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META-ANALYSIS

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Foliar nutrient resorption differs between arbuscular mycorrhizal and ectomycorrhizal trees at local and global scales

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Abstract

Aim: Trees associating with ectomycorrhizal (ECM) fungi typically occur in infertile soils and use nutrients more conservatively than arbuscular mycorrhizal (AM) trees. We hypothesized that ECM trees would have greater nutrient resorption (i.e., proportion of nutrients resorbed during leaf senescence) than AM trees.

Location: Global.

Methods: We synthesized nitrogen (N) and phosphorus (P) resorption data from 378 species from sub/tropical, temperate and boreal forests, including 43 studies where ECM and AM trees co-occurred, and conducted a meta-analysis. Additionally, we quantified N resorption in 45 plots varying in ECM-AM tree abundances in the temperate deciduous forests of southern Indiana, USA.

Results: Overall, resorption patterns were driven primarily by mycorrhizal type, climate zone, and to a lesser degree, leaf habit. In the boreal forest, P resorption was 76% greater for ECM than AM trees ($p < .05$). In the sub/tropics, AM trees resorbed 30% more N than ECM trees. At the sites where AM and ECM trees co-occurred, ECM trees resorbed more N in temperate forests (15% greater; $p < .001$) whereas AM trees tended to resorb more N in sub/tropical forests (by 29%; $p = .08$). Besides, deciduous ECM trees resorbed more N (10%) and P (15%) than deciduous AM trees, while evergreen ECM and AM trees did not differ. In the deciduous forests of Indiana, where ECM and AM trees co-occurred, the relative abundance of ECM trees in a plot was positively correlated to plot-scale N resorption ($R^2 = .25$, $p = .001$), indicating greater nutrient conservatism with increasing ECM-dominance.

Main conclusions: Our results indicate that mycorrhizal association – in addition to other factors – is correlated with the degree to which trees recycle nutrients, with the strongest effects occurring for N resorption by temperate deciduous trees.

KEYWORDS
litter decomposition, mycorrhizal associations, nutrient conservation, nutrient retranslocation, nutrient use traits, plant–soil feedbacks

1 | INTRODUCTION

The extent to which plant species promote soil fertility feedbacks – either negative or positive – has been a long-standing question in ecology, and one of growing interest in light of human-caused shifts in species distributions (Hobbie, 1992; van Breemen & Finzi, 1998). Theory predicts that plants occurring in nutrient-poor soils have lower nutrient concentrations in their foliage, and thus, a more conservative nutrient use strategy than species occurring in more fertile sites (Aerts, 1996; Chapman, Langley, Hart, & Koch, 2006; Pastor, Aber, McClaugherty, & Melillo, 1984; Vitousek, 1982). An equally important, but less well-understood strategy for nutrient conservation is nutrient retranslocation or nutrient resorption. Nutrient resorption is the process by which plants withdraw nutrients from senescing tissues prior to abscission (Lü, Freschet, Flynn, & Han, 2012). Resorbed nutrients can account for ~31% of annual plant demand for nitrogen (N) and ~40% for phosphorus (P), and therefore have important consequences for primary productivity in forests (Cleveland et al., 2013). Moreover, nutrient resorption affects leaf litter quality, as litters with high C:nutrient ratios decay slowly or incompletely (Aerts & Chapin, 2000; Güsewell & Gessner, 2009; Hättenschwiler, Coq, Barantal, & Handa, 2011). Consequently, nutrient resorption not only affects the amount of nutrients that plants need to re-acquire from soil each year, but also affects the rate at which nutrients released to soil become available to plants and microbes.

Syntheses of nutrient resorption have investigated the role of leaf habit, climate and soil fertility as drivers of global variation in resorption (Brant & Chen, 2015; Reed, Townsend, Davidson, & Cleveland, 2012; Vergutz, Manzoni, Porporato, Novais, & Jackson, 2012; Yuan & Chen, 2009). While these studies have shed light on global patterns of resorption, there have been few efforts to link resorption dynamics to broader nutrient cycling strategies of plants such as a plant's mycorrhizal association. Ectomycorrhizal (ECM) plants dominate in high-latitude ecosystems where nutrients cycle slowly, whereas arbuscular mycorrhizal (AM) plants dominate in low-latitude ecosystems where nutrients cycle rapidly. Yet, whether ECM and AM plants differ in nutrient resorption – within biomes where both mycorrhizal types can dominate (e.g., temperate forests) or across biomes – has not been tested empirically.

A recent hypothesis suggests that the type of mycorrhizal fungi that plant species associate with can be used as a predictive framework for C and nutrient cycling within and across ecosystems (Phillips, Brzostek, & Midgley, 2013; Wurzburger, Brookshire, McCormack, & Lankau, 2017). ECM trees often possess leaf litters that decay more slowly than litters from AM trees (Cornelissen, Aerts, Cerabolini, Werger, & Van Der Heijden, 2001), which may lead to slower nutrient cycling (Lin, McCormack, Ma, & Guo, 2017) and soils with higher C-N ratios (Averill, Turner, & Finzi, 2014) in ECM-dominated relative to AM-dominated ecosystems. ECM plants also possess the capability to decompose organic matter directly via extracellular enzymes, leading to more conservative N cycling in ECM-dominated soils (Chapman et al., 2006); in contrast, AM plants (which generally show little or no saprotrophic capability) rely on free-living microbes to mineralize nutrients (Lindahl & Tunlid, 2015; Smith & Smith, 2011; Van Der Heijden, Martin, Selosse, & Sanders, 2015), which often results in large N leaching losses from AM-dominated soils (Lin et al., 2017; Phillips et al., 2013). Such differences in C and nutrient use may explain why ECM plants, but not AM plants, sustain high levels of productivity under elevated CO_2 especially in N-limited forests (Terrer, Vicca, Hungate, Phillips, & Prentice, 2016).

