Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts

Insu Jo

Songlin Fei
Purdue University, sfei@purdue.edu

Christopher M. Oswalt

Grant M. Domke

Richard P. Phillips

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Shifts in tree-mycorrhizal associations

Authors:

Insu Jo¹, Songlin Fei¹*, Christopher Oswalt², Grant M. Domke³, Richard P. Phillips⁴

Affiliations:

¹ Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA.
² Southern Research Station, Forest Service, United States Department of Agriculture, Knoxville, TN 37919, USA.
³ Northern Research Station, Forest Service, United States Department of Agriculture, St. Paul, MN 55108, USA.
⁴ Department of Biology, Indiana University, Bloomington, IN 47405, USA

*Correspondence to: Songlin Fei, Department of Forestry and Natural Resources, 715 West State St., Purdue University, West Lafayette, IN 47907, USA. Email: sfei@purdue.edu
Abstract:

Plant-fungal symbioses play critical roles in vegetation dynamics and nutrient cycling and in doing so, modulate the impacts of global changes on ecosystem functioning. Here, we used forest inventory data consisting of over three million trees to develop a spatially-resolved “mycorrhizal tree map” of the contiguous USA. We show that abundances of the two dominant mycorrhizal tree groups – arbuscular mycorrhizal (AM) and ectomycorrhizal trees – are associated primarily with climate. Further, we show that anthropogenic influences, primarily nitrogen (N) deposition and fire suppression, in concert with climate changes, have increased AM tree dominance during the past three decades in the eastern US. Given that most AM-dominated forests in this region are underlain by soils that are high in N availability, our results suggest that the increasing abundance of AM trees has the potential to induce nutrient acceleration, with critical consequences for forest productivity, ecosystem carbon and nutrient retention, and feedbacks to climate change.

One Sentence Summary:

Anthropogenic influences alter tree mycorrhizal associations inducing nutrient acceleration in the USA forests.
Main Text:

Introduction

The forests of North America are experiencing unprecedented change owing to the combined effects of climate change, nitrogen (N) deposition, changes in disturbance regime, fragmentation, and invasions of exotic species (1-5). While anthropogenic-induced shifts in the distribution and abundance of tree communities are well-described (1, 6), far less is known about the direct and indirect impacts of global changes on plant-fungal associations (7, 8). Over 90% of vascular plants associate with mycorrhizal fungi (9, 10), and there is emerging consensus that such plant-fungal associations have profound impacts on nutrient cycling and vegetation dynamics in ecosystems, particularly temperate forests (11-15). However, critical gaps remain in our understanding of biogeographic patterns of mycorrhizal associations, and our limited knowledge of the anthropogenic factors responsible for shifting plant-mycorrhizal distributions has hindered efforts to predict ecosystem feedbacks to climate change (16).

The two dominant types of fungi that associate with trees – arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) – differ greatly in their form and function. Consequently, tree mycorrhizal associations have been hypothesized to represent trait-integrating phenotypes that give rise to “biogeochemical syndromes” in forests (13), although the relative contribution of the plants vs. fungi to these syndromes is poorly quantified. EM-dominated forests often cycle carbon (C) and nutrients conservatively owing to the lower chemical quality of their litters relative to AM-dominated forests, which have more “open” C and nutrient cycles (17, 18). Such effects not only alter the degree to which these ecosystems store C and nutrients (19-22), but likely affect their sensitivity to human induced global changes (23-26). Here, using forest inventory data collected by the USDA Forest Service, Forest Inventory and Analysis (FIA)
program across the contiguous USA, we (i) map the tree mycorrhizal association patterns and identify underlying drivers of these observed associations, (ii) quantify the impacts of human induced global changes, primarily climate change, N deposition, and disturbance regimes, on tree mycorrhizal associations, and (iii) assess the potential feedback of mycorrhizal association shifts on soil C and nutrient dynamics.

