

Purdue University

**Purdue e-Pubs**

---

Purdue University Libraries Open Access  
Publishing Support Fund

Purdue Libraries and School of Information  
Studies

---

2019

## 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

Follow this and additional works at: <https://docs.lib.purdue.edu/fund>

---

### Recommended Citation

Jo, Insu; Fei, Songlin; Oswalt, Christopher M.; Domke, Grant M.; and Phillips, Richard P., "Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts" (2019). *Purdue University Libraries Open Access Publishing Support Fund*. Paper 13.  
<http://dx.doi.org/10.1126/sciadv.aav6358>

This document has been made available through Purdue e-Pubs, a service of the Purdue University Libraries.  
Please contact [epubs@purdue.edu](mailto:epubs@purdue.edu) for additional information.

1 **Title: Shifts in dominant tree-mycorrhizal associations in response to**  
2 **anthropogenic impacts**

3

4 **Shifts in tree-mycorrhizal associations**

5

6 **Authors:**

7 Insu Jo<sup>1</sup>, Songlin Fei<sup>1\*</sup>, Christopher Oswald<sup>2</sup>, Grant M. Domke<sup>3</sup>, Richard P. Phillips<sup>4</sup>

8

9 **Affiliations:**

10 <sup>1</sup> Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907,  
11 USA.

12 <sup>2</sup> Southern Research Station, Forest Service, United States Department of Agriculture, Knoxville,  
13 TN 37919, USA.

14 <sup>3</sup> Northern Research Station, Forest Service, United States Department of Agriculture, St. Paul,  
15 MN 55108, USA.

16 <sup>4</sup> Department of Biology, Indiana University, Bloomington, IN 47405, USA

17

18 \*Correspondence to: Songlin Fei, Department of Forestry and Natural Resources, 715 West  
19 State St., Purdue University, West Lafayette, IN 47907, USA. Email: [sfei@purdue.edu](mailto:sfei@purdue.edu)

20 **Abstract:**

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

33

34

35 **One Sentence Summary:**

36 Anthropogenic influences alter tree mycorrhizal associations inducing nutrient acceleration in the  
37 USA forests.

38

39 **Main Text:**

40 **Introduction**

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

52         The two dominant types of fungi that associate with trees – arbuscular mycorrhizal (AM)  
53 and ectomycorrhizal (EM) – differ greatly in their form and function. Consequently, tree  
54 mycorrhizal associations have been hypothesized to represent trait-integrating phenotypes that  
55 give rise to “biogeochemical syndromes” in forests (13), although the relative contribution of the  
56 plants vs. fungi to these syndromes is poorly quantified. EM-dominated forests often cycle  
57 carbon (C) and nutrients conservatively owing to the lower chemical quality of their litters  
58 relative to AM-dominated forests, which have more “open” C and nutrient cycles (17, 18). Such  
59 effects not only alter the degree to which these ecosystems store C and nutrients (19-22), but  
60 likely affect their sensitivity to human induced global changes (23-26). Here, using forest  
61 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.

### 67 **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

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 be 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**).

#### 147 **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<sub>2</sub> 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<sub>2</sub>. 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

## 231 **Materials and Methods**

### 232 Tree data collection

233 Tree inventory data were obtained from forest plots across the USA by the Forest Inventory and  
234 Analysis (FIA) program (US Forest Service; data available at  
235 <https://apps.fs.usda.gov/fia/datamart/>). The FIA program monitors forests resources at the  
236 national level, using permanent plots, which have a sampling intensity of approximately one plot  
237 every 2,428 ha. Each plot comprises four subplots (fixed-radius: 7.3 m) spaced 37 m apart in a  
238 triangular arrangement with one subplot in the center. For each FIA plot, we extracted tree basal  
239 area by species with diameter at breast height (dbh) > 12.7 cm as adult tree and dbh 5.1-12.7 cm  
240 as sapling (44).

### 241 Soil carbon and nitrogen stocks

242 FIA program collected soil samples on every 1/16th base intensity plot, distributed  
243 approximately every 38,848 ha (45). We compiled forest litter layer C and N concentrations and  
244 the associated litter layer thickness and bulk density, mineral soil C and N concentrations for 0-  
245 20 cm soil depth and the associated soil bulk density and coarse fraction at subplot-level where  
246 species-level vegetation inventory was available. Soil C and N measurements in FIA data are  
247 based on mineral soil (<2mm) and coarse particles (>2mm) are not included. Mineral soil C and  
248 N stocks ( $\text{kg m}^{-2}$ ) to a depth of 20 cm calculated based on soil C and N concentration (%), soil  
249 bulk density ( $\text{g cm}^{-3}$ ), after removing a proportion of coarse particle fraction (particle size >2mm)  
250 in the soil layer. Total soil C and N stocks were calculated by combining values for both mineral  
251 soil (0-20 cm depth) and litter layer. Since soil texture for mineral soil (0-20 cm depth) was  
252 categorized based on field measure, we assigned mean clay proportion for each texture type  
253 (loamy=45%, clayey=60%, sandy or coarse sand=10%), following Zhu *et al* (30). Soil data  
254 summary by ecoregion is available at **Table S2**.