Understanding whether mycorrhizal associations can be used an integrative trait for plant nutrient dynamics is essential for improving predictions of the sensitivity of ecosystems to environmental changes and the impact of climate change on the global C cycle (Clemmensen et al., 2013; Phillips et al., 2013; Wurzburger et al., 2017). Here, we combined a global dataset of nutrient concentrations in green and senesced leaves from Vergutz et al. (2012) with information on the plant–mycorrhizal association (ECM or AM) across different leaf habits (deciduous and evergreen) and climatic zones (boreal, temperate and sub/tropics). Given that ECM and AM plants tend to dominate in different biomes that have distinct environmental conditions (Kobe, Lepczyk, & Iyer, 2005; Lambers, Raven, Shaver, & Smith, 2008; Read, 1984), we also synthesized resorption data from studies where both ECM and AM plants co-occurred (Lin et al., 2017). We hypothesized that ECM trees would have higher resorption than AM trees – even after accounting for variation in climate zone (sub/tropics versus temperate) or the type of nutrient limitation (N versus P).

2 | MATERIALS AND METHODS

2.1 | Global dataset of co-occurring and not co-occurring ECM and AM trees

We synthesized N and P concentrations in green and senesced tree leaves from a global dataset (Vergutz et al., 2012), and identified the corresponding mycorrhizal type of each tree species (limiting our analyses to ECM and AM trees only). To determine mycorrhizal associations, we searched the ISI Web of Knowledge for studies that unambiguously reported information on the mycorrhizal type (Brundrett, 2009; Harley & Harley, 1987; Koele, Dickie, Oleksyn, Richardson, & Reich, 2012; Wang & Qiu, 2006; Supporting Information). We defined trees that have been reported to associate with both ECM and AM fungi (e.g., *Salix*, *Populus*, *Eucalyptus* spp.) to be ECM, as many ECM roots have small amounts of AM fungi (Allen et al., 1995; Chen, Brundrett, & Dell, 2000; Wagg, Pautler, Massicotte, & Peterson, 2008) and true 'dual colonists' are uncommon (5% of the total species in this study). When dual colonists were excluded from the analyses, the results were similar (for statistical results see Supporting Information); as such, we decided to include them. Nutrient resorption efficiency (NuR) was calculated as described by Killingbeck (1996); Van Heerwaarden, Toet, & Aerts (2003):

$$\mathrm{NuR}=\frac{(X_{\mathrm{gr}}-X_{\mathrm{sen}})\,*\,\mathrm{MLCF}}{X_{\mathrm{gr}}}\times 100\%$$

where X_{gr} and X_{sen} are nutrient concentrations of green and senesced leaves, respectively. To account for leaf mass loss during foliar senescence, a mass loss correction factor (MLCF, the percentage of leaf mass remaining in senesced leaves compared to green leaves) was applied (Vergutz et al., 2012). Given that species-specific MLCF values were unavailable, we used a mean MLCF value (0.78), following the methods of Vergutz et al. (2012).

We restricted our analysis to woody plants only as non-woody plants associate exclusively with AM fungi; thus, comparisons in nutrient resorption between ECM and AM woody plants are not confounded by plant growth form (Read, 1991; Wang & Qiu, 2006). Because other factors may influence the magnitude of difference between ECM and AM trees in nutrient resorption, we also included key geographic information (latitude, longitude, and study site), climatic parameters (mean annual temperature, MAT; mean annual precipitation,

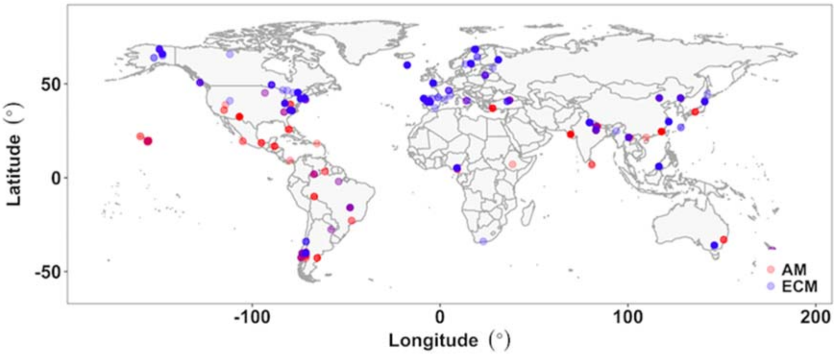

FIGURE 1 Global distribution of the nutrient resorption dataset for ectomycorrhizal (ECM, blue) and arbuscular mycorrhizal (AM, red) tree species. Points become darker when sites overlap in space

MAP) and plant characteristics (leaf habit, i.e., evergreen or deciduous; N-fixing status, i.e., leguminous or non-leguminous tree) from the original datasets into our analysis. Additionally, for each site we retrieved soil nutrient data (total N and labile inorganic P) at a depth of 0–30 cm from the IGBP-DIS dataset [available online from Oak Ridge National Laboratory Distributed Active Archive Center (http://daac.ornl.gov/)] (Xu, Thornton, & Post, 2013). Soil N and labile inorganic P data were extracted from the global gridded soil dataset at 1-degree (Scholes & de Colstoun, 2011) and 0.5-degree (Yang, Post, Thornton, & Jain, 2014) resolution, respectively.

