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Ectomycorrhizal impacts on plant nitrogen nutrition: emerging isotopic patterns, latitudinal variation, and hidden mechanisms

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Ectomycorrhizal impacts on plant nitrogen nutrition: emerging isotopic patterns, latitudinal variation, and hidden mechanisms

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ABSTRACT

Ectomycorrhizal (EcM) mediated nitrogen (N) acquisition is one main strategy used by terrestrial plants to facilitate growth. Measurements of natural abundance nitrogen isotope ratios (denoted as $\delta^{15}\text{N}$ relative to a standard) increasingly serve as integrative proxies for mycorrhiza-mediated N acquisition due to biological fractionation processes that alter $^{15}\text{N}:^{14}\text{N}$ ratios. Current understanding of these processes is based on studies from high latitude ecosystems where plant productivity is largely limited by N availability. Much less is known about the cause and utility of ecosystem $\delta^{15}\text{N}$ patterns in the tropics. Using structural equation models, model selection, and isotope mass balance we assessed relationships among co-occurring soil, mycorrhizal plants, and fungal N pools measured from 40 high and 9 low latitude ecosystems. At low latitudes ^{15}N -enrichment caused ecosystem components to significantly deviate from those in higher latitudes. Collectively, $\delta^{15}\text{N}$ patterns suggested reduced N-dependency and unique sources of EcM ^{15}N -enrichment under conditions of high N availability typical of the tropics. Understanding the role of mycorrhizae in global N cycles will require reevaluation of high latitude perspectives on fractionation sources that structure ecosystem $\delta^{15}\text{N}$ patterns, as well as better integration of EcM function with biogeochemical theories pertaining to climate-nutrient cycling relationships.

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INTRODUCTION

Soil N availability limits plant growth in many high latitude ecosystems due to the slow accumulation of biologically fixed N during ecosystem development (Chapin *et al.* 1986). In low latitude forests, phosphorus (P) is generally more limiting due to higher rates of biological N fixation and losses of P to soil weathering processes (Hedin *et al.* 2003; Menge *et al.* 2012). Arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) associations are two main types of mycorrhizae that play integral roles in helping plants meet mineral nutrient demands (Smith & Read 2008; Smith & Smith 2011). In general, most plants associate with AM fungi in the ancient, monophyletic phylum Glomeromycota, particularly tropical forest trees and herbaceous species. Ectomycorrhizal plants, while taxonomically more rare, are common within boreal and temperate forests (e.g. Pinaceae, Fagaceae, Betulaceae, Nothofagaceae, and others) (Tedersoo & Smith 2013), but also in several ecologically important tropical trees from the Amherstieae and Mirbelieae of Fabaceae, Dipterocarpaceae, Leptospermoideae of Myrtaceae, and others (Brundrett 2009). Ectomycorrhizal fungi include a diverse assemblage of families and genera of the Basidiomycota, and to a lesser extent Ascomycota (Smith & Read 2008).

Although both of these mycorrhizal types confer nutritive and other benefits to their host plants, they are functionally distinct due to differences in mode of interaction, hyphal morphology, cellular biochemistry, enzymatic capacity, and carbon costs to host plants (Taylor & Alexander 2005; Smith & Read 2008). For instance, EcM fungi are thought to provide plants with greater access to organic N bound in chitin, proteins, and tannins (Lucas & Casper 2008; Talbot *et al.* 2008; Wurzbarger & Hendrick 2009), whereas AM fungi predominantly access mineral or amino acid N due to very limited hydrolytic and oxidative capacity (Courty *et al.* 2010; Smith & Smith 2011). Because EcM plant litter and fungal residues are generally more refractory or gradually accumulate in soil, these two mycorrhizal types also differ in their

influence on carbon and mineral nutrient cycling (Cornelissen *et al.* 2001; Langley & Hungate 2003; Read & Perez-Moreno 2003; Phillips & Fahey 2006; Orwin *et al.* 2011; Clemmensen *et al.* 2013; Phillips *et al.* 2013; Averill *et al.* 2014).

There are few tools to evaluate mycorrhizal roles in N cycling *in situ*. Analyses of natural abundance N isotope ratios (^{15}N : ^{14}N expressed as $\delta^{15}\text{N}$ relative to standard), as an integrator of N-cycling, can provide a glimpse into mycorrhizal functional ecology within soil profiles and across biomes (Lindahl *et al.* 2007; Courty *et al.* 2011; Tedersoo *et al.* 2012b; Nave *et al.* 2013). This is possible because the isotopic imprint of the EcM symbiosis is manifest in both plant and fungal associates. Ectomycorrhizal plants are generally ^{15}N -depleted relative to AM or non-mycorrhizal plants (Schulze *et al.* 1994; Michelsen *et al.* 1998; Craine *et al.* 2009) and EcM fungi typically are ^{15}N -enriched relative to co-occurring saprotrophic fungi (reviewed in Mayor *et al.* 2009). Such observations suggest that relative (i.e. plant *and* fungal) $\delta^{15}\text{N}$ values provide a time-integrated, non-destructive tracer of not only soil N sources, but also the relative demand for EcM derived N (reviewed in Hobbie & Högberg 2012). This is because the relative N isotope concentrations in EcM plant and fungal symbionts are currently understood to result from the delivery of ^{15}N -depleted N transfer compounds to host plants and subsequent retention of ^{15}N -enriched N by fungi (Hobbie & Colpaert 2003). As a result of these apparently linked sources of ^{15}N -fractionation, one can estimate the proportion of plant N derived from EcM fungi across successional chronosequences, natural gradients, and under fertilization or N deposition regimes (Hobbie *et al.* 2005; Averill & Finzi 2011; Högberg *et al.* 2011; Mayor *et al.* 2012; Nave *et al.* 2013).

These ^{15}N mass balance frameworks were developed from a few intensively studied high latitude tundra and boreal ecosystems where plant productivity is predominantly N-limited (Hobbie & Hobbie 2008). It remains unknown if the same plant and fungal $\delta^{15}\text{N}$ patterns are present in lower latitude subtropical and tropical (hereafter sub/tropical) ecosystems where EcM

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3 99 trees are growing under conditions of more rapid N cycling (Kuyper 2012). Weathered soils,
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5 100 humid conditions, and low available P often result in high N losses and concomitantly ¹⁵N-
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7 101 enriched soils (Houlton *et al.* 2006; Brookshire *et al.* 2012). Thus, conditions of high N
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9 102 availability, combined with potentially enriched background $\delta^{15}\text{N}$, may obscure the formation of
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11 103 distinct $\delta^{15}\text{N}$ patterns and their subsequent utility in studying tropical EcM associations. This gap
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13 104 in understanding is particularly acute since 80% of EcM ecology literature occurred in only two
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15 105 predominantly high latitude plant groups (i.e. Pinaceae and Fagales; Dickie & Moyersoen 2008;
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17 106 Alexander & Selosse 2009).

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21 107 Evidence from EcM plant species in the tropics has suggested that relative ¹⁵N:¹⁴N ratios
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23 108 among EcM and AM trees are inconsistent with those described from high latitude forests. For
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25 109 instance, data from the Afro-tropics suggested that $\delta^{15}\text{N}$ values in some EcM trees are
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27 110 equivalent to or even higher than those of co-occurring AM trees (Högberg 1990; Högberg &
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29 111 Alexander 1995; Cerling *et al.* 2004; Tedersoo *et al.* 2012b). In addition, EcM plants in
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31 112 temperate forests subjected to high N deposition are occasionally ¹⁵N-enriched relative to co-
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33 113 occurring AM plants, suggesting that N saturation can obscure the EcM signal (Schulze *et al.*
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35 114 1994; Pardo *et al.* 2006). Such increases in EcM plant $\delta^{15}\text{N}$ values following N additions have
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37 115 been attributed to functional variation in associated EcM fungal taxa or to the bypassing of EcM
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39 116 mediated N uptake (Lilleskov *et al.* 2002, 2011; Högberg *et al.* 2011).

