

# Similar below-ground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests

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## Summary

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- Compared with ectomycorrhizal (ECM) forests, arbuscular mycorrhizal (AM) forests are hypothesized to have higher carbon (C) cycling rates and a more open nitrogen (N) cycle.
- To test this hypothesis, we synthesized 645 observations, including 22 variables related to below-ground C and N dynamics from 100 sites, where AM and ECM forests co-occurred at the same site.
- Leaf litter quality was lower in ECM than in AM trees, leading to greater forest floor C stocks in ECM forests. By contrast, AM forests had significantly higher mineral soil C concentrations, and this result was strongly mediated by plant traits and climate. No significant differences were found between AM and ECM forests in C fluxes and labile C concentrations. Furthermore, inorganic N concentrations, net N mineralization and nitrification rates were all higher in AM than in ECM forests, indicating ‘mineral’ N economy in AM but ‘organic’ N economy in ECM trees.
- AM and ECM forests show systematic differences in mineral vs organic N cycling, and thus mycorrhizal type may be useful in predicting how different tree species respond to multiple environmental change factors. By contrast, mycorrhizal type alone cannot reliably predict below-ground C dynamics without considering plant traits and climate.

## Introduction

Nearly all tree species are associated with either arbuscular mycorrhizal (AM) or ectomycorrhizal (ECM) fungi (Brundrett, 2009; van der Heijden *et al.*, 2015). The mycorrhizal type of a tree species largely relates to its phylogeny (Koele *et al.*, 2012), but the dominant mycorrhizal type of a forest community may also be constrained by climatic and soil conditions (Read, 1991; Read & Perez-Moreno, 2003). AM angiosperm families tend to dominate in lowland tropical and subtropical forests where nutrient mineralization processes are rapid, while families of ECM trees increase in dominance in cool to cold environments where organic matter decomposition is somewhat to severely inhibited (Read & Perez-Moreno, 2003; Soudzilovskaia *et al.*, 2015).

Given the differences in their adaptations and distribution patterns, AM and ECM trees may be expected to respond differently to global change factors (Phillips *et al.*, 2013). Indeed, previous studies have shown that tree species of different mycorrhizal types may display opposite responses in growth performance under long-term N deposition, with AM trees more often showing positive responses and some ECM trees exhibiting negative responses (Boggs *et al.*, 2005; Thomas *et al.*, 2010). Moreover, the spatial distributions of trees associating with AM or EM fungi may

expand or contract at different rates in response to climate changes (Lankau *et al.*, 2015). To understand how changes in forest community composition will affect ecosystem functioning, it will be important first to analyze whether trees with different mycorrhizal types vary in their effects on ecological processes, especially on below-ground carbon (C) and nitrogen (N) cycling.

In terms of C cycling, ECM forests are expected to have higher forest floor and mineral soil C stocks than AM forests (Read, 1991; Vesterdal *et al.*, 2013; Averill *et al.*, 2014). The expectation has been attributed to differences in plant and associated mycorrhizal fungal traits. For plant traits, compared with AM trees, ECM trees are considered to have lower relative growth rates as well as lower leaf litter quality (Read, 1991; Cornelissen *et al.*, 2001). Therefore, leaf litters of ECM plants should decompose more slowly than those of AM plants, leading to higher forest floor C stocks (Cornelissen *et al.*, 2001; Vesterdal *et al.*, 2013). Mycorrhizal fungal trait variation may also influence soil C stocks (Langley & Hungate, 2003; Talbot *et al.*, 2008). First, ECM fungi can produce extracellular enzymes facilitating organic nitrogen (N) uptake from soil organic matter (SOM), whereas AM fungi lack these enzymes and primarily take up inorganic N (Talbot *et al.*, 2008). This direct N uptake from soils causes competition for N between ECM fungi and free-living decomposers,

potentially decreasing SOM decomposition rates and then increasing C stocks in forest floors and mineral soils (Gadgil & Gadgil, 1971; Soudzilovskaia *et al.*, 2015; Averill & Hawkes, 2016; Fernandez & Kennedy, 2016). Second, compared with AM fungi, ECM fungi require more C from their host plants and have higher standing biomass of external mycelium (van der Heijden *et al.*, 2015; Soudzilovskaia *et al.*, 2015), which may lead to higher necromass production by ECM relative to AM fungi. The larger amounts of ECM fungal necromass entering the soil C pool may also contribute to greater C stocks in ECM-dominated forests, given that mycorrhizal fungal necromass is an important precursor for the formation of SOM (Godbold *et al.*, 2006; Clemmensen *et al.*, 2013). Despite these advances, previous studies have usually focused on the varying effects of AM and ECM forests on soil C stocks while neglecting C fluxes (Vesterdal *et al.*, 2013; Averill *et al.*, 2014), which are necessary to understand mycorrhizal-associated below-ground C budgets (Soudzilovskaia *et al.*, 2015).

Additionally, AM and ECM forests may have contrasting modes of below-ground N cycling (Chapman *et al.*, 2006; Phillips *et al.*, 2013). AM-dominated forests have previously been characterized by higher inorganic N : organic N ratios and higher nitrification rates, and show greater nitrate leaching in response to N deposition (Phillips *et al.*, 2013; Midgley & Phillips, 2014). However, such studies have only been conducted in temperate forests and it is unknown how applicable these findings would be to subtropical and tropical forests, which host many notable and ecologically important ECM tree species, particularly those in the families of Dipterocarpaceae and Myrtaceae and some in the Fabaceae (Brundrett, 2009). Available evidence seems to suggest that ECM-mediated uptake of organic N may be relatively unimportant in tropical forests, given that  $\delta^{15}\text{N}$  values of ECM trees, which can be used to indicate the relative importance of N transfer from ECM fungi to trees, are similar to or even higher than those of co-occurring AM trees (Tedersoo *et al.*, 2012; Mayor *et al.*, 2015). These results may indicate a generally more open and rapid N cycling in tropical forests, regardless of mycorrhizal type (Kuyper, 2012; but see Corrales *et al.*, 2016).

Overall, whether differences in soil C and N cycling are strongly associated with mycorrhizal type has not been firmly established across different biomes with contrasting plant phylogeny, climate, and rates of C and nutrient cycling. However, it

is not easy to parse out how different factors combined and separately influence a certain ecosystem process such as C sequestration. By synthesizing a global database, Averill *et al.* (2014) estimated that ECM-dominated ecosystems contained 1.7 times more C per unit soil N than AM-dominated ecosystems. The authors proposed that fundamental differences in the effects of AM and ECM fungi on soil C and N cycling were underlying this difference in C sequestration. However, this comparison was conducted across biomes and it was difficult to separate the effects of mycorrhizal type *per se* from effects mediated by environmental factors. To better understand the correlative relationships between mycorrhizal associations and below-ground C and N cycling dynamics, we compiled a database of 22 variables related to ecosystem C and N cycling and associated soil microbial communities from study sites where AM and ECM forests co-occurred under the same soil and climate conditions. Using this database we could test for differences in these variables within each site separately and thereby more confidently attribute these differences to the occurrence of AM vs ECM forests. Specifically, we aimed to answer the following questions: do AM forests have higher soil C cycling rates than ECM forests; and do AM forests have a more open N cycle dominated by inorganic N forms than ECM forests?