Our dataset contained 655 observations from 378 species taken from 88 studies carried out in 29 countries (Figure 1; Supporting Information Table S1). There were 626 data points for N and 446 for P (Supporting Information Table S1), respectively. The sites spanned a latitude from 43.0° S to 68.5° N, and longitude from 159.7° W to 176.9° E, with MAT ranging from −8.0 to 31.6 °C and MAP between 140 and 5500 mm. We classified these sites into three biomes (boreal, temperate, sub/tropics): the boreal biome included all forests north of 50° N while sites with an absolute latitude between 30° and 50° were classified as temperate forests. As there were relative few data points for ECM trees in the tropics, we grouped tropics and sub-tropics together as sub/tropics sites between 30° S and 30° N to avoid replicate number bias when comparing resorption data across biomes.

2.2 | Global dataset of co-occurring ECM and AM trees only

From our global dataset, we selected studies in which ECM and AM trees co-occurred at the same sites (based on information of study sites, i.e., similar climate, soil type and topography etc.). Given that only 25 individual studies for N and 17 for P from our current global datasets met our criteria, we further searched Web of Science and Google Scholar using the following keywords (a) nitrogen* OR phosphorus* OR nutrient* and (b) resorption* OR retranslocation and (c) woody* OR trees* OR forest*, focusing on studies that included nutrient resorption for both ECM and AM trees at the same site. Eventually, a total of 43 individual studies for N resorption and 31 for P resorption were included in the dataset (Supporting Information Figures S1 and S2, data from the additional 18 sites for N and 14 sites for P were eventually added into the complete global dataset, i.e., including both co-occurring and not co-occurring dataset). We averaged resorption values when data were measured multiple times over the course of a year within a given study site. As with our global dataset, key geographic information (latitude, longitude, and study site) and plant features (leaf habit and N-fixing status) were also incorporated into our co-occurring dataset. For each study site, we then calculated PD_Deciduous and PD_N_fixers as predictors for differences in nutrient resorption between ECM and AM trees in the subsequent meta-analysis. PD_Deciduous was defined by calculating the proportion of deciduous tree species that were ECM ($P\_Deciduous_{ECM}$) and AM ($P\_Deciduous_{AM}$) at each site, and subtracting the latter from the former (i.e., $PD\_Deciduous = P\_Deciduous_{ECM} - P\_Deciduous_{AM}$). PD_N_fixers was calculated according to the similar procedure as we replaced the 'proportion of deciduous' using the 'proportion of N_fixers'. As nutrient resorption depends on nutrient availability, we included soil N and labile inorganic P data from global gridded soil datasets as a potential predictor for the differences in nutrient resorption between ECM and AM trees.

2.3 | Plot-scale study in three temperate hardwood forests

Given that site-level factors can also influence nutrient resorption, we quantified N resorption in ECM and AM trees co-occurring at the plot scale across three temperate deciduous forests in south-central Indiana, USA. Here we did not focus on P resorption because Rosling et al. (2015) have investigated P cycling at these same field sites and found little effect of mycorrhizal type on litter P and inorganic P cycling, suggesting that differences in P resorption between ECM and AM forests should be relatively small in our temperate forests. The three forest sites – Griffy Woods (GW; 39°11′ N, 86°30′ W), Morgan Monroe State Forest (MMSF; 39°19′ N, 86°25′ W) and Lilly-Dickey Woods (LDW; 39°14′ N, 86°13′ W) – differ in species composition, soil type and land-use history (Cheeke et al., 2017), yet all are within 30 km from one another and thus experience the same climate. At each site, 15 permanent research plots (15 m × 15 m) were established that vary in the relative abundance of ECM and AM trees, offering a unique opportunity to explore relationships between mycorrhizal dominance and resorption. For plot-level foliar N, green foliage at each site was sampled in summer 2012 from approximately 20 ECM and 20 AM trees and from the dominant species for a given site. We calculated site-level mean foliar N values for all ECM and AM trees and then scaled down the foliar N concentration from site-level to plot-level based on the percentage of basal area of ECM trees in the plot. For plot-level litter N, litterfall was collected biweekly in autumn 2012 (from September to November) using litter baskets and sorted by mycorrhizal type. We calculated basket-level litter N for each mycorrhizal type within each plot, averaged across all litter collection time points and then scaled up the litter N concentration from basket-level to plot-level based on % ECM trees by basal area for the plot. Both foliar and litter samples were analysed using an elemental combustion system (Costech ECS 4010, Costech Analytical Technologies, Valencia, CA, USA) for total N concentration. Plot-level resorption efficiency was calculated as described above.

2.4 | Statistical analyses

We compared the differences of resorption between ECM and AM trees within each subgroup (i.e., leaf habit or climatic zone) for our global non-co-occurring dataset, using a two-tailed Wilcoxon rank sum test to account for small and uneven group sizes and/or non-normal error distribution. Mixed-effects models (*lmer* function in *lme4* packages) were applied to quantify the combined effects of mycorrhizal types, climate zones and leaf habit on N and P resorption at the global scale. Soil nutrient data (N and labile inorganic P) from global soil gridded datasets had no significant effect on plant nutrient resorption (N and P), even after considering study sites and species as random factors in the mixed-effects models (Supporting Information Figure S3). Therefore, in order to reduce model complexity we did not include soil nutrient data into our model selection processes. Mycorrhizal types, climate zones and leaf habit were treated as fixed factors, and site and species were treated as random factors to account for the non-independence of nutrient resorption within the same site or species. Model comparisons and selection were assessed using corrected Akaike's information criterion (AICc) while the significance of fixed-effects terms was assessed via ANOVA with *F* tests.

