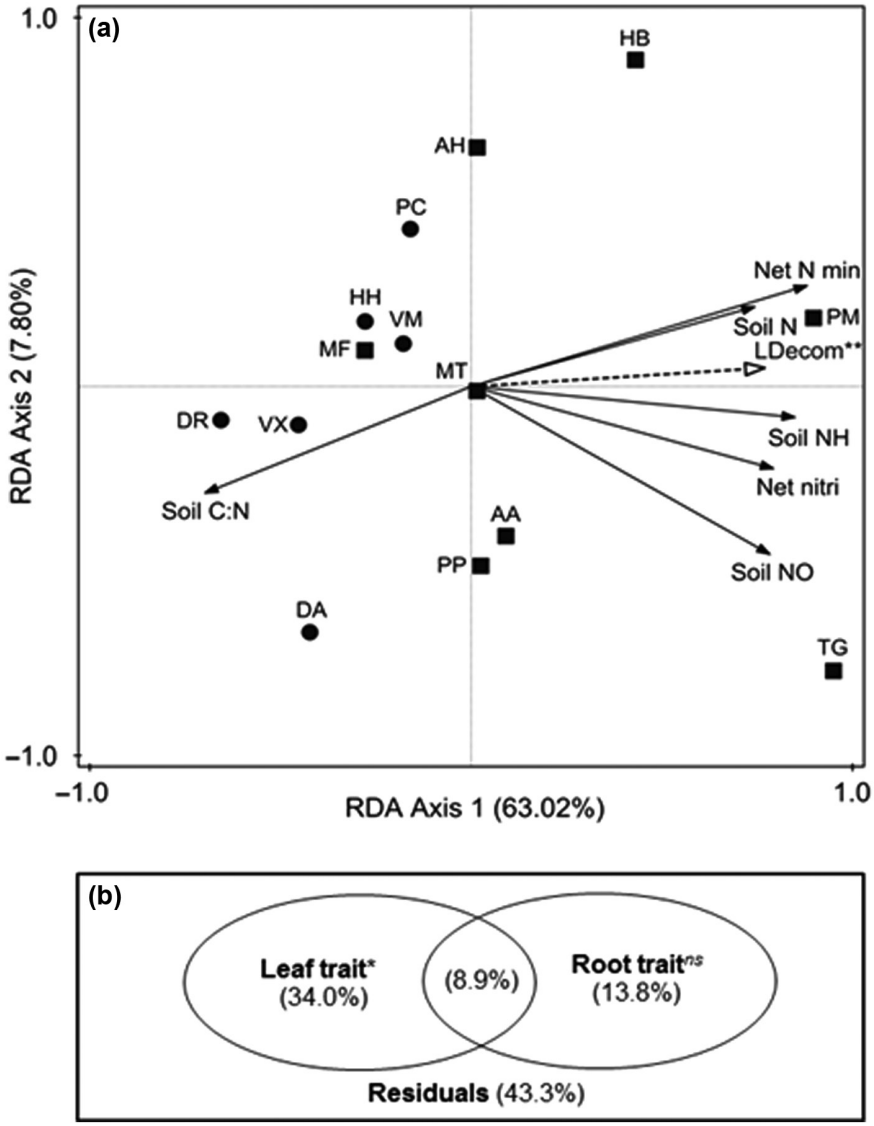

Figure 4. Linkages between plant traits and bulk soil N cycling as analyzed by a partial redundancy analysis (a) and a variation partitioning analysis (b). In the triplot of the partial redundancy analysis (a), circles and squares represent ECM and AM tree species, respectively. Solid lines are six variables related to bulk soil N cycling. Dashed line is the statistically significant plant trait determined by a forward selection with Monte Carlo permutation. Abbreviations of tree species and variables related to bulk soil N cycling are shown in Table 1 and 2, respectively. In variation partitioning analysis (b), each circle represents the percentage of variations explained by leaf or root traits. The overlap of circles represents shared variation between leaf and root traits. *, $p < 0.05$; **, $p < 0.01$; *ns*, not significant.

