



Climate mismatches with ectomycorrhizal fungi contribute to migration lag in North American tree range shifts

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Climate change will likely shift plant and microbial distributions, creating geographic mismatches between plant hosts and essential microbial symbionts (e.g., ectomycorrhizal fungi, EMF). The loss of historical interactions, or the gain of novel associations, can have important consequences for biodiversity, ecosystem processes, and plant migration potential, yet few analyses exist that measure where mycorrhizal symbioses could be lost or gained across landscapes. Here, we examine climate change impacts on tree-EMF codistributions at the continent scale. We built species distribution models for 400 EMF species and 50 tree species, integrating fungal sequencing data from North American forest ecosystems with tree species occurrence records and long-term forest inventory data. Our results show the following: 1) tree and EMF climate suitability to shift toward higher latitudes; 2) climate shifts increase the size of shared tree-EMF habitat overall, but 35% of tree-EMF pairs are at risk of declining habitat overlap; 3) climate mismatches between trees and EMF are projected to be greater at northern vs. southern boundaries; and 4) tree migration lag is correlated with lower richness of climatically suitable EMF partners. This work represents a concentrated effort to quantify the spatial extent and location of tree-EMF climate envelope mismatches. Our findings also support a biotic mechanism partially explaining the failure of northward tree species migrations with climate change: reduced diversity of co-occurring and climate-compatible EMF symbionts at higher latitudes. We highlight the conservation implications for identifying areas where tree and EMF responses to climate change may be highly divergent.

climate change | ectomycorrhizal fungi | mycorrhizal symbiosis | range shifts | species distribution modeling

Climate change is shifting the environmental context in which species interactions take place. Warming trends have been shown to create spatial and temporal mismatches between plants and their symbiotic partners, ultimately to the detriment of critical ecosystem functions and services (1, 2). As species migrate in response to climate change, historical interactions may collapse with declining niche overlap between partners, and novel interactions may form as species colonize newly suitable habitats (3, 4). Predicting where climate disruptions could uncouple species interactions or shift interaction hotspots will help conservation and management strategies adapt to protect against biodiversity loss and maintain ecosystem functioning. While this has begun for some aboveground species interactions (e.g., plant–pollinator networks; 5, 6), few studies have examined how climate change may create large-scale mismatches belowground, for example, between plant and soil microbial distributions.

Biogeographic mismatches driven by climate change might arise if plants and microbes respond to different climate variables, if they differ in their sensitivity to the same variable, or if they vary in migration potential (7). Plant species' risks to climate change are often considered based on shrinking climate suitability (8) or proximity to their climate niche edge (9). For example, forecasts of North American tree species distributions show that many species may lose suitable climate habitat, especially in the contiguous United States, but there is high species-level variation (10). While climate-based models predict rapid northward tree range shifts, these predictions do not match observations from large-scale forest inventory data (11–14). To explain this inconsistency, one hypothesis is that aboveground–belowground species interactions hinder tree migration. However, the possibility that climate disequilibrium with microbial symbionts is limiting tree range shifts has not been tested on a broad scale.

Ectomycorrhizal fungi (EMF) form symbiotic associations with plant roots and are important regulators of forest health and soil functioning (15–17), with estimates that 60% of all tree stems on Earth form EMF symbioses (18). Recent work predicts that warming could reduce EMF diversity in pine-dominated forests by over 25% in some regions (19). This assumes that tree and fungal species distributions are static and that plant–fungal interactions will respond similarly at different climate boundaries. These assumptions begin to fail when considering that EMF differ in dispersal abilities and climate envelope shifts (20, 21), are unequally distributed across plant host ranges (22), and can both facilitate host range expansions at leading edges

Significance

Predicting where climate change might disrupt species interactions is critical to protect against biodiversity loss and maintain ecosystem functioning. This is particularly true for tree symbioses with ectomycorrhizal fungi (EMF), which are widespread and regulate key aspects of forest productivity, species composition, and nutrient cycling. Here, we assess the risk of climate change to overlapping habitat suitability of tree species and their EMF partners across North American forest ecosystems. Our results show that climate change will negatively impact 35% of tree-EMF partnerships by shrinking their shared habitat conditions. We also find that tree migration lag is linked to reduced diversity of EMF partners, indicating that symbiotic disequilibrium is a challenge facing tree species responses to climate change.

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(23, 24) and limit host range contractions at trailing edges (25). Predicting the future state of forests thus requires an understanding of how spatial variation in tree species and EMF climate responses will create losses and gains of key symbioses and the implications for biodiversity and ecosystem functioning.

To this end, we assess the risk of climate disruptions to the codistribution of tree-ectomycorrhizal symbioses across North American forest ecosystems. To compare the climate suitability of tree species and EMF pairs, we used tree species occurrence records (26), forest inventory data (27), and soil fungal data from two continental-scale sequencing projects (28, 29). Combining these fungal datasets, encompassing 541 plots located across 110 sites and nearly 6,000 soil samples in total, created a unique opportunity to address this knowledge gap by providing EMF information at a relevant geographic and climatic scale to compare with their plant host distributions (SI Appendix, Fig. S1; 30). We created Maxent species distribution models (SDM, 31) for 50 common EMF-associating tree species using half a million occurrence records and 400 EMF species that were most prevalent across sites. The SDM approach incorporated AICc-based sensitivity analysis of Maxent tuning parameters, as well as five-fold random cross-validation for estimating robust cutoffs in habitat suitability to make binary spatial predictions of species' presence vs. absence. We filtered tree-EMF species comparisons based on plot-level co-occurrence data to account for mycorrhizal host specificity, acknowledging that these symbioses are a function of both phylogenetic and geographic proximity. This resulted in ~9,000 unique comparisons of climate niches between North American tree species and possible EMF partners (SI Appendix, Table S1). Using a previously described spatial analysis framework (SI Appendix, Fig. S1; 11), we developed four main research questions:

- 1) If tree and EMF suitable habitat is predicted to shift northward with climate change overall, do "hotspots" of climate overlap between tree-EMF pairs also increase in latitude?
- 2) How do future climate forecasts affect the amount of suitable climate overlap between trees and EMF partners?

- 3) Are climate envelope mismatches between tree-EMF pairs similar at northern and southern boundaries?
- 4) Does EMF diversity at climate boundaries predict tree species migration potential estimated from large-scale forest observations?

Results

The climate suitability for most tree and EMF species is projected to shift northward. Comparing future vs. present climate scenarios results in positive latitudinal changes at both northern and southern boundaries for 48 of 50 tree species ($\chi^2 = 135$, $P < 0.001$; Fig. 1A) and 296 of 400 EMF species ($\chi^2 = 556$, $P < 0.001$; Fig. 1B). A smaller portion of EMF species (84 of 400) show expanding latitudinal distributions with increasing suitable climate boundaries northward and southward. Climate envelope model performance was generally high; the SDM True Skill Statistic across all EMF species was 0.421 ± 0.148 (mean ± 1 SD), and across all tree species was 0.390 ± 0.010 (mean ± 1 SD).

Geographic changes in climate suitability affect the location and extent of climate niche overlap between tree-EMF pairs. Compiling EMF species climate niches for each tree family resulted in shared climate hotspots of EMF diversity (i.e., areas predicted to contain the most EMF species with similar climate tolerances). Comparing the peaks in predicted richness distributions, these hotspots move north by 3.8° latitude on average under future climates relative to present conditions (Fig. 2).