## Materials and Methods

### Data collection

To develop a comprehensive database, peer-reviewed articles were searched using the Web of Science and China National Knowledge Infrastructure with the following search terms: (*tree species* OR *plant species*) AND (*C cycling* OR *soil C* OR *soil respiration* OR *N cycling* OR *N mineralization* OR *nitrification* OR *microbial community*). We extracted papers from our search that matched the following criteria: co-occurring AM and ECM forests grew on the same climate, soil type and topography; comparisons between AM and ECM forests were done only on trees/forests of the same age, which were at least 10 yr old; and at least one response variable listed in Table 1 was reported. Furthermore, for plantations, we selected monoculture stands (i.e. composed by a single tree species) and excluded mixed stands. For natural forests, the selection standards were not as strict as for the plantation sites, to be able to include more samples. In our study,

**Table 1** Variables selected to evaluate the relative effects of arbuscular mycorrhizal (AM) forests and ectomycorrhizal (ECM) forests on soil carbon (C) and nitrogen (N) cycles

Category	Target variable (sample size)
Litter input and quality	Annual above-ground litter input (31), leaf litter C : N ratio (27), leaf litter lignin concentration (14), leaf litter lignin : N ratio (16)
C pools	Forest floor C stock (26), mineral soil C concentration (82), forest floor C : N ratio (16), mineral soil C : N ratio (74), dissolved organic C concentration (16)
C fluxes	C mineralization rate (24), soil respiration rate (13)
N pools	Forest floor N stock (16), mineral soil N concentration (68), inorganic N concentration (33), $\text{NH}_4^+$ -N concentration (29), $\text{NO}_3^-$ -N concentration (24), organic N : inorganic N ratio (26)
N fluxes	Net N mineralization rate (27), net nitrification rate (26)
Microbial biomass	Microbial biomass C (29), microbial biomass N (15), MBC : MBN ratio (13)

MBC, microbial biomass C; MBN, microbial biomass N.

some natural sites contained tree clusters (i.e. several trees of the same species growing together; e.g. Lovett *et al.* (2004)) or stands dominated by tree species of the same mycorrhizal type (e.g. Brzostek *et al.*, 2015). In addition, we also included studies on the effects of dominant tree species on soil processes where soils beneath the canopy of target species were analyzed (e.g. Finzi *et al.*, 1998). A total of 150 papers covering 100 study sites met these criteria and were included in our study (Fig. 1; Supporting Information Table S1).

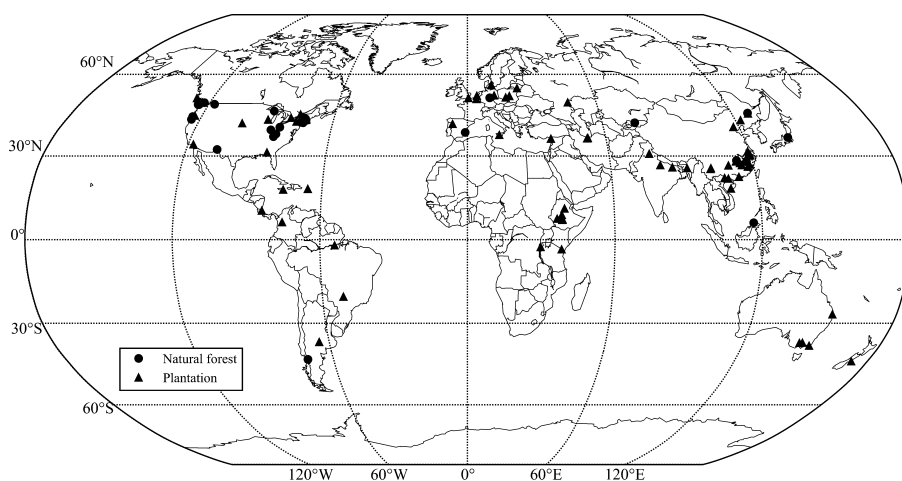
From each forest stand at each study site, we extracted mean values of each response variable listed in Table 1, which contained four response variables related to leaf litter quality and annual above-ground litter input, seven response variables related to C pools and fluxes, eight response variables related to N pools and fluxes, and three response variables related to soil microbial biomass. If necessary, data were taken from graphs using the GETDATA software (v.2.26; <http://getdata-graph-digitizer.com>). Forest floor and mineral soil layers were treated separately. C and N stocks ( $\text{Mg ha}^{-1}$ ) were used as metrics of forest floor C and N pools (Table S1). For mineral soils, concentrations ( $\text{g kg}^{-1}$ ) were used as metrics (Table S1), considering that the sample size was smaller when using stock rather than concentration as metrics (Fig. S1) and no significant differences were found between AM and ECM forests in mineral soil bulk density (Fig. S2). Furthermore, results were similar when analyzing differences between AM and ECM forests in mineral soil C and N pools when using concentration and stock as metrics (Fig. S1). If response variables were measured multiple times over the course of a year within a given study site, data were averaged across all sampling occasions. For studies including multiple sampling depths, we focused on the uppermost layer of mineral soil, which may best reflect tree species-specific effects on ecosystem processes. However, because the sampling depth of the uppermost mineral soil layer varied among studies (e.g. 0–10 cm in some studies compared with 0–30 cm in others), we were not able to compare pools of 'total' soil C and N (i.e. forest floor combined with mineral soil).

Given that other factors may influence the magnitude of differences between AM and ECM forests in ecosystem processes,

we incorporated key climate, site, and plant characteristics into our analysis. We collected data for soil sampling depth, mean annual temperature (MAT), mean annual precipitation (MAP), climate zone (temperate and tropical/subtropical forests) and forest type (plantation and natural forest) for each study site. When climatic factors were not reported, we extracted these data from the WorldClim database (<http://www.worldclim.org/>) based on site location information (latitude and longitude). For tree species characteristics, we collected information on taxonomic group (angiosperm or gymnosperm), N-fixation ability (N-fixing or non-N-fixing) and mycorrhizal type of trees. Subsequently, differences between AM and ECM trees in the proportions of angiosperms (DPA) and N-fixing trees (DPN) for each study site were calculated, as follows:  $\text{DPA (or DPN)} = R_{\text{AM}} - R_{\text{ECM}}$ , where  $R_{\text{AM}}$  and  $R_{\text{ECM}}$  are the ratios of species number of angiosperms (or N-fixing trees) in the number of AM and ECM trees in a study site, respectively. For mycorrhizal type, trees were classified into AM and ECM trees based on the reports of each study. If this information was not reported, mycorrhizal type was designated according to previous reviews (e.g. Wang & Qiu, 2006; Brundrett, 2009) or based on the reports describing mycorrhizal associations of closely related species (i.e. within genus or family) (Koele *et al.*, 2012; Phillips *et al.*, 2013). Trees dually colonized by both AM and ECM fungi (e.g. *Populus*, *Eucalyptus*) were either classified as ECM type or excluded in the following analyses to explore their influence. The results were broadly consistent between the two scenarios (Fig. S3) and in the following sections we only present results based on dually colonized trees considered as the ECM type.