We then conducted the meta-analysis for the global co-occurring dataset. Nutrient resorption values of each tree species were used to calculate average values for ECM and AM trees within a given site (or individual study). For each site, the effect size was calculated as the normalized mycorrhizal effects using the log response ratio [LnRR, i.e., ln (ECM/AM), log ratio of mean values for ECM compared with those of AM trees at the same site] in the meta-analysis. A positive LnRR indicated greater values in ECM than AM trees and vice versa. Thus, we had one LnRR value per study site to avoid pseudoreplication. For both N and P resorption, we included all individual studies to assess the overall mean effect size using random-effect models for the meta-analysis with the *metafor* package in R. As potential drivers of the nutrient resorption differences between ECM and AM trees, we then considered climate zones, the difference between deciduous proportion in ECM and in AM trees (PD_Deciduous, i.e., first, deciduous proportion was calculated for ECM and AM trees, respectively, and then the proportional difference between mycorrhizal types was consider as PD_Deciduous), the difference between N-fixer's proportion in ECM and in AM trees (PD_N_fixers, i.e., first, N-fixer's proportion was calculated for ECM and AM trees, respectively, and then the proportional difference between mycorrhizal types was consider as PD_N_fixers), and soil nutrients (N and labile inorganic P) in the specific site as the potential predictors. We applied model selection analysis, based on AICc with *glmulti* packages and averaged the top-ranked models using the MuMIn package (Barton, 2015) to determine which predictors were statistically significant and summarized the relative importance of each predictor. We selected important predictors based on the relative importance as a subgroup factor and applied the subgroup-meta analysis to further check for mycorrhizal effects on nutrient resorption within each subgroup. Given the rarity of AM trees in boreal forests, comparisons between ECM and AM trees were examined for temperate and sub-tropical/tropical (sub/tropical for abbreviation) biomes only.

For the Indiana study, we applied linear regression analysis to detect correlations between N resorption efficiency and percentage of ECM trees at the plot level. We used a linear mixed model with the study site as a random factor to test the effects of the percentage of ECM trees on N resorption efficiency. We also applied linear regression analysis to detect correlations between location/climatic variables (latitude, MAP or MAT) and nutrient resorption (based on the complete global dataset, i.e., including both co-occurring and not co-occurring dataset) for ECM and AM trees, respectively. All statistical analyses were performed using R version 3.0.2 (R Core Team, 2015).

3 | RESULTS

3.1 | Global-scale resorption differences between ECM and AM trees

Globally, ECM deciduous trees had significantly greater N and P resorption than AM deciduous trees, while resorption differences between the mycorrhizal types were not apparent in evergreen trees (Figure 2a,b). AM trees had significantly greater N resorption than ECM trees in the sub/tropics (Figure 2c). P resorption was significantly greater for ECM than AM trees, but only in the boreal forest (Figure 2d). When all data in the global dataset were analysed together, linear mixed models showed that the interaction of mycorrhizal types and climate zones significantly affected the variation in N resorption (Tables 1 and 2). Mycorrhizal type significantly explained variation in P resorption at the global scale (Tables 1 and 2).

3.2 | Global-scale resorption differences between co-occurring ECM and AM trees

When co-occurring in a single site, no significant differences for N and/or P resorption was found between ECM and AM trees across all three biomes (43 individual studies, see Supporting Information Figures S1 and S2). Model selection identified the two most important predictors for resorption differences between the two mycorrhizal types: climate zone and leaf habit (Figure 3a,c). Neither factor was significant for P resorption (Figure 3b,d). Within temperate forests, ECM trees had 15% greater N resorption than AM trees. We found the opposite trend in sub/tropical forests (ECM trees had 29% less resorption than AM trees), although this effect was not statistically significant ($p = .08$).

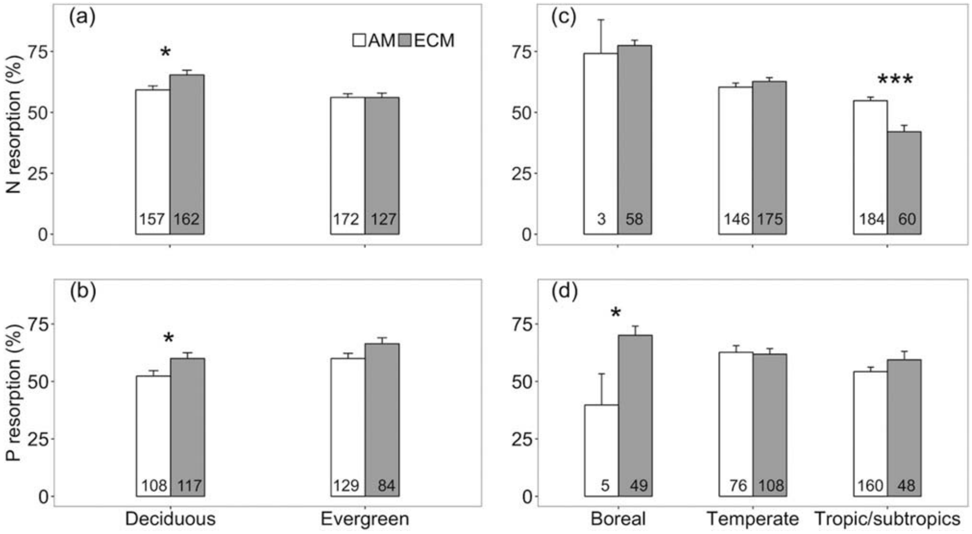

FIGURE 2 Means (± 1 *SE*) of resorption of nitrogen (N, a and c) and phosphorus (P, b and d) for ectomycorrhizal (ECM, grey) and arbuscular mycorrhizal (AM, white) trees across different plant leaf habits (deciduous and evergreen) and climate regions (boreal, temperate and sub/tropics). The number of observations is given within each bar. Statistically significant differences between the two mycorrhizal types are shown with asterisks (*** if $p < .001$, * if $p < .05$) according to the two-tailed Wilcoxon rank sum test. Overall statistical effects of mycorrhizal types, leaf habit and climate zones are given in Tables 1 and 2

3.3 | Case study in temperate deciduous forest

For the three forest sites in Indiana, N resorption increased with increasing dominance of ECM trees at the plot scale. Among the sites, the correlation was stronger at the Morgan Monroe State Forest ($R^2 = .39$, $p = .007$), and Lilly-Dickey Woods ($R^2 = .18$, $p = .07$) than at Griffy Woods ($R^2 = .00$, $p = .47$). When analysing the data from the three sites together, we found a significant positive correlation between N resorption and the dominance of ECM trees (Figure 4, $R^2 = .25$, $p = .001$).