Climate change increases the total area of suitable climate overlap between all tree-EMF pairs by 30% overall, or approximately 226,000 km² ($F_{1,17173} = 1,084.7$, $P < 0.001$; Fig. 3A). Most tree-EMF pairs show expanding amounts of climate overlap. Some of the biggest climate "winners" for tree species are *Populus deltoides*, *Quercus alba*, *Carpinus caroliniana*, and *Fagus grandifolia* that have increasing overlap with more than 80% of their potential EMF partners (SI Appendix, Fig. S2). However, 35% of all tree-EMF pairs are at risk of shrinking their total area of shared climate suitability (Fig. 3B). This includes

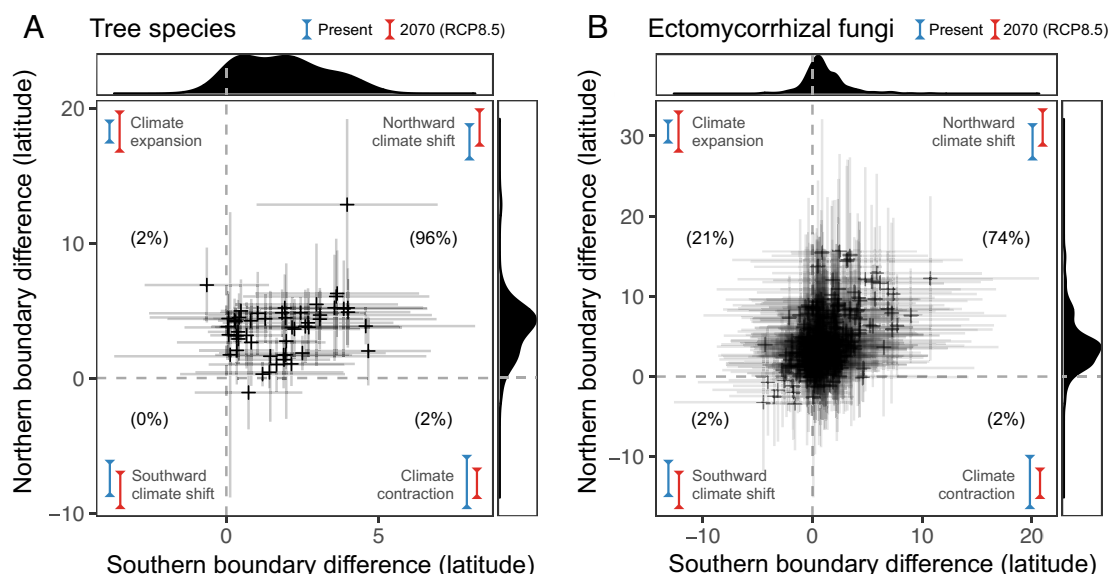


Fig. 1. Geographic changes in climate envelopes for tree species and EMF across North America. We analyzed how the suitable climate boundaries of 50 tree species (A) and 402 EMF species (B) change at southern and northern locations (2.5% and 97.5% percentiles, respectively) between present and future climates (2070 RCP8.5). The four quadrants show different climate suitability scenarios under climate change (illustrated with red and blue bars): expansion further north and south overall (Top Left); shift toward higher latitude at both northern and southern boundaries (Top Right); shift toward lower latitude at both northern and southern boundaries (Bottom Left); or contraction toward lower latitudes at northern boundaries and higher latitudes at southern boundaries (Bottom Right). Center points are mean latitude difference distribution values for each tree or EMF species summarized across longitude bands ± 1 SD (gray error bars).

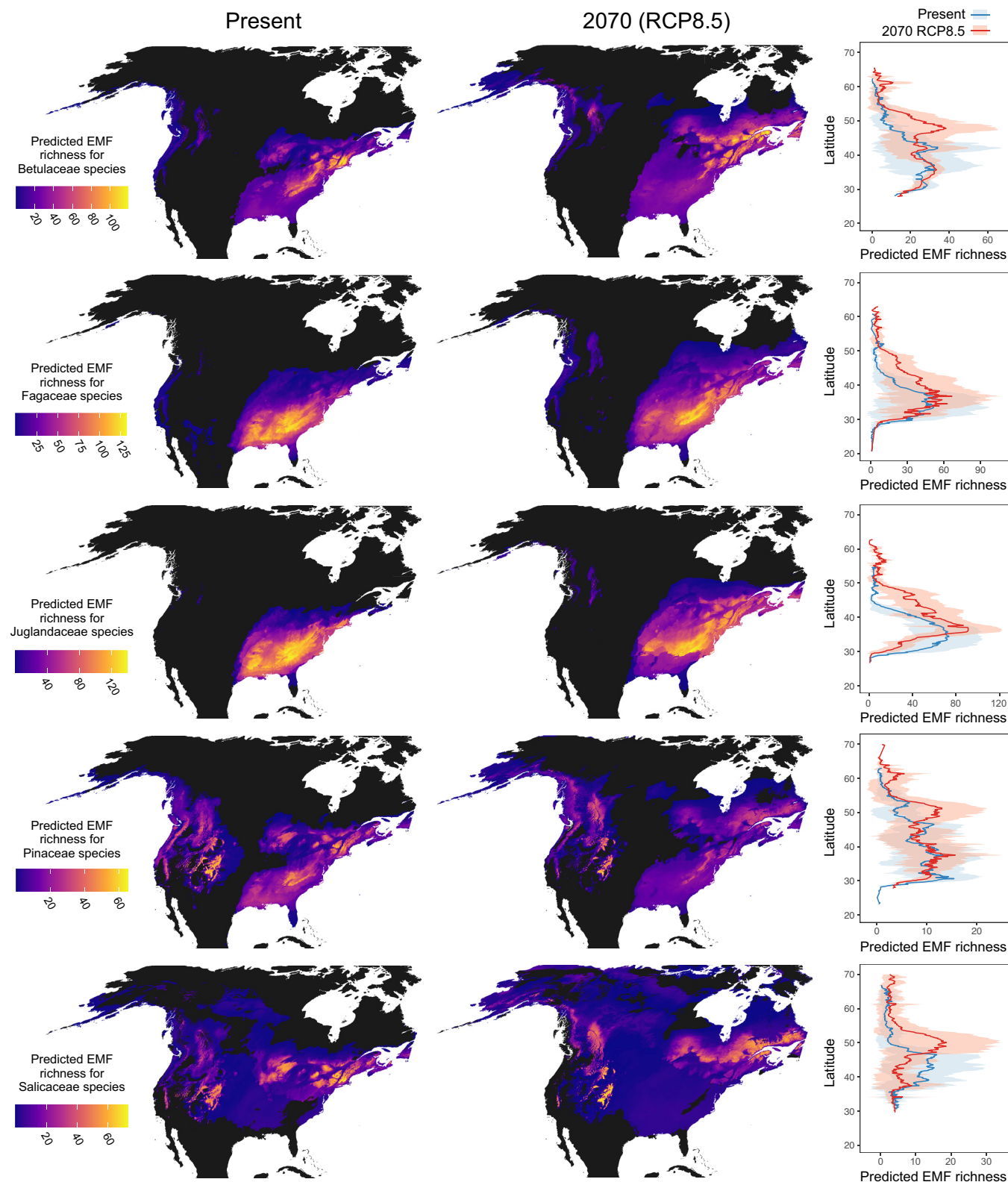


Fig. 2. Geographic hotspots of suitable climate overlap between tree-EMF species pairs. We analyzed how climate change affects the cumulative area where EMF SDMs predict overlapping climate suitability with co-occurring tree species. Predicted EMF richness maps reflect the sum of overlapping climate suitability between a given tree species and all their EMF partners. Maps show family-level trends as the sum divided by the number of tree species per family. Brighter colors indicate potential interaction hotspots—areas predicted to support a greater number of co-occurring and climatically compatible tree-EMF symbioses. Maps show tree-EMF hotspots under the present and future climate scenarios. Plots on the right show how predicted EMF richness changes with latitude for each climate scenario, with trend lines showing mean composite richness extracted across longitude bands ± 1 SD (shaded area).

mean negative trends across two or more host tree families for *Coltriciella*, *Gymnomyces*, *Laccaria*, *Phylloporus*, *Pisolithus*, *Tomentellopsis*, and *Tricholoma* fungal genera (Fig. 3C and *SI Appendix*, Fig. S3). Net

changes in total overlapping climate area with EMF partners vary by tree family (climate scenario $\times$ family interaction: $F_{4,17173} = 101.0$, $P < 0.001$; *SI Appendix*, Fig. S4), with Juglandaceae and Fagaceae