**Distribution and drivers of tree mycorrhizal association patterns**

Using FIA vegetation data and tree mycorrhizal type information, we mapped the relative abundance of over three million AM and EM trees across the conterminous USA (Fig. 1A). While patterns of mycorrhizal associations and associated drivers have been reported previously, these studies were based on species occurrence data (27-29), covered lesser spatial extent (30), and examined fewer vegetation survey plots than our study (31). Our results indicate that AM trees are more dominant in dry and warm ecoregions, while EM trees are more dominant in humid and cold ecoregions (Fig. 1, A and B). In the western USA, AM trees are dominant in the subtropical desert and steppe regions and EM trees are dominant in the northwestern and intermountain west regions (Fig. 1A, Fig. S1). AM and EM trees are well-mixed in eastern USA, with more AM trees in the hot continental region and more EM trees in the western portion of the warm continental region (Fig. 1, Fig. S1). Using a mixed-effects model that accounts for the spatial heterogeneity between plots in different sub-ecoregions, we found that climate is an important driver of tree mycorrhizal association patterns at the continental scale (Fig. 1C). Overall, AM tree dominance was negatively associated with mean annual precipitation (MAP) and positively associated with mean annual temperature (MAT) (Fig. 1C), although the magnitude and direction of effect sizes differed in some ecoregions. Forest tree basal area, which was used as an indicator of forest successional stage, had smaller effects on AM tree
dominance compared to climatic factors, implying that climate is a more important driver of the continental tree mycorrhizal association patterns (Fig. 1C).

**Shifts in tree mycorrhizal associations and associated drivers**

To understand the impacts of human-induced global changes on tree mycorrhizal associations, we used repeated measurements of forest inventories from the FIA program during the last three decades in eastern USA where rapid climate change has been observed (Fig. S2) (1). AM tree dominance has significantly increased in all parts of eastern USA during the last three decades (based on a paired Wilcoxon signed-rank test, \( P<0.05 \); Fig. 2A), especially in the central regions (17% increase in prairie and 15% increase in hot continental regions), due to both an increase in AM tree abundance (i.e. basal area; Fig. S3A) and decrease in EM tree abundance (Fig. S3B). AM tree dominance in southern and northern ecoregions also increased (5% increase in warm continental and 5% increase in subtropical, Fig. 2A), even though these regions had statistically significant increases in both AM and EM tree abundance (Fig. S3, A and B).

Particularly, the western portion of the warm continental region and northern portion of the subtropical region had similar increases in AM tree abundance, while the eastern portion of the warm continental region and southern portion of the subtropical region had the opposite trend (Fig. 2A).

Our analysis indicates that three factors – N deposition, fire frequency and climate change – likely contributed to the increases in AM tree dominance. First, we found a strong positive correlation between N deposition and shifts in AM tree dominance, consistent with earlier studies based on smaller spatial extent and shorter temporal scale (31). In temperate forests, most AM tree species have nutrient acquisitive traits (e.g., rapid root growth into nutrient hot spots and narrower C:N in leaf and root tissues) (17, 32-34) and often dominate stands
characterized by open (i.e., fast) N cycles (13, 30). Thus, the positive relationship between N deposition and AM dominance may result from AM trees being competitively superior at acquiring excess N – the nutrient that generally limits plant growth in these forests. Second, we found strong negative associations between fire frequency and AM tree dominance (Fig. 2B). While it is well-established that fire suppression following European settlement has led to oak (Quercus) regeneration failure and forest “mesophication” in the eastern US (35), our results indicate that this trend is not merely a result of EM-associating oaks being replaced by AM-associating maples (Acer). The change in AM tree dominance was not driven by a specific phylogenetic group of tree species, as the most common AM and EM tree genera had relatively similar effect sizes on the change (Fig. 2C). Changes of abundance in all five most common AM genera, with a few statistically non-significant exceptions, were positively associated with AM tree dominance change; while, the changes of abundance in EM genera were nearly all negatively associated with the AM tree dominance change (Fig. 2C). Possible explanations for the observed non-significant outliers (e.g., Prunus in prairie and Carya in warm continental region) could due to small sample sizes or potential preferential harvesting in these regions. The third factor contributing to increases in AM tree dominance is climate change. In general, increases in MAP were negatively associated with increases in AM tree dominance, while the associations with MAT were weak and variable (Fig. 2B).

