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Title: Climatic controls of decomposition drive the global biogeography of forest tree symbioses

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The identity of the dominant microbial symbionts in a forest determines the ability of trees to access limiting nutrients from atmospheric or soil pools[1,2], sequester carbon[3,4] and withstand the impacts of climate change[1-7]. Characterizing the global distribution of symbioses, and identifying the factors that control it, are thus integral to understanding present and future forest ecosystem functioning. Here we generate the first spatially explicit map of forest symbiotic status using a global database of 1.2 million forest inventory plots with over 28,000 tree species. Our analyses indicate that climatic variables, and in particular climatically-controlled variation in decomposition rate, are the primary drivers of the global distribution of major symbioses. We estimate that ectomycorrhizal (EM) trees, which represent only 2% of all plant species[8], constitute approximately 60% of

tree stems on Earth. EM symbiosis dominates forests where seasonally cold and dry climates inhibit decomposition, and are the predominant symbiosis at high latitudes and elevation. In contrast, arbuscular mycorrhizal (AM) trees dominate aseasonally warm tropical forests and occur with EM trees in temperate biomes where seasonally warm-and-wet climates enhance decomposition. Continental transitions between AM and EM dominated forests occur relatively abruptly along climate driven decomposition gradients, which is likely caused by positive plant-microbe feedbacks. Symbiotic N-fixers, which are insensitive to climatic controls on decomposition compared with mycorrhizal fungi, are most abundant in arid biomes with alkaline soils and high maximum temperatures. The climatically driven global symbiosis gradient we document represents the first spatially-explicit, quantitative understanding of microbial symbioses at the global scale and demonstrates the critical role of microbial mutualisms in shaping the distribution of plant species.

Microbial symbionts strongly influence the functioning of forest ecosystems. They exploit inorganic, organic[2] and/or atmospheric forms of nutrients that enable plant growth[1], determine how trees respond to elevated CO_2[6], regulate the respiratory activity of soil microbes[3,9], and affect plant species diversity by altering the strength of conspecific negative density dependence[10]. Despite growing recognition of the importance of root symbioses for forest functioning[1,6,11] and the potential to integrate symbiotic status into Earth system models that predict functional changes to the terrestrial biosphere[11,12], we lack spatially-explicit, quantitative maps of the different root symbioses at the global scale. Generating these quantitative maps of tree symbiotic states would link the biogeography of functional traits of belowground microbial symbionts with their 1.5 trillion host trees[13], spread across Earth's forests, woodlands, and savannas.

The dominant guilds of tree root symbionts, arbuscular mycorrhizal (AM) fungi, ectomycorrhizal (EM) fungi, ericoid mycorrhizal (ErM) fungi, and nitrogen (N)-fixing bacteria (N-fixer) are all based on the exchange of plant photosynthate for limiting macronutrients. The AM symbiosis is the oldest of the four, having evolved nearly 500 million years ago, with EM, ErM and N-fixer plant taxa having evolved multiple times from an AM basal state. Plants that form the AM symbiosis are markedly more diverse than the other symbiotic groups, comprising nearly 80% of all terrestrial plant species, and principally rely on AM fungi for enhancing mineral phosphorus (P) uptake[14]. EM fungi evolved more recently from saprotrophic ancestors, and as a result may be better than AM fungi at competing with free living soil microbes for resources[3]. As such, some EM fungal lineages are more capable of mobilizing organic sources of soil nutrients (particularly nitrogen) compared with AM fungi[15,16]. Association with EM fungi, but not AM fungi, has been shown to allow trees to accelerate photosynthesis in response to increased atmospheric CO_2 when soil nitrogen (N) is limiting[6] and to inhibit soil respiration by decomposer microbes[3,9] (but see [17]). Because increased plant photosynthesis and decreased soil respiration both reduce atmospheric CO_2 concentrations, the EM symbiosis is associated with buffering the Earth's climate against anthropogenic changes.

In contrast to mycorrhizal fungi, which extract nutrients from the soil, symbiotic N-fixers (Rhizobia and Actinobacteria) convert atmospheric N_2 to plant-usable forms. Symbiotic N-fixers are responsible for a large fraction of biological soil-N inputs, which can increase N-availability in forests where they are locally abundant[18]. Both N-fixing bacteria and EM fungi often demand more plant photosynthate than does the AM symbiosis[14,19,20]. Because tree growth and reproduction are limited by access to inorganic, organic and atmospheric sources of N, the distribution of these root symbioses is likely to reflect both environmental conditions that maximize the cost-benefit ratio of symbiotic exchange as well as physiological constraints on different symbionts.

