



Mycorrhizal dominance reduces local tree species diversity across US forests

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Ectomycorrhizas and arbuscular mycorrhizas, the two most widespread plant–fungal symbioses, are thought to differentially influence tree species diversity, with positive plant–soil feedbacks favouring locally abundant ectomycorrhizal tree species and negative feedbacks promoting species coexistence and diversity in arbuscular mycorrhizal forests. While seedling recruitment studies and cross-biome patterns of plant diversity and mycorrhizal dominance support this hypothesis, it remains to be tested at the forest stand level over continental scales. Here, we analyse approximately 82,000 forest plots across the USA to show that both ectomycorrhizal-dominated and arbuscular mycorrhizal-dominated forests show relatively low tree diversity, while forests with a mixture of mycorrhizal strategies support a higher number of tree species. Our findings suggest that mycorrhizal dominance, rather than mycorrhizal type, shapes tree diversity in forests.

Mycorrhizas—the most widespread terrestrial symbionts on Earth—have long been known for their nutritional benefits to plants¹. However, there is increasing interest in their role as drivers of local plant biodiversity². Species-rich tropical rainforests are mainly composed of arbuscular mycorrhizal (AM) trees³ while species-poor boreal forests are dominated by ectomycorrhizal (ECM) trees^{4,5}, suggesting that the AM strategy favours plant species coexistence and diversity while the ECM strategy promotes dominance by one or few species^{2,6}. Small-scale studies of seedling recruitment support this hypothesis: ECM seedlings perform better when growing in soils near (or conditioned by) conspecific individuals (that is, showing positive plant–soil feedbacks), whereas the opposite has been found for AM plants^{7,8}. Proposed mechanisms for positive feedback in ECM forests include greater protection to conspecific seedlings from soil-borne pathogens and improved nutrient acquisition, relative to AM forests^{6,9}. However, we do not know whether these short-term effects on recruitment dynamics translate into persistent effects on canopy tree species composition and diversity. Indeed, neither the historical biome-level observations nor the individual-level studies of seedling recruitment directly test the hypothesis that ECM-dominated forests sustain lower tree species diversity than AM-dominated forests; broad-scale analyses at the forest tree community level are needed to resolve this.

In this study, we used an extensive grid-based inventory of 82,393 naturally forested plots surveyed by the U.S. Department of Agriculture Forest Service (Forest Inventory and Analysis National Program) to explore the relationship between mycorrhizal dominance (ECM versus AM strategy) and local tree species diversity across broad environmental gradients at the continental scale. Selected plots (each consisting of 4 subplots of 168 m²) spanned the contiguous USA¹⁰, with the number of tree species per plot ranging from 1 to 18 (Fig. 1a). The mycorrhizal strategy for the 349 tree species present in the selected plots was extracted from a recently published database^{11,12}. As a predictor of plot-scale tree species diversity (that is, richness, Shannon's entropy index and the inverse of Simpson's concentration index), we calculated the proportion of total basal area, estimated from stem diameter measurements,

consisting of trees with the same mycorrhizal strategy. Because the vast majority of plots are dominated by ECM and/or AM strategies (Extended Data Fig. 1), with other strategies quite rare (for example, ericoid mycorrhizal or ERM), patterns of ECM and AM proportions are essentially mirror images (Fig. 1b and Extended Data Fig. 2). We hypothesized that tree diversity would decrease monotonically as dominance by ECM trees increased, such that AM forests would show the highest tree diversity (see the ectomycorrhizal dominance hypothesis; Fig. 2a). We tested for a relationship between tree diversity and ECM proportion in several ways: (1) using the simple bivariate relationship (results shown in the supplementary material); (2) after controlling for other environmental factors; and (3) after controlling for the statistical necessity that forests with multiple mycorrhizal types have a greater species pool of trees to draw from than forests with just one mycorrhizal type.