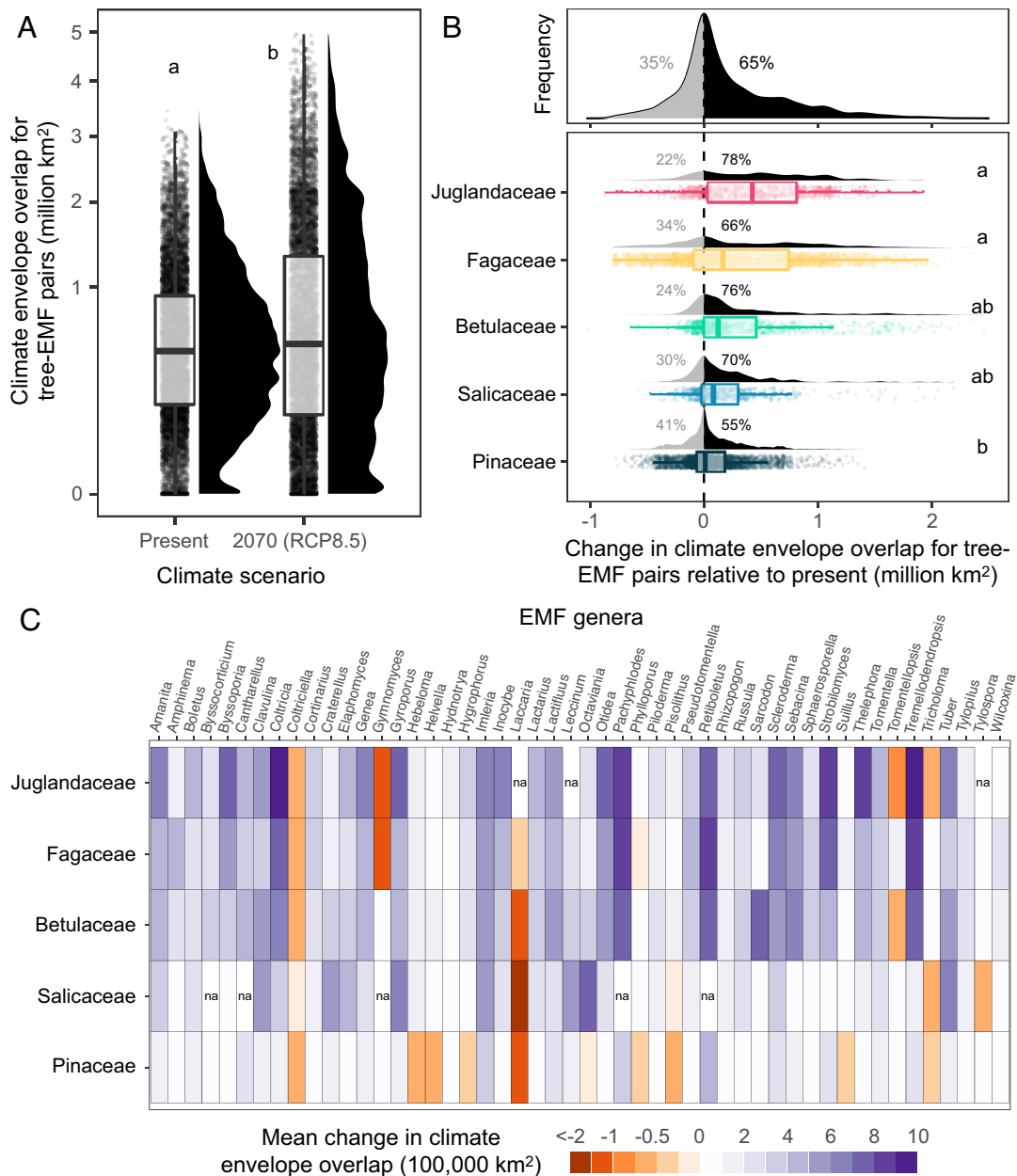


Fig. 3. Climate change effects on the total suitable climate overlap between tree-EMF pairs. (A) Total area of suitable climate overlap across all tree-EMF pairs. Note that the Y-axis is scaled by a square root transformation. (B) Changes in the extent of tree-EMF suitable climate overlap between current and future climate projections. The *Top* distribution shows that climate change may shrink the geographic extent of shared climate niches for 35% of tree-EMF pairs overall. The *Bottom* plot shows how this distribution varies among tree families. (C) Mean change in suitable climate overlap across the top 50 EMF genera for each tree family. Orange colors indicate negative change, and purple colors indicate positive change.

having the largest positive responses and Pinaceae having the most negative responses to climate change. Some of the most at-risk Pinaceae species include *Abies lasiocarpa*, *Pinus contorta*, *Pinus elliotii*, and *Pinus virginiana* that show reductions in future climate overlap with 70 to 90% of EMF partners (SI Appendix, Fig. S2).

Climate envelope mismatches between trees and EMF partners are greatest at northern climate boundaries. Mismatches are defined as the absolute latitudinal difference between a tree species and EMF partners at their climate niche edges (97.5th and 2.5th percentile of suitable climate areas). Climate change effects on tree-EMF mismatches are 67% larger at northern vs. southern boundaries (climate scenario $\times$ boundary interaction: $F_{1,34830} = 22.3$, $P < 0.001$; Fig. 4A). This equates to an average increase in climate suitability misalignment by 1.2° latitude at northern edges, and 0.6° latitude at southern edges.

For 60% of all tree-EMF pairs, mismatches become larger in future climates relative to present levels (Fig. 4B), but this proportion varies by tree family (SI Appendix, Fig. S5). In particular, Salicaceae have a higher proportion of EMF partners that become more mismatched in future climates than Fagaceae and Juglandaceae, which show a more even split of EMF partners becoming more aligned vs. mismatched at their climate niche edges (Fig. 4B).

As a consequence of greater climate envelope mismatch, the northern boundaries of tree hosts are expected to contain less diverse EMF communities. We predicted EMF richness by summing the present climate suitability predictions of all co-occurring EMF species across a given tree species climate envelope. We then used longitude band analysis to estimate the mean richness of climate-compatible EMF at the southern (2.5th percentile), center (50th percentile), and