255 Climate, N deposition, and fire frequency data

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 [www.worldclim.org](http://www.worldclim.org)) (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 <http://prism.oregonstate.edu/>) (47), were aggregated with mean.  
262 Annual mean of total N deposition ( $\text{kg N ha}^{-1} \text{ yr}^{-1}$ ) data over the past 15 years (2000-2015) were  
263 extracted from the National Atmospheric Deposition Program (available at  
264 <http://nadp.slh.wisc.edu/>) (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 ( $\text{per km}^2$ ) 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 Tree mycorrhizal type information

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

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<sup>2</sup>) 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 Statistical analysis

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).

328 **References and Notes:**

- 329 1 S. Fei, J. M. Desprez, K. M. Potter, I. Jo, J. A. Knott, C. M. Oswald, Divergence of  
330 species responses to climate change. *Sci. Adv.* **3** (2017).
- 331 2 R. Thomas, C. Canham, K. Weathers, C. Goodale, Increased tree carbon storage in  
332 response to nitrogen deposition in the US. *Nat. Geosci.* **3**, 13-17 (2009).
- 333 3 V. H. Dale, L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J.  
334 Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J.  
335 Stocks, B. M. Wotton, Climate change and forest disturbances: climate change can affect  
336 forests by altering the frequency, intensity, duration, and timing of fire, drought,  
337 introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or  
338 landslides. *BioScience* **51**, 723-734 (2001)
- 339 4 K. H. Riitters, J. D. Wickham, R. V. O'Neill, K. B. Jones, E. R. Smith, J. W. Coulston, T.  
340 G. Wade, J. H. Smith, Fragmentation of continental United States forests. *Ecosystems* **5**,  
341 815-822 (2002)
- 342 5 J. G. Ehrenfeld, P. Kourtev, W. Huang. Changes in soil functions following invasions of  
343 exotic understory plants in deciduous forests. *Ecol. Appl.* **11**, 1287-1300 (2001)
- 344 6 C. Parmesan, G. Yohe, A globally coherent fingerprint of climate change impacts across  
345 natural systems. *Nature* **421**, 37 (2003).
- 346 7 W. H. van der Putten, M. A. Bradford, E. P. Brinkman, T. F. J. van de Voorde, G. F.  
347 Veen, Where, when and how plant–soil feedback matters in a changing world. *Func.*  
348 *Ecol.* **30**, 1109-1121 (2016).

- 349 8 A. T. Classen, M. K. Sundqvist, J. A. Henning, G. S. Newman, J. A. M. Moore, M. A.  
350 Cregger, L. C. Moorhead, C. M. Patterson, Direct and indirect effects of climate change  
351 on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere* **6**, 1-  
352 21 (2015).
- 353 9 S. E. Smith, D. Read, *Mycorrhizal Symbiosis* (Academic Press, UK, 2008).
- 354 10 M. G. A. van der Heijden, F. M. Martin, M. –A. Selosse, I. R. Sanders, Mycorrhizal  
355 ecology and evolution: the past, the present, and the future. *New Phytol.* **205**, 1406-1423  
356 (2015).
- 357 11 J. A. Bennett, H. Maherali, K. O. Reinhart, Y. Lekberg, M. M. Hart, J. Klironomos,  
358 Plant-soil feedbacks and mycorrhizal type influence temperate forest population  
359 dynamics. *Science* **355**, 181-184 (2017).
- 360 12 I. Jo, K. M. Potter, G. M. Domke, S. Fei, Dominant forest tree mycorrhizal type mediates  
361 understory plant invasions. *Ecol. lett.* **21**, 217-224 (2018).
- 362 13 R. P. Phillips, E. Brzostek, M. G. Midgley, The mycorrhizal-associated nutrient  
363 economy: a new framework for predicting carbon-nutrient couplings in temperate forests.  
364 *New Phytol.* **199**, 41-51 (2013).
- 365 14 D. J. Read, J. Perez-Moreno. Mycorrhizas and nutrient cycling in ecosystems – a journey  
366 towards relevance? *New Phytol.* **157**, 475-492 (2003).