Results

Tree species diversity and mycorrhizal dominance. In line with our hypothesis, the bivariate relationship showed that tree species diversity was relatively low in ECM-dominated forests (Supplementary Fig. 1). However, contrary to our hypothesis, tree diversity was maximal when the ECM tree basal area was approximately 50% and tree species diversity declined under increasing dominance by AM trees (Supplementary Fig. 2; see the mycorrhizal mixture hypothesis in Fig. 2a). As such, tree species diversity was lowest in forests dominated by either the ECM or AM strategies and highest when there was an approximate mixture of both strategies.

Effect of local abiotic factors. Mycorrhizal distributions are known to be correlated with environmental factors that also influence plant diversity¹³ but the pattern in the bivariate relationship was strong after controlling for environmental variables (Fig. 2b). In models including effects of local abiotic factors (climatic, topographic and physiographic properties), we found that tree diversity was influenced by these factors, especially temperature, topography and water availability, but the negative effects of mycorrhizal dominance on tree diversity were strongest (Figs. 2b and Fig. 3).

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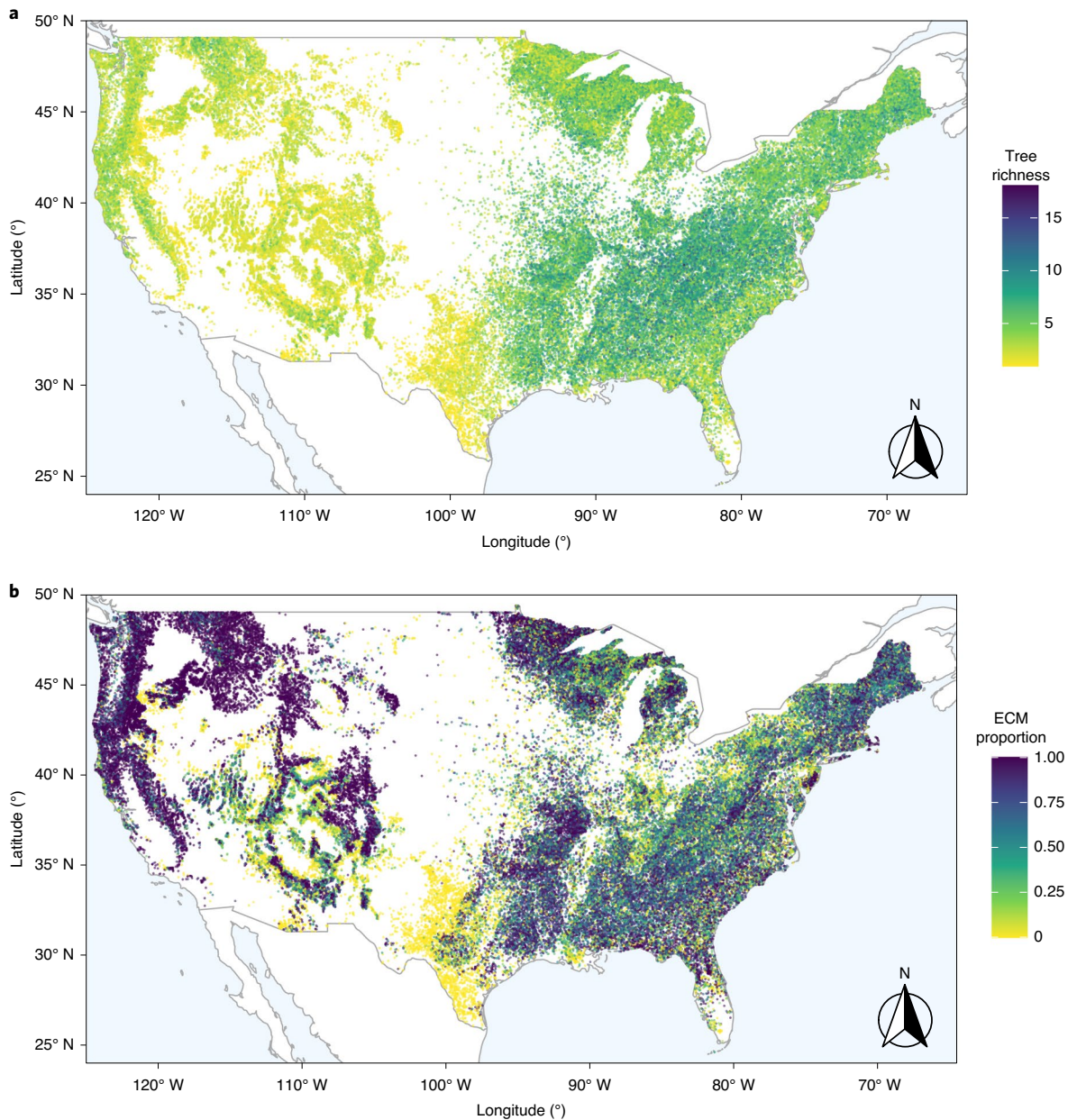