In one of the earliest efforts to understand the functional biogeography of plant root symbioses, Sir David Read[21] categorically classified biomes by their perceived dominant mycorrhizal type and hypothesized that seasonal climates favor hosts associating with EM fungi due to their ability to compete directly for organic N. By contrast, it has been proposed that sensitivity to low temperatures has prevented N-fixers from dominating outside the tropics, despite the potential for N-fixation to alleviate N-limitation in boreal forests[20,22]. However, global scale tests of these proposed biogeographic patterns and their proposed climate drivers are lacking or inconclusive[23-25] and we have no understanding of the regional variations in this proposed latitudinal trend. To address this research gap, we compiled the first global ground-sourced survey database to reveal numerical abundances of each symbiosis across the global forested biomes, rather than incidence (presence or absence, e.g.,[23-25]), which is essential for identifying the shapes and potential mechanisms underlying transitions in forest symbiotic state along climatic gradients[26,27].

We determined the abundance of tree symbioses using GFBi, an extension from the plot-based Global Forest Biodiversity (GFB[28]) database, which contains over 1.2 million forest inventory plots of individual-based measurement records from which we derive abundance information for entire tree communities (Figure 1).

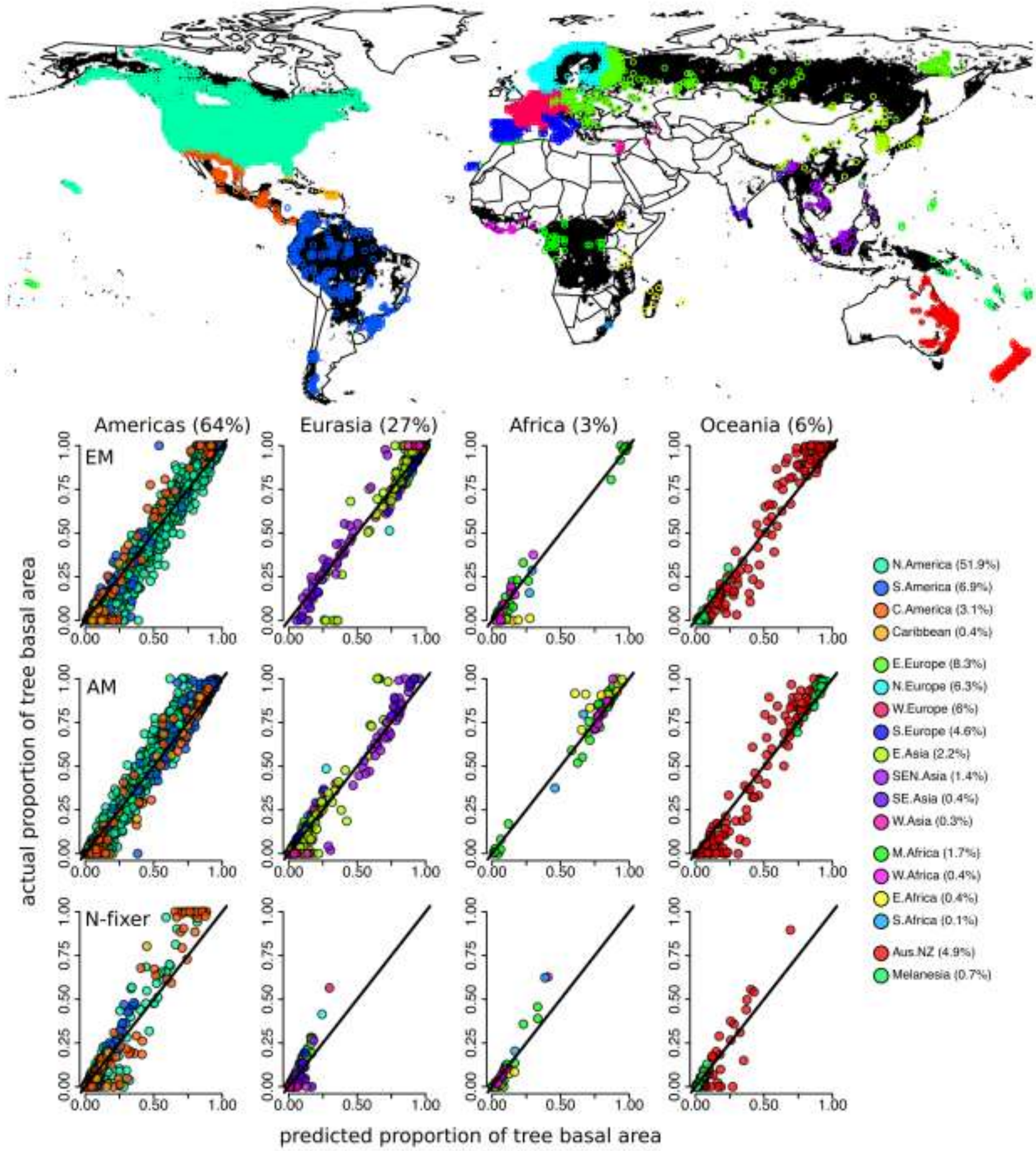

Figure 1. A map of 1 by 1 degree grid cells where we analyzed the proportion of tree stems and basal area for different symbiotic guilds (above). Circles show the location of training data, colored by geographic origin, while black squares show the extent of model projections. Panels below the map show actual vs. predicted proportion of basal area for ectomycorrhizal (EM), arbuscular mycorrhizal (AM), and N-fixer trees by continent and subregion, and demonstrate globally consistent model performance.