- 367 15 M. K. Taylor, R. A. Lankau, N. Wurzburger, Mycorrhizal associations of trees have  
368 different indirect effects on organic matter decomposition. *J. Ecol.* **104**, 1576-1584  
369 (2016).
- 370 16 M. Shi, J. B. Fisher, E. R. Brzostek, R. P. Phillips. Carbon cost of plant nitrogen  
371 acquisition: global carbon cycle impact from an improved plant nitrogen cycle in the  
372 Community Land Model. *Glob. Change Biol.* **22**, 1299-1314 (2016).
- 373 17 J. H. C. Cornelissen, R. Aerts, B. Cerabolini, M. J. A. Werger, M. G. A. van der Heijden,  
374 Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia*  
375 **129**, 611-619 (2001).
- 376 18 B. N. Sulman, E. R. Brzostek, C. Medici, E. Shevliakova, D. N. L. Menge, R. P. Phillips,  
377 Feedbacks between plant N demand and rhizosphere priming depend on type of  
378 mycorrhizal association. *Ecol. Lett.* **20**, 1043-1053 (2017).
- 379 19 C. Averill, B. L. Turner, A. C. Finzi, Mycorrhiza-mediated competition between plants  
380 and decomposers drives soil carbon storage. *Nature* **505**, 543-545 (2014).
- 381 20 C. Averill, C. V. Hawkes, Ectomycorrhizal fungi slow soil carbon cycling. *Ecol. Lett.* **19**,  
382 937-947 (2016).
- 383 21 N. A. Soudzilovskaia, M. G. A. van der Heijden, J. H. C. Cornelissen, M. I. Makarov, V.  
384 G. Onipchenko, M. N. Maslov, A. A. Akhmetzhanova, P. M. van Bodegom, Quantitative  
385 assessment of the differential impacts of arbuscular and ectomycorrhiza on soil carbon  
386 cycling. *New Phytol.* **208**, 280-293 (2015).

- 387 22 M. E. Craig, B. L. Turner, C. Liang, K. Clay, D. J. Johnson, R. P. Phillips, Tree  
388 mycorrhizal type predicts within-site variability in the storage and distribution of soil  
389 organic matter. *Glob. Change Biol.* **24**, 3317–3330 (2018).
- 390 23 C. Terrer, S. Vicca, B. A. Hungate, R. P. Phillips, I. C. Prentice, Mycorrhizal association  
391 as a primary control of the CO<sub>2</sub> fertilization effect. *Science* **353**, 72-74 (2016).
- 392 24 C. Terrer, S. Vicca, B. D. Stocker, B. A. Hungate, R. P. Phillips, P. B. Reich, A. C. Finzi,  
393 I. C. Prentice, Ecosystem responses to elevated CO<sub>2</sub> governed by plant–soil interactions  
394 and the cost of nitrogen acquisition. *New Phytol.* **217**, 507-522 (2018).
- 395 25 M. G. Midgley, R. P. Phillips, Mycorrhizal associations of dominant trees influence  
396 nitrate leaching responses to N deposition. *Biogeochemistry* **117**, 241-253 (2014).
- 397 26 C. A. Gehring, C. M. Sthultz, L. Flores-Rentería, A. V. Whipple, T. G. Whitham, Tree  
398 genetics defines fungal partner communities that may confer drought tolerance. *Proc.*  
399 *Natl. Acad. Sci.* **114**, 11169-11174 (2017).
- 400 27 N. A. Soudzilovskaia, S. Vaessen, M. van't Zelfde, N. Raes, “Global patterns of  
401 mycorrhizal distribution and their environmental drivers” in *Biogeography of*  
402 *Mycorrhizal Symbiosis*, L. Tedersoo, Eds. (Springer International Publishing, 2017), vol  
403 230, pp. 223-235.
- 404 28 R. Swaty, H. M. Michael, R. Deckert, C. A. Gehring, Mapping the potential mycorrhizal  
405 associations of the conterminous United States of America. *Fungal Ecol.* **24**, 139-147  
406 (2016).

- 407 29 D. J. Read, Mycorrhizas in ecosystems. *Experientia* **47**, 376-391 (1991).
- 408 30 K. Zhu, M. L. McCormack, R. A. Lankau, J. F. Egan, N. Wurzburger, Association of  
409 ectomycorrhizal trees with high carbon-to-nitrogen ratio soils across temperate forests is  
410 driven by smaller nitrogen not larger carbon stocks. *J. Ecol.* **106**, 524-535 (2018).
- 411 31 C. Averill, M. C. Dietze, J. M. Bhatnagar, Continental-scale nitrogen pollution is shifting  
412 forest mycorrhizal associations and soil carbon stocks. *Glob. Change Biol.* **24**, 4544-4553  
413 (2018).
- 414 32 W. Chen, R. T. Koide, T. S. Adams, J. L. DeForest, L. Cheng, D. M. Eissenstat, Root  
415 morphology and mycorrhizal symbioses together shape nutrient foraging strategies of  
416 temperate trees. *Proc. Natl. Acad. Sci.* **113**, 8741-8746 (2016).
- 417 33 G. Lin, M. L. McCormack, C. Ma, D. Guo. Similar below-ground carbon cycling  
418 dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and  
419 ectomycorrhizal forests. *New Phytol.* **213**, 1440-1451 (2017).
- 420 34 H.-Y. Zhang, X.-T. Lü, H. Hartmann, A. Keller, X.-G. Han, S. Trumbore, R. P. Phillips,  
421 Foliar nutrient resorption differs between arbuscular mycorrhizal and ectomycorrhizal  
422 trees at local and global scales. *Glob. Ecol. Biogeogr.* **27**, 875-885 (2018).
- 423 35 G. J. Nowacki, M. D. Abrams, The demise of fire and “mesophication” of forests in the  
424 eastern United States. *BioScience* **58**, 123-138 (2008).