Fig. 1 | Tree richness and ECM proportion at the plot scale across the USA. a, Map of tree richness (number of tree species). **b**, Map of ECM proportion (as the proportion of basal area per plot of trees with DBH > 12.7 cm known to associate with ECM fungi).

Effect of the regional species pool. Our results are also robust to the potential statistical artefact that forest plots with only one mycorrhizal type have lower *potential* diversity (that is, only tree species of that type can be present). Local plant diversity is determined by environmental filtering from the regional flora¹⁴ and species diversity depends on the size and composition of the regional species pool¹⁵. As such, we applied a null model to determine if mycorrhizal dominance had detectable effects on tree species diversity beyond what could be explained by the tree species composition of the regional flora. We assessed the expected relationship between tree diversity and the proportion of ECM tree basal area based on random sampling from the regional tree species pool, from which we calculated the deviation between observed and expected values for each plot (which we call ‘alpha-deviation’). The null model reassigned a species identity to each individual tree in a given plot based on a random

draw of species of the same mycorrhizal type (simplified as either ECM or ‘other’ strategies) from the regional pool, with probability weights proportional to species regional abundances. Our null model thus preserved the value of ECM proportion in each plot. Regional pools were defined within each of 25 ecoregions¹⁶, which represent geographical areas with relatively similar ecological and environmental conditions (Supplementary Fig. 3). Results of our null model analysis showed that the hump-shaped relationship with tree species diversity being lowest at low or high ECM basal area persisted (Fig. 2c and Supplementary Fig. 4). This means that the lower local tree species diversity observed in plots dominated by either the ECM or AM strategy was not only the result of the regional species pool containing a smaller number of tree species from either one of these strategies but rather an outcome of local processes reducing species diversity in ECM- or AM-dominated plots.

