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Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts

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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)

62   program across the contiguous USA, we (i) map the tree mycorrhizal association patterns and

63   identify underlying drivers of these observed associations, (ii) quantify the impacts of human

64   induced global changes, primarily climate change, N deposition, and disturbance regimes, on tree

65   mycorrhizal associations, and (iii) assess the potential feedback of mycorrhizal association shifts

66   on soil C and nutrient dynamics.

Distribution and drivers of tree mycorrhizal association patterns

68   Using FIA vegetation data and tree mycorrhizal type information, we mapped the relative

69   abundance of over three million AM and EM trees across the conterminous USA (**Fig. 1A**).

70   While patterns of mycorrhizal associations and associated drivers have been reported previously,

71   these studies were based on species occurrence data (*27-29*), covered lesser spatial extent (*30*),

72   and examined fewer vegetation survey plots than our study (*31*). Our results indicate that AM

73   trees are more dominant in dry and warm ecoregions, while EM trees are more dominant in

74   humid and cold ecoregions (**Fig. 1, A** and **B**). In the western USA, AM trees are dominant in the

75   subtropical desert and steppe regions and EM trees are dominant in the northwestern and

76   intermountain west regions (**Fig. 1A**, **Fig. S1**). AM and EM trees are well-mixed in eastern

77   USA, with more AM trees in the hot continental region and more EM trees in the western portion

78   of the warm continental region (**Fig. 1**, **Fig. S1**). Using a mixed-effects model that accounts for

79   the spatial heterogeneity between plots in different sub-ecoregions, we found that climate is an

80   important driver of tree mycorrhizal association patterns at the continental scale (**Fig. 1C**).

81   Overall, AM tree dominance was negatively associated with mean annual precipitation (MAP)

82   and positively associated with mean annual temperature (MAT) (**Fig. 1C**), although the

83   magnitude and direction of effect sizes differed in some ecoregions. Forest tree basal area,

84   which was used as an indicator of forest successional stage, had smaller effects on AM tree

4

85   dominance compared to climatic factors, implying that climate is a more important driver of the

86   continental tree mycorrhizal association patterns (**Fig. 1C**).

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

88   　　　To understand the impacts of human-induced global changes on tree mycorrhizal

89   associations, we used repeated measurements of forest inventories from the FIA program during

90   the last three decades in eastern USA where rapid climate change has been observed (**Fig. S2**)

91   (*1*). AM tree dominance has significantly increased in all parts of eastern USA during the last

92   three decades (based on a paired Wilcoxon signed-rank test, $P<0.05$; **Fig. 2A**), especially in the

93   central regions (17% increase in prairie and 15% increase in hot continental regions), due to both

94   an increase in AM tree abundance (i.e. basal area; **Fig. S3A**) and decrease in EM tree abundance

95   (**Fig. S3B**). AM tree dominance in southern and northern ecoregions also increased (5% increase

96   in warm continental and 5% increase in subtropical, **Fig. 2A**), even though these regions had

97   statistically significant increases in both AM and EM tree abundance (**Fig. S3, A** and **B**).

98   Particularly, the western portion of the warm continental region and northern portion of the

99   subtropical region had similar increases in AM tree abundance, while the eastern portion of the

100 warm continental region and southern portion of the subtropical region had the opposite trend

101 (**Fig. 2A**).

102 　　　Our analysis indicates that three factors – N deposition, fire frequency and climate

103 change – likely contributed to the increases in AM tree dominance. First, we found a strong

104 positive correlation between N deposition and shifts in AM tree dominance, consistent with

105 earlier studies based on smaller spatial extent and shorter temporal scale (*31*). In temperate

106 forests, most AM tree species have nutrient acquisitive traits (e.g., rapid root growth into nutrient

107 hot spots and narrower C:N in leaf and root tissues) (*17, 32-34*) and often dominate stands

108 characterized by open (i.e., fast) N cycles (*13*, *30*). Thus, the positive relationship between N

109 deposition and AM dominance may result from AM trees being competitively superior at

110 acquiring excess N – the nutrient that generally limits plant growth in these forests. Second, we

111 found strong negative associations between fire frequency and AM tree dominance (**Fig. 2B**).

112 While it is well-established that fire suppression following European settlement has led to oak

113 (*Quercus*) regeneration failure and forest "mesophication" in the eastern US (*35*), our results

114 indicate that this trend is not merely a result of EM-associating oaks being replaced by AM-

115 associating maples (*Acer*). The change in AM tree dominance was not driven by a specific

116 phylogenetic group of tree species, as the most common AM and EM tree genera had relatively

117 similar effect sizes on the change (**Fig. 2C**). Changes of abundance in all five most common

118 AM genera, with a few statistically non-significant exceptions, were positively associated with

119 AM tree dominance change; while, the changes of abundance in EM genera were nearly all

120 negatively associated with the AM tree dominance change (**Fig. 2C**). Possible explanations for

121 the observed non-significant outliers (e.g., *Prunus* in prairie and *Carya* in warm continental

122 region) could due to small sample sizes or potential preferential harvesting in these regions. The

123 third factor contributing to increases in AM tree dominance is climate change. In general,

124 increases in MAP were negatively associated with increases in AM tree dominance, while the

125 associations with MAT were weak and variable (**Fig. 2B**).