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43 117 Evidence also suggests that some tropical trees may rely on EcM-mediated N
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45 118 acquisition, particularly in monodominant forests with high soil organic matter and low N
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47 119 availability (Torti *et al.* 2001; Henkel *et al.* 2002; Brearley *et al.* 2003; Mayor & Henkel 2006;
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49 120 Newbery *et al.* 2006). Additionally, $\delta^{15}\text{N}$ values from some tropical fungi were consistently ¹⁵N-
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51 121 enriched relative to sympatric saprotrophic fungi independent of climate, geography, or
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53 122 substratum (Mayor *et al.* 2009). Thus, the observation of consistent ¹⁵N-enrichment of tropical
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3 123 EcM fungi, but not necessarily corresponding ^{15}N -depletion of tropical EcM plants, calls into
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5 124 question the current paradigm explicitly linking the two patterns.
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7 125 Until now, the paucity of datasets that included co-occurring soil, fungal, and plant $\delta^{15}\text{N}$
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9 126 values from low latitude ecosystems prevented full assessment of how changes to host-
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11 127 symbiont nutrient limitations influence $\delta^{15}\text{N}$ patterns across biomes. Here we seek to overcome
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13 128 this limitation by assessing if there are globally unifying or deviating trends in EcM plant N
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15 129 dynamics. To do this, we assembled several published and original datasets containing $\delta^{15}\text{N}$
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17 130 values representing the major co-occurring ecosystem components involved in N cycling: soils,
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19 131 sporocarps of EcM and saprotrophic fungi, and foliage from both EcM and AM plants. To
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21 132 address both direct and indirect causes of ecosystem $\delta^{15}\text{N}$ patterns at large scales, we
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23 133 compared structural equation models (SEM) to examine hypothetical causal pathways among
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25 134 ecosystem components (Grace *et al.* 2010; Lam & Maguire 2012). For instance, incorporation of
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27 135 indirect climatic influences over soil $\delta^{15}\text{N}$ and N concentrations, and the possibility of distinctive
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29 136 patterns in N cycling among AM and EcM systems, is made possible by comparing competing
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31 137 path diagrams in SEM. These data permit a balanced examination of relative ecosystem $\delta^{15}\text{N}$
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33 138 patterns so that: (1) the influence of EcM fungi over plant $\delta^{15}\text{N}$ patterns may be assessed in an
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35 139 inclusive global context; (2) any alternative pathways of causality can potentially be elucidated;
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37 140 and, (3) estimates of the importance of EcM fungi for the N nutrition of host plants may be
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39 141 placed within a context of biogeochemical predictions regarding plant nutrient limitations.
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41 142 Linking plant nutrient demands with the functional role of distinct mycorrhizal types has been
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43 143 highlighted as a research priority in ecosystem science (Phillips *et al.* 2013) and examining
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45 144 latitudinal variation in ecosystem $\delta^{15}\text{N}$ patterns offers a unique opportunity to assess the role of
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47 145 EcM in N cycling (Courty *et al.* 2010).
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MATERIALS AND METHODS

We compiled data from studies published up through July 2013 that included soil, plant, and fungal $\delta^{15}\text{N}$ along with similar original data obtained by the authors. Original samples were collected by the authors and silica dried in the field prior to transporting to one of several laboratories for isotopic analyses. To evaluate general trends across disparate studies, data were aggregated for sites <100 km distant. Compiling site-based variability in this manner permitted comparison at the global scale without potentially confounding effects of spatial autocorrelation. In some cases this meant averaging among sites that differed slightly in underlying parent material, elevation, or plant taxa (i.e. Fortuna Reserve, Panama, this study; Oregon, USA in Hobbie *et al.*, 2012; New Hampshire, USA in Colin & Averill, 2011). Due to floristic heterogeneity and/or sampling limitations, some sites contained only one dominant EcM plant species whereas others contained $\delta^{15}\text{N}$ values from many species (>8; see Table S1, S2 in Supporting Information). The number of sampled fungal taxa representing different trophic groups also varied by site (e.g. 2 to >50). In total, we averaged data from 47 sites taken from 22 published and 7 original studies (Fig. 1).

Mean annual temperature (MAT) and precipitation (MAP), along with geographical positions (lat./long.), were taken from the published studies, studies referred to therein, obtained on site, or extracted from a global climate database (New *et al.* 2002). Statistical analyses and graphical representations used absolute values of latitude. Stand age, elevation, and soil N concentrations ([N] mg g⁻¹) were also extracted if available. Owing to the varying methods across studies, soil [N] was measured from samples of varying layers or depths (0 to 5, and 5 to 10, 12, or 15 cm). When separate organic and mineral [N] were reported, these values were averaged over total core depths and are hereafter referred to as surface soil [N]. Similarly, “organic” and “mineral” layers may not necessarily coincide with strict definitions of C content

but such divisions were retained for $\delta^{15}\text{N}$ values to address presumed ^{15}N -enrichment with depth. Soil C content was infrequently reported, preventing use of C/N ratios in subsequent analyses. Several studies had missing values for one or more ecosystem components (e.g. saprotrophic fungi or AM plant $\delta^{15}\text{N}$ values). In such instances, the original authors were asked for additional metadata and to assess if serially published studies contained duplicated sample values. Site metadata and references are given in [Table S1](#). Taxonomic identities of organisms and geographic locations of original soil, fungal, and plant $\delta^{15}\text{N}$ values are included in [Table S2](#). Overall, sites varied widely in latitude (-13 to 74 °N), altitude (5 to 2780 m a.s.l.), mean annual precipitation (183 to 7032 mm yr⁻¹), and mean annual temperature (-9.8 to 26 °C). Surface soil N concentrations ([N]) ranged from 0.6 to 35.7 mg g⁻¹ and soil $\delta^{15}\text{N}$ values ranged from -4.6 to 8.7 ‰.

The included datasets have certain limitations. First, most studies involving ^{15}N analyses of both plants and fungi have been undertaken in arctic, boreal, and temperate ecosystems of the Northern Hemisphere, while studies in tropical regions are rare, and data from temperate forests of the Southern Hemisphere nearly non-existent. Second, data for other potentially important factors influencing the pathways of causality put forth in SEM, such as N and P availability, mineral N $\delta^{15}\text{N}$ values, or soil clay content, were lacking for most sites and therefore not included.

Statistical analyses

Graphical assessments and univariate linear regressions were performed in JMP[®] Pro 10.0.0 (SAS Institute Inc., Cary, NC). Generalized least squared model selections were conducted using the *nlme* package version 3.1-104 (Pinheiro *et al.* 2011) in the R statistical environment (R Development Core Team 2012). Structural equation modeling was performed using Amos Version 7.0 (SPSS, Chicago, IL). Explanatory variables were compared to normal distributions

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3 198 and outliers were assessed using Goodness of Fit tests. Two extreme outliers were
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5 199 subsequently removed from the *soil [N]* data that were heavily influenced by anthropogenic N
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7 200 deposition (*soil [N]* = 35.7, mg/g) and a single high $\delta^{15}\text{N}$ value in mineral soil from Gabon.
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10 201 Structural equation models are similar to many widely accepted statistical methods such
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12 202 as regression and path analysis, but are better suited to test assumptions regarding pathways
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14 203 (both direct and indirect) of causality among multiple ecosystem components in a theoretical
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16 204 context (Grace *et al.* 2010). Unlike regression and ANOVA analyses, SEM enable us to
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18 205 examine whether preconceived model structures (i.e. strength and direction of causality) match
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20 206 with theoretical frameworks based on *a priori* knowledge (Grace *et al.* 2010; Lam & Maguire
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22 207 2012). Use of SEM has been gaining traction in the biological and ecological literature (Shipley
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24 208 2000; Grace 2006; Lavorel & Grigulis 2013). Our SEM included $\delta^{15}\text{N}$ values taken from the main
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26 209 co-occurring pools of N: AM plants, EcM plants, saprotrophic fungi, EcM fungi, and surface
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28 210 soils. We also included available variables that were perceived to have direct (i.e. *soil [N]*) and
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30 211 indirect influence over the N cycling in these forested ecosystems (i.e. climate, elevation, forest
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32 212 age). The SEM were analyzed using an exploratory approach owing to initial uncertainty in the
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34 213 strength and direction of climatic influences over N cycling pathways. Initially, a full model
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36 214 including all available variables that may influence the demand for and pathways of N cycling
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38 215 were constructed using: *soil [N]* (mg/g), stand age (yr), elevation (m), MAT, MAP, high vs. low
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40 216 latitude, and lat./long. Climate (MAT and MAP) and the absolute value of latitude were also
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42 217 assessed as square root transformations to account for non-linearity. Variables were
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44 218 subsequently removed using backward elimination stepwise regression until only the minimum
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46 219 significant non-redundant variables remained. Model outputs supported the supplementation of
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48 220 climatic data with the strongly correlated ([see Fig. S4 in Supporting Information](#)), yet putatively
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50 221 more encompassing, latitudinal proxy ($R = 0.77$ and 0.61 for latitude vs. MAT and MAP,
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52 222 respectively) to best account for observed trends in isotopic gradients. The relatively small
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number of low latitude datasets prevented separate SEM constructions for high latitude and low latitude ecosystems to specifically contrast these ecosystem types; instead we included these categories as potentially exogenous model parameters. Categorical groupings of high vs. low latitude sites were made at $\pm 27^\circ$ latitude to allow for statistical contrasts. This break point was defined by the furthest site from the equator that retained a subtropical climate (e.g. Hou *et al.* 2012) but does not correspond to a globally universal latitudinal “break point” for sub/tropical conditions due to regional climatic variability.

During the process of model construction, separate models for the $\delta^{15}\text{N}$ values of saprotrophic fungi and EcM and AM plants were explored in order to ascertain distinct pathways and correlations of error terms among these components individually. Soil $\delta^{15}\text{N}$ values were initially modeled as exogenous with no causal agents in the exploratory models. Next, plausible relationships between all ecosystem $\delta^{15}\text{N}$ components were explored by assessing path diagrams and model fit parameters (i.e. chi square, root mean square error of approximation [RMSEA] and probability of a close fit [PClose]). A non-significant P value indicates that the model structure does not differ significantly and that the model is a feasible representation of the data (see goodness-of-fit tests below). Competing SEM were compared with the most parsimonious models based on corrected Aikake Information Criteria (AICc) output (see Table S3 in Supporting Information) for comparison of statistical methods. In addition, because of strong correlation among ecosystem $\delta^{15}\text{N}$ values, latent variables representing shared variation among observed variables were defined and incorporated when significant, but omitted from the final path diagram to simplify visual presentation and to prevent overly abstract construction of the role such latent variables might have in structuring ecosystem $\delta^{15}\text{N}$ values (see Grace *et al.* 2010 for a discussion of such theoretical constructs in ecosystem ecology). We used best-fit regression functions (linear, quadratic, cubic) and correlation analysis (Pearson-product moment) to examine relationships among ecosystem $\delta^{15}\text{N}$ values, or their relative differences,

with absolute values of latitude to more thoroughly examine relationships that emerged from the SEM and hypothetical predictions.