The extent to which other factors may contribute to future shifts in tree mycorrhizal associations is unknown. AM tree dominance tended to increase with basal area, an indicator of forest succession, as shade tolerant AM trees increase their abundance with the progression of forest succession. However, the effects of basal area were relatively small compared to the other drivers, suggesting that anthropogenic drivers (i.e., climate change, N deposition, fire
suppression) had far greater impact on recent demographic shifts. Other factors such as land use change and forest management, which directly affect tree species dominance, could impact shifts in tree mycorrhizal associations. Additionally, to the extent that pollution control and reduction reduces N loading to US forests, future shifts in mycorrhizal associations may lessen in importance in the coming decades.

A continuing shift to AM tree dominance is also predicted by our finding that saplings were more AM-dominated compared to adult trees in seven of 11 ecoregions (Fig. 3). In the eastern US, all ecoregions other than the warm continental region had greater AM tree dominance in saplings compared to adult trees (Fig. 3). The prairie, hot continental, and subtropical regions had over 54% greater sapling AM tree dominance compared to adult trees. The differences in AM tree dominance between saplings and adult trees were mixed in the western USA (Fig. 3). Compared to adult trees, more AM saplings were observed in the marine, Mediterranean, temperate steppe regions, but less AM saplings in the temperate desert, tropical/subtropical desert, tropical/subtropical steppe regions. In addition, the overall differences between adult and sapling AM tree dominance were smaller than those observed in the ecoregions in eastern USA (Fig. 3).

**Relationships between tree mycorrhizal associations and soil C and N**

To assess the potential consequences of mycorrhizal association shifts on C and N dynamics, we analyzed the relationships between AM tree dominance and soil C and N stocks (litter layer and 0-20 cm depth of the mineral soil) on plots where both soil attributes and associated vegetation were measured (2,113 plots) using linear regression models. In general, the associations between AM tree dominance and soil C and N stocks were positive in mesic temperate ecoregions but negative in dry ecoregions; however, most ecoregions had a negative
relationship between soil C:N ratio and AM tree dominance (Fig. 4, A to C). Across the study area, AM-dominated forests had 28% more soil N and 8% more soil C than EM-dominated forests (Fig. 4, A and B, Table S2). The greater increase in soil N stocks (relative to soil C stocks) in mesic ecoregions and the lower decrease in soil N stocks (relative to soil C stocks) in dry ecoregions resulted in a negative relationship between soil C:N ratio and AM tree dominance along the continental AM tree dominance gradient (Fig. 4, A to C).

Using mixed-effects models, we further tested how forest mycorrhizal association and environmental factors are related to soil attributes for each ecoregion after accounting for the spatial heterogeneity between plots in different sub-ecoregions by adding sub-ecoregions as random intercepts in the models. We found that AM tree dominance, climate, and soil texture had significant associations with soil C and N stocks and C:N ratio, though with different effect sizes (Fig. 4, D to F). Overall, AM tree dominance was positively associated with soil C and N stocks and negatively with C:N ratio across the ecoregions – consistent with site-based patterns recently reported (22). Among the climatic factors, MAP tended to have positive associations with soil C and N stocks, while MAT have negative associations. Soil C and N stocks were similar between the top 20 cm of the mineral soil and the top 20 cm plus litter layer (Fig. S4) owing to the much smaller size of the litter C and N pools.

The observational nature of our data preclude us from determining whether AM trees are causing elevated N levels in soil (as opposed to merely responding to them). It is possible that AM trees can elevate soil N (pool sizes and transformation rates) by releasing high chemical quality litter to soil. Several studies of temperate trees have shown that AM litters generally decay faster than EM litters in common garden studies (36) and meta-analyses (37). And given that higher chemical quality litter leads to both greater rates of N transformations (38) and the
formation of more protected (i.e. stable) soil organic matter (*sensu* the MEMS hypothesis) (39), increasing AM dominance may lead to elevated N levels in soil (22). Contemporary theory of soil organic matter stabilization and turnover indicates that changes in AM vs EM dominance can alter C and N cycling in 30–45 years (18) – well-within the time frame detect changes in the FIA dataset. Thus, our contention that AM trees may be contributing, in part, to N accumulation is a testable hypothesis but requires further inquiry.

