Title: Climate drives the global biogeography of forest tree symbioses

Authors: *Steidinger BS*[1]***, *Crowther TW*[2]*†**, *Liang J†*[3,4]***, *Van Nuland ME*[1], *Werner GDA*[5], *[Full GFBI Author LIST]*[6], *and Peay KG*[1]*†*

Affiliations:
[1] Department of Biology, Stanford University, Stanford CA USA
[2] Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland
[3] Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA
[4] Research Center of Forest Management Engineering of State Forestry Administration, Beijing Forestry University, Beijing, China
[5] Department of Zoology, University of Oxford, Oxford UK

*These authors contributed equally to this work and share the first-author
†Corresponding authors: Email kpeay@stanford.edu; albeca.liang@gmail.com; tom.crowther@usys.ethz.ch

One Sentence Summary: Climate structures the turnover of functionally distinct tree-microbial symbioses across the world's forested biomes.

Abstract:

Given that the activity of most trees is underpinned by their associated symbiotic microorganisms in soil, identifying the factors controlling the distribution of symbiotic partners is integral to understanding 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 31 million stems representing over 28 thousand tree species. We reveal marked latitudinal turnover in major symbioses, with ectomycorrhizal and arbuscular mycorrhizal symbiosis dominating at high and low latitudes, respectively. Our analyses indicate that climate is the primary determinant of which symbiotic guild dominates a given biome. Ectomycorrhizal trees, which we estimate constitute 60% of all stems globally (and >80% outside of the tropics), dominate forests with cold wet-seasons and high seasonal variability in temperature. Arbuscular mycorrhizal trees, by contrast, occur in aseasonal forests with hot wet-seasons. Symbiotic N-fixers reach peak abundance in arid biomes with alkaline soils and high maximum temperatures. The existence of a climatically driven global symbiosis gradient, which we call Read's Rule, represents one of the most prominent biogeographic patterns on the planet, and demonstrates the tight coupling of nutrient exchange mutualisms with the global distribution of plant communities.

Main Manuscript:

An emerging body of evidence suggests that the functioning of forest trees is underpinned by their relationships with symbiotic microorganisms (*1-7*), and that the identity of the microbial symbionts in a given area determines the ability of trees to access limiting nutrients from the soil (*4, 5*), sequester carbon (*3, 6*) and withstand the impacts of climate change (*2*). Despite growing recognition of the importance of root symbioses for forest functioning (*2, 4, 8*) and the potential to integrate symbiotic status to earth system models that predict functional changes to the terrestrial biosphere (*8, 9*), little progress has been made in mapping their distribution at the global scale. The absence of such data represents an important gap in our understanding of the functional traits that influence plant distributions and our ability to anticipate how biomes will function in future environments.

The primary guilds of tree root symbionts, arbuscular mycorrhizal (AM) fungi, ectomycorrhizal (EM) fungi, and nitrogen (N)-fixing bacteria (N-fixer), differ markedly in evolutionary history but are all based on exchange of plant photosynthate for limiting macronutrients, coupling the cycling of atmospheric C with soil N and phosphorus (P) (*8*). AM symbiosis is the ancestral state of all land plants and AM fungi are particularly important for enhancing mineral P uptake (*10*). EM fungi evolved more recently from saprotrophic ancestors (10), and as a result are better competitors with free living soil microbes (*6*), and more effectively mobilize organic sources of soil nutrients (particularly N) compared with AM fungi (*11*). Likewise, by converting atmospheric N_2 to plant usable forms, symbiotic N-fixers (Rhizobia and Actinobacteria) are responsible for the majority of biological soil-N inputs, and act as "nitrostats" that enhance N-availability and productivity in forests where they are locally abundant (*4, 12*). However, EM fungi and N-fixing bacteria often require greater investment of plant photosynthate compared with AM symbiosis (*10*). As a result, the distribution of these associations will reflect both environmental conditions that maximize cost-benefit ratio of symbiotic exchange as well as physiological constraints on different symbionts.

In one of the original efforts to map the functional biogeography of symbiosis, Read (*13*) hypothesized that slower decomposition rates in colder, seasonal climates at high latitudes favors hosts associating with EM fungi with stronger decomposition abilities (enabling them to directly access organic N), whereas warmer, aseasonal climates at lower latitude regions select for AM symbioses. Similarly, temperature sensitivity has been proposed as a key limitation on the abundance of N-fixers outside the tropics (*14, 15*). However, empirical tests of the underlying distributional patterns and their proposed climate drivers to date are inconclusive, in part due to reliance on regional datasets that may miss key transitions if responses are non-linear or vary across biogeographic regions (*16, 17*), or use datasets that do not accurately represent plant abundance (e.g., (*18-20*)).