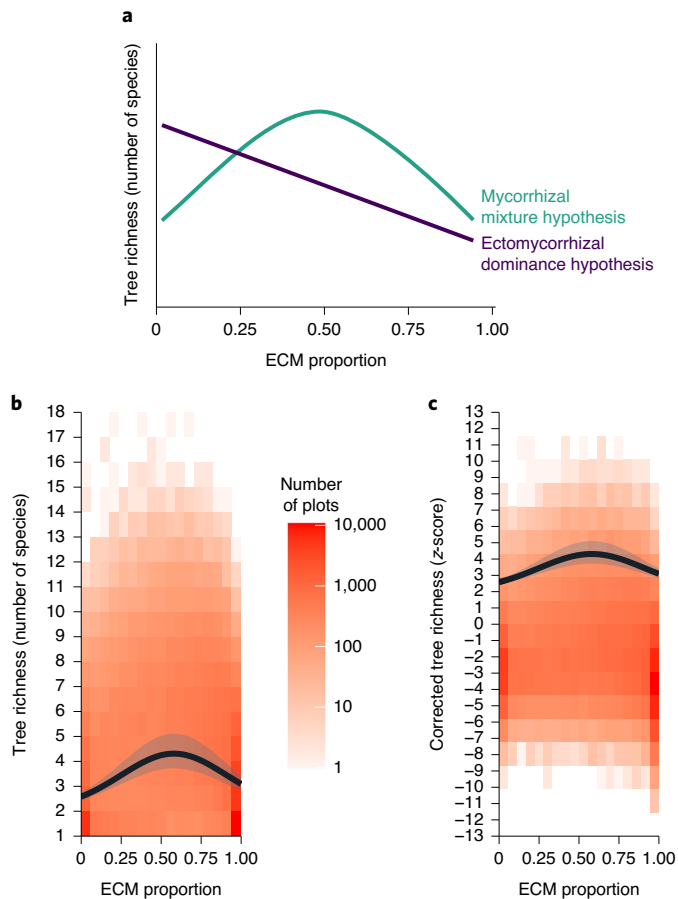


Fig. 2 | Relationships between ECM proportion and tree richness.

a, Hypothetical relationships. **b**, Observed ECM proportion versus predicted tree richness (number of species). **c**, ECM proportion versus corrected tree richness. Predictions in both **b** and **c** take into account potentially confounding environmental factors (elevation, physiography, precipitation, slope and temperature); the lines indicate the regression curves and the shaded areas represent the 95% credible intervals of the regression.

Discussion

Our results strongly suggest that dominance by either ECM or AM strategy, and not only the ECM strategy type, reduces local tree diversity across the forested USA. Several mechanisms involving mycorrhizal type may combine locally to influence plant diversity². First, positive plant–soil feedbacks commonly reported for ECM species at the seedling recruitment stages^{7,8}, could also apply to AM species but at later life stages (for example, saplings or small subcanopy trees), eventually leading to canopy dominance by certain AM tree species (Supplementary Fig. 5). While it is widely accepted that ECM plants may benefit more from ECM fungi in terms of mineral and organic nutrition and protection against root pathogens⁹, the higher maintenance costs of ECM fungi compared to AM fungi could mean that the net benefits of the two mycorrhizal types are similar¹⁷, thereby equalizing fitness differences among strategies. Furthermore, fine-scale niche partitioning could promote coexistence of different mycorrhizal types¹⁸ and ecosystems with a mixture of mycorrhizal strategies may also create environments that are more diverse and spatially heterogeneous¹⁹. Together, these processes could locally promote diversity where multiple plant nutrient acquisition strategies, such as mycorrhizal types, co-occur^{8,20}.

A number of studies have reported the positive effects of a diverse inoculum of AM fungi on plant diversity and ecosystem functions^{21,22}. Plant species richness as well as evenness increase in

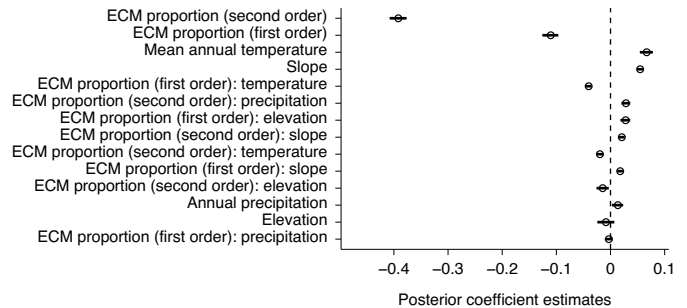


Fig. 3 | Posterior coefficient estimates for the effects on tree richness (number of species). Effects on tree species richness of ECM proportion (first- and second-order terms), local environmental factors (elevation, precipitation, slope, temperature) and their interactions. Medians are represented by the empty circles and the 95% credible intervals are represented by black vertical lines. Variables were standardized before modelling to permit quantitative comparison of coefficients. Terms are ordered based on the absolute values of the slopes.