TABLE 1 Model selection for nitrogen (N) resorption and phosphorus (P) resorption at the global scale; only the top five models (1 to 5) are shown

Resorption	Model	Fixed terms	K	LL	AICc	ΔAIC	Weight
N	1	ABCDE	12	−2,531.2	5,086.9	0.00	0.60
	2	ABCDEF	13	−2,531.0	5,088.7	1.83	0.24
	3	ABCDEFG	15	−2,529.8	5,090. 5	3.62	0.10
	4	ABCEF	11	−2,535.8	5,094.1	7.27	0.02
	5	ABCE	10	−2,537.0	5,094.3	7.47	0.01
P	1	C	5	−1,805.1	3,620.3	0.00	0.20
	2	~1	4	−1,806.5	3,621.0	0.76	0.14
	3	BC	6	−1,804.4	3,621.1	0.81	0.13
	4	B	5	−1,806.0	3,622.1	1.79	0.08
	5	AB	7	−1,804.1	3,622.5	2.27	0.06

Note. Models were sorted by increasing values of second-order Akaike's information criterion (AICc, AIC corrected for small sample sizes) and ΔAIC, which represents the difference in AICc between the current and the most appropriate model. Fixed terms definitions: Climate zones (A), leaf habit (B), mycorrhizal types (C); interaction climate zones:leaf habit (D), interaction climate zones:mycorrhizal types (E), interaction mycorrhizal types:leaf habit (F) and interaction climate zones:leaf habit: mycorrhizal types (G). Other variables are K = the number of parameter estimates; LL = log-likelihood; weight = conditional model probability or Akaike weight (model likelihood of model 1 divided by the sum of model likelihoods).

3.4 | Climatic influence on nutrient resorption for ECM and AM trees

For both ECM and AM trees, soil nutrients (N and labile inorganic P from global soil gridded dataset) had no significant correlation with plant nutrient resorption (N and P) (Supporting Information Figure S3). For ECM trees, N and P resorption were positively correlated with absolute latitude while negatively correlated with MAT and MAP. However, N and P resorption for AM trees had weak correlations with latitude or climatic variation at the global scale (Supporting Information Figure S4, Table 3).

4 | DISCUSSION

We found partial support for our hypothesis that ECM trees have higher nutrient resorption compared with AM trees, as resorption depended on nutrient type, climate zone and leaf habit. At the global scale, ECM trees exhibited greater P (but not N) resorption relative to

TABLE 2 ANOVA table of the corrected Akaike's information criterion (AICc)-best model (model 1 in Table 1) for nitrogen (N) resorption and phosphorus (P) resorption at the global scale

Resorption	Fixed term	Num d.f.	Den d.f.	*F*	*p*
N	Mycorrhizal types (Mt)	1	348	3.40	.07
	Climate zones (Cz)	2	240	41.00	< .001
	Leaf habit (Lh)	1	348	5.94	.02
	Cz: Lh	2	240	1.47	.231
	Mt:Cz	2	240	9.59	< .001
P	Mycorrhizal types (Mt)	1	271	11.00	.001

Den. d.f. = denominator degrees of freedom of the fixed term;
MAP = mean annual precipitation; MAT = mean annual temperature;
Num. d.f. = numerator degrees of freedom of the fixed term.