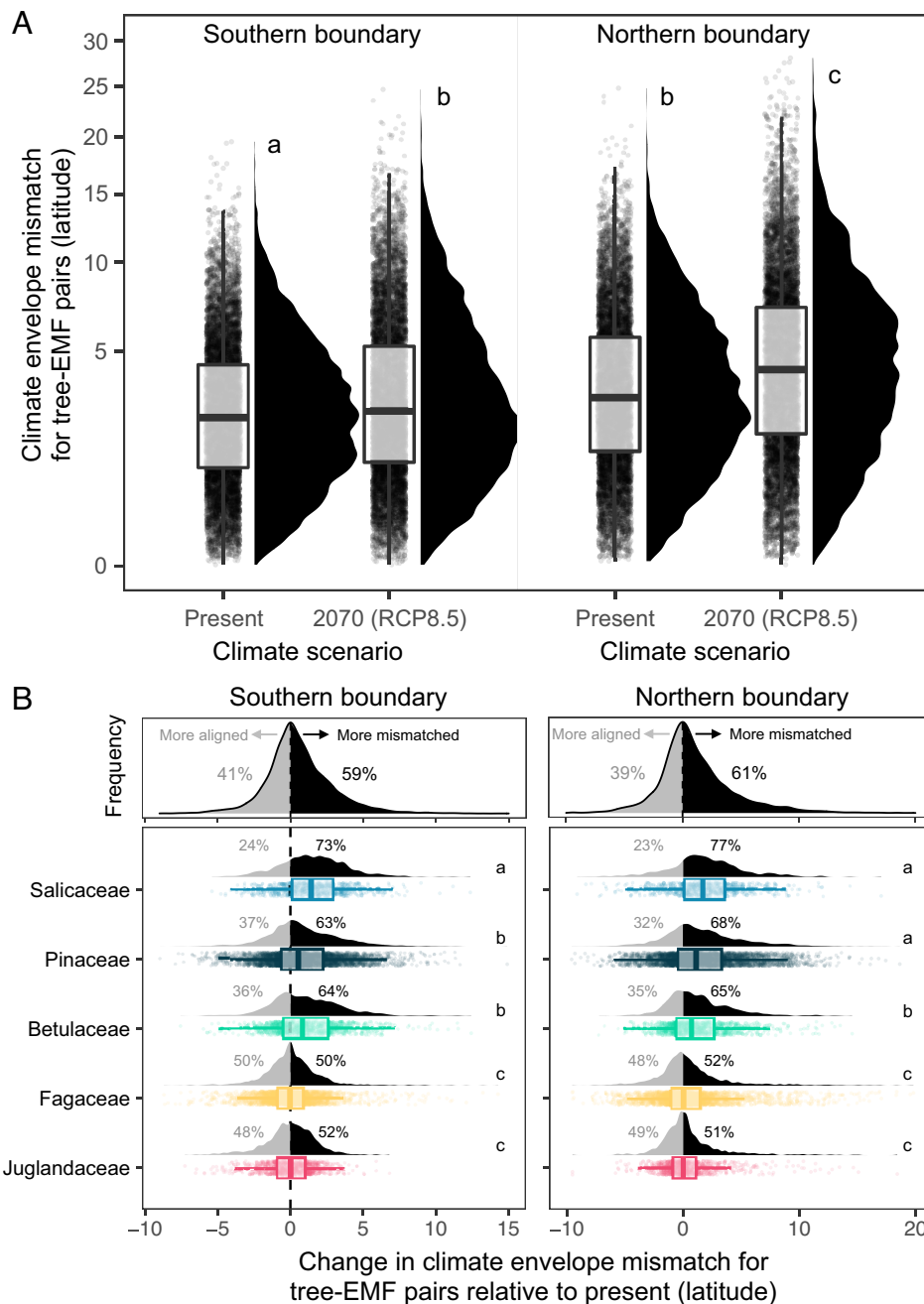


Fig. 4. Climate envelope mismatches between tree-EMF pairs. (A) We quantified mismatch as the absolute latitude difference in climate suitability between tree-EMF pairs at their southern and northern boundaries (2.5% and 97.5% percentiles of latitudinal distributions, respectively). (B) Latitude change in suitable climate mismatch between tree-EMF pairs at southern and northern boundaries. The *Top* distributions show how climate change is predicted to increase the latitudinal mismatch of climate suitability across all tree-EMF pairs. The *Lower* distributions show how this varies among tree families.

northern (97.5th percentile) latitude positions of tree species climate niches. On average, climate-compatible EMF richness is 65% lower at the northern limits vs. center locations of tree climate niches ($F_{2,135}=14.1$, $P < 0.001$; Fig. 5A).

We used large-scale forest inventory data (US Forest Inventory and Analysis, FIA) to estimate tree species migration potential as the current latitude difference between seedling vs. adult tree occurrences at their distribution extremes (97.5th and 2.5th percentiles of occurrence records). Because the FIA data are restricted to US states, we focused on the 25 tree species with predominantly US distributions. Only two of these species suggest limited evidence consistent with northward range shifts (uncertainty estimates overlap zero), compared to 22 species that show stronger signs of latitude contraction ($\chi^2 = 213$, $P < 0.001$; Fig. 5B).

Moreover, tree migration potential is positively associated with predicted EMF species richness ($r^2 = 0.07$, $P = 0.04$; Fig. 5C). Specifically, trees with greater latitude contraction have less diverse EMF species pools at range edges that contain climate-compatible partners. Oppositely, increasingly rich communities of co-occurring EMF climate partners seem to buffer against tree range contractions and trend toward promoting tree range shifts. This pattern only exists using data from co-occurring tree-EMF pairs. Repeating the analysis using total (unfiltered) predicted EMF richness showed no significant correlation with tree migration potential ($r^2 = 0.02$, $P = 0.16$; *SI Appendix, Fig. S6*), suggesting that the co-occurrence based screening of tree-EMF comparisons captures biologically meaningful aspects of these symbioses.

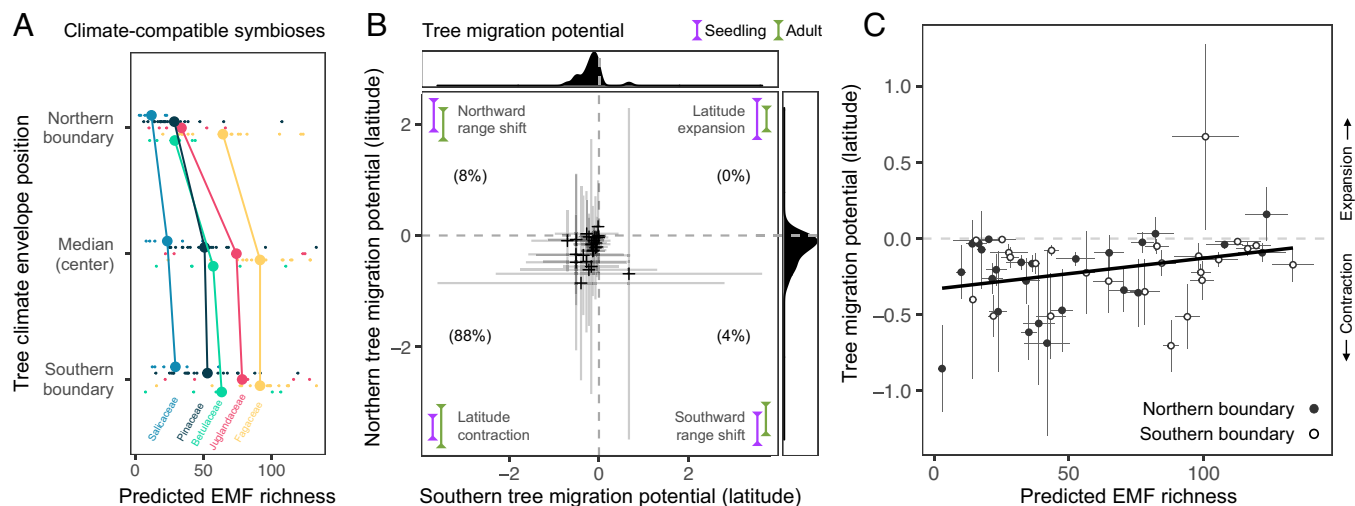


Fig. 5. Reduced diversity of climate-compatible EMF partners corresponds with lower tree migration potential. (A) We predicted EMF richness for each tree species by summing the climate suitability models of all co-occurring EMF partners based on overlap with their host tree climate niche. We then calculated the species pool of climate-compatible EMF partners at the southern, central, and northern climate positions of tree hosts. The line plot shows how the predicted EMF species pool richness varies across these positions. Colors indicate tree families, small points are tree species, and large points are tree family averages. (B) We used large-scale forest inventory measurements to estimate tree species migration potential by calculating latitude differences between seedlings vs. adult trees at their southern and northern extremes (2.5% and 97.5% percentiles of occurrence records, respectively). The four quadrants represent the possible migration scenarios: seedlings at higher latitudes than adult trees at both northern and southern boundaries (*Top Left*); seedlings expand further north and south than adult trees (*Top Right*); adult trees expand further north and south than seedlings (*Bottom Left*); and seedlings at lower latitudes than adult trees at both northern and southern boundaries (*Bottom Right*). Center points are mean latitude difference distribution values for each seedling–adult tree species comparisons summarized across longitude bands ± 1 SD (gray error bars). (C) Comparison of tree species migration potential and predicted richness of climate-compatible EMF partners. Center points are mean values summarized across longitude bands ± 1 SE (error bars).

Discussion

Climate change research has largely focused on understanding risks at the species level, but interactions among species will ultimately be responsible for significant community and ecosystem-level changes. For trees, an extensive body of literature has documented the critical role of competition in determining the species composition (32)—and thus function—of the forests they comprise. More recently, microbial interactions have been identified as key modifiers of competitive interactions between plants (33, 34). For example, the type of mycorrhizal association a tree forms and the availability of mycorrhizal fungi change key demographic rates (35–37) and tree species coexistence (38). Despite this, there is still little concrete information on how plant–mycorrhizal interactions will likely change in the future due to shifting climate conditions. Our goal was to link tree species and EMF distributions under changing climate scenarios to predict the likelihood and extent of geographic mismatches in these important symbioses. By doing so, we show that trees and many of their fungal mutualists have nonidentical climate niches, meaning that interactions (not just species) are at risk of local extinction from geographic detachment of shared habitat suitability—changes that are likely to affect broader forest resilience to climate change.

Interaction mismatches have been discussed in the context of plant and microbial climate change responses (4, 7) but are rarely measured in a spatially explicit way. This work represents a large-scale attempt to characterize the spatial extent and positioning of such mismatches for tree–EMF associations across North America. One consequence of our modeling approach is that while EMF and their host plants are both considered to be functionally obligate participants in this mutualism (15), the lack of strong host specificity on the plant and fungal side means that their environmental niches and realized distributions are to some extent independent. This is implied by other studies on fungal species distributions (39) or host specificity (40), but here, we quantify the degree of independence across species climate envelopes

(Fig. 3). Although some tree hosts and EMF have nonoverlapping climate tolerances, our results show that climate change is expected to shift habitat suitability toward higher latitudes overall. Moving the geographic center for these interactions has implications for mycorrhizal-mediated ecosystem functions (41–43) and soil biodiversity conservation (44) if interaction diversity hotspots do not align with existing protected areas (Fig. 2).