Finally, separating cause and effect in this instance may be of limited importance given that tree species often modify soils in ways that tend to exacerbate or enhance the pre-existing biogeochemical condition (40). Thus, while we can’t rule out that the species are merely responding to the high N soils, both processes likely contribute to the maintenance of the biogeochemical syndromes observed. More experiments and/or long-term repeated measures of soil stocks are needed to test the mechanisms of these associations. Nevertheless, the consistent large-scale patterns in forests across multiple ecoregions suggests that dominant tree mycorrhizal type could be an important driver of nutrient and C dynamics in forests through positive/negative feedbacks associated with AM/EM plant traits (40).

Given that AM-dominated forests tend to be underlain by soils with lower C:N than EM-dominated soils (30,33; **Fig. 4C**), the increasing dominance of AM trees could have consequences for forest ecosystem functions and services. Low or small ratios are often used as proxies for rates of microbial N transformations in soils such as nitrification, nitrate leaching losses (38), as well as for ecosystem sensitivity to N deposition (41). Thus, forests of eastern USA may be experiencing an acceleration of N cycling – owing to the shifts in AM dominance. The consequences of nutrient amplification would likely be profound for water quality if for example, elevated nitrification rates enhance nitrate export to lakes and rivers.
The consequences of nutrient acceleration may be most profound for forest productivity, which can feed-back to affect climate change. Most AM-dominated ecosystems cannot sustain high level of productivity under elevated CO$_2$ unless the availability of soil N is high (23). Thus, if increases in AM tree dominance lead to an acceleration of N cycling, AM-dominated forests in eastern USA may be strong sinks for atmospheric CO$_2$. However, if the AM-induced acceleration of N cycling leads to significant ecosystem N losses (25) or results in N stabilization in soil organic matter (22), there may be little stimulation of forest productivity. In addition, shifting balance of AM-EM vegetation could also be influenced by N-induced Phosphorus (P) limitation and more severe drought periods (42). While N-induced P limitation has long been considered as something that would only occur in forests south of the last glacial maximum (where mineral P levels are extremely low), recent evidence from northern ecosystems challenges the paradigm (43). Either way, our results indicate that changes in N cycling owing to increasing AM tree dominance could have profound consequences for C and N retention and loss in forests and hence, the degree to which forests feedback to climate change.

Conclusions

Our study provides the first comprehensive distribution map of tree-mycorrhizal association in the contiguous USA. More importantly, we provide empirical evidence based on national forest inventory data for how global changes may have impacted the shift of mycorrhizal associations at the continental scale. We found that AM tree dominance was positively associated with both soil C and N stocks, particularly for temperate forests, which challenges the prevailing idea that EM dominant ecosystems store more C than AM tree dominant ecosystems (15, 19-21). We note, however, that soil C:N ratio was negatively associated with AM tree dominance, supporting recent findings that showed the positive
association between soil C:N ratio and EM tree dominance driven by low soil N instead of high C stock in EM dominant ecosystems (22, 30). Our results suggest that increases in AM tree dominance in the eastern USA may increase soil N stocks, inducing a positive feedback of nutrient acceleration, at least in the upper surface soils. A better understanding of the role of dominant forest mycorrhizal association type in ecosystem processes at global scales and the mechanisms responsible for forest soil C storage is critical for improving ecosystem models to predict forest ecosystem processes and functions in global climate change.
Materials and Methods

Tree data collection

Tree inventory data were obtained from forest plots across the USA by the Forest Inventory and Analysis (FIA) program (US Forest Service; data available at https://apps.fs.usda.gov/fia/datamart/). The FIA program monitors forests resources at the national level, using permanent plots, which have a sampling intensity of approximately one plot every 2,428 ha. Each plot comprises four subplots (fixed-radius: 7.3 m) spaced 37 m apart in a triangular arrangement with one subplot in the center. For each FIA plot, we extracted tree basal area by species with diameter at breast height (dbh) > 12.7 cm as adult tree and dbh 5.1-12.7 cm as sapling.