response to AM fungi inoculation²³ and plant–soil feedbacks involving seedlings tend to be more negative in AM tree species⁷. These results lead to the expectation of a positive effect of AM dominance on tree diversity. However, studies at the community level are typically conducted in grasslands²⁴, which may not apply to long-lived trees in forests. Thus, the few studies of trees are typically at the level of individual seedlings^{7,8,25} and these short-term effects on seedling recruitment might not necessarily translate to canopy-level patterns involving mature trees. It is also worth noting that even though most tropical rainforests are both AM-dominated and host high tree species diversity, there are also several hyper-dominant tropical tree species forming AM associations²⁶. Therefore, not all tropical forest communities are species-rich, even in neotropical forests where AM trees dominate²⁷. In addition, our study included only trees, while an important component of total plant diversity in forests is attributable to understory herbs, which may be favoured in forests dominated by AM trees²⁸. Nonetheless, recent evidence cast doubt on the conventional hypothesis of lower plant diversity in ECM compared to AM systems in temperate and boreal sites²⁹. Using data at the continental scale, both within and across ecoregions, our results show that mycorrhizal dominance—regardless of mycorrhizal type—shapes tree species diversity in forests, with diversity maximized when different mycorrhizal strategies coexist.

In sum, patterns of mycorrhizal dominance and tree diversity have been historically considered among distant biomes, leading to the hypothesis that the ECM symbiosis reduces plant diversity, while AM symbiosis promotes plant diversity^{2,13}. The impact of mycorrhizal fungi on plant nutrition and plant–soil feedbacks, often studied at the individual level, have provided indirect support for these hypotheses². However, forest trees interact locally over prolonged periods and results from our study at the community and canopy level suggest that short-term effects, such as negative plant–soil feedback effects involving AM seedlings at the recruitment stage, do not persist in the longer term to influence canopy tree species diversity. In fact, we find that mycorrhizal dominance (either AM or ECM) favours dominance by a single species, thus reducing diversity and potentially leading to alternative stable states in forest tree species composition³⁰. Even though mycorrhizal dominance can be determined at several scales (for example, root system, stand, biome), our study highlights the importance of considering the impact of mycorrhizas on ecological processes at the scale of the forest plot or stand (<1 km²). At this scale, coexisting mycorrhizal strategies may act as a promoter of plant diversity, which might only be detected by studying the entire gradient of mycorrhizal

proportions. Forests with a mixture of mycorrhizal strategies are sometimes overlooked because they are considered less common⁴. However, this is not the case across North America (52% of plots have between 10 and 90% ECM proportion; Supplementary Fig. 5) and forests with diverse nutrient acquisition strategies may represent a crucial avenue for research and forest management targeting greater ecosystem services and adaptation to climate change.

Methods

Data collection. For this study, we used publicly available data from the U.S. Department of Agriculture Forest Service, known as the Forest Inventory and Analysis (FIA) programme. Data were accessed from https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html on 28 February 2020. The primary objective of the FIA is to determine the extent, condition, volume, growth and use of trees on US forest land to frame realistic forest policies and programmes¹⁰. This database has been used to address many ecological questions across large scales and gradients^{11,31,32}. Plots are distributed relatively evenly in forested areas across all of the lower 48 contiguous states. Plot location uncertainty is generally <1.6 km but locations are sometimes deliberately exchanged within a given county due to potential issues regarding plot integrity and landowner privacy¹⁰. Each standard plot consists of four 7.3 m radius circular subplots (168 m²) within which all stems >12.7 cm diameter at breast height (DBH) are identified to species and measured. There is one centre subplot surrounded by the 3 peripheral subplots, each at a distance of 36.6 m from the centre subplot.