126 The extent to which other factors may contribute to future shifts in tree mycorrhizal

127 associations is unknown. AM tree dominance tended to increase with basal area, an indicator of

128 forest succession, as shade tolerant AM trees increase their abundance with the progression of

129 forest succession. However, the effects of basal area were relatively small compared to the other

130 drivers, suggesting that anthropogenic drivers (i.e., climate change, N deposition, fire

131 suppression) had far greater impact on recent demographic shifts. Other factors such as land use

132 change and forest management, which directly affect tree species dominance, could impact shifts

133 in tree mycorrhizal associations. Additionally, to the extent that pollution control and reduction

134 reduces N loading to US forests, future shifts in mycorrhizal associations may lessen in

135 importance in the coming decades.

136   A continuing shift to AM tree dominance is also predicted by our finding that saplings

137 were more AM-dominated compared to adult trees in seven of 11 ecoregions (**Fig. 3**). In the

138 eastern US, all ecoregions other than the warm continental region had greater AM tree

139 dominance in saplings compared to adult trees (**Fig. 3**). The prairie, hot continental, and

140 subtropical regions had over 54% greater sapling AM tree dominance compared to adult trees.

141 The differences in AM tree dominance between saplings and adult trees were mixed in the

142 western USA (**Fig. 3**). Compared to adult trees, more AM saplings were observed in the marine,

143 Mediterranean, temperate steppe regions, but less AM saplings in the temperate desert,

144 tropical/subtropical desert, tropical/subtropical steppe regions. In addition, the overall

145 differences between adult and sapling AM tree dominance were smaller than those observed in

146 the ecoregions in eastern USA (**Fig. 3**).

Relationships between tree mycorrhizal associations and soil C and N

148   To assess the potential consequences of mycorrhizal association shifts on C and N

149 dynamics, we analyzed the relationships between AM tree dominance and soil C and N stocks

150 (litter layer and 0-20 cm depth of the mineral soil) on plots where both soil attributes and

151 associated vegetation were measured (2,113 plots) using linear regression models. In general,

152 the associations between AM tree dominance and soil C and N stocks were positive in mesic

153 temperate ecoregions but negative in dry ecoregions; however, most ecoregions had a negative

154 relationship between soil C:N ratio and AM tree dominance (**Fig. 4, A to C**). Across the study

155 area, AM-dominated forests had 28% more soil N and 8% more soil C than EM-dominated

156 forests (**Fig. 4, A** and **B, Table S2**). The greater increase in soil N stocks (relative to soil C

157 stocks) in mesic ecoregions and the lower decrease in soil N stocks (relative to soil C stocks) in

158 dry ecoregions resulted in a negative relationship between soil C:N ratio and AM tree dominance

159 along the continental AM tree dominance gradient (**Fig. 4, A to C**).

160 Using mixed-effects models, we further tested how forest mycorrhizal association and

161 environmental factors are related to soil attributes for each ecoregion after accounting for the

162 spatial heterogeneity between plots in different sub-ecoregions by adding sub-ecoregions as

163 random intercepts in the models. We found that AM tree dominance, climate, and soil texture

164 had significant associations with soil C and N stocks and C:N ratio, though with different effect

165 sizes (**Fig. 4, D to F**). Overall, AM tree dominance was positively associated with soil C and N

166 stocks and negatively with C:N ratio across the ecoregions – consistent with site-based patterns

167 recently reported (*22*). Among the climatic factors, MAP tended to have positive associations

168 with soil C and N stocks, while MAT have negative associations. Soil C and N stocks were

169 similar between the top 20 cm of the mineral soil and the top 20 cm plus litter layer (**Fig. S4**)

170 owing to the much smaller size of the litter C and N pools.

171 The observational nature of our data preclude us from determining whether AM trees are

172 causing elevated N levels in soil (as opposed to merely responding to them). It is possible that

173 AM trees can elevate soil N (pool sizes and transformation rates) by releasing high chemical

174 quality litter to soil. Several studies of temperate trees have shown that AM litters generally

175 decay faster than EM litters in common garden studies (*36*) and meta-analyses (*37*). And given

176 that higher chemical quality litter leads to both greater rates of N transformations (*38*) and the

177   formation of more protected (i.e. stable) soil organic matter (*sensu* the MEMS hypothesis) (*39*),

178   increasing AM dominance may lead to elevated N levels in soil (*22*). Contemporary theory of

179   soil organic matter stabilization and turnover indicates that changes in AM vs EM dominance

180   can alter C and N cycling in 30-45 years (*18*) – well-within the time frame detect changes in the

181   FIA dataset. Thus, our contention that AM trees may be contributing, in part, to N accumulation

182   is a testable hypothesis but requires further inquiry.