Mycorrhizal fungi can strongly influence local biogeochemical cycles (16, 45), with clear evidence for different effects between mycorrhizal associations (i.e., EM vs. AM forests). However, it is less clear how compositional variation within mycorrhizal types affects ecosystem scale processes (46). Some evidence points toward key functions mediated by particular fungal groups, like how the genus *Tomentella* was strongly associated with differences in mycorrhizal-mediated carbon cycling in pine and oak forests (47). Similarly, the genus *Cortinarius* has been identified as critical for organic matter decomposition due to its large complement of manganese peroxidase enzymes (48). Yet, for many of the taxa for which we predict large changes in climate overlap with potential host trees, it is unclear what this may mean functionally, both for large contractions (e.g., *Coltriciella*, *Laccaria*) or expansions (e.g., *Coltricia*, *Tremellodendropsis*). This is in part because many of these taxa do not have sequenced genomes or have not been studied functionally due to difficulties propagating them. It is also unclear how much functional redundancy is present in EMF communities (28), compositional differences in local EMF communities have also been shown to alter N-uptake pathways and mediate tree growth response to eCO_2 (49). While it seems likely the mismatches we predict and the concomitant differences in community structure will alter ecosystem function in these areas, it remains to be determined exactly what these effects will be and whether they will be adaptive or maladaptive. Moving forward, new conservation and management approaches may need to be designed

that focus on areas where large mismatches in plant and fungal niches are anticipated to develop.

We used a bottom-up modeling approach to compare tree-EMF distributions, and top-down modeling (as in ref. 19) or integrated modeling (e.g., joint SDMs) might show different patterns. For instance, combining multiple single-species SDMs is known to overestimate community-level measures because it does not account for biotic filtering effects on community assembly (50). We do find that predicted EMF richness estimates from summed SDMs are positively correlated with observed EMF richness measured across sites (*SI Appendix, Fig. S7*), indicating that this approach is generally able to identify climate zones which support a higher diversity of EMF co-occurrences with a given tree species. However, modeling only the climate component of species fundamental niches is a limitation of this study, and future efforts comparing the realized niches of trees and fungi will likely improve predictions of at-risk symbioses by encompassing more of the biotic effects involved in shaping species distributions. For instance, joint species distribution modeling between trees and EMF would provide an interesting comparison to our results, but a full contrast is beyond the scope of the current study. Additionally, we did not incorporate SDM uncertainty into downstream analyses of climate niche comparisons between species, though we note that our cross-validation approach was designed to avoid strongly biased outputs. This could be an important step in future analyses for evaluating changes in tree-EMF symbioses with species distributions that are strongly vs. weakly controlled by climate. Nonetheless, our findings and approach offer a starting point to consider how the spatial extent of shared habitat suitability changes between plant hosts and a diverse group of belowground microbial symbionts.

We used local co-occurrence of tree and EMF species to screen for symbiont comparisons. This could be both underestimating and/or overestimating the actual number of partnerships. However, we note that 1) root tip sequencing and root-tracing to confirm established tree-EMF symbioses is unfeasible at this geographic scale, 2) the host breadth for most EMF species is largely unknown, and 3) our results support the biological relevance for screening tree-EMF pairs (*SI Appendix, Fig. S6*). As a result, we believe filtering comparisons based on local co-occurrence is a reasonable and reproducible way to balance possible biases in over- or underestimating symbiont pairs.

Climate change is expected to create winners and “losers” for tree-EMF symbioses in terms of total climate niche overlap. For example, *Laccaria*, a common fungal genus in many forests, is predicted to lose much of its shared climate habitat with four of the five tree families we included, and up to 200,000 km². Similarly, Pinaceae trees, which dominate many high-elevation and high-latitude forests, are expected to see shared climate contractions with 40% of the EMF we modeled. Previous work on mycorrhizal symbiosis and climate change has predominantly treated either mycorrhizal communities or tree hosts as fixed, like the recent predicted declines in EMF diversity and associated tree hosts near southern boreal forests (18, 19). Our approach is unique in that it explicitly accounts for the possibility that these interactions might shift their suitable climate distributions, providing important context for evaluating climate change impacts on mycorrhizal associations.

Species ranges are hypothesized to be determined by different ecological factors at opposing range boundaries, often summarized as northern edges limited by climate and southern edges limited by competition (51–53). Our results suggest that from a mycorrhizal perspective, climate change impacts on the codistribution of North American trees and EMF partners will be more apparent at northern boundaries. A number of other studies show that

boreal forests are a major area of concern for climate tipping points in soil fungal community change (30) where warming-induced shifts in EMF community structure have been linked to poor tree host performance (54). At the opposite end, EMF species appeared much less prone to southern climate contractions than trees (southern boundary difference near zero in Fig. 1*B*). This trend might indicate that EMF southern range limits are generally not controlled by climate, but more work is necessary to test alternative explanations. Compellingly, the longitude band analysis could be adapted to quantify localized trends in species dynamics at their latitude extremes, possibly revealing finer-scale patterns in range expansions and contractions across the entire length of a species’ boundary.

One simplifying assumption of many future range projections is that plant species will be able to migrate to keep pace with climate change. This assumption has been questioned with respect to differences in climate velocity across landscapes (55) as well as dispersal barriers (56). Here, we identify a unique biotic challenge to tree migration—symbiosis mismatch in climate compatibility. By comparing adult and seedling distributions in a large tree demographic database, we find that tree migration lag at northern range limits is correlated to fewer co-occurring EMF species with matching climate suitability. Certain tree species even appear to be retreating southward, indicating that broad-based seedling recruitment failure might be driving range contractions. For instance, fewer EMF species at tree range limits—which has been observed before (22)—could be amplifying the negative effects of nonclimatic stressors on recruitment (e.g., fire suppression, canopy closure, and deer overbrowsing) for some eastern temperate forest species. Lack of compatible EMF symbionts has been shown to hinder tree establishment during the invasion of new biogeographic regions (23) or in patchy habitats with contrasting mycorrhizal associations (20, 57). Given that most of the dominant trees in temperate and boreal forests are associated with EMF, this suggests that it is not simply the presence of EMF, but the presence of a diverse community of preferred, climatically compatible EMF partners that may be critical for promoting tree range shifts and buffering against range contractions. Mycorrhizal signatures on plant–soil feedback patterns (35) also suggest some degree of EMF host preference among temperate North American tree species, and other studies have found that tree species or genotypes may not perform well when paired with soil microbes outside their normal range (58, 59). While more empirical work on this topic is certainly warranted, it may help explain previous observations of migration failure among a wide range of North American tree species (11). Consequently, our findings suggest that mycorrhizal fungi will need to be carefully considered as part of any assisted migration strategies for North American tree species.

Materials and Methods

Fungal Occurrence Data. We combined soil fungal data from two continental-scale sequencing projects (*SI Appendix, Fig. S1*), the National ecological observation network (NEON) and the Dimensions of Biodiversity of EMF survey (DoB-Fun). NEON samples included 42 terrestrial sites containing woody vegetation, distributed across major ecoclimatic zones in the United States, from which we compiled fungal sequence data collected in 2016 through 2018 using the “neonMicrobe” R package (29). DoB-Fun soil samples encompassed 68 sites spanning mature North American Pinaceae forests collected in 2011 to 2012 (28). In total, this combination resulted in 5,940 total soil samples from 541 plots across 110 sites. Both projects use similar sampling approaches during peak growing seasons from 40 m square plots with consistent PCR methods targeting the ITS1 region of fungal rRNA (ITS1F-ITS2 primer pair; 60), allowing for meaningful comparisons across projects (61).