- 425 36 J. Cornelissen, R. Aerts, B. Cerabolini, M. Werger, M. Van Der Heijden, Carbon cycling  
426 traits of plant species are linked with mycorrhizal strategy. *Oecologia* **129**, 611-619  
427 (2001).
- 428 37 A. B. Keller, R. P. Phillips, Leaf litter decay rates differ between mycorrhizal groups in  
429 temperate, but not tropical, forests. *New Phytol.* in press, doi:10.1111/nph.15524.
- 430 38 G. M. Lovett, K. C. Weathers, M. A. Arthur, Control of nitrogen loss from forested  
431 watersheds by soil carbon: nitrogen ratio and tree species composition. *Ecosystems* **5**,  
432 0712-0718 (2002).
- 433 39 M. F. Cotrufo, M. D. Wallenstein, C. M. Boot, K. Denef, E. Paul, The microbial e  
434 fficiency-matrix stabilization (mems) framework integrates plant litter decomposition  
435 with soil organic matter stabilization: Do labile plant inputs form stable soil organic  
436 matter? *Glob. Change Biol.* **19**, 988-995 (2013).
- 437 40 S. E. Hobbie, Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends*  
438 *Ecol. Evol.* **30**, 357-363 (2015).
- 439 41 M. G. Midgley, R. P. Phillips, Resource stoichiometry and the biogeochemical  
440 consequences of nitrogen deposition in a mixed deciduous forest. *Ecology* **97**, 3369-3378  
441 (2016).
- 442 42 K. K. Treseder, E. B. Allen, L. M. Egerton-Warburton, M. M. Hart, J. N. Klironomos, H.  
443 Maherali, L. Tedersoo, Arbuscular mycorrhizal fungi as mediators of ecosystem  
444 responses to nitrogen deposition: A trait-based predictive framework. *J. Ecol.* **106**, 480–  
445 489 (2018).

446 43 S. Goswami, M. C. Fisk, M. A. Vadeboncoeur, M. Garrison-Johnston, R. D. Yanai, T. J.  
447 Fahey, Phosphorus limitation of aboveground production in northern hardwood forests.  
448 *Ecology*, **99**, 438-449 (2018).

449 44 U.S. Department of Agriculture, Forest Service, (USDA Forest Service), “The forest  
450 inventory and analysis database: database description and user guide for Phase 2 (version  
451 7.2)” (USDA FS, 2018; [https://www.fia.fs.fed.us/library/database-](https://www.fia.fs.fed.us/library/database-documentation/current/ver72/FIADB%20User%20Guide%20P2_7-2_final.pdf)  
452 [documentation/current/ver72/FIADB%20User%20Guide%20P2\\_7-2\\_final.pdf](https://www.fia.fs.fed.us/library/database-documentation/current/ver72/FIADB%20User%20Guide%20P2_7-2_final.pdf)).

453 45 U.S. Department of Agriculture, Forest Service, (USDA Forest Service), “The forest  
454 inventory and analysis database: database description and user guide for Phase 3 (version  
455 6.0.1)” (USDA FS, 2014; [https://www.fia.fs.fed.us/library/database-](https://www.fia.fs.fed.us/library/database-documentation/current/ver60/FIADB%20User%20Guide%20P3_6-0-1_final.pdf)  
456 [documentation/current/ver60/FIADB%20User%20Guide%20P3\\_6-0-1\\_final.pdf](https://www.fia.fs.fed.us/library/database-documentation/current/ver60/FIADB%20User%20Guide%20P3_6-0-1_final.pdf)).

457 46 R. J. Hijmans, S.E. Cameron, J.L. Parra, P.G. Jones, A. Jarvis, Very high resolution  
458 interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965-1978 (2005).