183   Finally, separating cause and effect in this instance may be of limited importance given

184   that tree species often modify soils in ways that tend to exacerbate or enhance the pre-existing

185   biogeochemical condition (*40*). Thus, while we can't rule out that the species are merely

186   responding to the high N soils, both processes likely contribute to the maintenance of the

187   biogeochemical syndromes observed. More experiments and/or long-term repeated measures of

188   soil stocks are needed to test the mechanisms of these associations. Nevertheless, the consistent

189   large-scale patterns in forests across multiple ecoregions suggests that dominant tree mycorrhizal

190   type could be an important driver of nutrient and C dynamics in forests through positive/negative

191   feedbacks associated with AM/EM plant traits (*40*).

192   Given that AM-dominated forests tend to be underlain by soils with lower C:N than EM-

193   dominated soils (*30,33*; **Fig. 4C**), the increasing dominance of AM trees could have

194   consequences for forest ecosystem functions and services. Low or small ratios are often used as

195   proxies for rates of microbial N transformations in soils such as nitrification, nitrate leaching

196   losses (*38*), as well as for ecosystem sensitivity to N deposition (*41*). Thus, forests of eastern

197   USA may be experiencing an acceleration of N cycling – owing to the shifts in AM dominance.

198   The consequences of nutrient amplification would likely be profound for water quality if for

199   example, elevated nitrification rates enhance nitrate export to lakes and rivers.

200   The consequences of nutrient acceleration may be most profound for forest productivity,

201   which can feed-back to affect climate change. Most AM-dominated ecosystems cannot sustain

202   high level of productivity under elevated CO_2 unless the availability of soil N is high (*23*). Thus,

203   if increases in AM tree dominance lead to an acceleration of N cycling, AM-dominated forests in

204   eastern USA may be strong sinks for atmospheric CO_2. However, if the AM-induced

205   acceleration of N cycling leads to significant ecosystem N losses (*25*) or results in N stabilization

206   in soil organic matter (*22*), there may be little stimulation of forest productivity. In addition,

207   shifting balance of AM-EM vegetation could also be influenced by N-induced Phosphorus (P)

208   limitation and more severe drought periods (*42*). While N-induced P limitation has long been

209   considered as something that would only occur in forests south of the last glacial maximum

210   (where mineral P levels are extremely low), recent evidence from northern ecosystems

211   challenges the paradigm (*43*). Either way, our results indicate that changes in N cycling owing

212   to increasing AM tree dominance could have profound consequences for C and N retention and

213   loss in forests and hence, the degree to which forests feedback to climate change.

214   **Conclusions**

215   Our study provides the first comprehensive distribution map of tree-mycorrhizal

216   association in the contiguous USA. More importantly, we provide empirical evidence based on

217   national forest inventory data for how global changes may have impacted the shift of

218   mycorrhizal associations at the continental scale. We found that AM tree dominance was

219   positively associated with both soil C and N stocks, particularly for temperate forests, which

220   challenges the prevailing idea that EM dominant ecosystems store more C than AM tree

221   dominant ecosystems (*15*, *19-21*). We note, however, that soil C:N ratio was negatively

222   associated with AM tree dominance, supporting recent findings that showed the positive

223   association between soil C:N ratio and EM tree dominance driven by low soil N instead of high

224   C stock in EM dominant ecosystems (*22*, *30*). Our results suggest that increases in AM tree

225   dominance in the eastern USA may increase soil N stocks, inducing a positive feedback of

226   nutrient acceleration, at least in the upper surface soils. A better understanding of the role of

227   dominant forest mycorrhizal association type in ecosystem processes at global scales and the

228   mechanisms responsible for forest soil C storage is critical for improving ecosystem models to

229   predict forest ecosystem processes and functions in global climate change.

230

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 (*44*).

Soil carbon and nitrogen stocks

FIA program collected soil samples on every 1/16th base intensity plot, distributed

approximately every 38,848 ha (*45*). 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**.

<u>Climate, N deposition, and fire frequency data</u>

256 At the plot level, mean annual temperature (MAT) and mean annual precipitation (MAP) of

257 current climate conditions were derived from the Global Climate Data - WorldClim Version 1.4

258 (1-km spatial resolution; available at <u>www.worldclim.org</u>) (*46*). At the hexagon level, MAT and

259 MAP changes over the past three decades, calculated by subtracting mean values of the recent

260 period (1981-2015) and the recent past (1951-1980) from the PRISM Climate Group (4-km

261 spatial resolution; available at <u>http://prism.oregonstate.edu/</u>) (*47*), were aggregated with mean.

262 Annual mean of total N deposition (kg N ha^{-1} yr^{-1}) data over the past 15 years (2000-2015) were

263 extracted from the National Atmospheric Deposition Program (available at

264 <u>http://nadp.slh.wisc.edu/</u>) (*48*) and aggregated with mean at the hexagon level. Although wet N

265 deposition data are available from 1985 to 2016, we used total N deposition data, which includes

266 wet and dry N deposition of both organic and inorganic forms, given that recent N deposition

267 data reflect the historical N deposition patterns (*31*). Fire frequency data were compiled from

268 spatial wildfire occurrence data in the USA over 24 years (1992-2015) (*49*). The point locations

269 of fire occurrence during the period were converted to kernel density (per km^2) raster (1-km

270 spatial resolution) using ArcGIS (ver. 10.5, Esri Inc., USA), and then aggregated with mean at

271 the hexagon level. Spatial patterns of these data are available in **Fig. S2**.