We also examined if the following system of ^{15}N mass balance models developed in high latitude forests (equations from Hobbie & Högberg 2012) were able to provide reasonable estimates for N transferred in the EcM symbiosis using averaged $\delta^{15}\text{N}$ values from the high and low latitude sites.

$$\delta^{15}\text{N}_{\text{EcM plant}} = \delta^{15}\text{N}_{\text{available N}} + \Delta \times (\log_e \times f) / (1 - f) \quad \text{Eqn. 1}$$

$$\delta^{15}\text{N}_{\text{EcM fungi}} = \delta^{15}\text{N}_{\text{available N}} - \Delta \times \log_e \times (1 - f) \quad \text{Eqn. 2}$$

$$\Delta = (\delta^{15}\text{N}_{\text{available N}} - \delta^{15}\text{N}_{\text{EcM plant}}) / (1 + \delta^{15}\text{N}_{\text{EcM plant}}) \quad \text{Eqn. 3}$$

Where $\delta^{15}\text{N}_{\text{available N}}$ represents the combined value of all available soil N sources used, Δ represents the effective discrimination against ^{15}N during the production of N transfer compounds from available N by EcM fungi, and f represents the proportion of total tree N comprised of those compounds. Assignment of three of the parameters used in each of these simultaneous equations permits solving for the fourth unknown parameter of interest. For instance, using plant and fungal $\delta^{15}\text{N}$ values reported in datasets, Δ values estimated from laboratory studies, and a range of $\delta^{15}\text{N}_{\text{available N}}$ values approximating actual soil measurements, estimates are possible of the upper and lower proportional bounds of N transferred by EcM (f).

RESULTS

Patterns among soil, plant, and fungal $\delta^{15}\text{N}$ values

The $\delta^{15}\text{N}$ values of mineral and organic soil horizons were positively correlated across sites ($R = 0.70$, $n = 27$), and mineral soils were on average $3 \pm 1.6 \text{ ‰}$ (mean \pm s.d.) more ^{15}N -enriched than those of organic soils (matched pairs t-test: $P < 0.001$, $n = 27$). Soil $\delta^{15}\text{N}$ values from

surface organic layers were negatively correlated with latitude (quadratic polynomial: $R^2 = 0.30$, $P = 0.001$, $n = 42$; $\gamma = 0.36 - 0.029 \times \chi + 0.0021 \times (\chi - 42.02)^2$; Fig. 2a), leading to significant ^{15}N -enrichment of sub/tropical forest soils compared to those of higher latitude ecosystems ($P = 0.036$, unequal variance t-test; Fig. 2a). In pursuit of inherent biases in our dataset, we examined the possibility that the highest latitude soil $\delta^{15}\text{N}$ values were driving the relationships by removing all sites above 51° and refitting the same regression models. Removal of these high-latitude sites did not decrease the variance explained or the significance of model formulations seen in Fig. 2 (see Figure S5 in Supporting Information).

Foliar $\delta^{15}\text{N}$ values of EcM plants were negatively correlated with latitude ($R^2 = 0.52$, $P < 0.001$, $n = 47$; $\gamma = 1.6 - 0.10 \times \chi$) and foliar $\delta^{15}\text{N}$ values from AM plants exhibited a comparable but non-linear relationship with latitude (quadratic polynomial, $R^2 = 0.37$, $P = 0.012$, $n = 22$; $y = 2.95 - 0.0059 \times \chi + 0.0033 \times (\chi - 40.04)^2$; Fig. 2b). Mean annual temperature and precipitation generally explained less variance than latitude for EcM plants (i.e. $R^2 = 0.25$, $P < 0.001$ and $R^2 = 0.26$, $P = 0.001$, respectively) and AM plants ($R^2 = 0.39$, $P = 0.009$ and $R^2 = 0.05$, $P = 0.60$, for quadratic polynomials, respectively see Figure S4 in Supporting Information). Foliar $\delta^{15}\text{N}$ values of sub/tropical EcM plants were 3.4‰ greater than EcM plants from higher latitudes (unequal variance t-test: $t = 3.49$; $P = 0.004$; Fig. 2b) and those for AM plants were 1.9‰ greater in sub/tropical forests ($t = 1.59$, $P = 0.07$; Fig. 2b). Accordingly the $\delta^{15}\text{N}$ differences between co-occurring EcM and AM plants were negatively correlated with latitude (cubic polynomial fit: $R^2 = 0.58$, $P = 0.001$, $n = 22$), and these average differences statistically compared according to high and low latitude groupings (Fig. 3a). Significant differences were present only in higher latitude groupings (i.e. $\Delta\delta^{15}\text{N}_{\text{EcM-AM}} = 0.6 \pm 0.5\text{‰}$ vs. $-1.6 \pm 0.7\text{‰}$ in low and high latitudes, respectively; unequal variance t-test: $t = 2.51$, $P = 0.01$). Removal of the two highest latitude sites required a quadratic (vs. cubic) polynomial to achieve statistical significance of the fitted relationship ($P = 0.05$, $n = 20$; data not shown). Isotopic fractionation ($\Delta = \delta^{15}\text{N}_{\text{plant}} - \delta^{15}\text{N}_{\text{organic}}$

soil) during the uptake and/or translocation of soil N was compared as a metric to assess latitudinal differences among fractionation in EcM and AM plants. The average fractionation of EcM plants was greater than that of AM plants (avg. $\Delta\delta^{15}\text{N}_{\text{EcM plants}} = -2.6\text{‰}$ vs. $\Delta\delta^{15}\text{N}_{\text{AM plants}} = -1.7\text{‰}$) and comparison of the slopes of fitted lines indicated minimal fractionation of relatively ^{15}N -depleted soil N and increasing fractionation of relatively ^{15}N -enriched soil N ($\delta^{15}\text{N}_{\text{EcM plant}}$ slope = 0.63 and $\delta^{15}\text{N}_{\text{AM plant}}$ slope = 0.76) with similar intercepts of c. -7‰ where fractionation from source N is expected to no longer occur (Fig. 4a,b).

Sporocarp $\delta^{15}\text{N}$ values from saprotrophic fungi were negatively correlated with latitude ($R^2 = 0.18$, $P = 0.007$, $n = 39$; $\gamma = 3.396 - 0.070 \times \chi$) whereas those from EcM fungi showed no significant relationship (Fig. 2c). On average EcM sporocarp $\delta^{15}\text{N}$ values were 4.3‰ more enriched than saprotrophic fungi (Fig. 2c; matched pairs test: $t = -8.99$, $P < 0.001$, $n = 31$). These enrichment differences were slightly, but not significantly, smaller in low latitude forests owing to overall trends in both trophic groups ($\Delta\delta^{15}\text{N}_{\text{ECMF-SAPF}} = 4.6$ vs. 3.9‰ , respectively). Similarly, the differential ^{15}N -enrichments of tropical EcM systems caused the differences between EcM plants and fungi, ranging from 2.3 to 15.3‰ , to be smallest in low latitude forests (average difference = 5.5 vs. 7.8‰ , respectively; unequal variance t-test: $t = -2.20$, $P = 0.026$) and to be positively correlated with latitude ($R^2 = 0.13$, $P = 0.01$, $n = 44$; Fig. 3b). Although both EcM sporocarp $\delta^{15}\text{N}$ and surface soil total [N] were unrelated to latitude, EcM sporocarp $\delta^{15}\text{N}$ was negatively correlated with soil [N] ($R^2 = 0.34$, $P < 0.001$; Fig. 5a) and positively correlated with EcM plant $\delta^{15}\text{N}$ across all sites ($R^2 = 0.23$, $p = 0.001$, $n = 44$; Fig. 5b).

Mass balance mixing models

Using averaged values from high-latitude datasets, mass balance solutions for EcM plant $\delta^{15}\text{N}$ values were only possible with several parameter modifications. First, the effective discrimination (Δ in Eqn.'s 1-3) magnitude was reduced below that derived for *Pinus* EcM