Before our analyses, the dataset was filtered using several criteria according to the FIA user guide for phase 2 (ref. ¹⁰). First, we only kept census data from the most recent year for a given plot (range: 1995–2019; median: 2015), in cases where a plot was sampled more than once. Second, we retained plots following both standard production and standardized methods (that is, ‘sample kind code’ of 1, 2 or 3) and a similar sampling design within the 4 subplots where all stems >12.7 cm DBH were measured (that is, with a ‘plot design code’ of 1, 220, 240, 311, 314, 328, 502 or 505). Finally, we only used data taken using the National Field procedures in forested, natural and undisturbed stands with no observable recent silvicultural treatment. If data were missing for any measured values or variables, the plots were excluded. Otherwise, plots were retained for further analyses if more than four individual trees were present. From 1,557,871 available plots measurements, we analysed data for 82,393 plots containing 1,984,883 trees.

For each selected plot, topographic data (elevation, slope) and physiographic class (estimate of moisture available to trees) were accessed directly from the FIA database. Elevation is defined as the vertical distance above mean sea level ranging from 0 to 3,746 m with a median of 366 m. The percentage slope ranges from 0 to 155% with a median of 10%. Climatic data (that is, mean annual temperature, mean annual precipitation) were accessed from the Parameter-elevation Regressions on Independent Slopes Model Climate Group (800 m spatial resolution; <http://prism.oregonstate.edu/>). The mean annual temperature ranged from –3.3 to 25.3°C with a median of 9.9°C; mean annual precipitation ranged from 50 to 5,647 mm with a median of 1,072 mm.

From the stem diameter measurements, the total basal area was calculated for each species in each plot. The mycorrhizal strategy for each tree species was determined using a recently published database^{11,12}. Species were listed as either ECM, AM, ERM, non-mycorrhizal or both AM and ECM (AM + ECM). The basal area of dual AM/ECM tree species was assigned as half AM and half ECM in the calculation of mycorrhizal proportion. The distribution of dual AM/ECM proportion is shown in Supplementary Fig. 6.

Tree species richness was calculated as the number of observed tree species with a DBH > 12.7 cm. Species richness (Fig. 1a) followed large-scale tree diversity gradients previously mapped for the USA³³. Abundance was incorporated into diversity indices using the exponential of Shannon's entropy index ($q = 1$) and the inverse of Simpson's concentration index ($q = 2$), calculated as proposed by Chao et al.³⁴. Individual-based rarefaction was also conducted by resampling 10 individual trees per plot (below); a total of 70,641 plots were used for these calculations excluding plots containing fewer than 10 individual trees. The potential impact of grain size was assessed by modelling tree diversity and mycorrhizal dominance also at the subplot level, using 191,327 subplots. To test whether the results were robust to uncertainties in species mycorrhizal status, we modelled the relationship between tree richness and ECM proportion using only species for which mycorrhizal strategy was determined at the species level¹² (that is, 176 species in 71,089 plots).

Following the ‘national hierarchical framework of ecological units’¹⁶, we defined 25 ecoregions and assigned 1 for each plot depending on its location (Supplementary Fig. 3). Ecological units are defined as areas of similar surficial geology, lithology, geomorphic processes, soil groups and subregional climate.

Null model. We used a null model that reassigned the species identity of the individual trees in each plot based on random draws from the regional pool of tree species within ecoregions (Supplementary Fig. 3), while keeping the total number of individual trees per plot and the proportion ECM constant. Each

species' abundance (that is, its probability of being chosen by the null model) was calculated as its number of tree stems in the ecoregion, divided by the total number of stems across species. We ran 100 randomizations from which we calculated the diversity ‘deviation’ (or ‘corrected’ diversity) as the observed diversity minus the mean of the null distribution of diversity values, divided by the s.d. of this distribution. Diversity measures were the same as for the observed data. Negative values of corrected diversity represent lower diversity than expected given random draws from the regional species pool, which can be the result of environmental, demographic and stochastic processes that exclude some species locally. The null model was implemented in R³⁵.