272 <u>Tree mycorrhizal type information</u>

273 Mycorrhizal type was assigned for each tree species present in FIA plots based on peer-reviewed

274 journal publications (*50-53*). If the species-level mycorrhizal type was not available, we assigned

275 the most frequent mycorrhizal type within genus (or family). To avoid potential false conclusions

276 due to misclassification of mycorrhizal association (*54*), we further revised the ectomycorrhizal

277 tree information based on Tedersoo and Brundrett (*55*). We then calculated the AM tree

278 dominance (based on basal area) for each plot by dividing total AM tree basal area by the sum of

279   AM and EM mycorrhizal tree basal area. For some species categorized as both AM and EM, we

280   tested if assigning them as AM (or EM) changes the patterns of mycorrhizal associations and

281   found no significant effects, therefore, we assigned them a half of the basal area each to AM and

282   EM.

283   <u>Changes in AM-EM tree dominance during the past three decades</u>

284   To test changes in AM-EM tree dominance over the past three decades, we utilized

285   repeated measures of forest plot inventory available in eastern USA by US Forest Service, the

286   first inventory, collected between 1980 and 1995 (T1; mean inventory year: 1986; 83,866 plots)

287   and the second inventory was the latest completed inventory, which was finished in 2015 for

288   most states (T2; mean inventory year: 2015; 70,715 plots). We only included eastern USA since

289   repeated FIA measures are rarely available for the western USA. Because T2 inventory measures

290   were not necessarily done in the same plot locations with T1 plots, we aggregated plot-level AM

291   tree dominance and total tree basal area to the hexagon-level (a spatial tessellation design used

292   by FIA), following Fei *et al* (*1*). The size of hexagon (1,452 km^2) is approximately the mean size

293   of counties in eastern USA. We only included hexagons with at least 10 plots each for both T1

294   and T2 inventories (mean plot number per each T1 hexagon: 47; mean plot number per each T2

295   hexagon: 40), resulted in 1,785 hexagons for the final analysis.

296   <u>Statistical analysis</u>

297   We determined relative effects of climate and total tree basal area (as a surrogate for

298   succession status) on AM tree dominance across the ecoregions (plot level data) using mixed-

299   effects models with a beta distribution and logit link function using R package '*glmmTMB*' (*56*).

300   Since AM tree dominance data in our inventory plots included many zeros (only EM trees

301   present in the plot) and ones (only AM trees present), we transformed the data as $y' =$

302 $\frac{y \times (N-1) + 0.5}{N}$ where y is AM tree dominance and N is sample size, following Averill *et al* (*31*).

303 We added sub-ecoregions (nested units within ecoregion, **Fig. 1A**) as a random effect in the

304 model to account for the spatial heterogeneity between plots in different sub-ecoregions. We

305 excluded plots with any missing variables and ended up with 132,956 plots for analyses. All

306 predictor variables were standardized by subtracting mean and dividing by two standard

307 deviations to make the regression coefficients for the predictors comparable. AM tree dominance

308 differences between two inventories (T1 and T2) (hexagon level data) and between saplings and

309 adult trees (plot level data) were tested using a paired Wilcoxon signed-rank test for each

310 ecoregion. At the ecoregion level, effects of global change drivers (i.e. MAP and MAT changes,

311 N deposition, fire frequency), AM tree dominance at T1, and basal area on the AM tree

312 dominance change during the past three decades (T2-T1) were tested using mixed-effects models

313 with a Gaussian error distribution and sub-ecoregions as a random effect (see **Fig. S2** for the

314 spatial patterns of the predictor variables). We also tested effects of genus-level tree dominance

315 changes in 10 most abundant tree genera (57) in the studied plots on the AM tree dominance

316 change, using the same mixed effects model structure described above. The AM tree genera

317 included *Acer, Fraxinus, Prunus*, *Nyssa*, and *Ulmus* and the EM tree genera included *Quercus,*

318 *Pinus, Carya, Betula,* and *Populus*. Fire frequency was log-transformed to meet normality

319 assumptions and all predictor variables were standardized. Bivariate relationships between soil C

320 and N stocks and C:N ratio and AM tree dominance were tested using a linear regression. We

321 further determined relative effects of AM tree dominance and environmental factors on soil

322 attributes, using a mixed effects modeling approach. At the ecoregion level, we modeled each of

323 soil attributes (soil C and N stocks and C:N ratio) with a Gaussian error distribution as a function

324 of AM tree dominance, MAP, MAT, basal area, and clay proportion, nested within sub-

325   ecoregions. Soil attributes were log-transformed to meet normality assumptions and all predictor

326   variables were standardized. All statistical analyses were performed in the R statistical

327   programming environment, version 3.3.2 (*58*).