Using published literature on the evolutionary histories of mycorrhizal and N-fixer symbioses[8,25,29-33], we assigned plant species from the GFBi to one of 5 symbiotic guilds: AM, EM, ErM, N-fixer, and non- or weakly-mycorrhizal (NM). Most plants with symbioses derived from the AM state retain the genetic potential to associate with AM fungi[14]. Thus, consistent with other studies in this field[29], we assigned tree species to the AM-exclusive guild if they were not EM, ericoid mycorrhizal, non-mycorrhizal, or N-fixers. While there is some uncertainty in such assignments, direct investigation of mycorrhizal status when done supports this assumption[34]. Because individual measurements of mycorrhizal colonization are not possible at this scale, our models represent potential symbiotic associations.

To identify the key factors structuring symbiotic distributions we assembled 70 global predictor layers: 19 climatic (annual, monthly, and quarterly temperature and precipitation variables), 14 soil chemical (total soil N density, microbial N, C:N ratios and soil P fractions, pH, cation exchange capacity), 5 soil physical (soil texture and bulk density), 26 vegetative indices (leaf area index, total stem density, enhanced vegetation index means and variances), and 5 topographic variables (elevation, hillshade) (Table S7). Because decomposition is the dominant process by which soil nutrients become available to plants, we generated 5 additional layers that estimate the climatic control of decomposition. We parameterized decomposition coefficients according to the Yasso07 model[35,36] using the following equation:

$$k = \mathrm{Exp}(0.095T_i - 0.00014\, T_i^2)\,(1\text{-}\mathrm{Exp}[\,-1.21\, P_i]), \qquad (1)$$

where P_i and T_i are precipitation and mean temperature, either quarterly or annually, and the constants 0.0095 ($=\beta_1$) -0.00014 ($=\beta_2$) , and -1.21 ($=\gamma$) are parameters fit using a previous global study of leaf litter mass-loss[36]. Although local decomposition rates can vary significantly based on litter quality or microbial community composition[37], climate is the primary control at the global scale[36]. Decomposition coefficients describe how fast different chemical pools of leaf litter lose mass over time relative to a parameter, α, that accounts for leaf-chemistry. Decomposition coefficients (k) with values of 0.5 and 2 indicate a halving and doubling of decomposition rates relative to α, respectively (Supplemental Materials).

Given the large set of possible environmental predictors, we used the random forest machine-learning algorithm to identify the best predictors of global symbiosis distributions. The random forest algorithm averages multiple regression trees, each of which uses a random subset of all the model variables to predict a response. These regression trees identify optimal values along a predictor-gradient to "split" the model response into different nodes (e.g., predictions could be "split" into nodes of 50 or 75% of EM basal area depending on whether mean annual temperature is > or < 20°C). We ranked the importance of each variable according to inc node purity, which measures the decrease in model error that occurs whenever the response is split on that variable (Figure 2ABC). We first determined the influence and relationship of all 75 predictor layers on forest symbiotic state and then optimized our models using a stepwise reduction in variables, from least- to most-important. Soil chemical, vegetative, and topographic variables were the first to be eliminated from our models in this way. In a subsequent model that included only layers of climate, decomposition, and certain soil physical and chemical information, we found that the 4 most important variables accounted for >85% of the explained variability. We plot the partial-fits of these four variables for each symbiotic guild (Figure 2ABC).