In contrast, mixed results were found for studies conducted in tropical forests with ECM trees showing a more closed N cycling in some studies (Corrales et al. 2016, Waring et al. 2016, Lin et al. 2017a) but not in others (Tedersoo et al. 2012, Mayor et al. 2015). Inconsistent results among these tropical studies may be partly due to differences in soil N availability in their study sites, considering the interactive effects of mycorrhizal association and N availability on soil N transformation rates (Midgley and Phillips 2016, Terrer et al. 2016). For example, the differential effects of ECM and AM trees on net N mineralization rates were found to be reduced with N addition (Midgley and Phillips 2016). Therefore, for studies conducted in sites with high soil N availability, there should be no systematic differential effects between AM and ECM trees on soil N cycling (Tedersoo et al. 2012, Mayor et al. 2015). However, for our studied common garden, a previous study has shown that N rather than P is the key limiting nutrient for tree growth via analyzing leaf N and P resorption efficiency (Zhang et al. 2015). Thus, N-limited condition of our study site cannot mask mycorrhizal type effects on soil N cycling.

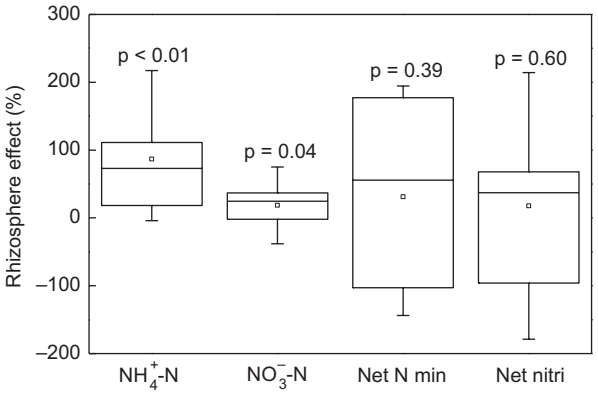

Figure 5. Rhizosphere effects on NH4⁺-N concentration, NO3⁻-N concentration, net N mineralization (net N min) and net nitrification rates (net nitri) across 14 tree species. p-values are obtained from one-sample *t*-tests. Box plots represent medians (horizontal lines in boxes), means (squares in boxes), interquartile ranges, and 5th and 95th percentiles (whiskers).

Linkages between plant traits and bulk soil N cycling

Contrasting effects of ECM and AM trees on soil N cycling have been suggested to be due to their intrinsic differences in plant traits (Phillips et al. 2013). Our results showed that ECM trees had significantly poorer leaf litter decomposability and higher root tissue density than AM trees (Table 2), which supported our hypothesis that ECM trees would have resource-conservative traits relative to resource-exploitive traits of AM trees. In line with our study, previous studies have also reported that leaf and root litters of ECM trees are characterized by lower quality and slower decomposition rates (Midgley et al. 2015, Taylor et al. 2016, Lin et al. 2017a). However, it should be noted that our studied ECM trees are from a single family (Dipterocarpaceae), while AM trees are from other eight plant families (Table 1). It is therefore possible that our results are driven by phylogenetic similarities rather than mycorrhizal type (Koele et al. 2012).

Conceptual models and experimental studies have expected that plants with resource-conservative traits support fungal dominated soil food webs accompanied by slow and closed soil N cycling, whereas plants with resource-exploitive traits support bacterial dominated soil food webs accompanied by fast and open soil N cycling (Wardle et al. 2004, Orwin et al. 2010, Hobbie 2015). Consistent with this expectation, we found that soil N availability was positively related to leaf litter decomposability and negatively related to root tissue density (Fig. 3). Furthermore, Cheeke et al. (2017)