459 47 PRISM Climate Group, Oregon State University, “PRISM climate data” (2004;  
460 <http://prism.oregonstate.edu>)

461 48 NADP Program Office, “National atmospheric deposition program, (NRSP-3)” (WI,  
462 USA, 2018; <http://nadp.slh.wisc.edu/>)

463 49 K. C. Short, Spatial wildfire occurrence data for the United States, 1992-2015 [FPA FOD  
464 20170508] (4<sup>th</sup> Edition). *Forest Service Research Data Archive* (Fort Collins, CO, USA,  
465 2017; <https://doi.org/10.2737/RDS-2013-0009.4>)



- 466 50 M. Brundrett, G. Murase, B. Kendrick, Comparative anatomy of roots and mycorrhizae  
467 of common Ontario trees. *Can. J. Bot.* **68**, 551-578 (1990).
- 468 51 C. G. Bueno *et al.* Plant mycorrhizal status, but not type, shifts with latitude and elevation  
469 in Europe. *Glob. Ecol. Biogeogr.* **26**, 690-699 (2017).
- 470 52 B. Wang, Y. L. Qiu, Phylogenetic distribution and evolution of mycorrhizas in land  
471 plants. *Mycorrhiza* **16**, 299-363 (2006).
- 472 53 A. A. Akhmetzhanova, N. A. Soudzilovskaia, V. G. Onipchenko, W. K. Cornwell, V. A.  
473 Agafonov, I. A. Selivanov, J. H. C. Cornelissen, A rediscovered treasure: mycorrhizal  
474 intensity database for 3000 vascular plant species across the former Soviet Union:  
475 Ecological Archives E093-059. *Ecology* **93**, 689-690 (2012).
- 476 54 M. Brundrett, L. Tedersoo, Misdiagnosis of mycorrhizas and inappropriate recycling of  
477 data can lead to false conclusions. *New Phytol.* in press, doi:10.1111/nph.15440.
- 478 55 L. Tedersoo, M. C. Brundrett, "Evolution of ectomycorrhizal symbiosis in plants" in  
479 *Biogeography of Mycorrhizal Symbiosis*, L. Tedersoo, Eds. (Springer International  
480 Publishing, 2017), vol 230, pp. 407-467.
- 481 56 A. Magnusson, H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van  
482 Bentham, B. Bolker, M. Brooks, Generalized linear mixed models using template model  
483 builder (2017; <https://cran.r-project.org/web/packages/glmmTMB/glmmTMB.pdf>).
- 484 57 J.A.Knott, J.M. Desprez, C.M. Oswalt, S. Fei, Shifts in forest composition in the eastern  
485 United States. *Forest Ecol and Mgmt* **433**, 176-183 (2019).

486 58 R Development Core Team. *R: A language and environment for statistical computing*  
487 (Vienna, Austria, 2014).

488 59 D. Cleland, J. Freeouf, J. Keys, G. Nowacki, C. Carpenter, W. McNab, *Ecological*  
489 *subregions: sections and subsections for the conterminous United States* (2007).

490

491

492 **Funding:**

493 This research was partially supported by the NSF Macrosystems Biology Program (#1638702)  
494 and USDA McIntire-Stennis program to S. Fei, and by the DOE Terrestrial Ecosystem Science  
495 program (# DESC0016188) to RP. Phillips.