Soil carbon and nitrogen stocks

FIA program collected soil samples on every 1/16th base intensity plot, distributed approximately every 38,848 ha. We compiled forest litter layer C and N concentrations and the associated litter layer thickness and bulk density, mineral soil C and N concentrations for 0-20 cm soil depth and the associated soil bulk density and coarse fraction at subplot-level where species-level vegetation inventory was available. Soil C and N measurements in FIA data are based on mineral soil (<2mm) and coarse particles (>2mm) are not included. Mineral soil C and N stocks (kg m$^{-2}$) to a depth of 20 cm calculated based on soil C and N concentration (%), soil bulk density (g cm$^{-3}$), after removing a proportion of coarse particle fraction (particle size >2mm) in the soil layer. Total soil C and N stocks were calculated by combining values for both mineral soil (0-20 cm depth) and litter layer. Since soil texture for mineral soil (0-20 cm depth) was categorized based on field measure, we assigned mean clay proportion for each texture type (loamy=45%, clayey=60%, sandy or coarse sand=10%), following Zhu et al (30). Soil data summary by ecoregion is available at Table S2.
Climate, N deposition, and fire frequency data

At the plot level, mean annual temperature (MAT) and mean annual precipitation (MAP) of current climate conditions were derived from the Global Climate Data - WorldClim Version 1.4 (1-km spatial resolution; available at [www.worldclim.org](http://www.worldclim.org) (46)). At the hexagon level, MAT and MAP changes over the past three decades, calculated by subtracting mean values of the recent period (1981-2015) and the recent past (1951-1980) from the PRISM Climate Group (4-km spatial resolution; available at [http://prism.oregonstate.edu/](http://prism.oregonstate.edu/)) (47), were aggregated with mean. Annual mean of total N deposition (kg N ha\(^{-1}\) yr\(^{-1}\)) data over the past 15 years (2000-2015) were extracted from the National Atmospheric Deposition Program (available at [http://nadp.slh.wisc.edu/](http://nadp.slh.wisc.edu/)) (48) and aggregated with mean at the hexagon level. Although wet N deposition data are available from 1985 to 2016, we used total N deposition data, which includes wet and dry N deposition of both organic and inorganic forms, given that recent N deposition data reflect the historical N deposition patterns (31). Fire frequency data were compiled from spatial wildfire occurrence data in the USA over 24 years (1992-2015) (49). The point locations of fire occurrence during the period were converted to kernel density (per km\(^2\)) raster (1-km spatial resolution) using ArcGIS (ver. 10.5, Esri Inc., USA), and then aggregated with mean at the hexagon level. Spatial patterns of these data are available in Fig. S2.

Tree mycorrhizal type information

Mycorrhizal type was assigned for each tree species present in FIA plots based on peer-reviewed journal publications (50-53). If the species-level mycorrhizal type was not available, we assigned the most frequent mycorrhizal type within genus (or family). To avoid potential false conclusions due to misclassification of mycorrhizal association (54), we further revised the ectomycorrhizal tree information based on Tedersoo and Brundrett (55). We then calculated the AM tree dominance (based on basal area) for each plot by dividing total AM tree basal area by the sum of
AM and EM mycorrhizal tree basal area. For some species categorized as both AM and EM, we tested if assigning them as AM (or EM) changes the patterns of mycorrhizal associations and found no significant effects, therefore, we assigned them a half of the basal area each to AM and EM.

Changes in AM-EM tree dominance during the past three decades

To test changes in AM-EM tree dominance over the past three decades, we utilized repeated measures of forest plot inventory available in eastern USA by US Forest Service, the first inventory, collected between 1980 and 1995 (T1; mean inventory year: 1986; 83,866 plots) and the second inventory was the latest completed inventory, which was finished in 2015 for most states (T2; mean inventory year: 2015; 70,715 plots). We only included eastern USA since repeated FIA measures are rarely available for the western USA. Because T2 inventory measures were not necessarily done in the same plot locations with T1 plots, we aggregated plot-level AM tree dominance and total tree basal area to the hexagon-level (a spatial tessellation design used by FIA), following Fei et al (1). The size of hexagon (1,452 km$^2$) is approximately the mean size of counties in eastern USA. We only included hexagons with at least 10 plots each for both T1 and T2 inventories (mean plot number per each T1 hexagon: 47; mean plot number per each T2 hexagon: 40), resulted in 1,785 hexagons for the final analysis.