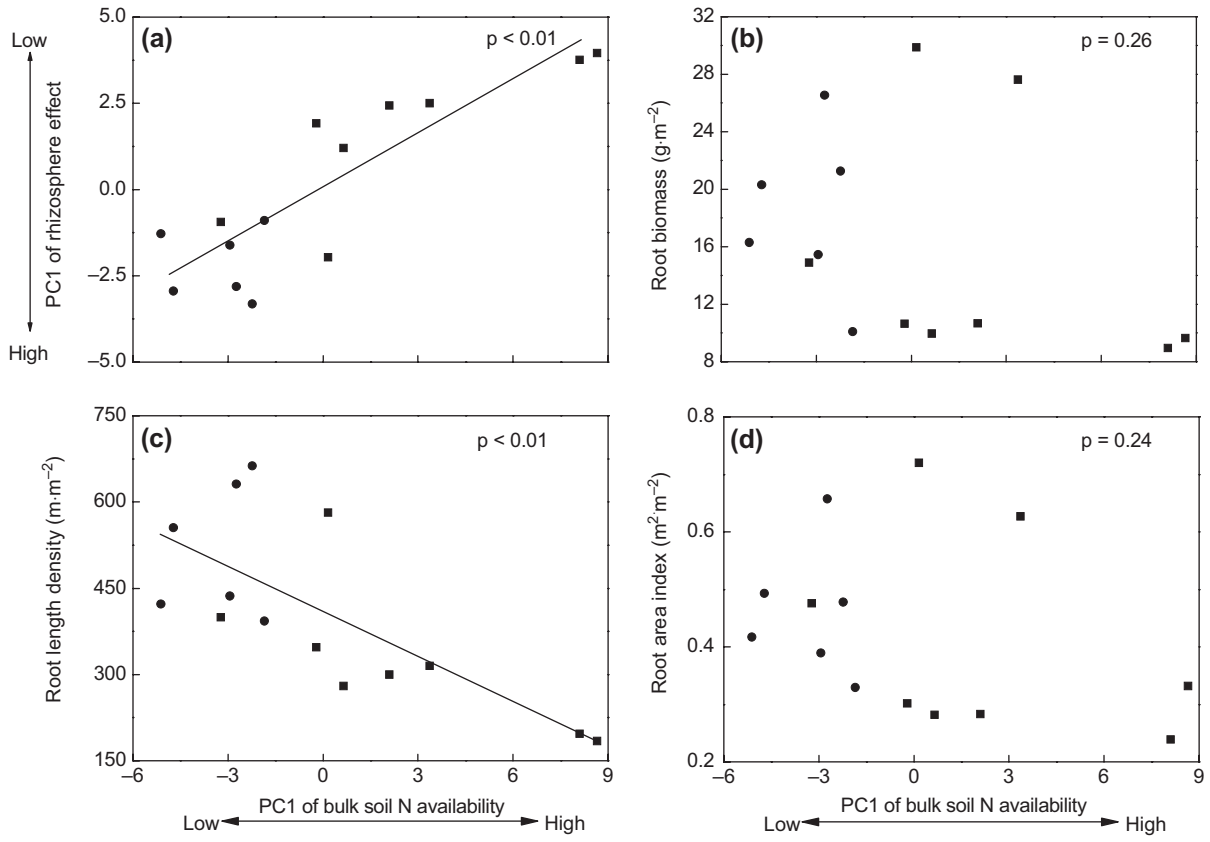

Figure 6. Relationships between species scores along the first axis of principal component analysis (PC1) representing bulk soil N cycling and PC1 of rhizosphere effect (a), root biomass (b), root length density (c) and root area index (d). PC1 of rhizosphere effect, calculated by principal component analysis, is a combined index representing interspecific differences in rhizosphere effects on NH4⁺-N concentration, NO3⁻-N concentration, net N mineralization and net nitrification rates. p-values are obtained from linear regression analyses.

showed that forests dominated by ECM trees had higher soil fungal biomass and greater fungal:bacterial ratios than those dominated by AM trees. These results indicate that the more closed soil N cycling induced by ECM trees may attribute to their resource-conservative traits, which support fungal dominated soil food webs.