323 forests, from 9 to 7 ‰ (Hobbie & Colpaert 2003), and ^{15}N -enriched soil N sources ($\delta^{15}\text{N}_{\text{available N}}$)
 324 were assigned above the available bulk surface soil $\delta^{15}\text{N}$ values. Both assumptions are
 325 reasonable given the likelihood that non-*Pinus* EcM systems may vary in effective discrimination
 326 magnitudes and that bulk soils may not approximate EcM access to ^{15}N -enriched soil N sources
 327 either at greater soil depths or in dissolved organic forms (Mayor *et al.* 2012; Hobbie *et al.*
 328 2013). The solution space resulting from the simultaneous equations required $\delta^{15}\text{N}_{\text{available N}}$
 329 values from 3.8 to 6.5 ‰ based on trees receiving 50–100% of their N from EcM, respectively.
 330 These high proportional dependencies and enriched $\delta^{15}\text{N}_{\text{available N}}$ sources agreed with field
 331 studies in arctic, alpine, boreal, and temperate ecosystems (Hobbie & Hobbie 2006; Averill &
 332 Finzi 2011; Mayor *et al.* 2012; Nave *et al.* 2013). However, solving for sub/tropical EcM plant
 333 $\delta^{15}\text{N}$ values required even more ^{15}N -enriched soil N sources, ranging from 2.9 to 9.4 ‰ despite
 334 being coupled with a reduced proportion of EcM-derived N from 10–50 %, respectively. Such
 335 ^{15}N -enriched N sources appear to encompass mineral and organic N forms based on detailed
 336 soil $\delta^{15}\text{N}$ measurements made from one of our tropical sites ($\delta^{15}\text{N}_{\text{NH}_4} = 1.0$ ‰, $\delta^{15}\text{N}_{\text{NO}_3} = -2.9$ ‰,
 337 $\delta^{15}\text{N}_{\text{DON}} = 7.6$ ‰; Fortuna, Panama; J. Mayor, unpublished data). Furthermore, solution spaces
 338 for sub/tropical EcM forests required us to nearly eliminate EcM discrimination to $\Delta = 2$ ‰.
 339 Following estimation of possible solutions for the simultaneous parameters that matched
 340 observed plant $\delta^{15}\text{N}$, we unsuccessfully attempted to further constrain these estimates with
 341 inclusion of observed $\delta^{15}\text{N}_{\text{EcM fungi}}$ values in Eqn. 2. For instance, in high latitude ecosystems,
 342 estimated parameters could not approximate $\delta^{15}\text{N}_{\text{EcM fungi}}$ values within even 5 ‰ of those
 343 observed. Further, the proportional dependencies on EcM N became highly sensitive to small
 344 increases in assigned $\delta^{15}\text{N}_{\text{available N}}$ (e.g. small shifts in $\delta^{15}\text{N}_{\text{available N}}$ from 4.5 to 5.5 ‰ produced f
 345 values ranging from 10 to 50 % of total tree N supply, respectively). In conclusion, the mass
 346 balance models derived from high latitude N-limited ecosystems failed to approximate observed

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3 347 EcM $\delta^{15}\text{N}$ values, particularly in sub/tropical forests, despite various concessions begin made in
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5 348 assignment of model parameters.
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10 350 **Structural equation modeling**

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12 351 The *a priori* model fit for $\delta^{15}\text{N}$ values of EcM plant foliage ($\chi^2 = 7.73$, $df = 5$, $P = 0.172$) had a
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14 352 RMSEA of 0.11 and a PClose of 0.23. This model suggests that the $\delta^{15}\text{N}$ values of EcM plant
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16 353 foliage were directly effected by latitude (coefficient estimate = -0.65) and indirectly by the
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18 354 competing influences of soil [N] and $\delta^{15}\text{N}$ values as mediated by the $\delta^{15}\text{N}$ values of co-occurring
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20 355 EcM sporocarps (coefficient estimate = 0.38). The *a priori* model fit for $\delta^{15}\text{N}$ values of AM plant
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22 356 foliage ($\chi^2 = 0.01$, $df = 1$, $P = 0.919$) had a RMSEA of 0.00 and PClose of 0.92. This model
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24 357 suggests that the $\delta^{15}\text{N}$ values of AM plant foliage were directly effected by organic soil $\delta^{15}\text{N}$
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26 358 values (coefficient estimate = 0.73) as mediated by the indirect affect of latitude (coefficient
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28 359 estimate = -0.35). The *a priori* model fit for $\delta^{15}\text{N}$ values of EcM sporocarps ($\chi^2 = 4.04$, $df = 2$, $P =$
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30 360 0.133) had a RMSEA of 0.15 and PClose of 0.17. This model suggests that the $\delta^{15}\text{N}$ values of
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32 361 EcM sporocarps were directly effected by latitude (coefficient estimate = 0.341) and soil [N]
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34 362 (coefficient estimate = -0.48). The *a priori* model fit for $\delta^{15}\text{N}$ values of saprotrophic sporocarps
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36 363 ($\chi^2 = 0.92$, $df = 1$, $P = 0.337$) had a RMSEA of 0.00 and PClose of 0.37, suggesting that
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38 364 saprotrophic fungal $\delta^{15}\text{N}$ values were directly effected by surface soil $\delta^{15}\text{N}$ values (coefficient
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40 365 estimate = 0.54) as mediated by the indirect affect of latitude (coefficient estimate = -0.36).
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46 366 A final unified path diagram depicting relationship among all observed variables had a
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48 367 RMSEA of 0.10 and PClose of 0.18 ($\chi^2 = 19.59$, $df = 13$, $P = 0.106$). The final fitted model shows
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50 368 the distinctive relationships of ecosystem $\delta^{15}\text{N}$ in both fungal and plant components and the
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52 369 complexity of causes influencing $\delta^{15}\text{N}$ values of EcM symbioses at broad scales (Fig. 6). A
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54 370 correlated error term co-influencing EcM and saprotrophic sporocarp $\delta^{15}\text{N}$ (coefficient estimate =
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56 371 -1.86, $P = 0.043$) produced fits that were marginally better (ΔAICc reduction of 2.36), but was
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omitted from graphical presentations for clarity. The model pathways previously identified in *a priori* SEM were retained in the fitted diagram for the $\delta^{15}\text{N}$ value of both EcM and AM plants (SEM $R^2 = 0.63$ and 0.55 , respectively). The two fungal trophic groups also retained distinctive pathways influencing sporocarp $\delta^{15}\text{N}$ values; the $\delta^{15}\text{N}$ values of both EcM (SEM $R^2 = 0.39$) and saprotrophic (SEM $R^2 = 0.34$) fungi were positively effected by the $\delta^{15}\text{N}$ of organic soils, as mediated by latitude-dependent processes. However, in contrast to *a priori* model specifications, EcM fungal $\delta^{15}\text{N}$ values were also effected by surface soil [N]. Therefore, the net effect of both soil [N] and $\delta^{15}\text{N}$ values affect the $\delta^{15}\text{N}$ values of EcM sporocarps directly and EcM plants indirectly. The SEM variables retained as influencing ecosystem component $\delta^{15}\text{N}$ values were also retained in all high AICc-ranked models, lending additional support to the interpretation of the SEM (See Table S3 in Supporting Information). The provisioning of indirect and direct pathways in the SEM is an advantage over multiple regression models.

DISCUSSION

Despite large variation in soils, plants, and fungi at the global scale, ecosystem components in lower latitudes exhibited ^{15}N -enrichment indicative of more rapid N cycling. In the context of this background variation in ecosystem $\delta^{15}\text{N}$, we explicitly sought to determine if latitudinal variation in *relative* $\delta^{15}\text{N}$ patterns correspond to theoretical shifts in mycorrhizal mediation of plant N demands. Below, we evaluate biome-scale differences in the pattern and function of EcM systems in order to critically evaluate mechanisms structuring ecosystem $\delta^{15}\text{N}$ patterns.

Soil $\delta^{15}\text{N}$ patterns

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3 396 Consistent with previous meta-analyses, soil $\delta^{15}\text{N}$ values were significantly more ^{15}N -enriched in
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5 397 sub/tropical forests (Martinelli *et al.* 1999; Amundson *et al.* 2003). Similarly, deeper soil layers
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7 398 were more ^{15}N -enriched and comparable in value to that seen in previous analyses of soil $\delta^{15}\text{N}$
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10 399 profiles (Hobbie & Ouimette 2009). Organic soil $\delta^{15}\text{N}$ values from the 21 sites containing only
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12 400 EcM plants were marginally more ^{15}N -depleted (-0.8‰) than soils from the 19 sites containing
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14 401 both AM and EcM plants (0.5‰ ; $P = 0.099$, one-way t-test assuming equal variances). Based
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16 402 on surveys of temperate forests, EcM-associated soil ^{15}N -depletion might result from greater
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18 403 nitrate retention in EcM-dominated stands relative to AM-dominated stands (Phillips *et al.* 2013;
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20 404 Midgley & Phillips 2014). As expected, the ^{15}N -enrichment of organic- relative to mineral soils
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22 405 was slightly smaller in sites containing only EcM trees (-2.7‰ vs. -3.8‰ , respectively; $P =$
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24 406 0.08 , one-way t-test assuming equal variance, $n = 23$) in contrast to the opposite prediction in a
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26 407 previous analysis (Hobbie & Ouimette 2009). Whereas soil ^{15}N -profiles in high latitude forests
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28 408 are largely due to the accumulation of EcM mycelial residues (Hobbie & Ouimette 2009;
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30 409 Clemmensen *et al.* 2013), fractionating gaseous losses also influence soil ^{15}N -enrichment in the
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32 410 tropics. Soil anoxia induced by high precipitation, combined with rapid rates of N cycling, leads
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34 411 to increased ratios of gaseous-to-hydrological N losses during nitrification and denitrification
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36 412 (Schlesinger & Bernhardt 2013). Such fractionating losses leave behind ^{15}N -rich N that can
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38 413 adhere to weathered clays, and ultimately contribute to soil and plant ^{15}N -enrichment over time
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40 414 (Kramer *et al.* 2003; Houlton *et al.* 2006; Hietz *et al.* 2011; Mayor *et al.* 2014). It is therefore
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42 415 apparent that the drivers of soil $\delta^{15}\text{N}$ profiles from high- and low-latitude ecosystems may be
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44 416 caused by fundamentally different mechanisms.
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52 418 ***Plant $\delta^{15}\text{N}$ patterns***

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54 419 Previous meta-analyses have shown that EcM plants are typically ^{15}N -depleted relative to AM
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56 420 and non-mycorrhizal plants at the global scale, irrespective of co-occurrence of both mycorrhizal
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types within individual sites (e.g. Craine *et al.* 2009). In the present study this distinction was absent from sub/tropical forests containing both AM and EcM trees. As the mechanism commonly evoked to explain ^{15}N -depletion of EcM plants relative to AM plants requires EcM-mediated delivery of ^{15}N -depleted N to host plants (reviewed in Hobbie & Högberg 2012), our results suggest a distinct functional role of EcM associations in sub/tropical forest N cycles. One hypothetical mechanism is that EcM trees in sub/tropical forests take up the majority of their N directly from soils, without mediation by mycorrhizae. This is unlikely given the high degree of root colonization in most EcM genera (personal observations), the dominance of the same EcM fungal lineages along the latitudinal gradient (Tedersoo *et al.* 2012a), and the SEM results. Alternatively, sub/tropical EcM fungi deliver comparable amounts of N to host plants but without ^{15}N -depletion of source N during transfer. Such reductions in the magnitude of effective isotopic fractionation are supported by the mass balance exercises requiring smaller Δ values.