Statistical analysis

We determined relative effects of climate and total tree basal area (as a surrogate for succession status) on AM tree dominance across the ecoregions (plot level data) using mixed-effects models with a beta distribution and logit link function using R package ‘glmmTMB’ (56). Since AM tree dominance data in our inventory plots included many zeros (only EM trees present in the plot) and ones (only AM trees present), we transformed the data as $y' = \frac{y}{(1+y)}$.
\[
\frac{y \times (N-1) + 0.5}{N}
\]
where \(y\) is AM tree dominance and \(N\) is sample size, following Averill et al (31).

We added sub-ecoregions (nested units within ecoregion, Fig. 1A) as a random effect in the model to account for the spatial heterogeneity between plots in different sub-ecoregions. We excluded plots with any missing variables and ended up with 132,956 plots for analyses. All predictor variables were standardized by subtracting mean and dividing by two standard deviations to make the regression coefficients for the predictors comparable.

AM tree dominance differences between two inventories (T1 and T2) (hexagon level data) and between saplings and adult trees (plot level data) were tested using a paired Wilcoxon signed-rank test for each ecoregion. At the ecoregion level, effects of global change drivers (i.e. MAP and MAT changes, N deposition, fire frequency), AM tree dominance at T1, and basal area on the AM tree dominance change during the past three decades (T2-T1) were tested using mixed-effects models with a Gaussian error distribution and sub-ecoregions as a random effect (see Fig. S2 for the spatial patterns of the predictor variables). We also tested effects of genus-level tree dominance changes in 10 most abundant tree genera (57) in the studied plots on the AM tree dominance change, using the same mixed effects model structure described above. The AM tree genera included Acer, Fraxinus, Prunus, Nyssa, and Ulmus and the EM tree genera included Quercus, Pinus, Carya, Betula, and Populus. Fire frequency was log-transformed to meet normality assumptions and all predictor variables were standardized. Bivariate relationships between soil C and N stocks and C:N ratio and AM tree dominance were tested using a linear regression. We further determined relative effects of AM tree dominance and environmental factors on soil attributes, using a mixed effects modeling approach. At the ecoregion level, we modeled each of soil attributes (soil C and N stocks and C:N ratio) with a Gaussian error distribution as a function of AM tree dominance, MAP, MAT, basal area, and clay proportion, nested within sub-
ecoregions. Soil attributes were log-transformed to meet normality assumptions and all predictor variables were standardized. All statistical analyses were performed in the R statistical programming environment, version 3.3.2 (58).
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Author contributions:

I.J. and S.F. conceived the study. C.O. and G.D. provided forest inventory data. IJ performed the analyses and drafted the manuscript. All authors contributed substantially to revisions and confirmed the final version of the manuscript.

Competing interests:

Authors declare no competing interests.

Data and materials availability:

All data used in the analyses is available at an open data repository (Purdue University Research Repository; DOI:10.4231/R76D5R7S). Vegetation and soil data is available at FIA DataMart – US Forest Service (https://apps.fs.usda.gov/fia/datamart/); Climate data is available at the Global Climate Data – WorldClim (www.worldclim.org) and the PRISM Climate Group (http://prism.oregonstate.edu/); N deposition data is available at the National Atmospheric Deposition Program (http://nadp.slh.wisc.edu/); Fire frequency data is available at US Forest Service Research Data Archive (DOI:10.2737/RDS-2013-0009.4).
Figure 1

A

Ecoregion

1. Marine
2. Mediterranean
3. Temperate desert
4. Temperate steppe
5. Tropical/subtropical desert
6. Tropical/subtropical steppe
7. Prairie
8. Warm continental
9. Hot continental
10. Subtropical
11. Savannah

AM tree dominance

EM dominant ↔ AM dominant

0
0.25
0.5
0.75
1

B

C

AM tree dominance

Mean coefficient estimate

MAT (°C)