Owing to the strong collinearity among plant traits (Supplementary material Appendix 1 Table A1), redundancy analysis was conducted to select the best predictors in explaining tree species-specific effects on soil N cycling. Leaf litter decomposability was the only retained significant predictor (Fig. 4a). Moreover, variation partitioning analysis also showed that leaf traits rather than root traits significantly explained variations in soil N cycling (Fig. 4b). These results are surprising, considering that root traits are increasingly found to be better in explaining soil microbial community composition (Legay et al. 2014), as well as soil N availability and N cycling rate than leaf traits (Orwin et al. 2010, Cantarel et al. 2015). Consistent with previous studies (Craine et al. 2001, Laliberté and Tylianakis 2012), the insignificant effect of root traits in our study may be because their effects can be captured through leaf traits, given the strong relationships between root and leaf traits (Supplementary material Appendix 1 Table A1) indicating that root traits may be matched by leaf traits along the exploitive-conservative resource spectrum (Reich 2014). However, owing to the proposed multidimensional framework of root traits, the three morphological traits analyzed in our study may be not enough to thoroughly represent their effects on ecosystem processes (Kong et al. 2014, Weemstra et al. 2016). For example, using meta-level analysis, root morphological traits were found to be unrelated to chemical traits (Weemstra et al. 2016) which were shown to be more important in predicting root functions (Roumet et al. 2016). Therefore, much more work is needed to study ecosystem functions of root traits from multidimensional perspectives.

Mycorrhizal type associated N acquisition capacities

Releasing C to soils as root exudates, which can simulate microorganism activities in the rhizosphere where nutrient availability may be altered relative to the surrounding bulk soils (i.e. rhizosphere effects, Phillips and Fahey 2006), has been expected to be a critical approach to meet plant N demand (Jones et al. 2004, Finzi et al. 2015). Although only a small proportion of C fixed by photosynthesis was consumed by root exudates, Finzi et al. (2015) found that rhizosphere related N mineralization can account for up to one third of total N mineralization in forest soils. According to C allocation theory, plants may allocate more C to root exudates under N limitation, which can increase rhizosphere N availability via priming effects (Phillips and Fahey 2008, Dijkstra et al. 2013). Consistent with this theory, our results showed that the magnitude of rhizosphere effects was negatively correlated with bulk soil N availability (Fig. 6a). Furthermore, for adapting to their induced lower soil N availability, ECM trees should allocate more C to rhizosphere and then have greater rhizosphere effects on N transformations compared with AM trees (Yin et al. 2014). Indeed, we found that ECM trees had significantly greater rhizosphere effects on NO_3^--N concentration, net N mineralization and net nitrification rates relative to AM trees (Table 2, Supplementary material Appendix 1 Fig. A1). This finding was in line with other studies showing that ECM trees had more than two times greater root exudation rates (Phillips and Fahey 2005, Yin et al. 2014) and greater rhizosphere effects on N transformation than AM trees (Phillips and Fahey 2006, Yin et al. 2014, Brzostek et al. 2015). These results suggest that, to meet N demand, ECM trees may activate N transformation in the rhizosphere via allocating more C to rhizosphere associated microorganisms. By contrast, N absorbed by AM trees is primarily supplied by a bulk soil process driven by free-living microorganisms.

In addition to mining N from SOM via rhizosphere effects, plants are also suggested to scavenge N via increasing investment in root construction to expand exploited soil volume under N limitation (Jackson et al. 2008, Taylor et al. 2014). In this study, ECM trees were found to have higher soil exploration relative to AM trees in terms of root length density (Table 2), which was negatively correlated with soil N availability (Fig. 6c). Theoretical and experimental studies have demonstrated that plants with higher root length density can acquire nutrients at a greater rate and are more competitive in N uptake compared with their neighbors and soil microorganisms (Raynaud and Leadley 2005, Jackson et al. 2008, Fort et al. 2014). Therefore, the greater rhizosphere effects and higher soil exploration of ECM trees suggest that these two strategies may work in tandem to increase N acquisition. However, there was no significant relationship between fine root biomass and soil N availability (Fig. 6b). These results indicate that root length density rather than fine root biomass may be the primary metric representing root function in N uptake, as suggested by other studies (Eissenstat 1992, Taylor et al. 2014).