In the present study pre-existing ^{15}N mass balance models were unable to match observed EcM plant and fungal $\delta^{15}\text{N}$ values and therefore could not quantitatively estimate presumed changes in the proportion of plant N derived from EcM fungi across the broad array of ecosystems. This shortcoming could not be avoided despite flexibility assigned to several of the parameters used in the system of mass balance equations. Of those changes, the reduction in effective fractionation magnitudes (Δ), an adjustment requiring a particularly large reduction in sub/tropical forest solutions, highlights a potential uncertainty regarding the physiological function of EcM in the tropics. It is therefore apparent that universal application of these mass balance equations will not only require better assessment of soil N $\delta^{15}\text{N}$ values (a parameter we also permitted to vary widely from bulk soil $\delta^{15}\text{N}$ measurements based on data from one tropical site included here), but also the elucidation of additional mechanisms by which low-latitude EcM sporocarps become ^{15}N -enriched independent of presumably lower host plant N demands (discussed below).

The SEM path analysis suggests that despite any latitudinally distinct processing of N by EcM, fungal activity remains an important direct affect over host plant $\delta^{15}\text{N}$ variability. Latitude (a crude proxy for climate, soil weathering, etc.) negatively affected EcM plant $\delta^{15}\text{N}$ in the path diagram, but EcM fungal $\delta^{15}\text{N}$ values positively affected EcM plant $\delta^{15}\text{N}$ with no significant interaction between them (coefficient estimate = 0.05, $P = 0.626$). However, the SEM path diagram highlighted competing indirect soil variables that appear to affect EcM plant $\delta^{15}\text{N}$ by differentially affecting EcM fungal $\delta^{15}\text{N}$. This indirect influence could result from access to and demand for soil N being inversely related to one another. In other words, high soil N availability leads to lower ^{15}N retained in EcM fungi, as shown in [Fig. 5a](#), when either N demand by host plants is low (Hobbie & Högberg 2012; but see Näsholm *et al.* 2013) or when high mineral N availability makes accessing ^{15}N -enriched organically-bound N an unnecessary enzymatic expenditure (Bödeker *et al.* 2014). Under this scenario fungal sporocarp $\delta^{15}\text{N}$ values closely match the $\delta^{15}\text{N}$ values of soil N sources when ^{15}N -fractionating (i.e. high Δ) N delivery to host plants is reduced. Evidence for this interpretation are seen in the eight sites containing the most ^{15}N -enriched EcM fungal values also being among those with the lowest soil [N] (average $\delta^{15}\text{N}_{\text{EcM fungi}} = 9.2\text{‰}$ in sites with average [N] = 2.83 mg g^{-1} , representing the upper and lower quartiles, respectively; sites: 8, 16, 17, 21, 29, 32, 38, 44 in [Table S1](#)).

In contrast to EcM plants, the relationship between AM plant $\delta^{15}\text{N}$ values and latitude-dependent processes were indirect. While AM plants were more ^{15}N -enriched in low latitudes, there was evidence for enrichment in some higher latitude sites as well (although these did not drive the resulting regression once sites above 51° were removed; [Figure S5](#)). Based on [Fig. 2b](#) and the SEM path diagram, the non-linear AM plant $\delta^{15}\text{N}$ relationship appears due to the close tracing of soil $\delta^{15}\text{N}$ values by AM plants independently of soil [N]. This relationship, and the fractionation magnitude observed in [Fig. 4b](#), suggests that surface soil $\delta^{15}\text{N}$ values at least approximate the N forms available to AM plants over a broad range of ecosystems. The

average ^{15}N -fractionation magnitude was comparable to previous estimates (c. 2 ‰ or less) of fractionation associated with uptake and translocation of N in AM plants in Australian woodland and the subarctic (Pate *et al.* 1993; Michelsen *et al.* 1998).

Fungal $\delta^{15}\text{N}$ patterns

Unlike soils, plants, and saprotrophic fungi, EcM fungi were not significantly ^{15}N -enriched at low latitudes — a pattern comparable to previous and ongoing meta-analyses of EcM fungal $\delta^{15}\text{N}$ patterns (Mayor *et al.* 2009; Erik Hobbie, personal communication). The question then becomes what could maintain uniformity in EcM fungal $\delta^{15}\text{N}$ values across these diverse biomes that vary in plant and soil $\delta^{15}\text{N}$ values, soil nutrient availabilities, and climate?

The SEM path diagram suggests that both EcM and saprotrophic fungi are positively effected by soil $\delta^{15}\text{N}$, yet EcM $\delta^{15}\text{N}$ values are also strongly effected by the competing influences of soil [N] and the presumed demand of N by host plants (discussed in the preceding section). Based on the framework of mass balance equations mathematically linking fungal and plant $\delta^{15}\text{N}$, we anticipated the $\delta^{15}\text{N}$ differences between EcM plants and sporocarps would become smaller in sub/tropical forests because of an expected reduction in overall N demands by sub/tropical plants growing under conditions of greater relative P limitation (Vitousek *et al.* 2010). The regression in Fig. 3b indicates that ^{15}N -differences between co-occurring EcM sporocarps and plants were indeed diminished in lower latitude ecosystems as expected. Yet the regressions and SEM path diagram indicate that the relative trend seen in Fig. 3b was driven largely by latitude associated variation in EcM plant $\delta^{15}\text{N}$ values. If the relative ^{15}N -enrichment of tropical EcM plants is caused by a reduced reliance on EcM fungi for soil N and possibly use of ^{15}N -enriched soil N sources, then there must be physiological mechanisms that account for the consistent ^{15}N -enrichment of EcM fungi in sub/tropical forests irrespective of N delivery to host plants.

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497 **Alternative hypotheses for EcM function in sub/tropical forests**

498 As mentioned, we have assumed, based on relative $\delta^{15}\text{N}$ patterns, that EcM fungi deliver N to
499 associated tropical trees without a high degree of ^{15}N -fractionation during synthesis of N transfer
500 compounds. In the absence of this typical high-latitude fractionating outlet, there are several
501 non-exclusive mechanisms that we speculate could lead to consistent ^{15}N -enrichment of EcM
502 fungi in the tropics. For instance, sub/tropical EcM fungi may: (1) acquire N from sources that
503 are uniquely ^{15}N -enriched (e.g. proteins; Emmerton *et al.* 2001; Hobbie & Högberg 2012); (2)
504 forage at greater soil depths (Hobbie & Ouimette 2009); (3) be disproportionately dominated by
505 taxa that are characteristically ^{15}N -enriched (e.g. *Cortinarius*; Hobbie & Agerer 2009; Cox *et al.*
506 2010); (4) undergo accelerated hyphal turnover times with concomitantly greater internal ^{15}N -
507 recycling (Hobbie *et al.* 2012; Ekblad *et al.* 2013; Pena *et al.* 2013); or, (5) have additional
508 unrecognized N outlets by which the fungal mycelium loses disproportionately more ^{14}N to
509 surrounding soil during processes such as acquisition of P or other limiting mineral nutrients
510 from weathered tropical forest soils (Lambers *et al.* 2008; Lucas & Casper 2008; Marklein &
511 Houlton 2011; Pritsch & Garbaye 2011; Tedersoo *et al.* 2012b). We suggest that any
512 combination of these non-exclusive processes could contribute to relative ^{15}N -enrichment of
513 EcM fungi in the tropics and that such differences in EcM mediation of plant-soil N cycling might
514 also contribute to sporocarp $\delta^{15}\text{N}$ variability in high latitude ecosystems as well (Lilleskov *et al.*
515 2011). Evaluation of these largely physiological mechanisms within sub/tropical forests is
516 necessary to produce globally consistent frameworks relating N cycling process with the $\delta^{15}\text{N}$
517 values of EcM components (Alexander & Selosse 2009).