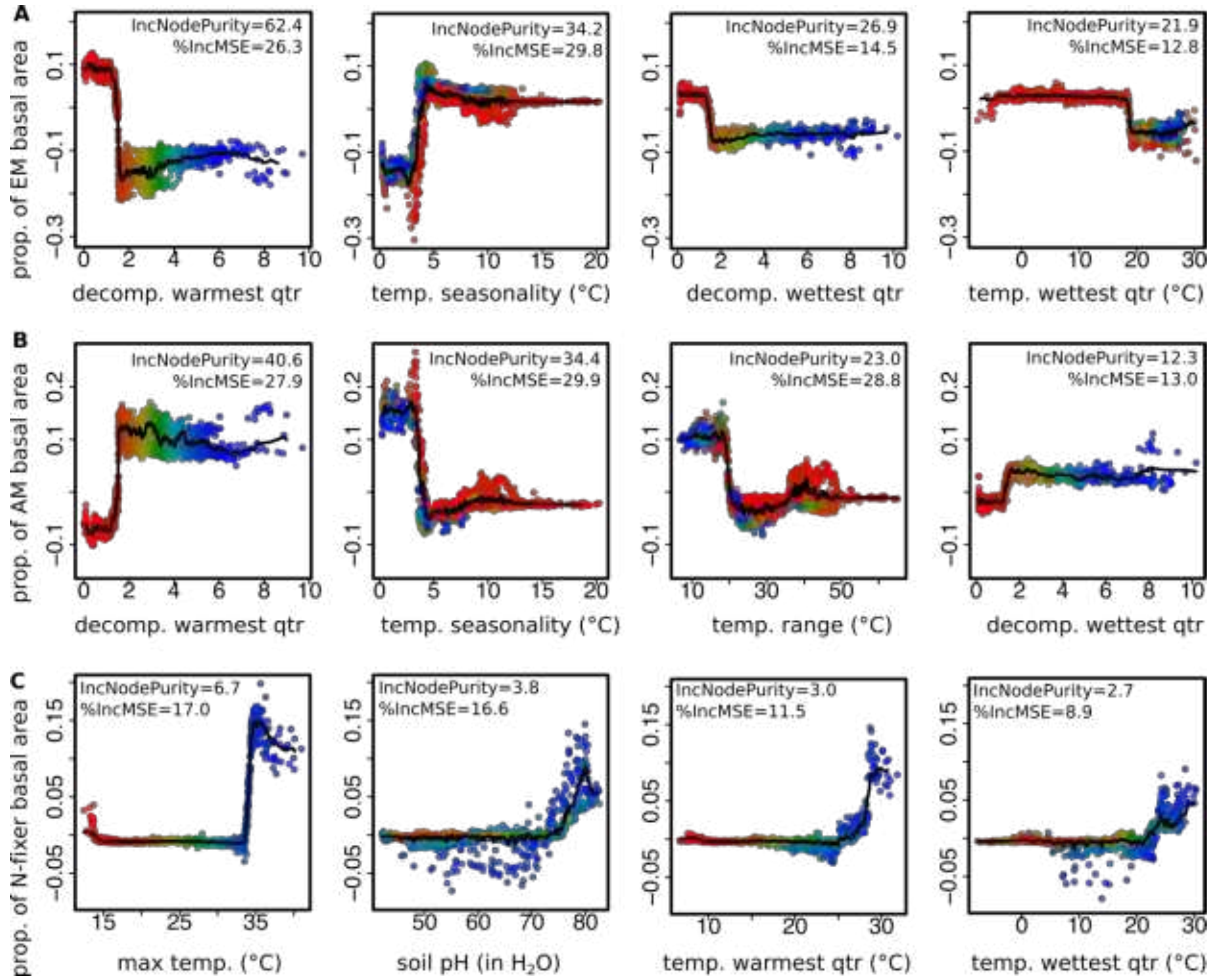

Figure 2. Partial plots of residual variation explained by the four most important predictors of the proportion of tree basal area belonging to the (A) ectomycorrhizal (EM), (B) arbuscular mycorrhizal (AM), and (C) N-fixer symbiotic guilds. Variables are listed in declining importance from left to right, as determined by inc node purity, with points colored with a red-green-blue gradient according to their position on the x-axis of the most important variable (left-most panels for each guild), allowing cross visualization between predictors. Each panel lists two measures of variable importance, inc node purity (used for sorting) and %IncMSE (see Supplemental Information for description). Decomposition rates in (A) and (B) are in units of leaf litter mass loss per quarter. The abundance of each symbiont type transitions sharply along climatic gradients, suggesting that sites near the threshold are particularly vulnerable to switching their dominant symbiont guild with climate changes.

The three most numerically abundant tree symbiotic guilds each have reliable environmental signatures, with the four most important predictors accounting for 81, 79, and 52% of the total variability in EM, AM, and N-fixer relative basal area, respectively. Models for

ErM and NM lack strong predictive power given the relative rarity of these symbiotic states amongst trees, although the raw data do identify some local abundance hotspots for ErM (Figure S1). As a result, we focus the remainder of results and discussion on the three major tree symbiotic states (EM, AM, N-fixer). Despite the fact that data from N. and S. America constitute 65% of the training data (at the 1 by 1 degree grid scale), our models accurately predict the proportional abundances of the three major symbioses across all major geographic regions (Figure 1). The high performance of our models, which is robust to both K-fold cross-validation and rarefying samples so that all continents are represented with equal depth (Figures S10-12), suggest that regional variations in climate (including indirect effects on decomposition) and soil pH (for N-fixers) are the primary factors influencing the relative dominance of each guild at the global scale (geographic origin only explained ~2-5% of the variability in residual relative abundance) (Figure 1BCD, Table S8).