### Statistical analyses

For each study site, values of each response variable for each tree species were used to calculate average values for AM and ECM forests. For each response variable, effect size was calculated as the natural log response ratio ( $R$ ) of its mean values of AM forest plots compared with those of ECM forest plots at the same site. Consequently, the number of response ratios (i.e. sample size) for a given response variable was one per study site to avoid



**Fig. 1** Map showing the geographical distribution of the 100 study sites used in this study.

pseudoreplication. Because mean effect size estimates in meta-analysis are based on how individual studies were weighted, four different weighting functions were used in our study: weighted by number of tree species,  $W_1 = (N_{AM} \times N_{ECM}) / (N_{AM} + N_{ECM})$ , where  $N_{AM}$  and  $N_{ECM}$  are number of AM and ECM tree species in a study site, respectively; weighted by replication,  $W_2 = (n_{am} \times n_{ecm}) / (n_{am} + n_{ecm})$ , where  $n_{am}$  and  $n_{ecm}$  are the average number of replications under AM and ECM tree species in a study site, respectively; weighted by number of tree species and replications,  $W_3 = n \times W_1$ , where  $n$  is the average number of replications of all tree species in a study site; and unweighted,  $W_4 = 1$ , where all observations were assigned equal weights. Mean effect sizes were calculated using random-effect models. Bootstrapping procedures (9999 iterations) were used to calculate 95% confidence intervals (CIs) of the mean effect sizes. If the 95% CIs of effect sizes for response variables did not overlap with zero, these response variables were considered significantly different between AM and ECM forests. Given that similar results were obtained for each of the different weighting functions (Table S2), only mean effect sizes weighted by number of tree species and replicates ( $W_3$ ) were reported. These analyses were performed using the METAWIN software, v.2.0 (Rosenberg *et al.*, 2000).

For each response variable, mixed linear models were performed in R using the NLME package (Pinheiro *et al.*, 2016) to analyze the influence of other factors on mycorrhizal-associated ecological processes. In these models, soil sampling depth, MAP, MAT, forest type, climate zone, DPA and DPN were considered as fixed factors. Furthermore, identity of study site was also included in models as a random factor. From these initial models, second-order Akaike information criterion ( $AIC_c$ ) values were calculated for all possible submodels.  $AIC_c$  was chosen because of the small sample sizes relative to the number of factors contained in some initial models (Burnham & Anderson, 2002). From these submodels, we selected top-ranked models, which contained all models within two units of  $AIC_c$  values (Grueber *et al.*, 2011). These top-ranked models were averaged using the MUMIN package (Barton, 2016) in R to determine which factors were statistically significant and to measure the relative importance (RI) of each factor. RI is referred to as the sum of the Akaike weights across all the top-ranked models containing the factor of interest (Grueber *et al.*, 2011). The RI ranges from 0 to 1 and a factor with  $RI > 0.5$  indicates that it is relatively important (Burnham & Anderson, 2002).

In addition to analyzing the indexes of DPA and DPN, taxonomic group and N-fixation ability were further analyzed to explore their effects on response ratios of selected variables. Specifically, we calculated mean effect sizes and their 95% CIs for each response variable when only including angiosperms and non-N-fixing trees using the methods described earlier. We did not analyze differences between AM and ECM forests in ecological processes when they were composed by gymnosperms or N-fixing trees, given that sample sizes of these comparisons were  $< 10$ . These small sample sizes may lead to type II error, considering that power analysis, using the PWR package in R, showed that sample sizes should be larger than nine to provide 80% chance of

correctly rejecting the null hypothesis when the significant level was set at 0.05 and assuming that mycorrhizal type explained 49% of the variation in ecological processes.

## Results

In total, 150 published papers from 100 study sites were included in our analyses (Fig. 1; Table S1). Across the 100 study sites, 76% were plantations and 47% were located in temperate zone. A database consisting of 645 observations was used to calculate effect sizes of 22 response variables. This database contained 173 tree species from 34 families, representing 81 AM and 92 ECM tree species (Table S3).

### Leaf litter quality and annual above-ground litter input

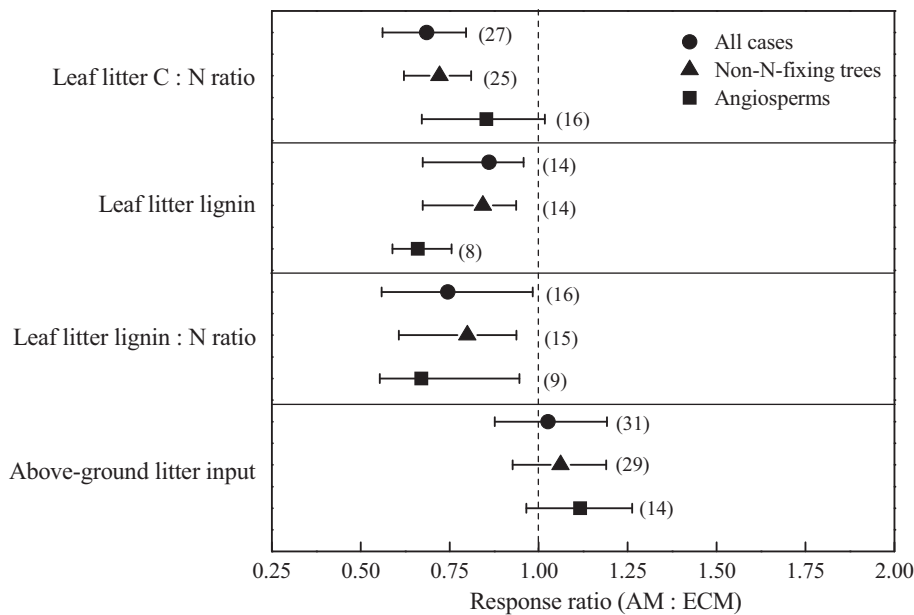
Leaf litter of AM trees had significantly lower lignin concentration, C : N ratio, and lignin : N ratio than ECM trees (Fig. 2), when all cases and non-N-fixing trees were analyzed. When only considering angiosperms, there was no significant difference between AM and ECM trees in leaf litter C : N ratio, but leaf litter of AM trees still displayed lower lignin concentration and lignin : N ratio than that of ECM trees (Fig. 2).