496

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

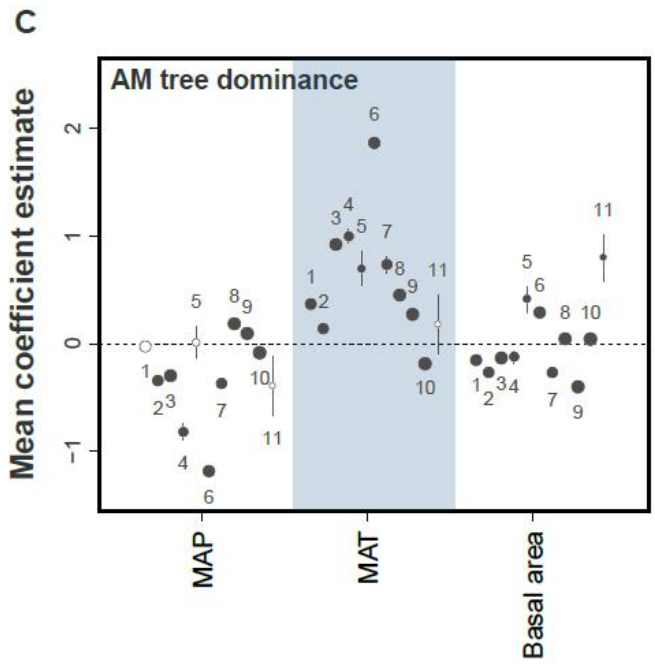
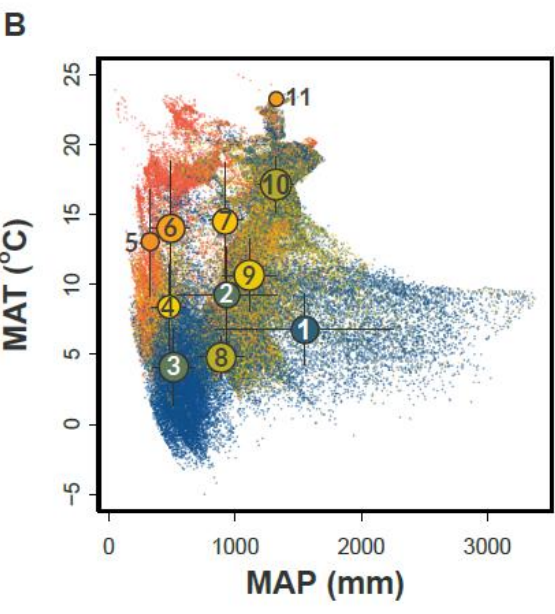
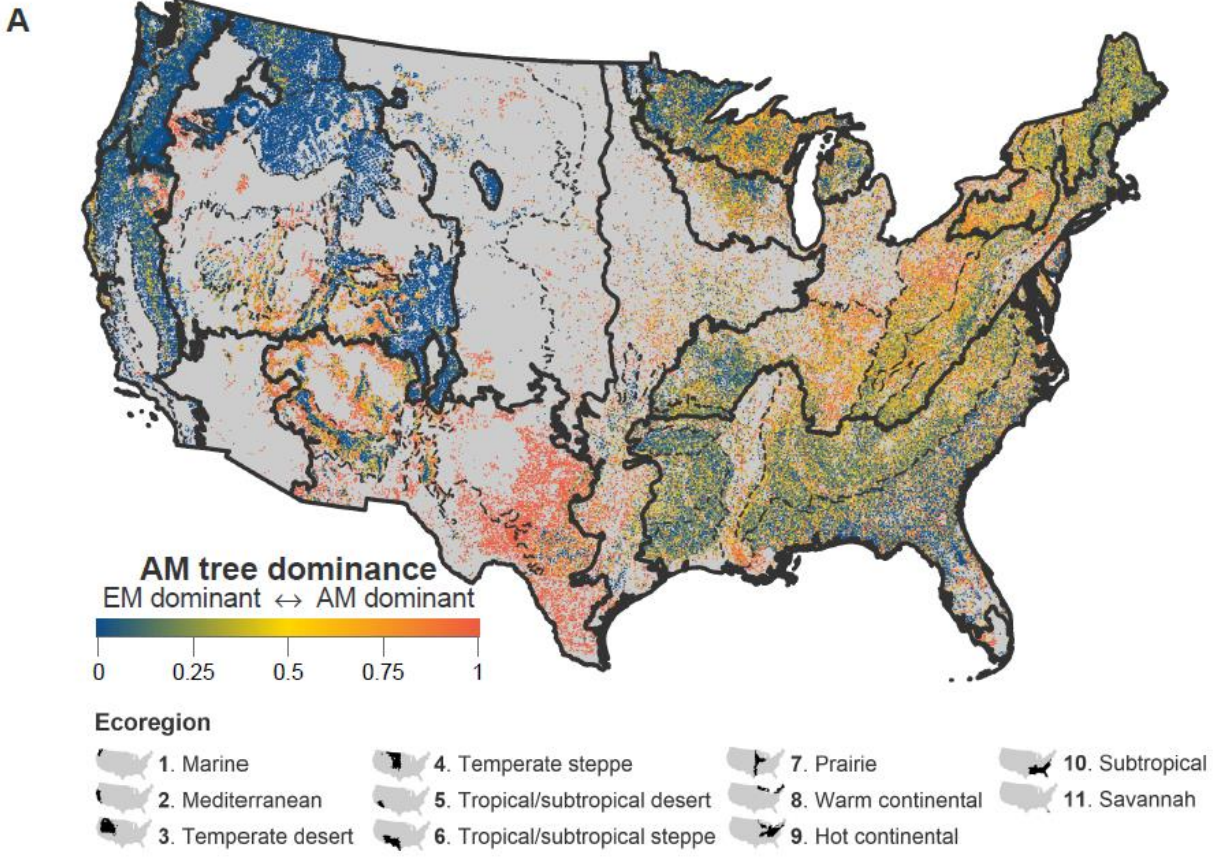
502 **Competing interests:**

503 Authors declare no competing interests.

504

505 **Data and materials availability:**

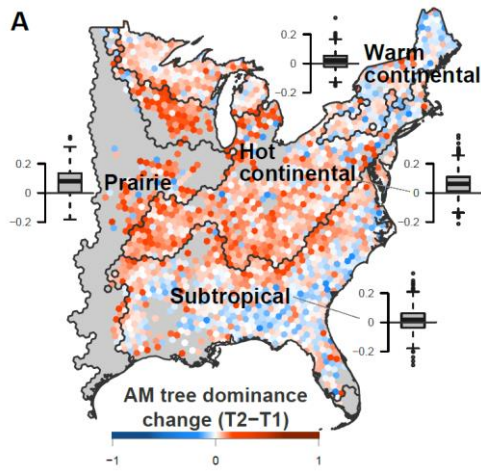
506 All data used in the analyses is available at an open data repository (Purdue University Research  
507 Repository; DOI:10.4231/R76D5R7S). Vegetation and soil data is available at FIA DataMart –  
508 US Forest Service (<https://apps.fs.usda.gov/fia/datamart/>); Climate data is available at the Global  
509 Climate Data – WorldClim ([www.worldclim.org](http://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).