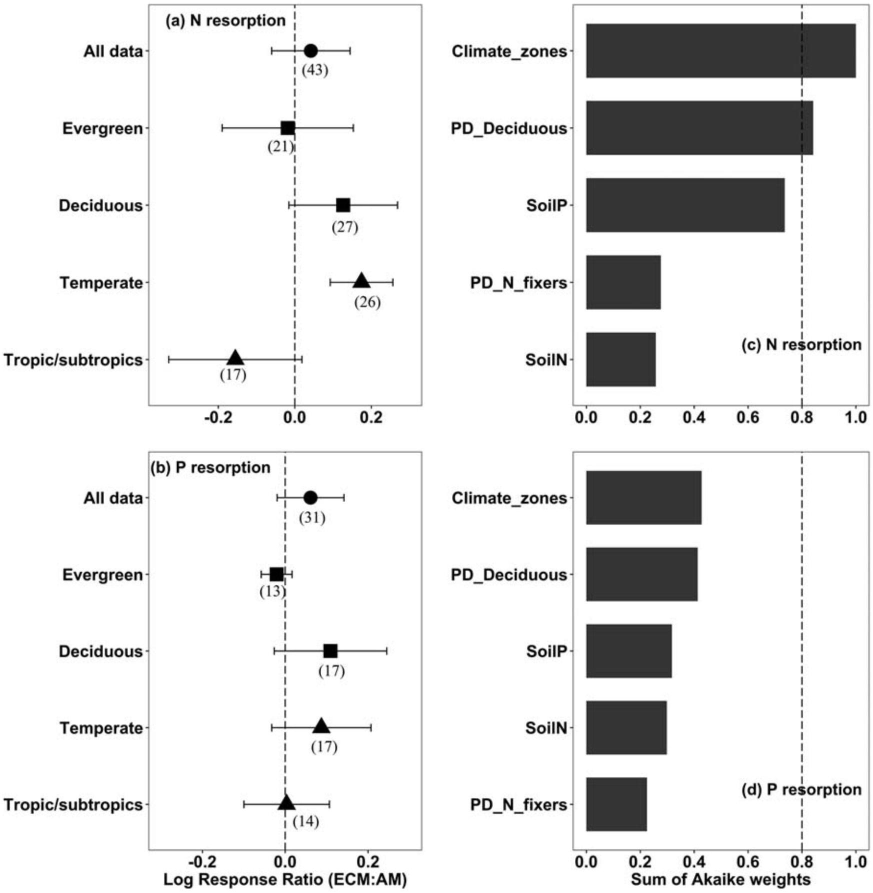

FIGURE 3 Mean difference of nitrogen (N, a) and phosphorus (P, b) resorption between ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) trees co-occurring at the same site. Values are given for all studies (circles), evergreen or deciduous trees only (squares) and temperate trees only or sub/tropical trees only (triangles). A value of 0 indicates no difference between ECM and AM trees and positive values represent a greater value for ECM trees. Error bars displayed for mean values indicate 95% bootstrap confidence intervals. The sample size for each variable is shown in parentheses. Model-average importance of the predictors of resorption differences between AM and ECM trees is shown for N (c) and P (d). The importance is based on the sum of Akaike weights derived from the model selection using Akaike's information criterion corrected for small samples (AICc). The cut-off (dashed line) is set at 0.8 in order to differentiate among the most important predictors. PD_Deciduous = the proportional difference between deciduous proportion in ECM and in AM trees; PD_N_fixers = the proportional difference between N-fixer's proportion in ECM and in AM trees in a study site

AM trees. At sites where both AM and ECM trees co-occurred, ECM trees resorbed more N (in temperate forests) whereas AM trees tended to resorb more N (in sub/tropical forests). Notably, this pattern was supported by our analysis of N resorption across a gradient of relative abundances of ECM and AM trees in three temperate forests, with plot-level N resorption increasing with increasing plot dominance of ECM trees. These results suggest that while ECM trees may not always be more conservative in nutrient use than AM trees, mycorrhizal type can explain resorption patterns in some ecosystems, such as N resorption in deciduous trees of the temperate zone.

4.1 | Mycorrhizal differences in high latitude ecosystems

The resorption of nutrients prior to leaf senescence has long been hypothesized to be an effective strategy for plants to compete for nutrients in low fertility environments (Aerts, 1999). Given that ECM trees often occur in soils where much of the soil N exists in organic forms (Corrales, Mangan, Turner, & Dalling, 2016; Phillips et al., 2013; Waring, Adams, Branco, & Powers, 2016), our finding that ECM trees resorb more N than AM trees at high latitudes supports this hypothesis. An important question then is whether resorption differences between ECM and AM trees are correlated with mycorrhizal fungi *per se*, or from variation in soil properties (e.g., soil C:N; Averill et al., 2014) induced by the different mycorrhizal types. Recent studies have reported that mycorrhizal fungi influence soil organic matter through their enzyme activities, turnover or effects on other decomposers (Clemmensen et al., 2013; Orwin, Kirschbaum, St John, & Dickie, 2011), but an equally plausible explanation for observed differences in soil C:N relates to variations in leaf litter. Our results indicate that aboveground processes, such as nutrient resorption and the resulting litter inputs, may be equally important in driving mycorrhiza-mediated differentiation of soil C dynamics.

Greater N resorption can lead to low N availability in soil, as N-poor litter can limit microbial decomposition and lead to the accumulation of detritus at the soil surface. However, ECM fungi, unlike AM

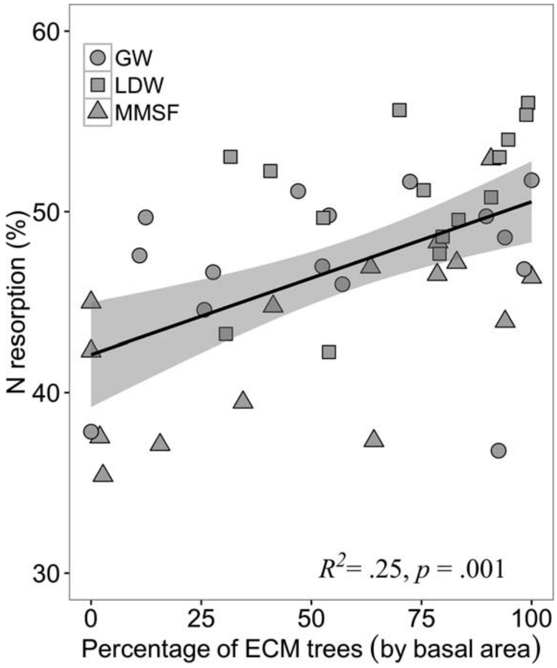

FIGURE 4 Plot-level N resorption efficiency for 45 plots (15 m^2) that represent a gradient of % ectomycorrhizal (ECM) trees (by basal area) across three temperate hardwood forest sites (GW = Griffy Woods; LDW = Lilly-Dickey Woods; MMSF = Morgan Monroe State Forest)

fungi, have the capability to take up large amounts of organic N (Hodge & Storer, 2015; Read & Perez-Moreno, 2003; Wurzburger & Brookshire, 2017). As such, the mycorrhizae themselves may not drive resorption directly, but rather influence nutrient use by minimizing the negative effects to trees of having low-quality, slow-cycling litter. Future studies that explicitly link tree mycorrhizal status with soil nutrient status are essential for further advances in this area.