518 As a theoretical exercise, we diagramed how mechanisms (1) and (5), the use of ^{15}N -
519 enriched proteins and an additional enzymatic N loss pathway, could modify mass balance
520 models to account for the patterns observed in this study. This exercise illustrates how the

relative importance of two different N loss pathways from fungal mycelium, combined by the resulting usage of ^{15}N -enriched N sources, could result in the observed $\delta^{15}\text{N}$ values in both high and low latitude EcM systems, respectively (see Fig. S6 in Supporting Information). Continued research in low latitude EcM forests could expand mechanistic understanding of mycorrhizal functional roles in ecosystem nutrient economies (e.g. Phillips *et al.* 2013), as well as the functional relevance of differences among fungal lineages (Buée *et al.* 2007). Our study, using simultaneous analyses of the major ecosystem $\delta^{15}\text{N}$ components across broad latitudinal gradients, has identified latitudinal discrepancies and distinct avenues for continued research.

Conclusions

In previous syntheses, mycorrhizal types were implicated in having global influences on plant $\delta^{15}\text{N}$ values (Amundson *et al.* 2003; Craine *et al.* 2009). Our study places these findings into a more nuanced context by including original datasets from the tropics with more exhaustive measurements from co-occurring soil, fungi, and plants. The presence of an EcM isotopic “signal” in typically N-limited higher latitude ecosystems (tundra, boreal, and temperate forests) appears absent from plants, but not fungi, in sub/tropical EcM forests. This deviation in the tropics could result from differential processes related to N availability in excess of plant demand, access to ^{15}N -enriched soil N sources, and/or unique, as yet undetermined, ^{15}N -fractionation outlets in tropical EcM fungi. Therefore, ^{15}N -based mixing models derived from high latitude EcM associations lack utility when applied to the high N conditions typical of tropical ecosystems. Understanding EcM symbioses in the context of global N cycles will allow better integration of mycorrhizal functional processes with theories pertaining to climate-nutrient cycling relationships.

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FIGURE CAPTIONS

Fig. 1. Approximate geographic locations of the published (filled circle) and original (open triangle) sites used in this study.

Fig. 2. Average values for high latitude and low latitude components (\pm s.e.), divided by dotted lines, are presented to the right of main figures and categorized based on site descriptions of sub/tropical climatic influences. **(a)** Organic soil vs. |latitude|: quadratic polynomial, $R^2 = 0.30$, $P = 0.001$, $n = 42$; Mineral soil vs. |latitude|: $R^2 = 0.09$, $P = 0.14$, $n = 27$; Low-latitude organic and mineral soil $\delta^{15}\text{N}$ values were significantly enriched ($P = 0.0085$ and 0.075 , respectively); **(b)** Ectomycorrhizal plant vs. |latitude|: $R^2 = 0.52$, $P < 0.001$, $n = 47$; AM plant: $R^2 = 0.37$, $P = 0.012$, $n = 22$; Low latitude EcM and AM plant $\delta^{15}\text{N}$ values were significantly enriched ($P = 0.019$, $P = 0.07$, respectively); **(c)** Saprotrophic fungal sporocarps vs. |latitude|: $R^2 = 0.18$, $P = 0.007$, $n = 39$; EcM fungal sporocarps vs. |latitude|: $R^2 = 0.03$, $P = 0.26$, $n = 46$).

Fig. 3. Relative differences among plant $\delta^{15}\text{N}$ values in relation to absolute values of latitudinal origin. **(a)** The $\delta^{15}\text{N}$ difference between EcM and AM plants, a metric of the relative influence of the EcM habit, was negatively related to latitude ($\gamma = 2.3 - 0.055 \times \chi - 0.0026 \times (\chi - 40.04)^2 - 5.016\text{e-}5 \times (\chi - 40.04)^3$; $R^2 = 0.59$, $P = 0.0003$, $n = 22$), with the “typical” differences present only in higher latitude ecosystems. **(b)** The difference between the $\delta^{15}\text{N}$ values of EcM fungi and plants, a metric of fractionation associated with EcM N delivery, was positively correlated with latitude ($\gamma = 4.62 + 0.065 \times \chi$; $R^2 = 0.13$, $P = 0.01$, $n = 44$).

Fig. 4. $\delta^{15}\text{N}$ fractionation values of EcM and AM plants and underlying organic soils. Deviation of fitted models from the 1:1 line (dashed) are a metric of the isotopic fractionation ($\Delta = \delta^{15}\text{N}_{\text{plant}} - \delta^{15}\text{N}_{\text{organic soil}}$) of plants during uptake, transfer, and translocation of this metric of soil N. **(a)** EcM: $R^2 = 0.37$, $P < 0.0001$, $n = 40$. **(b)** AM: $R^2 = 0.59$, $P = 0.0001$, $n = 19$.

Fig. 5. Significant relationships of $\delta^{15}\text{N}$ values from EcM fungi, plants, and surface soil [N]. **(a)** The $\delta^{15}\text{N}$ values of EcM sporocarps were negatively related to surface soil [N] across sites ($R^2 = 0.34$, $P < 0.001$) suggesting their ^{15}N -enrichment is partially a function of growth under low-N conditions. **(b)** The $\delta^{15}\text{N}$ values of EcM plants and fungi were positively correlated with one

another across the broad range of sites ($R^2 = 0.23$, $p < 0.001$, $n = 43$) illustrating the N cycling dependency of the relationship.

Fig. 6. Final path diagram fit from competing SEM relating ecosystem $\delta^{15}\text{N}$ values, soil N concentrations [N], and latitudinal position of sites. The weights of pathway arrows correspond to the size of coefficient estimates (direct effects) within circles. Squared multiple correlations (R^2) are included alongside each endogenous latent variable.

SUPPORTING INFORMATION

TO BE MADE AVAILABLE ON-LINE ONLY

Table S1. List of site averaged metrics extracted from published and original datasets, global climate data, and geographical position of sites.

Table S2. $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, %N, and %C of all plants, fungi, and soil from original data sets used in this study.

Table S3. List of AICc model weightings derived from generalized least squares model selection; an independent statistical examination of predictions from the SEM.

Figure S4. Scatterplot matrix regressing ecosystem $\delta^{15}\text{N}$ values with climate (MAT, MAP) and latitude.

Figure S5. Comparison of ecosystem component regressions used in Figure 2 of main text with and without all sites $> 51^\circ$ removed to demonstrate the robustness of the $\delta^{15}\text{N}$ patterns.

Figure S6. Hypothetical mass balance mixing model relationships for high latitude and low latitude EcM systems highlighting the potential of extracellular enzyme outlets and N sources to influence $\delta^{15}\text{N}$ values of EcM plants and fungi.