Random forest models should not be projected across predictor gradients that fall outside the ranges of their training data (e.g., grid cells with higher mean annual temperatures than the maximum used to fit the models). To prevent the over-projecting of our models over pixels where we lacked training data, we subset a global grid of predictor layers depending on whether (1) the grid cell fell within the top 60% of land surface with respect to tree stem density[13] and either (2) fell within the univariate distribution of all the predictor layers from our training data and/or (3) fell within an 8-dimensional hypervolume defined by the unique set of the 4-best predictors of the relative abundance of each guild (Figure 2, Supplemental Materials). We then projected our models across only those grid cells that met these criteria, which constitutes 46% of the global land surface and 88% of global tree stems (Figure 1; Figure S16). While model validation indicates that our projections are robust, additional ground truthing of predictions to identify any discrepancies would be incredibly valuable. If such discrepancies exist they can help fine tune climate-symbiosis models, or identify areas where climate might favors invasion by symbioses that have not yet evolved or dispersed to a particular biogeographic region.

In contrast to a recent global analysis of root traits, which concluded that plant evolution has favored reduced dependence on mycorrhizal fungi[38], we find that trees associating with the relatively more C-demanding and recently-derived EM fungi[14,19] represent the dominant tree-symbiosis. By taking the average proportion of EM trees, weighted by spatially-explicit global predictions for tree stem density[13], we estimate that approximately 60% of trees on earth are EM, despite the fact that only 2% of plant species associate with EM fungi (vs. 80% associating with AM fungi)[8,29]. Outside of the tropics, the estimate for EM relative abundance increases to approximately 80% of trees.

Turnover among the major symbiotic guilds results in a tri-modal latitudinal abundance gradient, with the proportion of EM trees increasing (and AM trees decreasing) with distance from the equator, while N-fixing trees reach peak abundance in the arid zone around 30 degrees (Figure 3A, Figure 4). These trends are driven by abrupt transitional regions along continental climatic gradients (Figure 2), which skew the distribution of symbioses among biomes (Figure 3A) and drive strong patterns across geographic and topographic features that influence climate. For example, moving north or south from the equator, the first transitional zone separates warm (aseasonal), AM-dominated, tropical broadleaf forests (>75% median basal area, vs. 8% for EM trees) from the rest of the EM-dominated world forest system (Figure 2AB; Figure 3A). It stretches longitudinally across 25 degrees N and S, just beyond the dry tropical broadleaf forests (with 25% EM tree basal area; Figure 3A), where average monthly temperature variation reaches 3-5°C (Figure 2AB).