Fungal DNA extraction methods are described in the NEON standard operating procedures (Battelle Memorial Institute, 2018, 2022) and ref. 28 for DoB-Fun samples. Following ITS amplification, all NEON samples, and most DoB-Fun samples, were sequenced on the Illumina MiSeq platform, while the remaining DoB-Fun samples were sequenced using 454 pyrosequencing. Bioinformatic pipeline details are described in [SI Appendix](#) and ref. 29, which involved processing and denoising Illumina reads with DADA2 (62) and 454 pyrosequencing reads with QIIME and USEARCH (63). Denoised sequences were clustered into operational taxonomic units (OTUs) at 97% similarity and taxonomy assignments were made using a naïve Bayesian classifier against the UNITE v9 database (64). In total, this approach yielded more than 68,000 fungal OTUs that we assigned to functional guilds using the FungalTraits database (65), resulting in over 9,000 EMF OTUs. We merged samples at the plot level by summing EMF OTU read counts across soil cores taken within the 40 × 40 m plots located at a given site ([SI Appendix, Fig. S1](#)), across all years that plot was sampled. We then agglomerated taxa at the species level (removing EMF taxa that lacked species-level assignments), and subset the top 1,000 most dominant EMF species. Finally, we removed EMF species present in less than 15 plots to reduce the variance associated with environmental niche modeling on sparse occurrence datasets. This process resulted in georeferenced, plot-level occurrence data for 402 EMF species to create individual environmental niche models. These species comprised the vast majority of the total sequenced reads assigned as EMF (89% on average), and their community sequencing coverage did not show strong latitudinal or longitudinal bias.

Tree Species Occurrence Data. We gathered 6.3 million occurrence records for 50 tree species that form EMF associations (66) using the “BIEN” R package (26). This includes 20 Pinaceae (*Abies balsamea*, *A. lasiocarpa*, *Abies grandis*, *Picea engelmannii*, *Picea glauca*, *Picea mariana*, *Picea rubens*, *Pinus banksiana*, *P. contorta*, *Pinus echinata*, *P. elliotii*, *Pinus flexilis*, *Pinus glabra*, *Pinus ponderosa*, *Pinus strobus*, *Pinus taeda*, *P. virginiana*, *Pseudotsuga menziesii*, *Tsuga canadensis*, *Tsuga heterophylla*), 15 Fagaceae (*F. grandifolia*, *Q. alba*, *Quercus chrysolepis*, *Quercus coccinea*, *Quercus falcata*, *Quercus hemisphaerica*, *Quercus laevis*, *Quercus margarettae*, *Quercus marilandica*, *Quercus montana*, *Quercus muehlenbergii*, *Quercus nigra*, *Quercus rubra*, *Quercus stellata*, and *Quercus velutina*), 5 Betulaceae (*Alnus rubra*, *Betula alleghaniensis*, *Betula lenta*, *Betula papyrifera*, and *C. caroliniana*), 5 Juglandaceae (*Carya aquatica*, *Carya cordiformis*, *Carya glabra*, *Carya ovata*, and *Carya tomentosa*), and 5 Salicaceae (*Populus balsamifera*, *P. deltoides*, *Populus grandidentata*, *Populus tremuloides*, and *Salix bebbiana*) species. These tree species were selected based on their frequency and dominance across sites using the woody vegetation dataset from NEON plots (compiled from 2014 to 2019) and forest composition metadata collected during DoB-Fun sampling. Each species occurrence records were initially mapped to manually check and remove outliers (e.g., points in the ocean or very far away from the nearest observation). To limit sampling bias effects on environmental niche models, occurrence records for each tree species were downsampled by removing duplicate records per raster cell (see below). This thinning reduced occurrences by an average of 85% per species but still retained over 535,000 total observations of tree species across North America.

Species Distribution Modeling. We used elevation and four bioclim climate variables from WorldClim v2 (67) at 2.5 arc-minute resolution (approximately 5 km² at the equator): mean annual temperature, annual precipitation, temperature seasonality, and precipitation seasonality. Present conditions reflect average climates for the years 1970 to 2000. Future climate rasters of the same bioclim variables were averaged across 17 global circulation models for the year 2070 under worst-case scenario predictions (Relative Concentration Pathway 8.5). Given the importance of nutrient cycling rates for explaining large-scale distributions of forest mycorrhizal symbioses (18), we calculated leaf litter decomposition rates using temperature and precipitation raster data based on the Yasso07 model of climate controls on mass-loss rates of different leaf litter nutrient pools (68). All environmental rasters were clipped to the study extent, which was defined as all North American ecoregions containing NEON and DoB-Fun sites, plus all the adjacent ecoregions.

We created individual SDMs for each tree and fungal species based on Maxent algorithms using “maxnet” (31) and “enmSdm” (69) R packages. Maxent models were trained with species presence data and 10,000 random background sites. We also incorporated dynamic AICc-based tuning of Maxent’s beta regularization parameter, testing beta values set at 0.5, 1, 2, and 5 (70), using the “glmnet” R

package (71). Continuous spatial predictions of habitat suitability were converted to binary predictions of species presence-absence based on threshold cutoffs. Cutoffs were chosen that maximize the sum of sensitivity and specificity, meaning the thresholds give equal weight to false positive and false negative rates (72). We used random cross-validation with five k-folds to reduce model deviance and calculated the average cutoff across folds for thresholding.

Climate Envelope Shifts. Species climate suitability shifts were calculated between present and future climate models using longitude band analysis (described in ref. 11). This approach measures the upper and lower latitudinal extremes of a species’ distribution across stratified longitude bands (3° wide) covering the species’ climate envelope ([SI Appendix, Fig. S1](#)). Within each band, we identified the 2.5th (southern) and 97.5th (northern) percentile of a species’ habitat suitability under present and future climates. We calculated the difference between percentiles in future vs. present climates for each longitude pair, resulting in latitudinal difference distribution (LDD):

$$LDD_{j,x} = q_{j,x}^{(future)} - q_{j,x}^{(present)},$$

where $q_{j,x}$ is the latitude at percentile x in the j th longitude band. Mean LDD were summarized at north and south boundaries to reflect a species’ climate envelope shifts at leading and trailing edges. Positive values indicate shifts toward higher latitudes. We used contingency analysis with chi-square tests to examine the proportion of tree and EMF species that fall into four mutually exclusive categories: northward climate shift, overall latitude expansion, overall latitude contraction, or southward climate shift.

Climate Envelope Overlap. There were 20,100 possible comparisons between the 50 tree species and 402 EMF species, but not all of these species pairs will form mycorrhizal symbioses. We filtered tree-EMF species comparisons based on co-occurrence data such that only trees and fungal species that were present in the same plot at least once were analyzed together. This was done to incorporate host specificity in mycorrhizal symbioses and to avoid comparisons between discordant tree-EMF associations as best we could at this scale. Tree species lists for each site were created from NEON woody vegetation tables and forest data collected during DoB-Fun project sampling. Ultimately, this filtering approach resulted in 8,814 total unique comparisons between North American trees and EMF species.

We calculated the total area of suitable climate overlap between individual tree species and all relevant EMF pairs (based on the filtered EMF species list above) in present and future climate conditions. The amount of overlapping area represents the extent of shared climate envelopes between trees and each of their putative EMF partners. To test how climate change might impact total tree-EMF niche overlap, we created a linear mixed effects model (LMER) with total overlap as the response (square root transformed), climate scenario (present or future), tree family, and climate × family interaction as fixed effects, and tree species nested within family and EMF species as random effects. We also calculated the change in niche overlap between future and present climates for each tree-EMF pair to quantify the distribution of mycorrhizal symbioses at risk of shrinking shared climate suitability between fungal species and plant hosts. Finally, we stacked all overlapping tree-EMF climate ranges within tree families to visualize geographic patterns and climate-driven changes in potential interaction hotspots that are defined by high composite densities of EMF species per pixel. Hotspot locations were identified by the max composite value (in degrees latitude), and climate change effects were measured as the latitudinal change in future vs. current hotspot locations. Although stacking individual species models can inflate community measures (50), we find that predicted EMF richness was positively correlated with observed levels of EMF richness ($r^2 = 0.28$, $P < 0.001$, RMSE = 1.18; [SI Appendix, Fig. S7](#)), suggesting this approach may be useful for this specific purpose.