To counter this limitation, we determined the abundance of tree symbioses using GFBi, an extension from the plot-based global forest biodiversity database (GFB, (*21*)), which contains individual-based measurement records from which we derive real abundance information for entire tree communities. We used published literature on the evolutionary histories of mycorrhizal and N-fixer symbioses to assign plant species from the GFBi to one of 3 symbiotic guilds – EM, AM, or N-fixer (ericoid mycorrhizal and non- or weakly-mycorrhizal trees were classified but represented only a small fraction of individuals so were excluded from further analysis). Because AM symbiosis is the ancestral state of all land plants and because most EM and N-fixing plants retain the genetic potential to associate with AM fungi (10), we modeled AM-only trees as the disjoint of all other states. While there is some uncertainty in such assignments, direct investigation of mycorrhizal status when done supports this assumption (*22*). Thus, while some new cases of EM or N-fixing symbioses are likely to be discovered in the future they are unlikely to significantly influence our results. We aggregated the plot level abundance (basal area and number of stems) of each symbiotic type to a 1 by 1 degree grid (Figure 1) along with 19 bioclimatic (*23*) and 10 soil-physical/chemical characteristics (Supplmental Methods). Next, we used the randomForest algorithm to determine how soil and climatic factors influence the proportional abundance of each guild (Figure 2) and projected our statistical models across a global grid of predictors (Figures 3

& 4) (see Supplemental Materials for full description). Because individual measurements of mycorrhizal colonization are not possible at this scale it is important to note that our models represent potential symbiotic associations and not colonization intensity.

We found that tree symbiotic guilds have reliable climatic signatures, with seasonal temperatures accounting for the majority of variability in the proportion of EM, AM, and N-fixer basal area (83, 79, and 52% explained variability, respectively; Figure 1BCD). Including total soil N or P, microbial N, 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 were dropped from our analysis. Our models performed well across all major geographic regions (Figure 1), indicating that climate, rather than biogeographic history, is generally the dominant factor influencing relative dominance of each guild (geographic origin explained ~2-5% of the variability in residual relative abundance). However, residuals do indicate a few locations which deviate somewhat from global trends. For example, the island of Borneo has higher abundance of EM symbiosis than expected given its climate (48% vs. 10% predicted, see Eurasian outliers in Figure 1B). Whether such deviations arises from unmeasured environmental variables or unique evolutionary history is an important question for future research.

Latitudinal trends in the dominant symbiotic guild are driven by abrupt transitions along climatic gradients. As a result, the distribution of symbioses are highly skewed (Figure 2). EM trees reached maximum abundance where it is cold during the wet season, temperatures vary seasonally, and annual high temperatures are suitably low (Figure 2A). As a result they dominate boreal, tundra, and temperate coniferous forest biomes and are the least common in tropical broadleaf forests (>90% vs. 8% median basal area, respectively) (Figure 3). AM trees have the opposite trend, reaching peaks in a-seasonal forests with hot wet-seasons (Figure 2B), dominating tropical broadleaf forest biomes (79%) but occurring at low densities in boreal and tundra forests (<3%) (Figure 3). These patterns in turnover among the dominant symbiotic guilds are reflected in a tri-modal latitudinal abundance gradient, with the proportion of EM trees increasing (and AM trees decreasing) moving away from the equator, while N-fixing trees increase in abundance in the arid zone around 30 degrees (Figure 4). Projection of climate models to the extent of global forests allows us to estimate that 60% of tree stems on earth are EM (and 80% of stems outside of the tropics), despite the fact that only 2% of plant species associate with EM fungi (vs. 80% associating with AM fungi) (*24*, *25*). N-fixing trees form a lower proportion of global forest stems (~7%). Global dominance of EM symbiosis in forests is particularly notable given the much older evolutionary origin of AM symbiosis. While AM fungi have been identified in fossilized roots from the early Devonian (400 mya (*26*)), the oldest EM fungal fossils are associated with the late Jurassic or early Cretaceous (156 mya (*27*)). This suggests that since their evolution EM fungi have displaced AM fungi as the dominant symbionts of trees from all extra-tropical forest biomes (Figure 4ab).

The transition from AM to EM dominance corresponds with a general shift from P to N limitation with increasing latitude (*15, 28, 29*). While soil variables were not predictive of mycorrhizal dominance at the global scale, climate exerts strong control over rates of decomposition and nutrient availability (*30*), and available global data on nutrient standing stocks may not adequately represent nutrient availability (*31*). Thus, while climate is a key state factor influencing global patterns in mycorrhizal symbiosis, the effect is likely indirect through controls over local nutrient cycles. While experiments are necessary to understand the precise mechanisms determining the competitive dominance of AM and EM symbioses (*32*), David Read hypothesized (*13*) that slow decomposition and N limitation at high latitude favors EM fungi due to their increased capacity to liberate organic nutrients, which is supported by recent genomic and physiological studies (*5*). Thus, we propose that the latitudinal transition from AM to EM dominated forests be called Read's Rule. While our analyses were conducted on plots aggregated at a large scale (i.e. one degree cells), recent empirical and theoretical studies examining fine-scale variation in the abundance of AM and EM symbioses are consistent with this mechanism. For example, in the tropics, where high temperature and precipitation promotes faster decomposition and regional AM dominance (Figure 3), EM trees can dominate in sites where poor soil quality and recalcitrant litter slow decomposition and N mineralization (*16*).