Conclusions

From the 'phytocentric' perspective, this study aimed to explain potential mechanisms underlying the differential effects of ECM and AM trees on soil N cycling and their corresponding adaptive strategies in terms of N acquisition capacity. Our results showed that, compared with the eight AM trees, the slower soil N cycling and lower N availability caused by six Dipterocarpaceae ECM trees could be explained by their resource-conservative traits, especially the poorer leaf litter decomposability. To adapt to their induced lower soil N availability, ECM trees were found to have greater rhizosphere effects on N transformations to mine N from SOM and higher soil exploration in terms of root length density to scavenge N from soils. Apart from Dipterocarpaceae in southeast Asia, ECM associations can also be formed in tropical trees from other phylogenetic groups, including Caesalpinioids in South America and Africa, and Nyctaginaceae in South America (Wurzburger et al. 2017). Therefore,

much more evidence is needed to verify whether differences between Dipterocarpaceae ECM trees and AM trees in plant traits, N acquisition capacities and effects on soil N cycling observed in our study can also be found between other plant lineages of tropical ECM trees and their co-occurring AM trees.

If a general pattern can be held across tropical forests, these findings can have two important implications. First, these results provide a potential explanation for the monodominant patches of some ECM species in high-diversity tropical forests (Bunyavejchewin 1999, van der Velden et al. 2014). Specifically, the slower soil N cycling rates and lower N availability induced by ECM trees may result in N limitation for co-existing AM trees, but not for ECM trees owing to their higher N mining and scavenging capacities, which may be conductive to their monodominance. Second, the differences between ECM and AM trees in N acquisition capacities may be useful in predicting responses and feedbacks of forest community to global change. For example, the higher N acquisition capacity of ECM trees could confer their competitive advantages over AM trees under the context of N limitation caused by global change factors (e.g. elevated CO_2). This shift in forest community composition may have significant feedbacks to global change, considering the varying effects of ECM and AM trees on ecosystem functioning (Phillips et al. 2013, Averill 2016, Lin et al. 2017a).