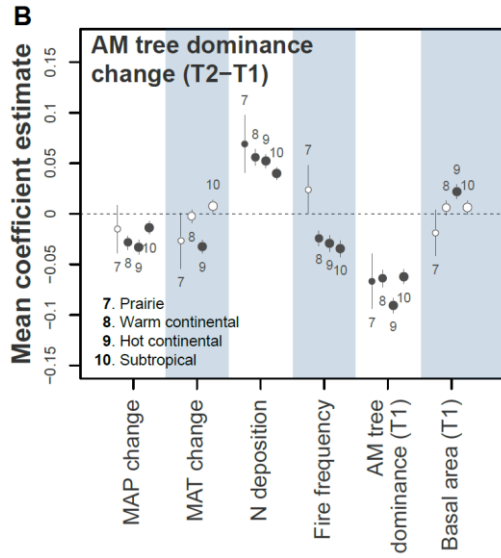
515 **Distribution of forest tree mycorrhizal types and their associated factors in forests of the**  
516 **contiguous USA.** (A) Geographical distribution of AM tree dominance. (B) Distribution of AM  
517 tree dominance in climatic space (MAP, mean annual precipitation; MAT, mean annual  
518 temperature). (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.

530

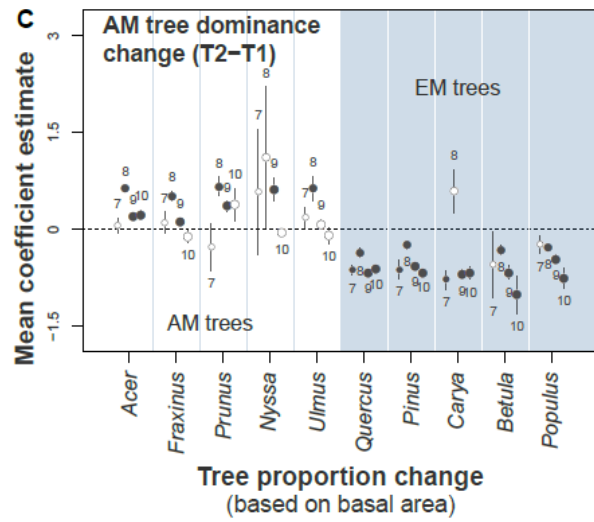
531 **Figure 2**



532



533

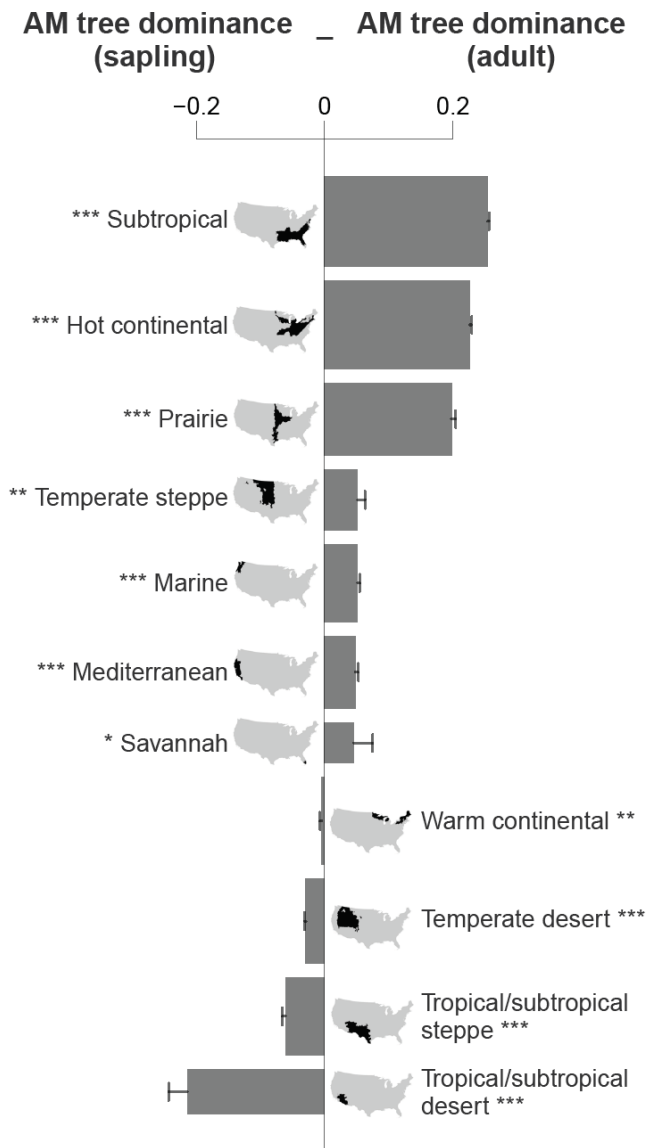


534

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.