Climate Envelope Mismatches. Climate mismatches are defined by the degree of misalignment in suitable climate boundaries. We calculated climate envelope mismatches between trees and EMF partners at northern and southern boundaries using a similar longitudinal band approach as for climate suitability shifts ([SI Appendix, Fig. S1](#)). For the x th latitude percentile (2.5th or 97.5th):

$$LDD_{j,x} = q_{j,x}^{(tree)} - q_{j,x}^{(EMF)},$$

where $q_{j,x}$ is the latitude at percentile x in the j th longitude band for a tree species or one EMF species. Here, the mean $LDD_{j,x}$ at a suitable climate boundary quantifies the degree of climate mismatch between a tree species and a single EMF partner. Put another way, it measures the latitudinal difference in tree vs. EMF climate niche edges. We measured the absolute value of climate envelope mismatches between tree-EMF pairs in present and future climates. Absolute tree-EMF mismatch removes directionality (e.g., whether trees or EMF are further north or south than the other), and instead isolates the intensity of climate misalignment between trees and symbionts regardless of their relative latitude positions. To test how climate change might affect the overall level of tree-EMF mismatches, we created a LMER model with absolute tree-EMF mismatches as the response (square root transformed), climate scenario, boundary (southern or northern), tree family, and all interactions as fixed effects, and tree species nested within family and EMF species as random effects.

Climate-Compatible EMF Richness and Tree Migration Potential. We compared predicted levels of EMF richness with tree species migration potential to test whether the diversity of co-occurring and climate-compatible fungal symbionts relates to observed tree species range dynamics. For each tree species, we estimated the mean and SD of predicted EMF richness at southern (2.5th percentile), center (median), and northern (97.5th percentile) suitable climate boundaries of the tree host. This was done by summing all binary SDM suitability output from the list of putative EMF partners (as described above), followed by splitting the stacked richness maps into longitude bands and then calculating mean richness estimates at each latitude position (as in *SI Appendix, Fig. S1*). This process results in predicted EMF richness values representing the total number of fungal species with overlapping climate suitability at a given tree species' southern, central, and northern climate niche positions. We used a linear model to test whether richness varies by niche position, with predicted EMF richness as the response and tree niche position, tree family, and position $\times$ family as fixed effects.

We estimated tree species migration potential using a similar longitude band analysis as above with seedling and adult tree observations in the United States Department of Agriculture FIA database. Latitude differences between seedlings and adult tree longitude pairs show novel seedling establishment, which is a strong proxy for range shifts (11, 73). We calculated tree species migration potential at

northern (97.5th percentile) and southern (2.5th percentile) boundaries. Because we only had access to FIA data in US states, we limited this analysis to 25 tree species with predominantly US distributions to avoid biased estimates of migration potential. Specifically, tree migration potential LDD was calculated as

$$LDD_{j,x} = q_{j,x}^{(\text{seedling})} - q_{j,x}^{(\text{adult})},$$

where $q_{j,x}$ is the latitude at percentile x in the j th longitude band for a seedling or adult tree species. At northern boundaries, positive $LDD_{j,x}$ indicates northern range expansion (seedlings at higher latitudes than adults), whereas positive $LDD_{j,x}$ at southern boundaries is consistent with southern range contraction (northward retreat of seedlings). We created a linear model to test whether tree migration potential relates to the predicted richness of climate-compatible EMF species using tree migration potential as the response and predicted EMF richness, climate boundary (north or south), and richness $\times$ boundary as fixed effects. We also repeated this analysis using the total stacked predicted EMF richness (i.e., not filtered by co-occurring tree-EMF pairs) to explore the effects of the screening process.

Data, Materials, and Software Availability. Data forming the basis of this study are available from the National Ecological Observatory Network at <http://doi.org/10.48443/ybys-zv89>, RELEASE-2021 (DP1.10086.001). Microbial sequence data are available through the neonMicrobe R package (ref. 29) and the NCBI SRA (accession number: [PRJNA950128](https://doi.org/10.5281/zenodo.11003760)). R code is archived on Zenodo (DOI: [10.5281/zenodo.11003760](https://doi.org/10.5281/zenodo.11003760)).

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1. J. Memmott, P. G. Craze, N. M. Waser, M. V. Price, Global warming and the disruption of plant-pollinator interactions. *Ecol. Lett.* **10**, 710–717 (2007).
2. S. K. Richman, J. M. Levine, L. Stefan, C. A. Johnson, Asynchronous range shifts drive alpine plant-pollinator interactions and reduce plant fitness. *Glob. Change Biol.* **26**, 3052–3064 (2020).
3. J. M. Montoya, D. Raffaelli, Climate change, biotic interactions and ecosystem services. *Philos. Trans. R. Soc. B. Biol. Sci.* **365**, 2013–2018 (2010).
4. W. H. Van der Putten, Climate change, aboveground-belowground interactions, and species' range shifts. *Ann. Rev. Ecol. Syst.* **43**, 365–383 (2012).
5. E. P. Gómez-Ruiz, T. E. Lacher Jr., Climate change, range shifts, and the disruption of a pollinator-plant complex. *Sci. Rep.* **9**, 14048 (2019).
6. J. C. Fowler, M. L. Donald, J. L. Bronstein, T. E. Miller, The geographic footprint of mutualism: How mutualists influence species' range limits. *Ecol. Monographs* **93**, e1558 (2023).
7. J. A. Rudgers et al., Climate disruption of plant-microbe interactions. *Ann. Rev. Ecol. Syst.* **51**, 561–586 (2020).
8. M. Pillet et al., Elevated extinction risk of cacti under climate change. *Nat. Plants* **8**, 366–372 (2022).
9. M. Esperon-Rodriguez et al., Climate change increases global risk to urban forests. *Nat. Clim. Change* **12**, 950–955 (2022).
10. A. Prasad et al., Combining US and Canadian forest inventories to assess habitat suitability and migration potential of 25 tree species under climate change. *Divers. Distrib.* **26**, 1142–1159 (2020).
11. K. Zhu, C. W. Woodall, J. S. Clark, Failure to migrate: Lack of tree range expansion in response to climate change. *Glob. Change Biol.* **18**, 1042–1052 (2012).
12. F. Sittaro, A. Paquette, C. Messier, C. A. Nock, Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Glob. Change Biol.* **23**, 3292–3301 (2017).
13. S. Sharma et al., North American tree migration paced by climate in the West, lagging in the East. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2116691118 (2022).
14. A. P. Hill, C. J. Nolan, K. S. Hemes, T. W. Cambron, C. B. Field, Low-elevation conifers in California's Sierra Nevada are out of equilibrium with climate. *PNAS Nexus* **2**, pgad004 (2023).
15. S. E. Smith, D. J. Read, *Mycorrhizal Symbiosis* (Academic press, 2010).
16. R. P. Phillips, E. Brzostek, M. G. Midgley, The mycorrhizal-associated nutrient economy: A new framework for predicting carbon-nutrient couplings in temperate forests. *New Phytol.* **199**, 41–51 (2013).
17. M. G. A. van der Heijden, F. M. Martin, M.-A. Selosse, I. R. Sanders, Mycorrhizal ecology and evolution: The past, the present, and the future. *New Phytol.* **205**, 1406–1423 (2015).
18. B. S. Steidinger et al., Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* **569**, 404–408 (2019).
19. B. S. Steidinger et al., Ectomycorrhizal fungal diversity predicted to substantially decline due to climate changes in North American Pinaceae forests. *J. Biogeography* **47**, 772–782 (2020).
20. K. G. Peay, M. G. Schubert, N. H. Nguyen, T. D. Bruns, Measuring ectomycorrhizal fungal dispersal: Macroecological patterns driven by microscopic propagules. *Mol. Ecol.* **21**, 4122–4136 (2012).
21. J. Diez et al., Altitudinal upwards shifts in fungal fruiting in the Alps. *Proc. R. Soc. B* **287**, 20192348 (2020).
22. R. A. Lankau, D. P. Keymer, Ectomycorrhizal fungal richness declines towards the host species' range edge. *Mol. Ecol.* **25**, 3224–3241 (2016).
23. M. A. Nuñez, T. R. Horton, D. Simberloff, Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology* **90**, 2352–2359 (2009).
24. J. Pither, B. J. Pickles, S. W. Simard, A. Ordóñez, J. W. Williams, Below-ground biotic interactions moderated the postglacial range dynamics of trees. *New Phytol.* **220**, 1148–1160 (2018).
25. R. A. Lankau, K. Zhu, A. Ordóñez, Mycorrhizal strategies of tree species correlate with trailing range edge responses to current and past climate change. *Ecology* **96**, 1451–1458 (2015).
26. B. S. Maitner et al., The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods Ecol. Evol.* **9**, 373–379 (2018).
27. USDA Forest Service, "Forest inventory and analysis National program" (United States Department of Agriculture, 2019).
28. J. M. Talbot et al., Endemism and functional convergence across the North American soil microbiome. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 6341–6346 (2014).
29. C. Qin et al., From DNA sequences to microbial ecology: Wrangling NEON soil microbe data with the neonMicrobe R package. *Ecosphere* **12**, e03842 (2021).
30. C. Qin, P. T. Pellitier, M. E. Van Nuland, K. G. Peay, K. Zhu, Niche modelling predicts that soil fungi occupy a precarious climate in boreal forests. *Glob. Ecol. Biogeogr.* **32**, 1127–1139 (2023), 10.1111/geb.13684.
31. S. J. Phillips, R. P. Anderson, M. Dudík, R. E. Schapire, M. E. Blair, Opening the black box: An open-source release of Maxent. *Ecography* **40**, 887–893 (2017).
32. S. W. Pacala et al., Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecol. Monographs* **66**, 1–43 (1996).
33. S. A. Mangan et al., Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466**, 752–755 (2010).
34. K. Hazelwood, H. Beck, C. T. Paine, Negative density dependence in the mortality and growth of tropical tree seedlings is strong, and primarily caused by fungal pathogens. *J. Ecol.* **109**, 1909–1918 (2021).
35. J. A. Bennett et al., Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* **355**, 181–184 (2017).
36. R. M. Segnitz, S. E. Russo, S. J. Davies, K. G. Peay, Ectomycorrhizal fungi drive positive phylogenetic plant-soil feedbacks in a regionally dominant tropical plant family. *Ecology* **101**, e03083 (2020).
37. X. Pu, M. Weemstra, G. Jin, M. N. Umaña, Tree mycorrhizal type mediates conspecific negative density dependence effects on seedling herbivory, growth, and survival. *Oecologia* **199**, 907–918 (2022).
38. M. E. Van Nuland, P. J. Ke, J. Wan, K. G. Peay, Mycorrhizal nutrient acquisition strategies shape tree competition and coexistence dynamics. *J. Ecol.* **111**, 564–577 (2023).