To what degree do the C costs of nutrient resorption relate to the C costs of nutrient acquisition from the soil? Trees that expend substantial amounts of C to resorb nutrients presumably need fewer nutrients from the soil, and thus may allocate less C belowground. However, as greater N resorption typically results in N-poor litter and the accumulation of detritus at the soil surface, greater belowground C allocation may be needed to mine nutrients from soil organic matter. Our results suggest that the latter mechanism may be more common, as the trees with the greatest nutrient resorption (ECM trees) are known to allocate more C belowground to support their mycorrhizal symbionts (Read & Perez-Moreno, 2003). This would indicate that the C costs of nutrient resorption may be small relative to the costs of nutrient uptake from the soil, and that a tree's nutrient use strategies may be coordinated (e.g., aboveground and belowground conservatism). Notably, previous nutrient resorption studies mainly focus on leaves (Brant & Chen, 2015), yet given the relatively higher turnover rates in both fine roots and mycelia, belowground nutrient resorption may have stronger effects on plant nutrient budget and organic matter dynamics. Thus, future studies that investigate nutrient resorption dynamics from fine roots and mycelia and the links between belowground C allocation and nutrient resorption are critically needed.

TABLE 3 Correlations between plant nitrogen (NuR_N) or phosphorus (NuR_P) resorption and location/climate (see Figure S4) for ectomycorrhizal (ECM) and arbuscular (AM) mycorrhizal trees

	Myco	d.f.	Latitude		MAT		MAP	
			Slope	R^2	Slope	R^2	Slope	R^2
NuR_N	ECM	270	0.82	.28***	−1.76	.31***	−0.009	.16***
	AM	323	0.33	.03***	−0.28	.00$^{n.s.}$	−0.002	.02*
NuR_P	ECM	179	0.51	.14***	−0.90	.10***	−0.006	.09***
	AM	226	−0.12	.00$^{n.s.}$	−0.70	.03**	0.005	.02*

****Note*. Myco, representing mycorrhizal types. Latitude (absolute value) variation, climatic variations (MAT = mean annual temperature; MAP = mean annual precipitation) across the global scale; d.f. = degrees of freedom. *** if $p < 0.001$, ** if $p < .01$, * if $p < .05$ and n.s. = non-significant for the preceding regression coefficient.

Temperate forests are arguably the most logical place to compare resorption between ECM and AM trees given that both types frequently co-occur and either can dominate (Phillips et al., 2013), unlike biomes where there is dominance by a single mycorrhizal type (AM trees in the tropics, ECM trees in the boreal forest). We found that N resorption increased with increasing dominance of ECM trees at the plot scale in Indiana deciduous forests, consistent with the results of our cross-biome meta-analysis. Increases in ECM dominance have been associated with reduced nitrification rates and greater N retention (Lin et al., 2017; Midgley & Phillips, 2014; Phillips et al., 2013). It is intuitive for tree species that inhibit N losses to have high N resorption, as both strategies are adaptations to low N availability. Most temperate forests are N limited (LeBauer & Treseder, 2008; Vitousek & Howarth, 1991), and thus greater N resorption or reduced N losses of ECM trees may enable them to be competitive in low nutrient environments. Thus, the greater resorption of N by ECM trees in temperate forests could lead to greater ECM dominance in temperate forests over time as nutrient limitation becomes exacerbated by rising CO_2 in the atmosphere (Terrer et al., 2016).

Collectively, our results complement Read's theory that the global distribution of ECM and AM forests are driven by climate effects on organic matter quantity and nutrient availability (Read, 1991) by suggesting that differences in nutrient resorption may be vital to reinforcing nutrient cycling syndromes in ECM- and AM-dominated stands. Nevertheless, future studies are needed to test this hypothesis, especially those that examine whether the C costs of nutrient acquisition are directly linked to resorption efficiency patterns in temperate and boreal forests, and whether such processes shape competitive interactions among ECM and AM tree species.

4.2 | Mycorrhizal associations in sub-tropical/tropical forests

We found lower N resorption for ECM versus AM trees at low latitude, consistent with the findings of Chuyong, Newbery, and Songwe (2000), who reported that N resorption was nearly twofold lower in ECM plants than non-ectomycorrhizal (mainly AM) plants in a central African tropical forest. Nutrient resorption may be less consequential for nutrient acquisition in sub/tropical forests, where warm wet climates ensure rapid litter decay (Bothwell, Selmants, Giardina, & Litton, 2014), regardless of litter quality. Further, tropical ECM trees, which typically form monodominant stands, might have lesser need to resorb nutrients if they can access N via a common mycelial network (He, Critchley, & Bledsoe, 2003; Selosse, Richard, He, & Simard, 2006). Supporting this, Soudzilovskaia et al. (2015) showed that ECM fungal colonization had high infection rate for roots at sites in tropical forests of Southeast Asia and central Amazonia. Another piece of evidence comes from Chuyong et al. (2000), who showed that ECM trees, compared to AM trees, had stronger nutrient recapturing capability owing to their greater allocation to absorptive fine roots and the ECM hyphal network in the upper portion of the soil (Chuyong et al., 2000).

Analyses of natural abundance N isotope ratios can provide information on mycorrhizal functional roles in N cycling (Nave et al., 2013). ECM plants are generally ^{15}N-depleted relative to AM plants (Craine et al., 2009; Schulze, Chapin, & Gebauer, 1994) as ECM fungi deliver depleted ^{15}N to host plants (reviewed in Hobbie & Högberg, 2012). However, Mayor et al. (2015) showed that such variation in isotopic patterns between ECM and AM trees may be biome-specific, suggesting a distinct functional role of ECM associations in the sub/tropical ECM forests. Our study also identified similar latitudinal discrepancies and continued research in low-latitude ECM forests is needed to expand mechanistic and biogeographic understanding of mycorrhizal functional roles in ecosystem nutrient economies (Phillips et al., 2013).