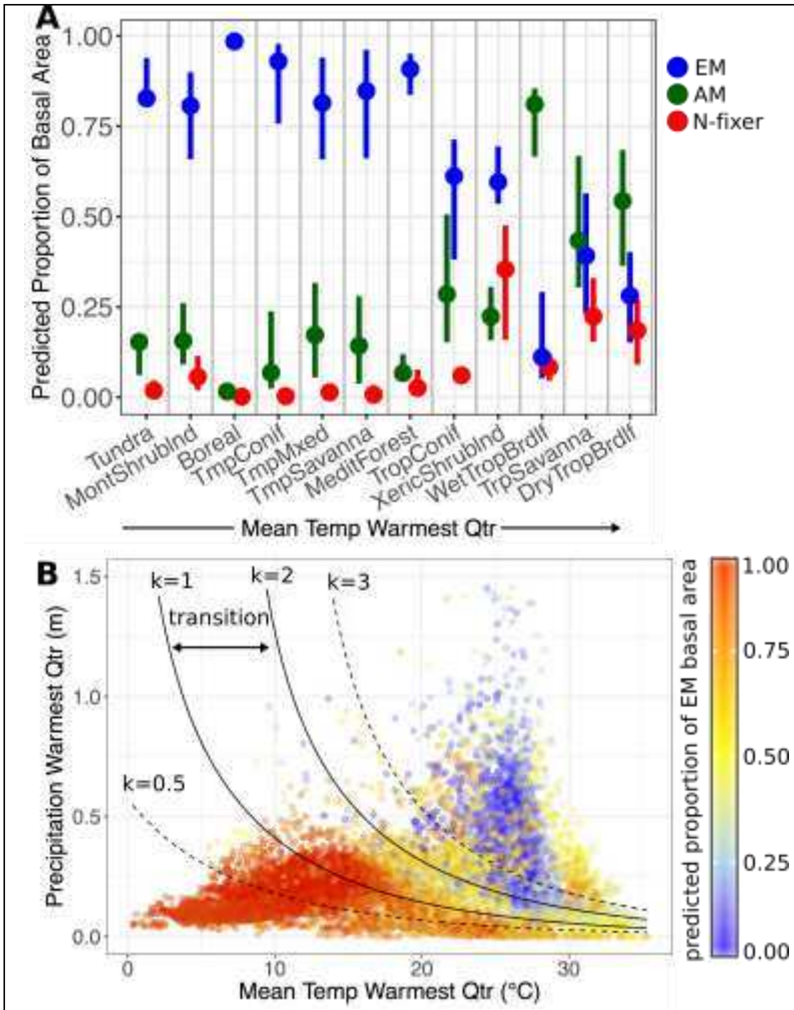

Figure 3. (A) The median proportion of tree basal area per biome (arranged in order of increasing mean temperature of the warmest quarter) for ectomycorrhizal (EM), arbuscular mycorrhizal (AM), and N-fixer symbiotic guilds. EM trees dominate all extra-tropical biomes. (B) The dependency of decomposition coefficients (k, solid and dotted lines) on temperature and precipitation during the warmest quarter with respect to predicted dominance of mycorrhizal symbiosis. AM forests transition to EM forests abruptly in the region between k=1 and 2, which is consistent with positive feedback between climatic and biological controls of decomposition.

Moving further N or S, the second transitional climate zone separates regions where decomposition coefficients during the warmest quarter of the year are less than 2 (see Figure 3B for the associated temperature and precipitation ranges). In N. America and China, this transition zone spans longitudinally around 50 degrees N, separating the mixed AM / EM temperate forests from their neighboring EM dominated boreal forests (75 vs 100% EM tree basal area, respectively; Figure 3A). This transitional decomposition zone bypasses W. Europe, which has temperature seasonality > 5°C, but lacks sufficiently wet summers to accelerate decomposition coefficients beyond values associated with mixed AM/EM forests. The latitudinal transitions in symbiotic state observed among biomes are mirrored by within-biome transitions along elevation gradients. For example, in tropical Mexico, warm and wet quarter decomposition coefficients < 2 occur along the slopes of the Sierra Madre, where mixed AM-exclusive and N-fixer woodlands in arid climates transition to EM dominated tropical coniferous forests (75% basal area, Figure 3A, Figure 4ABC, Figure S17-19). The southern hemisphere, which lacks the landmass to support extensive boreal forests, experiences a similar latitudinal transition in decomposition rates along the ecotone separating its tropical and temperate biomes, around 28 degrees S.

The abrupt transitions that we detected between forest symbiotic states along environmental gradients suggest that positive feedbacks may exist between climatic and biological controls of decomposition[11,36]. In contrast to AM fungi, some EM fungi can use oxidative enzymes to mineralize organic nutrients from leaf litter, converting nutrients to plant-usable forms before transferring them to their host trees[2,5]. Relative to AM trees, the leaf litter of EM trees is also chemically more resistant to decomposition, with higher C:N ratios and higher concentrations of decomposition-inhibiting secondary compounds[11]. Thus, EM leaf litter can exacerbate climatic barriers to decomposition, promoting conditions where EM fungi have superior nutrient-acquiring abilities to AM-fungi[5,11]. Such positive-feedbacks are known to cause abrupt ecosystem transitions along smooth environmental gradients between woodlands and grasses: trees suppress fires, which promotes seedling recruitment, while grass fuels fires, which kill tree seedlings[39]. Our study provides the first evidence that rapid transitions in tree community structure along climate gradients could also be governed by positive-feedbacks between symbiotic guilds and nutrient cycling; although other types of interactions, such as environmentally sensitive competition hierarchies among symbiotic guilds, could also lead to abrupt transitions without specifically invoking feedback effects. In either case, the existence of abrupt transitions suggests that trees and associated microbial symbionts in transitional regions along decomposition gradients should be susceptible to drastic turnover in symbiotic state with future environmental changes[40].

To illustrate the sensitivity of global patterns of tree symbiosis to climate change, we use the climate relationships we developed for current climate to project potential changes due to climate change. Relative to our global predictions using the most recent climate data, model predictions using the projected climates for 2070 suggest the abundance of EM trees will decline by as much as 10% (using a relative concentration pathway of 8.5 W/m^2; Figure S25). Due to their position along decomposition gradients relative to the abrupt shift from EM to AM forests (Figure 2AB), our models predict the largest declines in EM abundance will occur along the boreal-temperate ecotone, although declines in species abundances can lag decades, or even centuries or millennia, behind associated climatic changes[41]. The predicted decline in EM trees corroborates the results of common garden transfer and simulated warming experiments, which demonstrate that some important EM hosts will decline at the boreal-temperate ecotone in altered climates[42-44]. Because of the low tree diversity in boreal forests, tree species loss around transition zones may have major consequences for forest related economic activity[45].