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491

497   **Author contributions:**

498   I.J. and S.F. conceived the study. C.O. and G.D. provided forest inventory data. IJ performed the

499   analyses and drafted the manuscript. All authors contributed substantially to revisions and

500   confirmed the final version of the manuscript.

501

502   **Competing interests:**

503   Authors declare no competing interests.

504

505   **Data and materials availability:**

506   All data used in the analyses is available at an open data repository (Purdue University Research

507   Repository; DOI:10.4231/R76D5R7S). Vegetation and soil data is available at FIA DataMart –

508   US Forest Service (https://apps.fs.usda.gov/fia/datamart/); Climate data is available at the Global

509   Climate Data – WorldClim (www.worldclim.org) and the PRISM Climate Group

510   (http://prism.oregonstate.edu/); N deposition data is available at the National Atmospheric

511   Deposition Program (http://nadp.slh.wisc.edu/); Fire frequency data is available at US Forest

512   Service Research Data Archive (DOI:10.2737/RDS-2013-0009.4).

Figure 1
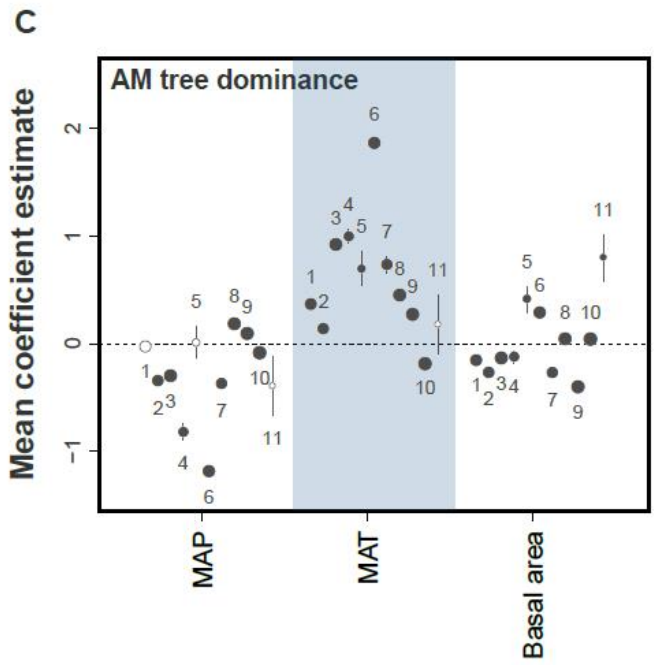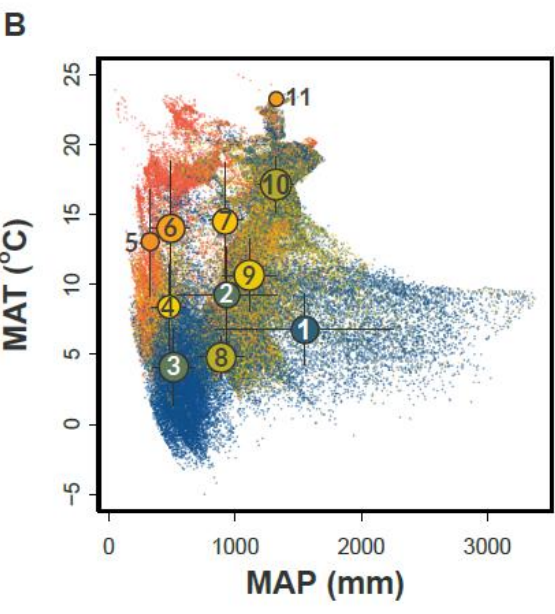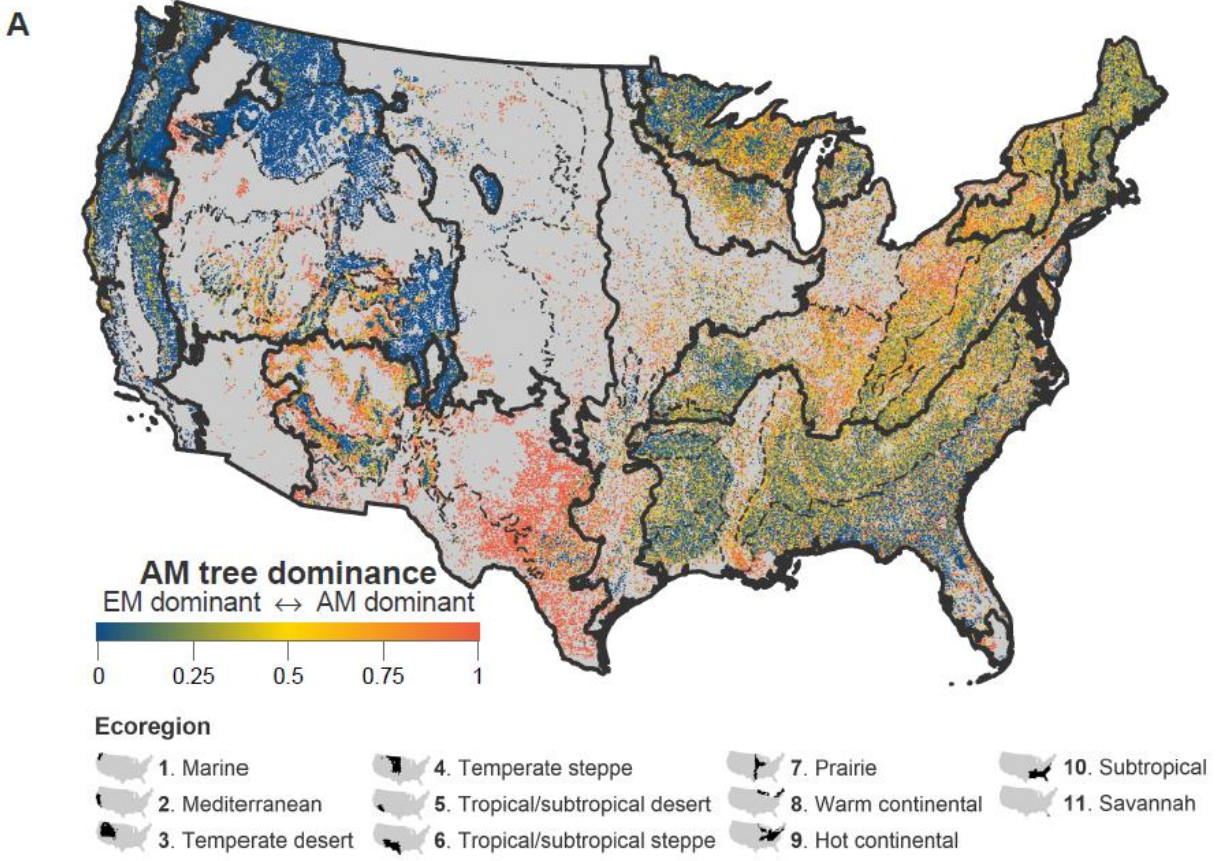
515 **Distribution of forest tree mycorrhizal types and their associated factors in forests of the**