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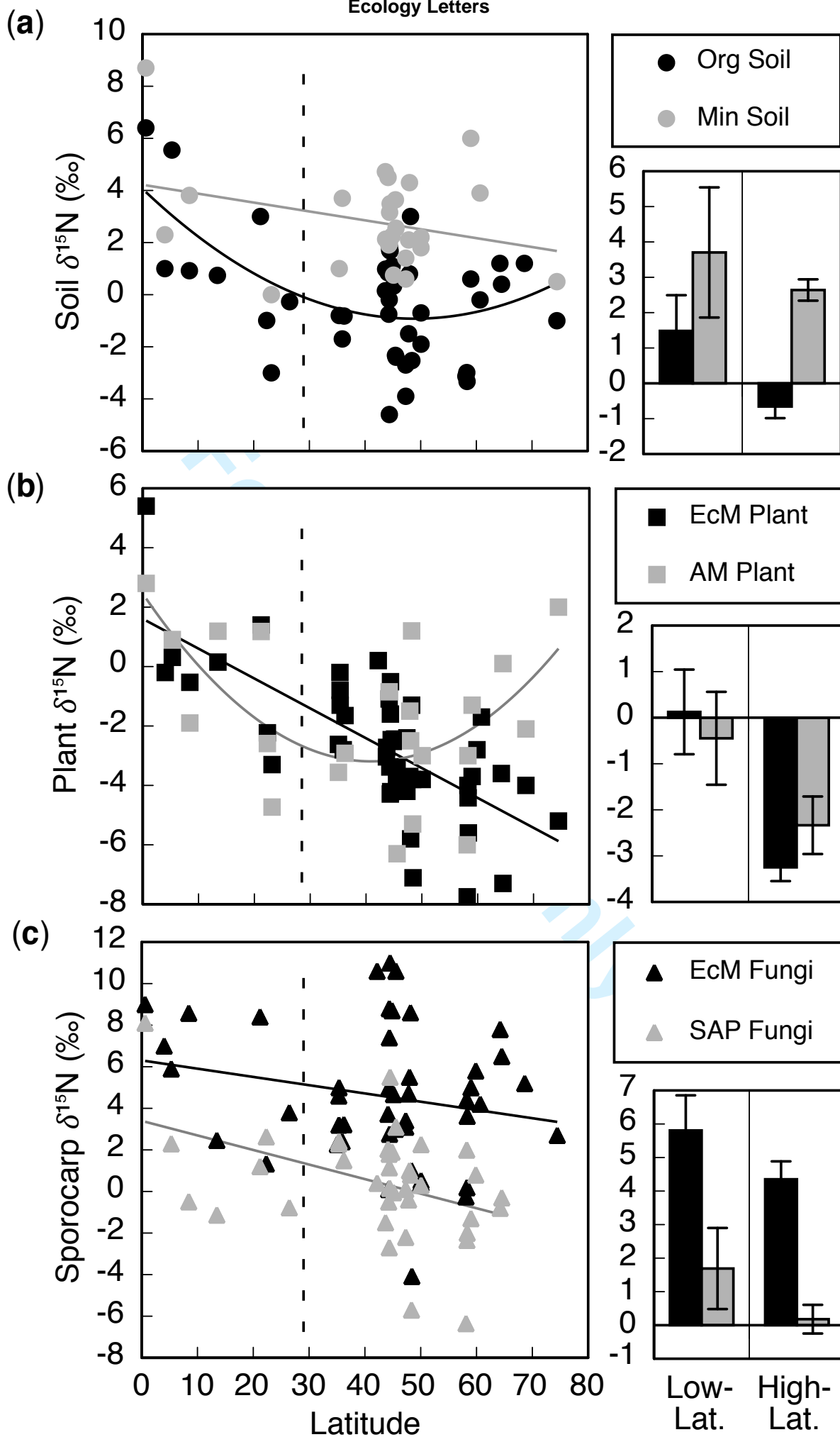
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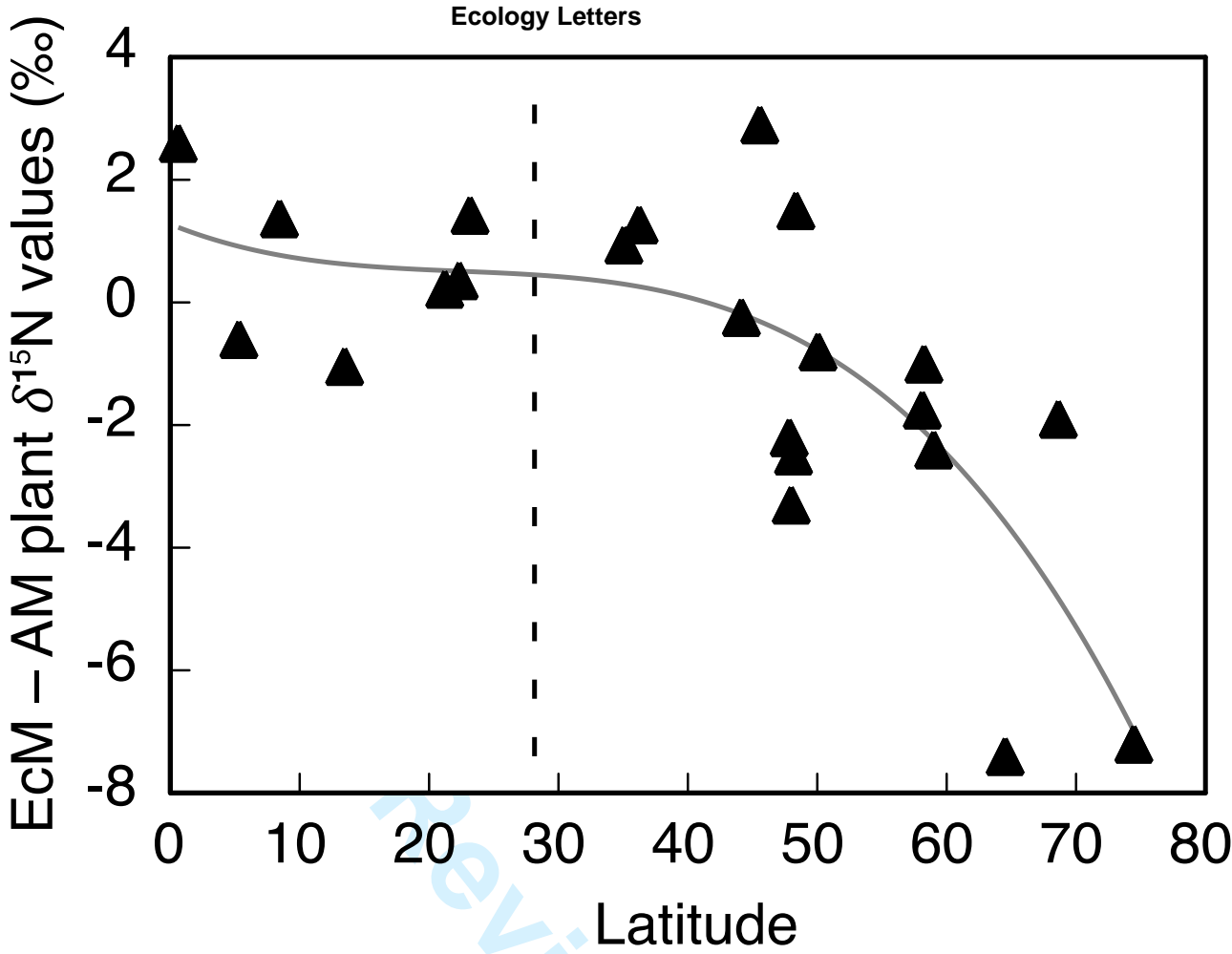
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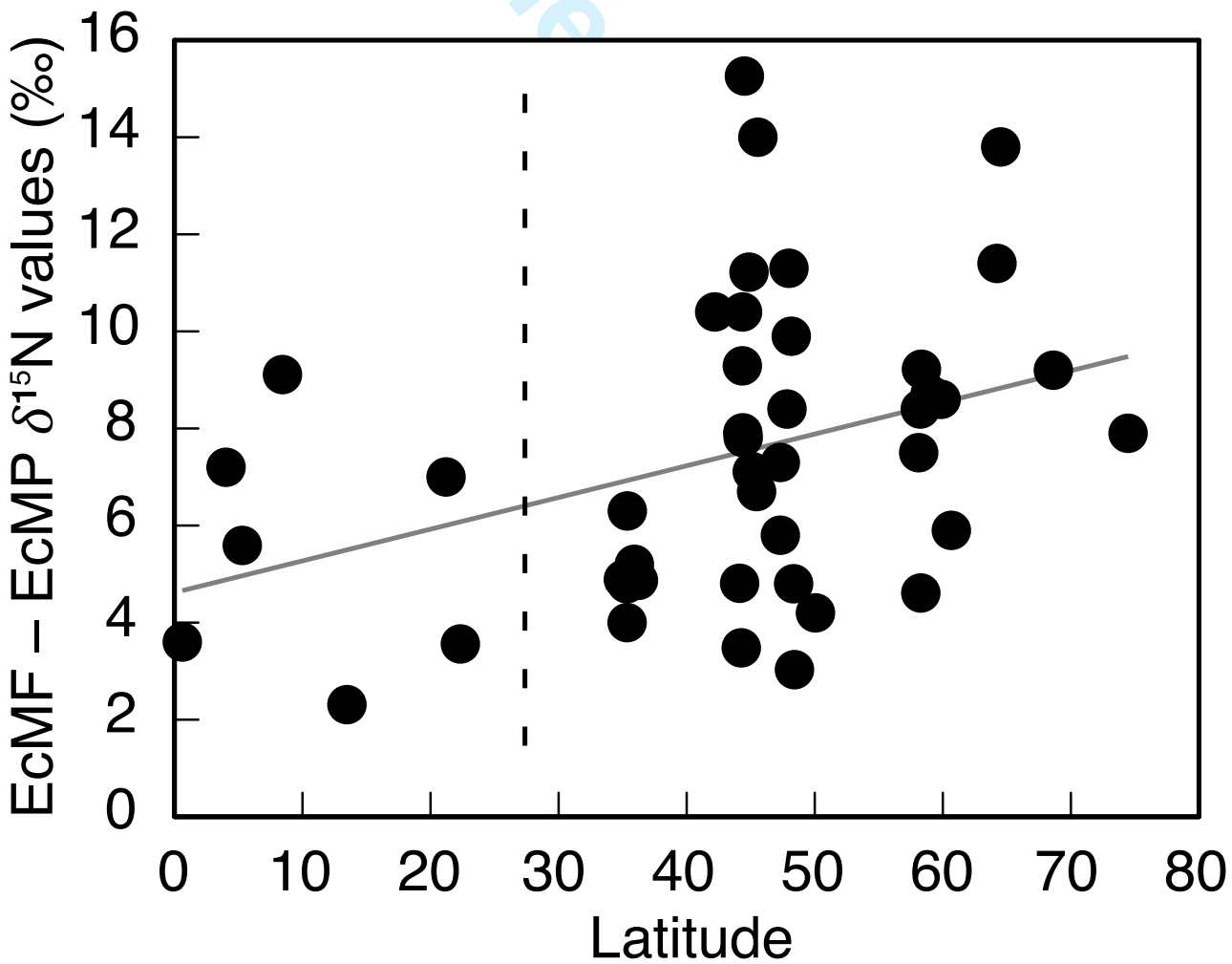