549

550 **Figure 3**



551

552 **AM tree dominance differences between adult trees and saplings in forests across 11**

553 **ecoregions of the USA.** The difference in AM tree dominance between adults and saplings for

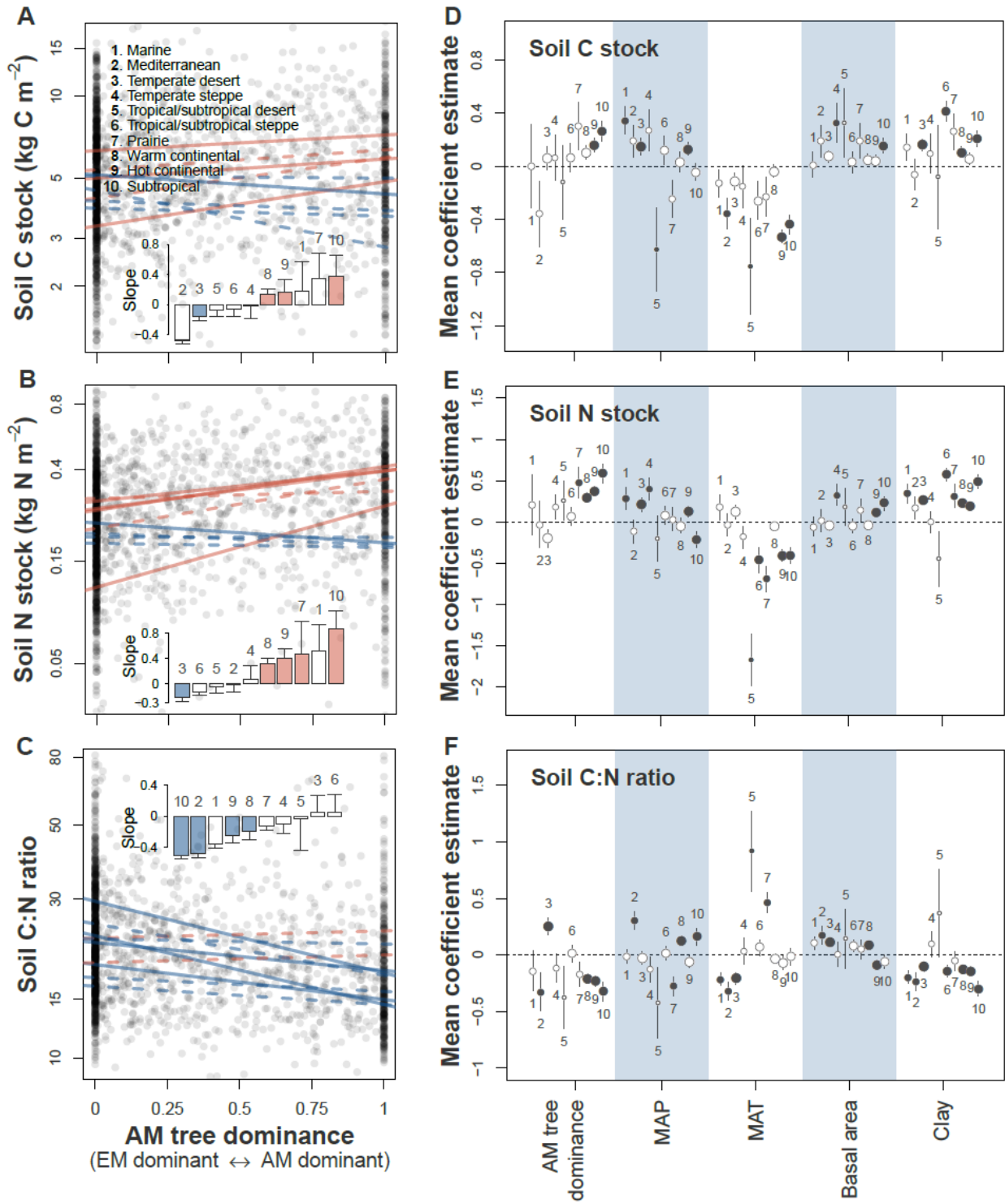
554 each ecological region were tested based on a paired Wilcoxon signed-rank test (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ).

555 Error bars are standard errors. The bar thickness is proportional to the

556 number of plots (log scale). Only plots where both adult trees and saplings are present are used

557 for the analysis (98,638 plots).





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 solid 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.