MAP (mm)
Distribution of forest tree mycorrhizal types and their associated factors in forests of the contiguous USA. (A) Geographical distribution of AM tree dominance. (B) Distribution of AM tree dominance in climatic space (MAP, mean annual precipitation; MAT, mean annual temperature). (C) Relative effects of MAP, MAT, and tree basal area on AM tree dominance. Each dot in (A) and (B) represents a plot and is colored based on the associated AM-EM tree dominance. Boundaries of ecoregions (solid line) and nested sub-ecoregions (dashed lines) in (A) are based on Cleland et al (55). Circles in (B) indicate ecoregion-level mean MAT and MAP values with the associated standard deviations. The circle is colored based on the mean AM tree dominance and the size is proportional to the number of plots (log scale). Effects of MAP, MAT, and basal area on AM tree dominance across ecoregions in the contiguous USA (C) were tested using generalized mixed effect models with sub-ecoregions included as a random effect in each model. Significant coefficient estimates are plotted in (C) as solid circles and non-significant ones as open circles. Circle size is proportional to the number of plots (log scale). The number beside each dot in (B) and (C) represents the associated ecoregion in (A). Error bars in (C) are standard errors.
Figure 2

A

B

C

- MAP change
- MAT change
- N deposition
- Fire frequency
- AM tree dominance (T1)
- Basal area (T1)

- Mean coefficient estimate

- AM tree dominance change (T2-T1)

- EM trees

- AM trees

- Tree proportion change (based on basal area)
Changes in forest AM tree dominance during the past three decades and the relative impacts of environmental changes on the mycorrhizal association changes in forests of eastern USA. (A) Changes in AM tree dominance over the two inventories (T2-T1). All ecoregions had a significant increase in AM tree dominance during the period based on a paired Wilcoxon signed-rank test ($P < 0.001$, inset figures are boxplots of hexagon-level changes by ecoregions). (B) Relative effects of climate and basal area change, AM tree dominance at the first inventory (T1), N deposition, and fire frequency on AM tree dominance change. (C) Effects of tree abundance change of the top 10 most abundant tree genera (genera on the left without shaded background are AM trees and genera on the right are EM trees) on AM tree dominance change. Mean coefficients in (B) and (C) were estimated at the ecoregion level based on generalized mixed effects models with sub-ecoregions included as a random effect. Significant coefficient estimates are plotted as solid circles and non-significant ones as open circles with the size being proportional to the number of hexagons (log scale). Error bars in (B) and (C) are standard errors.
AM tree dominance differences between adult trees and saplings in forests across 11 ecoregions of the USA. The difference in AM tree dominance between adults and saplings for each ecological region were tested based on a paired Wilcoxon signed-rank test (*, P < 0.05; **, P < 0.01; ***, P < 0.001). Error bars are standard errors. The bar thickness is proportional to the number of plots (log scale). Only plots where both adult trees and saplings are present are used for the analysis (98,638 plots).
Figure 4

A) Soil C stock (kg C m$^{-2}$)

B) Soil N stock (kg N m$^{-2}$)

C) Soil C:N ratio

D) Soil C stock

E) Soil N stock

F) Soil C:N ratio

AM tree dominance

(EM dominant ↔ AM dominant)
Associations between forest soil C and N with forest tree mycorrhizal type and environmental factors in forest ecosystems in the USA. (A-C) Relationships between AM tree dominance and soil (A) C stock, (B) N stock, and (C) C:N ratio (based on 0-20 cm depth mineral soil and litter layer). Linear regression lines were fitted by ecoregion (solid line: $P < 0.05$, dotted line: $P > 0.05$; red: positive slope, blue: negative slope). Inset figure shows coefficient (slope) estimate of the fitted line for each ecoregion (colored bars indicate significant relationship at $P < 0.05$; red: positive, blue: negative). (D-F) Effects of AM tree dominance and environmental factors on soil (A) C stock, (B) N stock, and (C) C:N ratio across ecoregions of the USA. Coefficient estimates in (D-F) are based on mixed effect models at ecoregion level with sub-ecoregions as a random effect. Significant coefficient estimates are plotted as sold circles and non-significant ones as open circles. Circle size is proportional to the number of plots (log scale). Error bars are standard errors. The number beside each bar in (A-C) and each dot in (D-F) represents the associated ecoregion in (A). Soil data summary is available in Table S2.