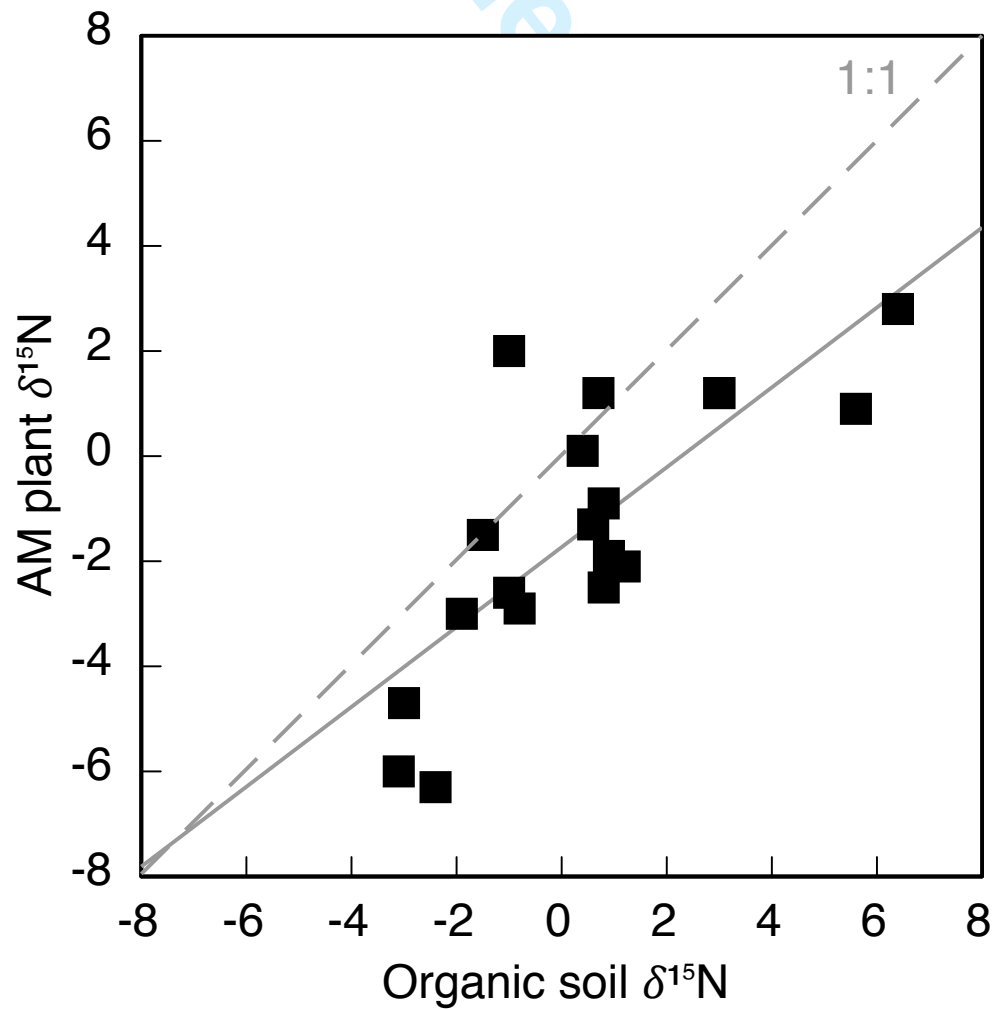
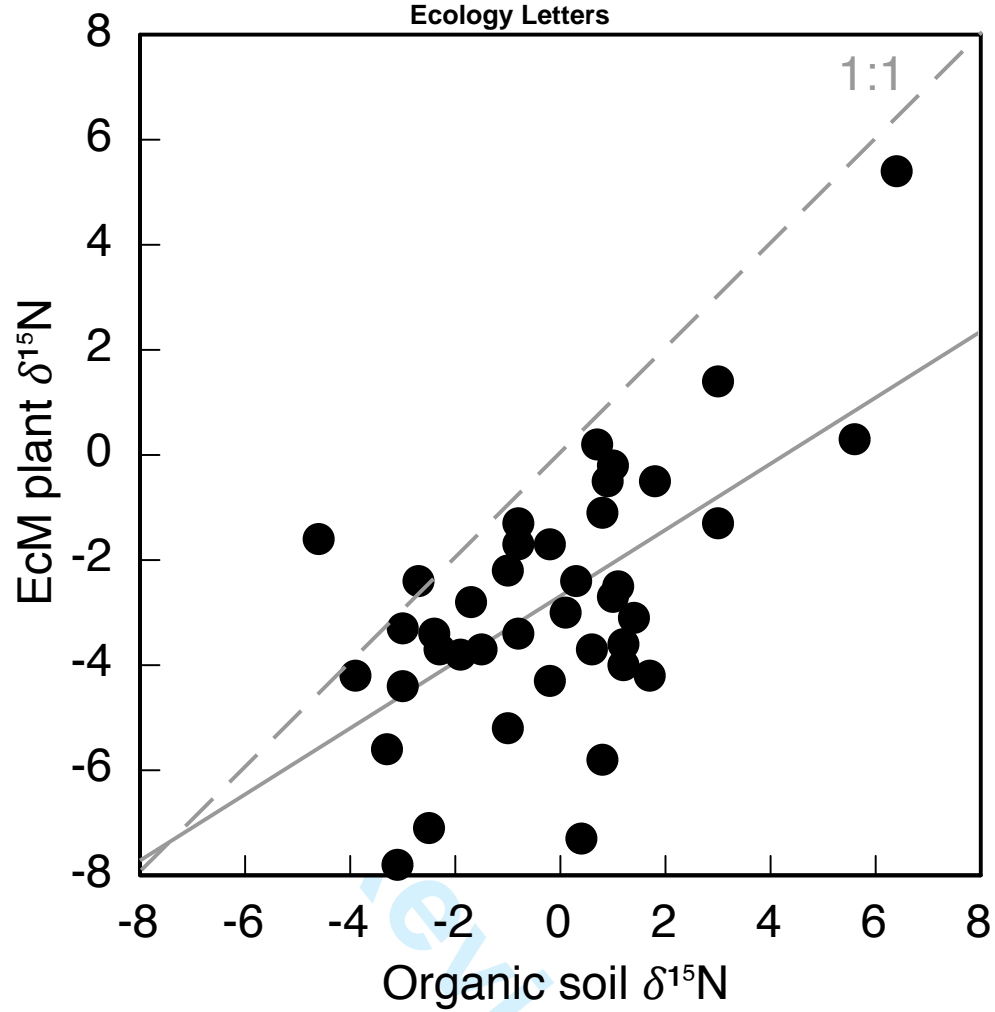


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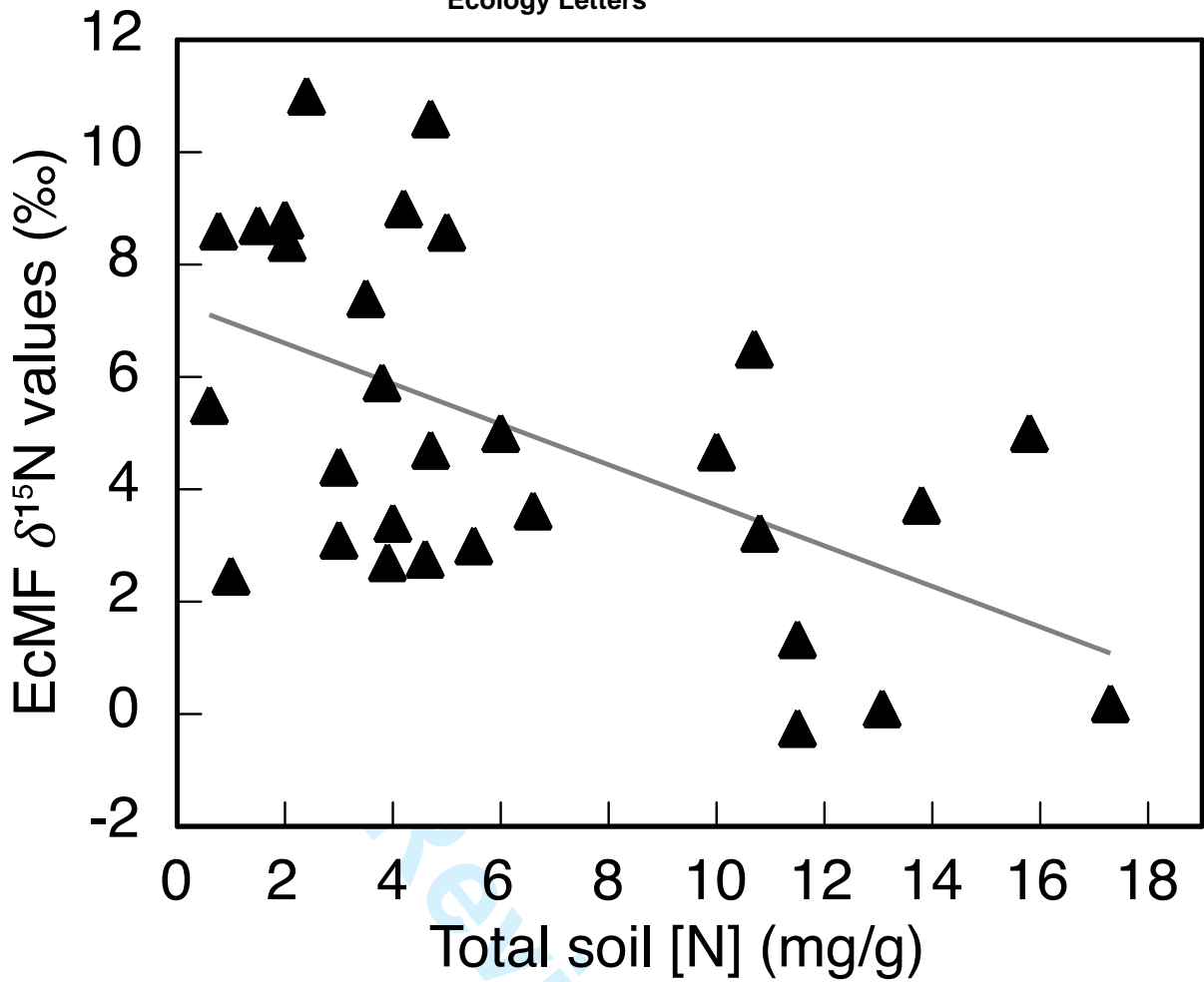
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