There was no significant difference in annual above-ground litter input between AM and ECM forests regardless of tree species characteristics (Fig. 2). Model selection resulted in three top-ranked models with  $\Delta AIC_c < 2.00$  (Table S4), which retained three fixed factors: climate zone, DPN and forest type (Table 2). Among these three factors, climate zone was the only factor that significantly explained variations in response ratio of annual above-ground litter input ( $P < 0.01$ ,  $RI = 0.82$ ; Table 2). Specifically, AM forests had significantly higher annual above-ground litter input than did ECM forests in temperate zones but not in tropical/subtropical zones (Fig. S4).

### C pools and fluxes

For C pools and concentrations, irrespective of tree species characteristics, AM forests had markedly less forest floor C stock than ECM forests (by 33.5–46.9%; Fig. 3). MAP significantly explained additional variation in the response ratio of forest floor C stock ( $P = 0.04$ ,  $RI = 0.55$ ; Table 2). Specifically, differences between AM and ECM forests in forest floor C stocks were gradually reduced with increasing MAP (Fig. S5). By contrast, AM forests had significantly higher mineral soil C concentration than ECM forests, when all cases were analyzed (8.0%; Fig. 3). Climate zone, DPA and DPN all had a significant influence on the magnitude and direction of the difference between AM and ECM forests in mineral soil C concentration (Table 2; Figs 3, S6, S7). As a result, AM forests had significantly higher mineral soil C concentration in tropical and subtropical zones but not in temperate zones (Fig. S4). Furthermore, when only considering non-N-fixing trees and angiosperms, there was no significant difference in mineral soil C concentration between AM and ECM forests (Fig. 3).

There was no significant overall difference between AM and ECM forests in concentrations of dissolved organic C (DOC)



**Fig. 2** Mean differences between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) tree species in annual above-ground litter input and leaf litter quality (carbon (C) : nitrogen (N) ratio, lignin, and lignin : N ratio) when all cases (circles) were considered, when only including non-N-fixing trees (triangles) and when only including angiosperms (squares). Analyses were considered significant when 95% bootstrap confidence intervals (error bars) did not overlap with the dashed line, indicating mean response ratio = 1. The sample size for each variable is shown in brackets.

when all cases and non-N-fixing trees were analyzed (Fig. 4), but climate zone significantly influenced the response ratio of DOC ( $P=0.01$ ,  $RI=0.68$ ; Table 2). Specifically, AM forests had significantly higher DOC concentration in tropical and subtropical zones but not in temperate zones (Fig. S4). For C fluxes, there were no consistent differences between AM and ECM forests in soil respiration and C mineralization rates (Fig. 5). DPA significantly influenced the magnitude of difference between AM and ECM forests in soil respiration rate ( $P<0.01$ ,  $RI=1.00$ ; Table 2) as AM forests had gradually higher soil respiration rates with increasing DPA values compared with ECM forests (Fig. S6).

### N pools and fluxes

There were no significant differences between AM and ECM forests in forest floor N stock irrespective of tree species characteristics (Fig. 3). No fixed factors were found to significantly explain variations in response ratio of forest floor N stock (Table 2). When all cases were analyzed, AM forests had markedly higher mineral soil N concentration than ECM forests (22.0%; Fig. 3). Furthermore, AM forest soils also had significantly higher inorganic N (40.2%),  $\text{NH}_4^+\text{-N}$  (18.6%) and  $\text{NO}_3^-\text{-N}$  (62.8%) concentrations, and lower organic N : inorganic N ratios (Fig. 4). For N fluxes, AM forest soils had significantly higher net N mineralization (55.6%) and nitrification (161.0%) rates than ECM forest soils (Fig. 5). DPN was the only factor that significantly explained the variations in magnitude of differences between AM and ECM forests in inorganic N,  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ , organic N : inorganic N ratio, net N mineralization, and net nitrification (Table 2; Fig. S7). However, there was no change in direction of differences between AM and ECM forests in the above-mentioned response variables when N-fixing trees were removed from the analysis (Figs 4, 5).

Forest floor C : N ratio was not markedly different when only considering non-N-fixing trees or angiosperms, but was

significantly higher in ECM than in AM forests when all cases were analyzed together (Fig. 3). Furthermore, AM forests had significantly lower forest floor C : N ratio than ECM forests in tropical and subtropical zones but not in temperate zones ( $P=0.03$ ,  $RI=1.00$ ; Table 2; Fig. S4). AM forests also had significantly lower (7.6–12.6%) mineral soil C : N ratio than ECM forests irrespective of tree species characteristics (Fig. 3). Soil sampling depth significantly explained variations in response ratios of mineral soil C : N ratio ( $P<0.01$ ,  $RI=1.00$ ; Table 2). Specifically, AM forests had gradually lower mineral soil C : N ratio than ECM forests with increasing soil sampling depth (Fig. S5).

### Microbial biomass and community structure

There were no significant differences between AM and ECM forests in microbial biomass C (MBC) and microbial biomass N (MBN) (Fig. S8) when all cases were analyzed. No additional fixed factors were found to significantly explain variation in the response ratios of MBC (Table 2), but DPA did significantly influence the response ratio of MBN ( $P<0.01$ ,  $RI=1.00$ ; Table 2). Specifically, AM forests had gradually higher MBN than did ECM forests with increasing DPA values (Fig. S6). The MBC : MBN ratio was significantly different between AM and ECM forests, with the MBC : MBN ratio being 9.8% lower in AM than in ECM forests when analyzing all cases together (Fig. S8). Furthermore, there was some indication of an increasing difference between AM and ECM forests in MBC : MBN ratio with increasing soil sampling depth ( $P=0.01$ ,  $RI=0.73$ ; Table 2), but this potential difference should be viewed conservatively given the limited sample size available for this comparison (Fig. S5).

### Discussion

To better understand the correlative relationships between mycorrhizal associations and ecosystem processes, we conducted a

**Table 2** Fixed factors retained in the top ranked models with  $\Delta AIC_c < 2.0$  and their significant levels and relative importance