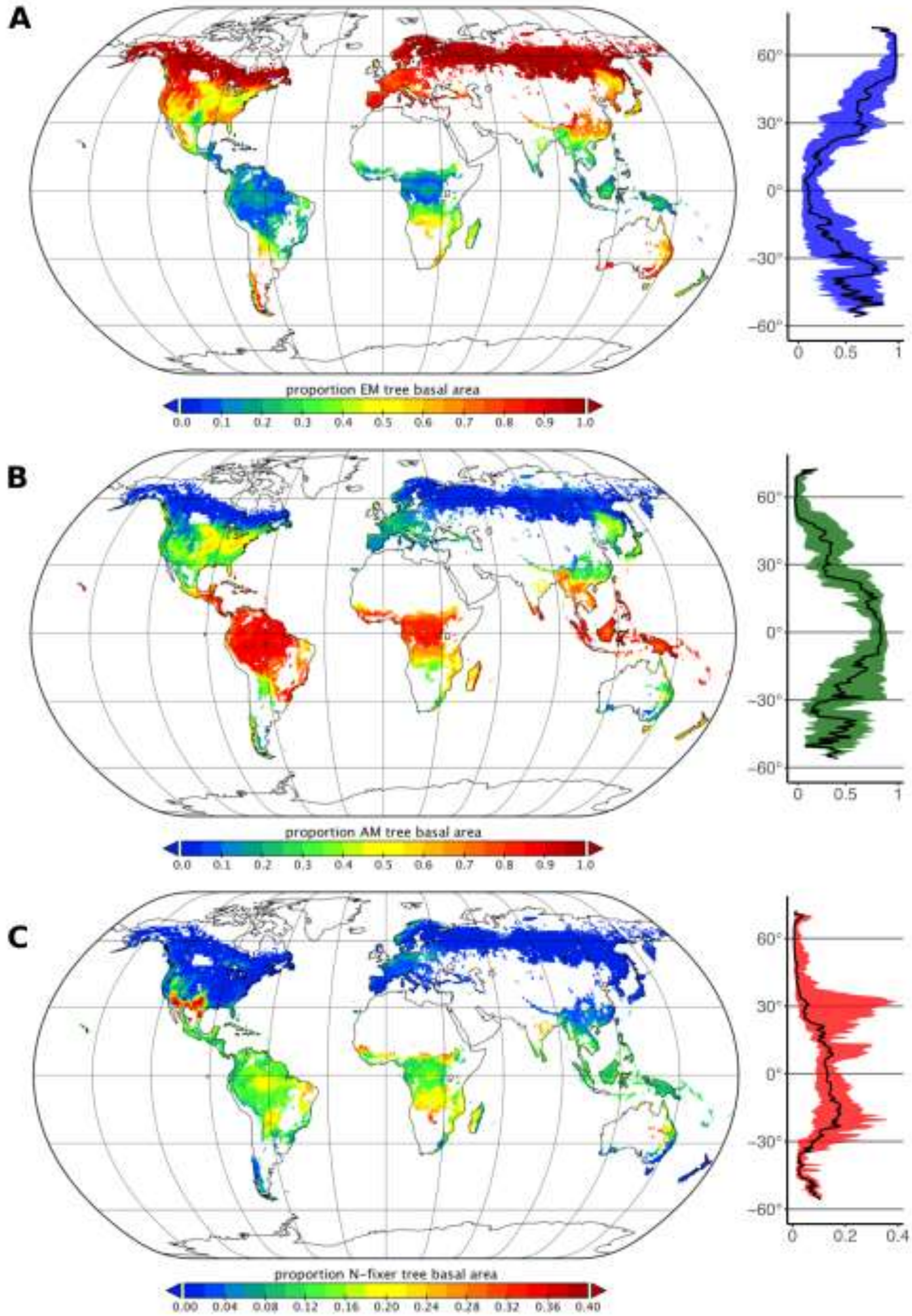

Figure 4. Predicted global maps (left) and latitudinal gradients (right, with solid line indicating the median and colored ribbon spanning the range from the 5% and 95% quantiles) of the proportion of tree basal area for (A) ectomycorrhizal (EM), (B) arbuscular mycorrhizal (AM), and (C) N-fixer symbiotic guilds.