516 **contiguous USA.** (A) Geographical distribution of AM tree dominance. (B) Distribution of AM

517 tree dominance in climatic space (MAP, mean annual precipitation; MAT, mean annual

518 temperature). (C) Relative effects of MAP, MAT, and tree basal area on AM tree dominance.

519 Each dot in (A) and (B) represents a plot and is colored based on the associated AM-EM tree

520 dominance. Boundaries of ecoregions (solid line) and nested sub-ecoregions (dashed lines) in

521 (A) are based on Cleland *et al* (*55*). Circles in (B) indicate ecoregion-level mean MAT and MAP

522 values with the associated standard deviations. The circle is colored based on the mean AM tree

523 dominance and the size is proportional to the number of plots (log scale). Effects of MAP, MAT,

524 and basal area on AM tree dominance across ecoregions in the contiguous USA (C) were tested

525 using generalized mixed effect models with sub-ecoregions included as a random effect in each

526 model. Significant coefficient estimates are plotted in (C) as solid circles and non-significant

527 ones as open circles. Circle size is proportional to the number of plots (log scale). The number

528 beside each dot in (B) and (C) represents the associated ecoregion in (A). Error bars in (C) are
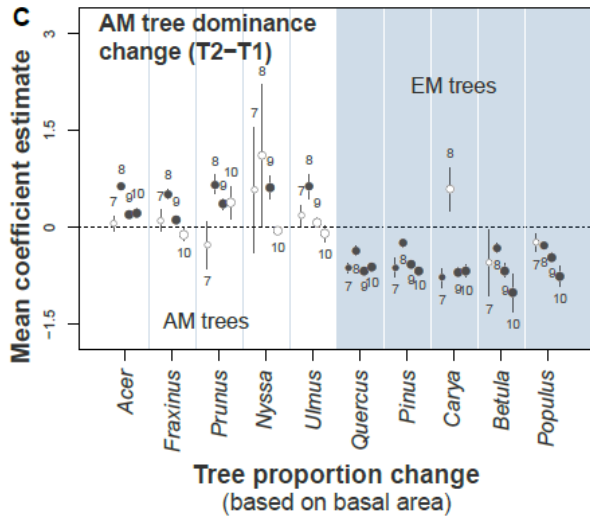
529 standard errors.