	Selected factors	Z-value	P-value	Relative importance
Annual above-ground litter input	<i>Climate zone</i>	3.16	<b>&lt; 0.01</b>	0.82
	DPN	1.87	0.06	0.35
	Forest type	1.18	0.19	0.18
Forest floor carbon (C) stocks	<i>MAP</i>	2.09	<b>0.04</b>	0.55
	MAT	1.16	0.19	0.21
Forest floor nitrogen (N) stocks	DPA	1.83	0.06	0.36
	<i>Climate zone</i>	1.63	0.13	0.29
Forest floor C : N ratio	<i>Climate zone</i>	2.18	<b>0.03</b>	1.00
Mineral soil C concentration	<i>Climate zone</i>	2.76	<b>&lt; 0.01</b>	1.00
	DPA	2.27	<b>0.02</b>	1.00
	DPN	2.07	<b>0.04</b>	0.56
Mineral soil N concentration	NA			
Mineral soil C : N ratio	<i>Soil sampling depth</i>	3.15	<b>&lt; 0.01</b>	1.00
	MAP	1.65	0.12	0.29
Dissolved organic C concentration	<i>Climate zone</i>	2.51	<b>0.01</b>	0.68
Inorganic N concentration	DPN	4.75	<b>&lt; 0.01</b>	1.00
	NA			
NH <sub>4</sub> <sup>+</sup> -N concentration	DPN	2.49	<b>0.01</b>	1.00
NO <sub>3</sub> <sup>-</sup> -N concentration	DPN	2.82	<b>&lt; 0.01</b>	0.70
	Forest type	1.47	0.14	0.30
Organic N : Inorganic N ratio	DPN	2.63	<b>&lt; 0.01</b>	1.00
C mineralization rate	NA			
Soil respiration rate	DPA	5.66	<b>&lt; 0.01</b>	1.00
Net N mineralization rate	DPN	3.20	<b>&lt; 0.01</b>	1.00
	MAP	0.66	0.31	0.32
Net nitrification rate	DPN	2.28	<b>0.02</b>	1.00
	Forest type	1.41	0.15	0.24
	<i>Climate zone</i>	0.98	0.23	0.17
Microbial biomass C	DPA	1.69	0.09	0.30
Microbial biomass N	DPA	3.55	<b>&lt; 0.01</b>	1.00
	Forest type	1.39	0.15	0.41
	<i>Climate zone</i>	0.70	0.29	0.23
MBC : MBN ratio	<i>Soil sampling depth</i>	2.45	<b>0.01</b>	0.73

See Supporting Information Table S4 for the full list of top-ranked models. MAT, mean annual temperature; MAP, mean annual precipitation. MBC, microbial biomass C; MBN, microbial biomass N; NA, no fixed factors were included in the top-ranked models; DPA, DPN, differences between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) trees in the proportions of angiosperms and N-fixing trees in a study site, respectively. Statistically significant factors and P-values are indicated in italic and bold text, respectively.

meta-analysis with 645 observations of 22 response variables related to below-ground C and N dynamics from 100 study sites where AM and ECM trees co-occurred under the same climate and soil conditions. In general, the effect of mycorrhizal type on soil C processes was less pronounced than previously reported (Orwin *et al.*, 2011; Averill *et al.*, 2014) and was strongly mediated by factors related to climate and plant traits. By contrast, the effect of mycorrhizal type on soil N processes was strong and highly predictable, with AM forests generally having a fast, inorganic and 'open' N cycle (Fig. 6), which related to their higher mineral soil N concentrations and lower C : N ratios (Fig. 3).

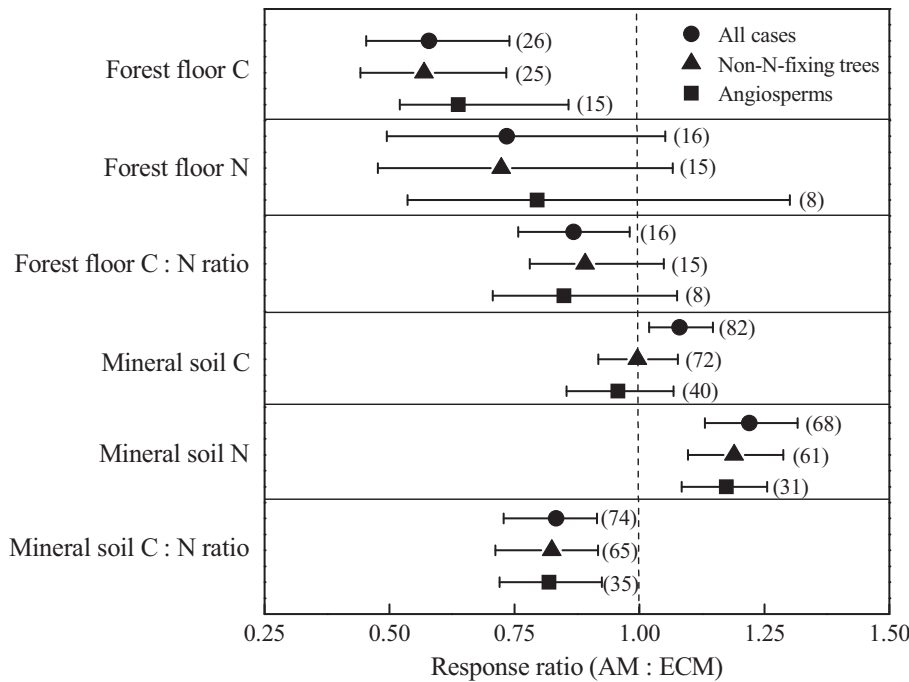
## Effects of mycorrhizal type on soil C cycling

Our results showed that ECM forests consistently had higher forest floor C stocks compared with AM forests (Fig. 3). Given that there were no significant differences in annual above-ground litter inputs between AM and ECM forests in our dataset (Fig. 2), the higher forest floor C stocks in ECM forests should be a result of their lower litter decomposition rates. Indeed, we found that leaf litters of ECM trees had higher lignin concentrations, C : N ratios and lignin : N ratios (Figs 2, 6), all of which contribute to slower decomposition rates; thus these findings were consistent with previous studies (Cornelissen *et al.*, 2001; Hobbie *et al.*, 2006).