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References

Averill, C. 2016. Slowed decomposition in ectomycorrhizal ecosystems is independent of plant chemistry. – Soil Biol. Biochem. 102: 52–54.
Ayres, E. et al. 2009. Home-field advantage accelerates leaf litter decomposition in forests. – Soil Biol. Biochem. 41: 606–610.
Bae, K. et al. 2015. Soil nitrogen availability affects belowground carbon allocation and soil respiration in northern hardwood forests of New Hampshire. – Ecosystems 18: 1179–1191.
Bardgett, R. D. et al. 2014. Going underground: root traits as drivers of ecosystem processes. – Trends Ecol. Evol. 29: 692–699.
Brzostek, E. R. et al. 2015. Mycorrhizal type determines the magnitude and direction of root-induced changes in decomposition in a temperate forest. – New Phytol. 206: 1274–1282.
Bunyavejchewin, S. 1999. Structure and dynamics in seasonal dry evergreen forest in northeastern Thailand. – J. Veg. Sci. 10: 787–792.
Cantarel, A. A. M. et al. 2015. Using plant traits to explain plant–microbe relationships involved in nitrogen acquisition. – Ecology 96: 788–799.
Cheeke, T. E. et al. 2017. Dominant mycorrhizal association of trees alters carbon and nutrient cycling by selecting for microbial groups with distinct enzyme function. – New Phytol. 214: 432–442.
Cornelissen, J. H. C. et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. – Aust. J. Bot. 51: 335–380.
Corrales, A. et al. 2016. An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. – Ecol. Lett. 19: 383–392.
Craine, J. M. et al. 2001. The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. – Oikos 93: 274–285.
Dijkstra, F. A. et al. 2013. Rhizosphere priming: a nutrient perspective. – Front. Microbiol. 4: 216.
Eissenstat, D. M. 1992. Costs and benefits of constructing roots of small diameter. – J. Plant Nutr. 15: 763–782.
Eviner, V. T. and Chapin, F. S. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. – Annu. Rev. Ecol. Evol. Syst. 34: 455–485.
Finzi, A. C. et al. 2015. Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. – Global Change Biol. 21: 2082–2094.
Fort, F. et al. 2014. Hierarchy of root functional trait values and plasticity drive early-stage competition for water and phosphorus among grasses. – Funct. Ecol. 28: 1030–1040.
Guo, D. L. et al. 2004. Fine root branch orders respond differentially to carbon source–sink manipulations in a longleaf pine forest. – Oecologia 140: 450–457.
Hobbie, S. E. 2015. Plant species effects on nutrient cycling: revisiting litter feedbacks. – Trends Ecol. Evol. 30: 357–363.
Hobbie, S. E. et al. 2010. Fine root decomposition rates do not mirror those of leaf litter among temperate tree species. – Oecologia 162: 505–513.
Jackson, B. G. et al. 2013. Are functional traits and litter decomposability coordinated across leaves, twigs and wood? A test using temperate rainforest tree species. – Oikos 122: 1131–1142.
Jackson, L. E. et al. 2008. Roots, nitrogen transformations, and ecosystem services. – Annu. Rev. Plant Biol. 59: 341–363.
Jones, D. L. et al. 2004. Plant and mycorrhizal regulation of rhizodeposition. – New Phytol. 163: 459–480.
Koele, N. et al. 2012. No globally consistent effect of ectomycorrhizal status on foliar traits. – New Phytol. 196: 845–852.
Kong, D. L. et al. 2014. Leading dimensions in absorptive root trait variation across 96 subtropical forest species. – New Phytol. 203: 863–872.
Laliberté, E. and Tylianakis, J. M. 2012. Cascading effects of long-term land-use changes on plant traits and ecosystem functioning. – Ecology 93: 145–155.
Lankau, R. A. et al. 2015. Mycorrhizal strategies of tree species correlate with trailing range edge responses to current and past climate change. – Ecology 96: 1451–1458.
Legay, N. et al. 2014. Contribution of above- and below-ground plant traits to the structure and function of grassland soil microbial communities. – Ann. Bot. 114: 1011–1021.
Lin, G. G. and Zeng, D. H. 2017. Heterogeneity in decomposition rates and annual litter inputs within fine-root architecture of tree species: implications for forest soil carbon accumulation. – For. Ecol. Manage. 389: 386–394.