4.3 | Climatic influence on resorption for ECM and AM trees

Latitude and climatic conditions (MAP or MAT) explained much of the variability in global nutrient resorption for ECM but not for AM trees (Supporting Information Figure S4). The positive relationships between resorption (both in N and P) and absolute latitude for ECM trees were probably due to the relatively high resorption and the predominance of ECM trees in cold and high-latitude areas. Previous studies also showed that ECM trees, such as *Betula pubescens* at four different sites in Sweden (Nordell & Karlsson, 1995) and *Quercus variabilis* in 16 provinces in China (Sun et al., 2016), had higher nutrient resorption at higher latitudes. Moreover, Oleksyn, Reich, Zytkowiak, Karolewski, and Tjoelker (2003) found that even at the same site, ECM trees (*Pinus sylvestris*) from high latitudes still had higher nutrient resorption (both in N and P) than genotypes from low latitudes, suggesting that a more conservative nutrient use strategy for ECM trees may be a well-conserved adaptation to relatively harsh (i.e., cold and wet) climates.

ECM trees in boreal forests had significantly greater P resorption (Supporting Information Figure S4); this could explain the negative relationship between P resorption and climate observed in Vergutz et al. (2012) and our study. Vergutz et al. (2012) reported that P resorption increased with increasing MAP and MAT, while the opposite trend was found by Yuan and Chen (2009). By separating plants into different mycorrhizal types, our results are useful in reconciling such results. The dataset from Yuan and Chen (2009) had fewer data points for ECM plants in cold regions compared to the study by Vergutz et al. (2012). Specifically, for regions with $\text{MAP} < 500$ mm or $\text{MAT} < 5$ °C, there were only four or six data points, respectively, in the dataset from Yuan and Chen (2009) whereas there were 21 or 37 data points for ECM plants in Vergutz et al. (2012). Therefore, without considering mycorrhizal types, investigating how P resorption efficiency varies across global environmental gradients can lead to inconclusive interpretations.

We found largely congruent resorption of N and P in temperate forests, but relatively high P versus N resorption in sub/tropical forests (Figure 2c,d). Similarly, McGroddy, Daufresne, and Hedin (2004) reported that litter N:P ratios remain roughly similar to the foliar N:P ratios in high latitudes but increase dramatically relative to foliage at low latitudes. Recently, Reed et al. (2012) reported that N:P resorption ratios are higher in high-latitude areas and lower in low-latitude areas. Consistent with those findings, we found greater P versus N resorption in the sub/tropical ecosystems, indicating the potential for P limitation at low latitudes. Moreover, this trend of greater P resorption in the sub/tropics was mainly driven by ECM but not AM trees (Figure 2c,d). Taken together, our results highlight the importance of considering mycorrhizal types when investigating latitudinal patterns of plant stoichiometry and nutrient cycling.

4.4 | Potential biases of the datasets

The main limitations of our dataset are spatial and phylogenetic distribution biases. First, we acknowledged that AM trees are too few in boreal forests to test our hypothesis at the global scale. In addition, previous work pointed out a strong phylogenetic bias in the mycorrhizal literature as more than 80% of the studies (up to 2008) on ECM plants were based on Pinaceae and Fagaceae (Dickie & Moyersoen, 2008). In our dataset, the major four families of ECM trees were Fagaceae, Pinaceae, Betulaceae and Salicaceae, making up approximately 35, 23, 11 and 9% of all species in our dataset, respectively. ECM trees from other 23 families accounted for 22% of the total species. Future investigations across a wide phylogenetic range will allow partitioning effects of phylogenetic similarity and mycorrhizal types. Lastly, it is important to note that the term ‘nutrient resorption’ in our study is largely limited to N and P due to data availability. Other mineral elements, such as K, Ca and Mg, might also play crucial roles in ecological function and processes (Campo, Maass, Jaramillo, & Yrízar, 2000; Huntington, 2000; Tripler, Kaushal, Likens, & Todd Walter, 2006). Comparison between co-existing ECM and AM trees for nutrient resorption of elements beyond N and P is worth further investigation.

5 | CONCLUSION

Collectively, our results indicate that trees with different mycorrhizal associations show different nutrient resorption patterns across global, biome and local scales. The relative abundance of mycorrhizal types within and among ecosystems is fluctuating at geologic and anthropogenic time-scales, with such vegetation shifts intensified under climatic and land-use changes (Dickie, Koele, Blum, Gleason, & McGlone, 2014). Our results suggest that if the relative abundance of ECM trees increases, ecosystem N recycling may increase in temperate forests given that ECM trees resorb more foliar N than do co-occurring AM trees. Meanwhile, an opposite pattern may play out in tropical forests. Further, our results indicate that the mycorrhizal effects are unlikely to be a tree species effect, as the plots across the 45-plot ‘mycorrhizal gradient’ in our Indiana forest case study contained six to eight canopy-dominant ECM and AM tree species. Our observation that ECM trees on average resorb more nutrients than AM trees may also help explain why AM litter generally decomposes more rapidly than ECM litter (Cornelissen et al., 2001; Lin et al., 2017; Midgley, Brzostek, & Phillips, 2015) despite no apparent differences in foliar chemistry (Koele et al., 2012). Environmental variables have a stronger effect on nutrient resorption for ECM trees than that for AM trees, suggesting that the impacts of environmental changes on a forest ecosystem would depend on the types of mycorrhizal association. Taken together, the results of our study emphasize the utility of considering mycorrhizal type as an integrative trait to better understand biogeochemical cycling from a geographic perspective.

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AUTHOR CONTRIBUTIONS

HZ, XL, RP and HH conceived and designed the experiments. HZ, AK and RP synthesized the data, performed the experiments and analysed the data. All the authors wrote the manuscript together.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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