39. Y. Miyamoto, Y. Terashima, K. Nara, Temperature niche position and breadth of ectomycorrhizal fungi: Reduced diversity under warming predicted by a nested community structure. *Glob. Change Biol.* **24**, 5724–5737 (2018).
40. K. G. Peay *et al.*, Lack of host specificity leads to independent assortment of dipterocarps and ectomycorrhizal fungi across a soil fertility gradient. *Ecol. Lett.* **18**, 807–816 (2015).
41. C. Terrer, S. Vicca, B. A. Hungate, R. P. Phillips, I. C. Prentice, Mycorrhizal association as a primary control of the CO₂ fertilization effect. *Science* **353**, 72–74 (2016).
42. N. A. Soudzilovskaia *et al.*, Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nat. Commun.* **10**, 5077 (2019).
43. D. R. Zak *et al.*, Exploring the role of ectomycorrhizal fungi in soil carbon dynamics. *New Phytolog.* **223**, 33–39 (2019).
44. C. A. Guerra *et al.*, Global hotspots for soil nature conservation. *Nature* **610**, 693–698 (2022).
45. K. Zhu, M. L. McCormack, R. A. Lankau, J. F. Egan, N. Wurzbarger, Association of ectomycorrhizal trees with high carbon-to-nitrogen ratio soils across temperate forests is driven by smaller nitrogen not larger carbon stocks. *J. Ecol.* **106**, 524–535 (2018).
46. G. R. Smith, K. G. Peay, Stepping forward from relevance in mycorrhizal ecology. *New Phytolog.* **226**, 292–294 (2020).
47. C. W. Fernandez, C. R. See, P. G. Kennedy, Decelerated carbon cycling by ectomycorrhizal fungi is controlled by substrate quality and community composition. *New Phytolog.* **226**, 569–582 (2020).
48. I. T. Bödeker *et al.*, Ectomycorrhizal *Cortinarius* species participate in enzymatic oxidation of humus in northern forest ecosystems. *New Phytolog.* **203**, 245–256 (2014).
49. P. T. Pellitier, I. Ibáñez, D. R. Zak, W. A. Argiroff, K. Acharya, Ectomycorrhizal access to organic nitrogen mediates CO₂ fertilization response in a dominant temperate tree. *Nat. Commun.* **12**, 5403 (2021).
50. J. S. Clark, A. E. Gelfand, C. W. Woodall, K. Zhu, More than the sum of the parts: Forest climate response from joint species distribution models. *Ecol. Appl.* **24**, 990–999 (2014).
51. T. Dobzhansky, Evolution in the tropics. *Am. Sci.* **38**, 209–221 (1950).
52. R. H. MacArthur, *Geographical Ecology* (Harper & Row Publishers, New York, 1972).
53. J. H. Brown, G. C. Stevens, D. M. Kaufman, The geographic range: Size, shape, boundaries, and internal structure. *Ann. Rev. Ecol. Syst.* **27**, 597–623 (1996).
54. C. W. Fernandez *et al.*, Ectomycorrhizal fungal response to warming is linked to poor host performance at the boreal-temperate ecotone. *Glob. Change Biol.* **23**, 1598–1609 (2017).
55. S. R. Loarie *et al.*, The velocity of climate change. *Nature* **462**, 1052–1055 (2009).
56. P. Caplat *et al.*, Looking beyond the mountain: Dispersal barriers in a changing world. *Front. Ecol. Environ.* **14**, 261–268 (2016).
57. K. G. Peay, Timing of mutualist arrival has a greater effect on *Pinus muricata* seedling growth than interspecific competition. *J. Ecol.* **106**, 514–523 (2018).
58. B. J. Pickles, M. A. Gorzelak, D. S. Green, K. N. Egger, H. B. Massicotte, Host and habitat filtering in seedling root-associated fungal communities: Taxonomic and functional diversity are altered in 'novel' soils. *Mycorrhiza* **25**, 517–531 (2015).
59. M. E. Van Nuland, J. K. Bailey, J. A. Schweitzer, Divergent plant–soil feedbacks could alter future elevation ranges and ecosystem dynamics. *Nat. Ecol. Evol.* **1**, 0150 (2017).
60. D. P. Smith, K. G. Peay, Sequence depth, not PCR replication, improves ecological inference from next generation DNA sequencing. *PLoS One* **9**, e90234 (2014).
61. B. D. Lindahl *et al.*, Fungal community analysis by high-throughput sequencing of amplified markers—A user's guide. *New Phytolog.* **199**, 288–299 (2013).
62. B. J. Callahan *et al.*, DADA2: High-resolution sample inference from Illumina amplicon data. *Nat. Methods* **13**, 581–583 (2016).
63. R. C. Edgar, Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* **26**, 2460–2461 (2010).
64. R. H. Nilsson *et al.*, The UNITE database for molecular identification of fungi: Handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Res.* **47**, D259–D264 (2019).
65. S. Pölme *et al.*, FungalTraits: A user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Divers.* **105**, 1–16 (2020).
66. M. C. Brundrett, Mycorrhizal associations and other means of nutrition of vascular plants: Understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant Soil* **320**, 37–77 (2009).
67. S. E. Fick, R. J. Hijmans, WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
68. M. Tuomi *et al.*, Leaf litter decomposition—Estimates of global variability based on Yasso07 model. *Ecol. Modelling* **220**, 3362–3371 (2009).
69. T. L. Morelli *et al.*, The fate of Madagascar's rainforest habitat. *Nat. Clim. Change* **10**, 89–96 (2020).
70. D. L. Warren, S. N. Seifert, Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* **21**, 335–342 (2011).
71. J. Friedman, T. Hastie, R. Tibshirani, Regularization paths for generalized linear models via coordinate descent. *J. Stat. Softw.* **33**, 1–22 (2010).
72. C. Liu, M. White, G. Newell, Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* **40**, 788–789 (2013).
73. A. P. Hill, C. B. Field, Forest fires and climate-induced tree range shifts in the western US. *Nat. Commun.* **12**, 6583 (2021).