The same logic implies that N-fixing trees, which have access to atmospheric pools of N, should also peak in abundance in temperate climates. Instead, our results highlight the global extent of the "N-cycling paradox," which describes how N-limitation is greater in the temperate zone (*28*), yet N-fixing trees are relatively more common in the tropics (*14, 15, 33*) (Figure 3c). We find that N-fixers dominate arid biomes with higher maximum temperatures and alkaline soils (particularly in North America and Africa, Figure 2C), and are the most common in xeric shrublands (24%), tropical savannas (21%), and dry broadleaf forest biomes (20%), but are nearly absent from boreal forests (<1%) (Figure 3). Our data is not capable of fully resolving the several hypotheses that have been proposed to reconcile the N-fixers paradox (*15, 34*). However, our results are consistent with model prediction (*14*) and recent empirical evidence (*17*) that N-fixing trees are particularly important in arid biomes. While past work has focused primarily on the difference between humid tropical and temperate forests (*15*), the humid-dry tropical forest transition deserves additional attention (*17*). Although not part of our investigation, regional studies have shown that equally important shifts in the identity of N-fixing symbionts, from rhizobial to actinorrhizal, also occur with increasing latitude (*14*). In addition, the tri-modal pattern we reveal suggests that N-fixing tree abundance should be also be considered in the light of other dominant root symbioses.

While the qualitative patterns we document here match long-standing hypotheses about the processes that regulative forest symbioses (*13, 35*), our models additionally identify the location of non-linear and abrupt transitions among symbiotic guilds along environmental gradients. The location and shape of these responses (Figure 3) have implications for how the global forest system is likely to change with anthropogenic climate changes. To illustrate, relative to our global predictions using historical climate data (1960-1980), substituting projected climates for 2070, the abundance of EM trees declines by as much as 10% (using a relative concentration pathway of 8.5 W/m^2; Supplemental Information). Our models predict the largest declines will occur along the boreal-temperate ecotone, where stimulated warming experiments also demonstrate that EM hosts will decline in altered climates (*36-38*). Given their longevity, tree declines would likely lag decades behind climatic change in the absence of extreme drought or fire events. However, given the low tree diversity in these biomes, tree species declines around transition zones may have major consequences for forest related economic activity (*39*).

Although soil microbes are a dominant component of forests, both in terms of diversity and ecosystem functioning (*1, 2, 8*), the identification of large-scale microbial biogeographic patterns have remained elusive (*40*). To our knowledge Read's Rule is the first biogeographic rule for microbial organisms. While this represents a fundamental biological pattern in the earth system, the predictions of our model, which we make available as a global raster layer, can be also applied as a "missing-link" in earth system models used to predict climate-biogeochemical feedbacks with couplings of atmospheric C with soil N and P. For example, our data layer can integrate the mycorrhizal associated nutrient economy (*8*), which describes differences in nutrient cycling between forests dominated by arbuscular and EM trees, into global Community Land Models that describe climate-biological feedbacks using plant function traits (*9*). Additionally, the proportion of N-fixing tree layer can be used to map the strength of forest nitrostats, which boost productivity by mobilizing atmospheric N and organic P. Finally, our predictive maps leverage the most comprehensive global forest dataset to generate the first quantitative global map of forest symbiosis, which describes the co-occurrence between plant and microbial functional traits across every forested biome on the planet earth.

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Figure Captions [Figures in Separate Document]

Figure 1. A) a map of 1 by 1 degree grid cells where we analyzed the proportion of tree stems and basal area for different symbiotic guilds, with points colored by geographic subregion. BCD) The actual vs. predicted proportion of basal area for ectomycorrhizal (EM), arbuscular mycorrhizal (AM), and N-fixers, respectively, by region. The model performs well across all geographic regions, suggesting that climate, rather than location, controls the relative abundance of each guild.

Figure 2. Partial plots of the four most important predictors of the proportion of tree basal area belonging to the ectomycorrhizal (A), arbuscular mycorrhizal (B), and (C) N-fixer guilds. Variables are listed in declining importance from left to right, as determined by inc node purity, with points colored according to their location along the gradient of the most important variable. The abundance of each symbiont type transitions sharply along climatic gradients, suggesting that sites that sit near the threshold are particularly vulnerable to climate changes.

Figure 3. A summary of the median proportion of tree basal area per biome (with bars indicating interquartile range) for ectomycorrhizal (EM), arbuscular mycorrhizal (AM), and N-fixer symbiotic guilds. EM trees dominate all extra-tropical biomes.

Figure 4. Predicted maps of the proportion of tree basal area for (a) ectomycorrhizal (EM), (b) arbuscular mycorrhizal (AM), and (c) N-fixer symbiotic guilds (left), along with the latitudinal gradients in relative abundance. Grid cells with fewer than 100 stems were omitted.

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