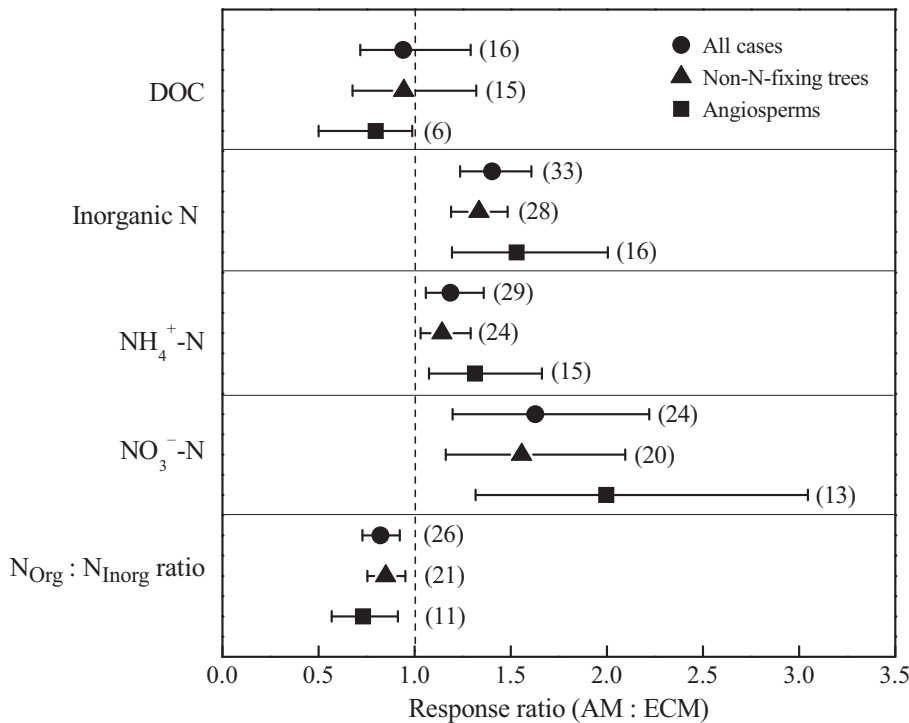
Apart from differences in plant litter quality, AM and ECM fungi also differ in their effects on litter decomposition, which may be another reason for the higher forest floor C stocks of ECM forests (Gadgil & Gadgil, 1971; Hodge *et al.*, 2001). Specifically, AM fungi may indirectly accelerate litter decomposition through their priming effects on soil bacterial communities (Hodge *et al.*, 2001; Nuccio *et al.*, 2013). ECM fungi can produce extracellular enzymes which may directly promote litter decomposition (Talbot *et al.*, 2008). For example, Phillips *et al.* (2014) found that ECM fungi-dominated systems had comparable or even higher concentrations of hydrolytic and oxidative enzymes in soil compared with saprotrophic fungi-dominated systems. In addition to the direct involvement of ECM fungi in litter decomposition, ECM fungi may indirectly retard litter decomposition in some situations by competing with saprotrophic microorganisms for soil N and water (Gadgil & Gadgil, 1971; Koide & Wu, 2003; Fernandez & Kennedy, 2016). Thus, the net effects of ECM fungi on litter decomposition may be negative, as the presence of ECM roots can suppresses litter decomposition, but the specific responses are likely to be species- and context-dependent (Fisher & Gosz, 1986; Fernandez & Kennedy, 2016).

The antagonistic relationships between ECM fungi and saprotrophic microorganisms competing for N might also lead to the expectation that ECM forests store more mineral soil C than do AM forests (Orwin *et al.*, 2011). This expectation has been supported by the evidence of higher standing biomass of ECM fungal mycelium whose residues are important precursors for the formation of SOM (Clemmensen *et al.*, 2013; Soudzilovskaia *et al.*, 2015). However, within the upper layers of mineral soil (with mean soil sampling depth of 15.1 cm; Table S1), our results showed that ECM forests had 8.0% lower mineral soil C concentrations than did AM forests (Fig. 6), and this difference occurred mainly in tropical/subtropical zones (Fig. S4). This finding may be explained by differences in plant litter quality between AM and ECM trees which can then influence soil C sequestration (Cotrufo *et al.*, 2013; Tamura & Tharayil, 2014). Therefore, to fully understand the effects of mycorrhizal type on mineral soil C, a suite of factors should be considered, including plant litter quality (above and below ground), mycorrhizal fungal traits, decomposition dynamics, and the conversion of forest floor C into mineral soil C (see more discussions later).

Additional evidence also suggests that ECM forests do not necessarily have higher C concentrations. For example, we observed



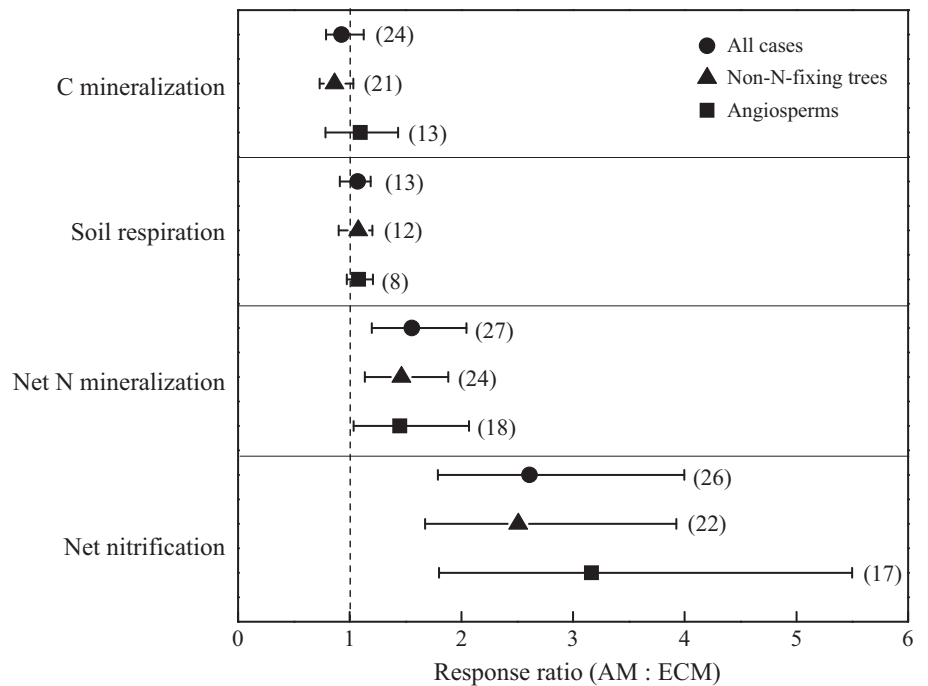
**Fig. 3** Mean differences between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) forests in carbon (C) and nitrogen (N) pools and C : N ratios of forest floor and mineral soil when all cases (circles) were considered, when only including non-N-fixing trees (triangles) and when only including angiosperms (squares). Analyses were considered significant when 95% bootstrap confidence intervals (error bars) did not overlap with the dashed line, indicating mean response ratio = 1. The sample size for each variable is shown in brackets.