The change in dominant nutrient exchange symbioses along climate gradients highlights the interconnection between atmospheric and soil compartments of the biosphere. The transition from AM to EM dominance corresponds with a shift from P to N limitation of plant growth with increasing latitude[46-48]. Including published global projections of total soil N or P, microbial N, or soil P fractions (labile, occluded, organic, and apatite) did not increase the amount of variation explained by the model or alter the variables identified as most important, and thus were dropped from our analysis. However, this does not necessarily mean that soil nutrient availability is unimportant at the global scale, as the best-available global data likely do not adequately represent local nutrient availability[49,50]. Rather, our finding that climatic controls of decomposition best predict the dominant mycorrhizal associations mechanistically links symbiont physiology with climatic controls of soil nutrient release from leaf litter. These findings are consistent with Read's hypothesis[21] that slow decomposition at high latitudes favors EM fungi due to their increased capacity to liberate organic nutrients[2]. Thus, while more experiments are necessary to understand the specific mechanism by which nutrient competition favors dominance of AM or EM symbioses[26], we propose that the latitudinal and elevational transitions from AM to EM dominated forests be called Read's Rule.

While our analyses focus on prediction at large spatial scales appropriate to the available data, our findings with respect to Read's Rule also provide insight into how soil factors structure the fine-scale distributions of tree symbioses within our grid cells. For example, while at a coarse scale we find that EM trees are relatively rare in many wet tropical forests, individual tropical sites in our raw data span the full range from 0 – 100 % EM basal area. In much of the wet tropics, these EM dominated sites exist as outliers within a matrix of predominantly AM trees. In an apparent exception that proves Read's Rule, in aseasonal warm neotropical climates, which accelerate leaf-decomposition and promote regional AM dominance (Figure 3), EM dominated tree stands can develop in sites where poor soils and recalcitrant litter slow decomposition and N mineralization[26,51]. Landscape-scale variation in the relative abundance of symbiotic states also changes along climate gradients, with variability highest in xeric and temperate biomes (Figure S2), suggesting that the potential of local nutrient variability to favor particular symbioses is contingent on climate.

Whereas EM trees are associated with ecosystems where plant growth is thought to be primarily N-limited, N-fixer trees are not. Our results highlight the global extent of the "N-cycling paradox," wherein some metrics suggest that N-limitation is greater in the temperate zone[46-48], yet N-fixing trees are relatively more common in the tropics[20,52,53] (Figure 3A). We find that N-fixers, which we estimate represent 7% of all trees, dominate forests with annual max temperatures >35°C and alkaline soils (particularly in North America and Africa, Figure 2C). They have the highest relative abundance in xeric shrublands (24%), tropical savannas (21%), and dry broadleaf forest biomes (20%), but are nearly absent from boreal forests (<1%) (Figure 3A, Figure 4). The decline in N-fixer tree abundance we observed with increasing latitude is also associated with a previously documented latitudinal shift in the identity of N-fixing microbes, from facultative N-fixing rhizobial bacteria in tropical forests to obligate N-fixing actinorhizal bacteria in temperate forests[52]. Our data are not capable of fully disentangling the several hypotheses that have been proposed to reconcile the N-cycling paradox[20,54]. However, our results are consistent with the model prediction[22] and regional empirical evidence[27,55,56] that N-fixing trees are particularly important in arid biomes. Based primarily on the observed positive, nonlinear association of N-fixer relative abundance with the mean temperature of the hottest month (Figure 2C), our models predict a two-fold increase in N-fixer relative abundance when transitioning from humid to dry tropical forest biomes (Figure 3A).

Although soil microbes are a dominant component of forests, both in terms of diversity and ecosystem functioning[5,6,11], identifying global-scale microbial biogeographic patterns remains an ongoing research priority. Our analyses confirm that Read's Rule, which is one of the first proposed biogeographic rules specific to microbial symbioses, successfully describes global transitions between mycorrhizal guilds. More generally, climate driven turnover among the major plant-microbe symbioses represents a fundamental biological pattern in the Earth system, as forests transition from low-latitude arbuscular mycorrhizal, to N-fixer, to high-latitude ectomycorrhizal ecosystems. The predictions of our model (which we make available as a global raster layer) can now be used to represent these critical ecosystem variations in global biogeochemical models used to predict climate-biogeochemical feedbacks within and between trees, soils, and the atmosphere. Additionally, the layer containing the proportion abundance of N-fixing trees can be used to map potential symbiotic N-fixation, which links together atmospheric pools of C and N. Future work can extend our findings to incorporate multiple plant growth forms and non-forested biomes, where similar patterns likely exist, to generate a complete global perspective. Our predictive maps leverage the most comprehensive global forest dataset to generate the first quantitative global map of forest tree symbioses, demonstrating how nutritional mutualisms are coupled with the global distribution of plant communities.

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