Lin, G. G. et al. 2013. Litter decomposition of a pine plantation is affected by species evenness and soil nitrogen availability. – Plant Soil 373: 649–657.
Lin, G. G. et al. 2017a. Similar below-ground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests. – New Phytol. 213: 1440–1451.
Lin, G. G. et al. 2017b. Data from: Contrasting effects of ectomycorrhizal and arbuscular mycorrhizal tropical tree species on soil nitrogen cycling: the potential mechanisms and corresponding adaptive strategies. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.2811b>.
Mayor, J. et al. 2015. Ectomycorrhizal impacts on plant nitrogen nutrition: emerging isotopic patterns, latitudinal variation and hidden mechanisms. – Ecol. Lett. 18: 96–107.
McCormack, M. L. et al. 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. – New Phytol. 207: 505–518.
Midgley, M. G. and Phillips, R. P. 2014. Mycorrhizal associations of dominant trees influence nitrate leaching responses to N deposition. – Biogeochemistry 117: 241–253.
Midgley, M. G. and Phillips, R. P. 2016. Resource stoichiometry and the biogeochemical consequences of nitrogen deposition in a mixed deciduous forest. – Ecology 97: 3369–3378.
Midgley, M. G. et al. 2015. Decay rates of leaf litters from arbuscular mycorrhizal trees are more sensitive to soil effects than litters from ectomycorrhizal trees. – J. Ecol. 103: 1454–1463.
Orwin, K. H. et al. 2010. Linkages of plant traits to soil properties and the functioning of temperate grassland. – J. Ecol. 98: 1074–1083.
Phillips, R. P. and Fahey, T. J. 2005. Patterns of rhizosphere carbon flux in sugar maple (*Acer saccharum*) and yellow birch (*Betula allegheniensis*) saplings. – Global Change Biol. 11: 983–995.
Phillips, R. P. and Fahey, T. J. 2006. Tree species and mycorrhizal associations influence the magnitude of rhizosphere effects. – Ecology 87: 1302–1313.
Phillips, R. P. and Fahey, T. J. 2008. The influence of soil fertility on rhizosphere effects in northern hardwood forest soils. – Soil Sci. Soc. Am. J. 72: 453–461.
Phillips, R. P. et al. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. – New Phytol. 199: 41–51.
Pinheiro, J. et al. 2017. nlme: Linear and nonlinear mixed effects models. – <https://cran.r-project.org/web/packages/nlme/>.
Raynaud, X. and Leadley, P. W. 2005. Symmetry of belowground competition in a spatially explicit model of nutrient competition. – Ecol. Model. 189: 447–453.
Read, D. J. 1991. Mycorrhizas in ecosystems. – Experientia 47: 376–391.
Read, D. J. and Perez-Moreno, J. 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? – New Phytol. 157: 475–492.
Reich, P. B. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. – J. Ecol. 102: 275–301.
Roumet, C. et al. 2016. Root structure–function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. – New Phytol. 210: 815–826.
Scott, N. A. and Binkley, D. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. – Oecologia 111: 151–159.
Šmilauer, P. and Lepš, J. 2014. Multivariate analysis of ecological data using CANOCO 5. – Cambridge Univ. Press.
Smith, S. E. and Read, D. J. 2008. Mycorrhizal symbiosis. – Academic Press.
Talbot, J. M. et al. 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. – Funct. Ecol. 22: 955–963.
Taylor, B. N. et al. 2014. Root length, biomass, tissue chemistry and mycorrhizal colonization following 14 years of CO_2 enrichment and 6 years of N fertilization in a warm temperate forest. – Tree Physiol. 34: 955–965.
Taylor, M. K. et al. 2016. Mycorrhizal associations of trees have different indirect effects on organic matter decomposition. – J. Ecol. 104: 1576–1584.
Tedersoo, L. et al. 2012. Enzymatic activities and stable isotope patterns of ectomycorrhizal fungi in relation to phylogeny and exploration types in an afrotropical rain forest. – New Phytol. 195: 832–843.
Terrer, C. et al. 2016. Mycorrhizal association as a primary control of the CO_2 fertilization effect. – Science 353: 72–74.
Thomas, R. Q. et al. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. – Nat. Geosci. 3: 13–17.
van der Velden, N. et al. 2014. Monodominance of *Parashorea chinensis* on fertile soils in a Chinese tropical rain forest. – J. Trop. Ecol. 30: 311–322.
Vitousek, P. M. et al. 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. – Ecol. Appl. 20: 5–15.
Wardle, D. A. et al. 2004. Ecological linkages between aboveground and belowground biota. – Science 304: 1629–1633.
Waring, B. G. et al. 2016. Scale-dependent variation in nitrogen cycling and soil fungal communities along gradients of forest composition and age in regenerating tropical dry forests. – New Phytol. 209: 845–854.
Weemstra, M. et al. 2016. Towards a multidimensional root trait framework: a tree root review. – New Phytol. 211: 1159–1169.
Wurzburger, N. and Brookshire, E. N. J. 2017. Experimental evidence that mycorrhizal nitrogen strategies affect soil carbon. – Ecology 98: 1491–1497.
Wurzburger, N. et al. 2017. Mycorrhizal fungi as drivers and modulators of terrestrial ecosystem processes. – New Phytol. 213: 996–999.
Yin, H. J. et al. 2014. Root-induced changes in nutrient cycling in forests depend on exudation rates. – Soil Biol. Biochem. 78: 213–221.
Zhang, J. L. et al. 2015. Nutrient resorption is associated with leaf vein density and growth performance of dipterocarp tree species. – J. Ecol. 103: 541–549.

Supplementary material (available online as Appendix oik-04751 at <www.oikosjournal.org/appendix/oik-04751>). Appendix 1.