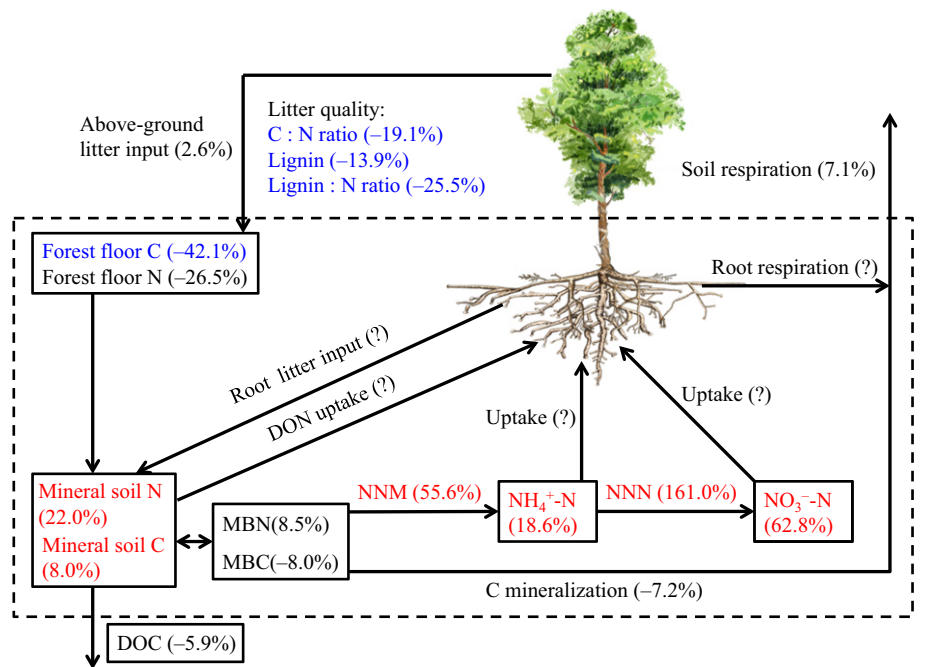
**Fig. 4** Mean differences between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) forests in dissolved organic carbon (DOC), inorganic nitrogen (N), NH<sub>4</sub><sup>+</sup>-N, NO<sub>3</sub><sup>-</sup>-N and the ratio of organic N to inorganic N concentrations (N<sub>Org</sub> : N<sub>Inorg</sub> ratio) when all cases (circles) were considered, when only including non-N-fixing trees (triangles) and when only including angiosperms (squares). Analyses were considered significant when 95% bootstrap confidence intervals (error bars) did not overlap with the dashed line, indicating mean response ratio = 1. The sample size for each variable is shown in brackets.

no effects of mycorrhizal type on C mineralization and soil respiration rates (Fig. 5). Neither did we observe significant differences in DOC concentration between AM and ECM forests, which is another important output pathway of soil C (Kindler *et al.*, 2011). Given that no marked differences in above-ground litter input and C output fluxes were found between AM and ECM forests, the higher mineral soil C concentrations in AM forests may be a result of a higher proportion of their floor C being incorporated into

mineral soil by soil fauna, especially for surface soil layers (Frouz *et al.*, 2013). Indeed, previous studies have reported that leaf litter quality positively correlates with soil fauna density (Hobbie *et al.*, 2006; Frouz *et al.*, 2013). Active soil fauna can incorporate litter C into soil aggregates, which protects soil C from decomposition (Frouz *et al.*, 2013). All these factors combined may explain the lower forest floor C stocks but higher mineral soil C concentrations in AM than in ECM forests, particularly in tropical/subtropical



**Fig. 5** Mean differences between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) forests in carbon (C) mineralization, soil respiration, net nitrogen mineralization (net N min) and net nitrification (net nit) rates when all cases (circles) were considered, when only including non-N-fixing trees (triangles) and when only including angiosperms (squares). Analyses were considered significant when 95% bootstrap confidence intervals (error bars) did not overlap with the dashed line, indicating mean response ratio = 1. The sample size for each variable is shown in brackets.



**Fig. 6** Percentage differences between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) forests in response variables related to carbon (C) and nitrogen (N) dynamics ((AM/ECM - 1) × 100%). Red and blue numbers represent pools or fluxes where AM forests have significantly higher (red) values or ECM forests have significantly higher values (blue). Black numbers represent pools or fluxes that are not significantly different between AM and ECM forests. Fluxes with '?' indicate key processes where there are not enough study cases available. DOC, dissolved organic C; DON, dissolved organic N; MBN, microbial biomass N; NNM, net N mineralization; NNN, net nitrification.

zones (Fig. S4) where decomposition is relatively rapid and soil fauna activity is high (Boča *et al.*, 2014).

Furthermore, differences in quantity and quality of below-ground litters, which have so far been ignored, may also explain the differences in mineral soil C concentrations between AM and ECM forests considering the higher litter quality and faster decomposition rates of root litters of AM trees (Makita & Fujii, 2015; Taylor *et al.*, 2016). However, owing to the data limitations, we could not target mycorrhizal-associated differences in quantity and quality of below-ground litters (Fig. 6). Therefore,

future studies should consider litter quantity and quality of roots and their associated fungi, which are important precursors of soil C (Clemmensen *et al.*, 2013).

### Effects of mycorrhizal type on soil C : N ratios and N cycling

Compared with more subtle and complex differences in soil C cycling between AM and ECM forests, the differences in N cycling between the two mycorrhizal types were highly systematic. AM forests had markedly higher (18.6–161.0%) inorganic



N concentrations, net N mineralization rates, and nitrification rates than did ECM forests, indicating faster N cycling rates in AM forests (Fig. 6). These findings are consistent with the hypothesis proposed by Read (1991) that, on the global scale, the differentiation between mycorrhizal types occurs primarily along a gradient of organic vs inorganic N cycling, and they are also consistent with the more recently updated 'Mycorrhizal-Associated Nutrient Economy' framework by Phillips *et al.* (2013), which associates the 'inorganic' N economy with AM trees and 'organic' N economy with ECM trees. Indeed, ECM fungi can mobilize N from SOM directly through the production of extracellular enzymes and are therefore less dependent on saprotrophic microbes for N uptake (Brzostek *et al.*, 2015; Lindahl & Tunlid, 2015). Conversely, AM fungi have limited hydrolytic ability and scavenge primarily for inorganic N released by saprotrophic microbes (Read & Perez-Moreno, 2003; Talbot *et al.*, 2008; Phillips *et al.*, 2013; Lindahl & Tunlid, 2015). Natural abundance N isotope and  $^{15}\text{N}$  labeling studies add further support for greater organic N uptake by ECM plants relative to co-occurring AM plants (Read & Perez-Moreno, 2003; Averill & Finzi, 2011).

Ectomycorrhizal fungi can selectively forage for N but not assimilate C from SOM, which may lead to a higher soil C:N ratio (Lindahl *et al.*, 2007; Clemmensen *et al.*, 2013; van der Heijden *et al.*, 2015). By assembling a global dataset of soil C and N stocks, Averill *et al.* (2014) indicated that ECM-dominated ecosystems stored 1.7 times more C per unit N than AM-dominated ecosystems (or 1.5 times more C per unit N when the comparison excluded grassland ecosystems). Our results suggest a much more conservative effect on overall C:N ratios, with ECM forests averaging 1.1 and 1.2 times higher C:N ratios than AM forests in their forest floor and mineral soil fractions, respectively (Fig. 3). This leaves open the possibility that individual tree species can exert significant controls on soil C:N ratios that go beyond broad mycorrhizal association. In line with this, Cools *et al.* (2014) synthesized data from >4000 plots to show that tree species explained the largest amount of variation in mineral soil C:N ratios and additional studies have further noted direct relationships between tree litter qualities and soil C:N ratios (Finzi *et al.*, 1998; Vesterdal *et al.*, 2008).