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531   **Figure 2**
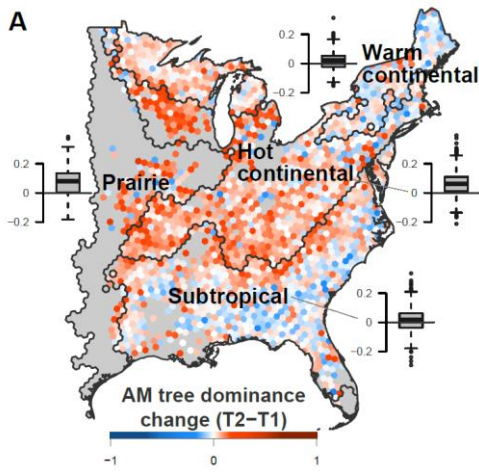
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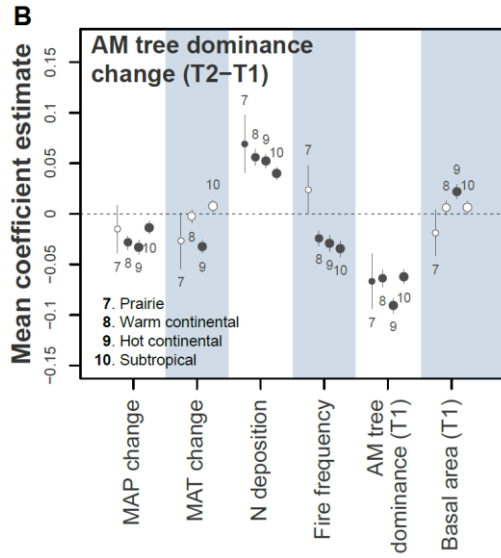
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535 **Changes in forest AM tree dominance during the past three decades and the relative**

536 **impacts of environmental changes on the mycorrhizal association changes in forests of**

537 **eastern USA.** (A) Changes in AM tree dominance over the two inventories (T2-T1). All

538 ecoregions had a significant increase in AM tree dominance during the period based on a paired

539 Wilcoxon signed-rank test ($P < 0.001$, inset figures are boxplots of hexagon-level changes by

540 ecoregions). (B) Relative effects of climate and basal area change, AM tree dominance at the

541 first inventory (T1), N deposition, and fire frequency on AM tree dominance change. (C) Effects

542 of tree abundance change of the top 10 most abundant tree genera (genera on the left without

543 shaded background are AM trees and genera on the right are EM trees) on AM tree dominance

544 change. Mean coefficients in (B) and (C) were estimated at the ecoregion level based on

545 generalized mixed effects models with sub-ecoregions included as a random effect. Significant

546 coefficient estimates are plotted as solid circles and non-significant ones as open circles with the

547 size being proportional to the number of hexagons (log scale). Error bars in (B) and (C) are

548 standard errors.