### Other factors influencing effects of mycorrhizal type on ecosystem functions

The effects of mycorrhizal type on N cycling were broadly consistent, but the effects of mycorrhizal type on C cycling were significantly influenced by the N-fixation capacity and plant group (i.e. angiosperms vs gymnosperms). Specifically, AM forests had higher mineral soil C concentrations and soil respiration rates than did ECM forests with increased DPA values (Table 2; Fig. S6), implying that the effects of AM association are largely confounded by the fact that AM trees have a higher propensity to be angiosperms. Furthermore, mineral soil C concentrations were significantly higher in AM than in ECM forests when all cases were considered, but not when AM and ECM trees were limited solely to non-N-fixing plants and angiosperms (Fig. 3). The

influence of N-fixation ability on soil C concentrations may be because most N-fixing trees form arbuscular mycorrhizas and N-fixing trees tend to promote soil C accumulation as a result of the extra N input, given the closely coupled relationships between soil C and N dynamics (Resh *et al.*, 2002; Cleveland & Liptzin, 2007). The influence of plant group may be because, compared with angiosperm trees, gymnosperm trees store less mineral soil C and more forest floor C (Laganier *et al.*, 2010), owing to their lower litter quality and root biomass allocation, and the lower soil fauna activity in gymnosperm forests (Cornwell *et al.*, 2008; Poorter *et al.*, 2012; Frouz *et al.*, 2013). Collectively, our results strongly suggest that variations in plant characteristics must be considered when analyzing whether mycorrhizal type has predictable effects on soil C cycling.

Apart from plant traits, climatic factors also constrained effects of mycorrhizal type on ecosystem processes (Table 2; Fig. S5). Differences in forest floor C stocks between AM and ECM forests were gradually reduced with increasing MAP (Fig. S5), which may be explained by the increasing similarity in decomposition rates among litters with different qualities accompanied by the increasing MAP (Meentemeyer, 1978; Zhang *et al.*, 2008; Boča *et al.*, 2014). Moreover, climate zone was found to significantly explain variations in response ratio of mineral soil C concentrations, with higher mineral soil C concentrations in AM than in ECM forests in tropical/subtropical zones but not in temperate zones (Table 2; Fig. S4). One possible reason for this result is the slower tree growth at higher latitudes with a longer period of time required to observe changes in C stocks after plantation establishment (76 of the 100 of sites in this study were plantations averaging 30 yr old; Table S1) (Laganier *et al.*, 2010). Another reason may be that the majority of N-fixing trees, which primarily form AM symbioses and tend to increase soil mineral C to a greater extent than non-N-fixing trees, occur in tropical/subtropical ecosystems (Table S3).

### Limitations and future research

The present study outlined major similarities and differences in below-ground C and N cycling between AM and ECM forests and enables a better understanding of potential relationships between mycorrhizal associations and ecosystem processes. However, our study has several limitations which should be resolved in future studies. First, constrained by available data, some important C and N fluxes were not fully considered here and should be investigated further (Fig. 6). For example, annual litter inputs of fine roots and their associated mycorrhizal fungal mycelium are suggested as the main precursors of soil C and probably account for more than half of annual litter production in many terrestrial ecosystems (Clemmensen *et al.*, 2013; Freschet *et al.*, 2013), yet accurate estimates of these inputs are lacking in most ecosystems. Second, while our study included species from 34 different plant families, most data were from a few families, including Sapindaceae, Fabaceae, Fagaceae, Myrtaceae, Cupressaceae, and Pinaceae (Table S3). It is therefore possible that our results were driven by phylogenetic similarities rather than mycorrhizal type (Koele *et al.*, 2012). Only increased

observations across a wide range of phylogenies can resolve this issue. Third, as with many previous studies, our analyses cannot fully separate effects of mycorrhizal type from effects of plant traits. In fact, in many cases, our results indicate the importance of considering both the mycorrhizal type and plant traits together. Thus, mycorrhizal type alone may not satisfactorily predict many key ecosystem processes, particularly those relating to C cycling.

## Conclusions

Through synthesizing 645 observations from 100 study sites, our results showed that AM trees generally produced higher-quality leaf litters compared with ECM trees. Without significant differences in annual above-ground litter inputs, ECM forests had higher forest floor C stocks relative to AM forests. Further, our study found that, in the surface soil layer, AM forests stored more mineral soil C than ECM forests in subtropical and tropical zones but not in temperate zones, driven in part by greater abundance of N-fixing trees which promotes soil C accumulation. Despite equal (in temperate forests) or lower (in subtropical and tropical forests) total mineral soil C, ECM forests had significantly higher C:N ratios in their mineral soil compared with AM forests. For N cycling, AM forests had significantly higher inorganic N concentrations, and net N mineralization and nitrification rates, indicating faster N cycling rates than in ECM forests, which instead had slower N cycling and relied more on organic sources.

The systematic differences in N cycling between AM and ECM forests may translate into predictable responses of these two types of trees to global change factors such as long-term N deposition and elevated atmospheric carbon dioxide concentration. ECM trees are likely to have advantages in ecosystems where organic N cycling dominates, yet with increasing N deposition, ECM trees may be at a disadvantage compared with AM trees (Thomas *et al.*, 2010; Phillips *et al.*, 2013; Midgley & Phillips, 2014). Furthermore, interactions between soil N availability and mycorrhizal type can help to explain variation in plant responses to elevated CO<sub>2</sub> (Terrer *et al.*, 2016). As such, our findings indicate the feasibility of incorporating mycorrhizal type into Earth system models, which may be useful in predicting forest ecosystem responses and feedbacks to global change.

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## Author contributions

G.L., M.L.M. and D.G. planned and designed the research. G.L. and C.M. collected and analyzed data. G.L., M.L.M. and D.G. wrote the manuscript.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

**Fig. S1** Differences between AM and ECM forests in mineral soil C and N pools when using concentration and stock as metrics.

**Fig. S2** Frequency distribution of response ratio of mineral soil bulk density.

**Fig. S3** Mean differences between AM and ECM forests in response variables when excluding tree species dually colonized by AM and ECM fungi.

**Fig. S4** Climate zone significantly explained variations in response ratios of annual litter input, forest floor C : N ratio, mineral soil C and dissolved organic C concentrations.

**Fig. S5** MAP and soil sampling depth significantly explained variations in response ratios of forest floor C stock, mineral soil C : N ratio and MBC : MBN ratio.

**Fig. S6** DPA significantly explained variations in response ratios of mineral soil C concentration, soil respiration rate and MBN.

**Fig. S7** DPN significantly explained variations in response ratios of mineral soil C, inorganic N  $\text{NH}_4^+$ -N,  $\text{NO}_3^-$ -N,  $\text{N}_{\text{Org}} : \text{N}_{\text{Inorg}}$  ratio, net N mineralization and net nitrification.

**Fig. S8** Mean differences between AM and ECM forests in response variables related to soil microbial biomass.

**Table S1** Detailed information of study sites, data, and references from which data were extracted

**Table S2** Results of meta-analyses based on four different weighting functions

**Table S3** Characteristics of tree species used in this study

**Table S4** The full list of top-ranked models with  $\Delta\text{AIC}_c < 2.00$

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