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Figure 3
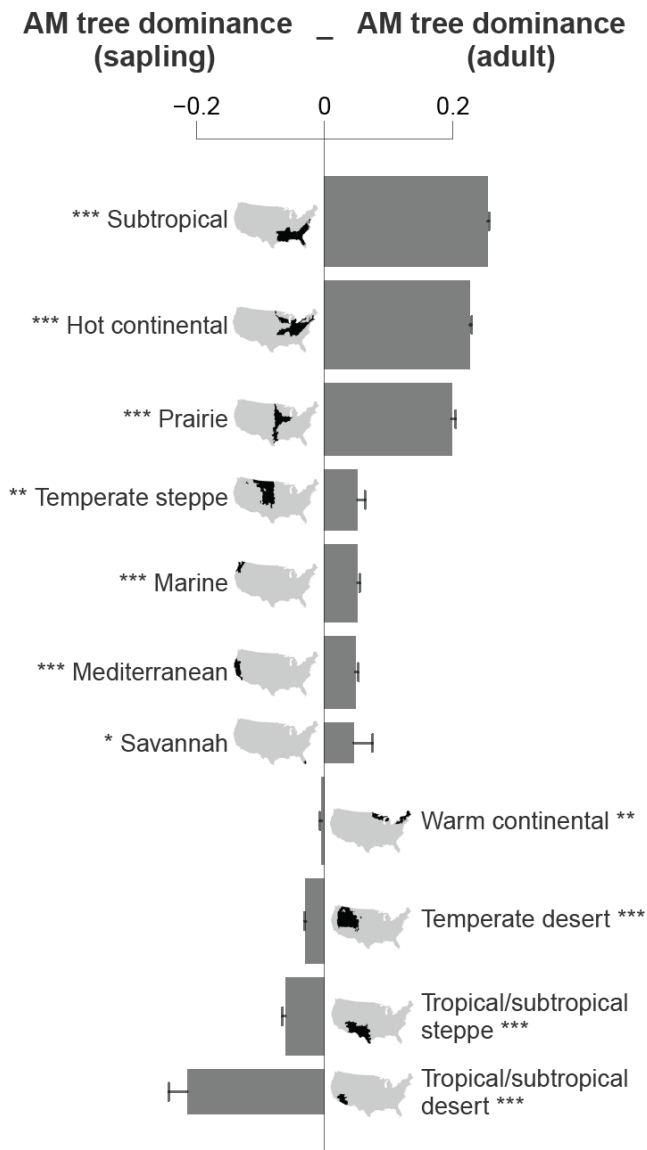
**AM tree dominance differences between adult trees and saplings in forests across 11 ecoregions of the USA**. The difference in AM tree dominance between adults and saplings for each ecological region were tested based on a paired Wilcoxon signed-rank test (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). 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
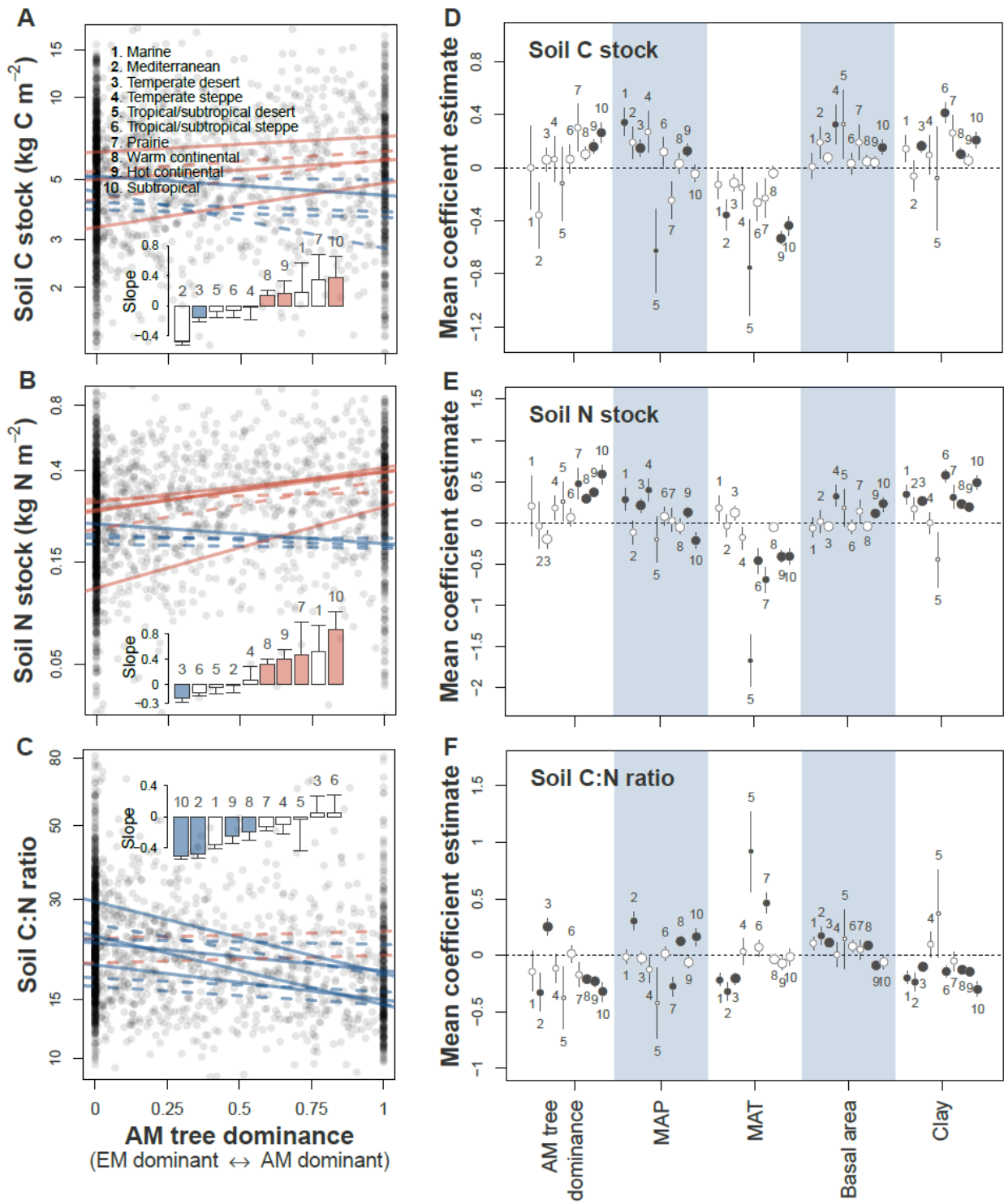
560 **Associations between forest soil C and N with forest tree mycorrhizal type and**

561 **environmental factors in forest ecosystems in the USA.** (A-C) Relationships between AM tree

562 dominance and soil (A) C stock, (B) N stock, and (C) C:N ratio (based on 0-20 cm depth mineral

563 soil and litter layer). Linear regression lines were fitted by ecoregion (solid line: $P < 0.05$, dotted

564 line: $P > 0.05$; red: positive slope, blue: negative slope). Inset figure shows coefficient (slope)

565 estimate of the fitted line for each ecoregion (colored bars indicate significant relationship at $P <$

566 0.05; red: positive, blue: negative). (D-F) Effects of AM tree dominance and environmental

567 factors on soil (A) C stock, (B) N stock, and (C) C:N ratio across ecoregions of the USA.

568 Coefficient estimates in (D-F) are based on mixed effect models at ecoregion level with sub-

569 ecoregions as a random effect. Significant coefficient estimates are plotted as sold circles and

570 non-significant ones as open circles. Circle size is proportional to the number of plots (log scale).

571 Error bars are standard errors. The number beside each bar in (A-C) and each dot in (D-F)

572 represents the associated ecoregion in (A). Soil data summary is available in Table S2.