Modelling. To quantify the effect of mycorrhizal proportion and the environmental variables on tree species diversity and corrected diversity, we used generalized linear mixed-effect models implemented in a Bayesian framework. Ecoregion was included as a random factor. For richness values ($q = 0$), we used a Poisson distribution; for $q = 1$, $q = 2$ and rarefied richness, we used the Gamma distribution. Because diversity values start at 1, distributions were truncated with a lower bound of <1. For the corrected diversity, we used a Gaussian distribution. Quadratic terms for mycorrhizal proportion were included in the models to test for non-linearity. When the 95% credible intervals did not overlap zero, they were considered significant and thus conserved in the second-order equations. Before modelling, variables were scaled by subtracting the mean and dividing by the s.d.

Analyses on diversity were conducted for rarefied richness, $q = 1$ and $q = 2$, which showed similar patterns as $q = 0$ (Supplementary Figs. 1 and 7). Robustness to the minimum number of trees per plot of the relationship between tree richness and ECM proportion was tested by running models with a threshold for a minimum number of individual trees per plot of 10 and 15 individual trees (Supplementary Fig. 8). They showed a similar pattern with a slight increase in maximum tree richness with an increasing threshold. The relationship between tree richness and ECM proportion was qualitatively the same at the subplot level (Supplementary Fig. 9), only with lower overall tree richness, as expected by the decrease in grain size. The relationship remained significant when using only species with mycorrhizal type assigned at the species level. The hump-shaped relationship was confirmed as significant (Supplementary Fig. 10; quadratic term -0.31 ± 0.1 95% credible interval).

The models ran on 4 parallel chains of length 5,000 with a burn-in of 1,000 iterations and a thinning rate of 10. Uninformative priors were used as provided in the brms package³⁶. Convergence was assessed for each parameter estimate by visually inspecting the Markov chains and considered sufficient when $\hat{R} = 1$.

Data manipulation and statistical analyses were done using the R platform³⁵ v.3.5.1 and the following main packages: brms³⁶v.2.12.0, data.table³⁷v.1.14.0, dplyr³⁸v.1.0.2, ggplot2 (ref. ³⁹) v.3.3.3, ggpubr⁴⁰v.0.4.0, ggsplot⁴¹v.1.1.1, raster⁴²v.3.4-5, reshape⁴³v.0.8.8, sf⁴⁴v.0.9-8, tidy⁴⁵v.1.1.0, vegan⁴⁶v.2.5-6.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are available from the FIA programme¹⁷ at <https://apps.fs.usda.gov/fia/datamart/CSV/ENTIRE.zip>. The data for the tree mycorrhizal associations are available from Jo and Fei¹² with the identifier <https://doi.org/10.4231/R76D5R7S>.

Code availability

The custom code of the analyses is available at Zenodo⁴⁸ with the identifier <https://doi.org/10.5281/zenodo.5713274>.

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References

- Smith, S. E. & Read, D. J. *Mycorrhizal Symbiosis* (Academic Press, 2008).
- Tedersoo, L., Bahram, M. & Zobel, M. How mycorrhizal associations drive plant population and community biology. *Science* **367**, eaba1223 (2020).
- Connell, J. H. & Lowman, M. D. Low-diversity tropical rain forests: some possible mechanisms for their existence. *Am. Nat.* **134**, 88–119 (1989).
- Brundrett, M. in *Advances in Ecological Research*, Vol. 21 (eds Begon M. et al.) 171–313 (Academic Press, 1991).
- Allen, E. B. et al. Patterns and regulation of mycorrhizal plant and fungal diversity. *Plant Soil* **170**, 47–62 (1995).
- Laliberté, E., Lambers, H., Burgess, T. I. & Wright, S. J. Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytol.* **206**, 507–521 (2015).
- Bennett, J. A. et al. Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* **355**, 181–184 (2017).
- Teste, F. P. et al. Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science* **355**, 173–176 (2017).

9. van der Heijden, M. G. A., Martin, F. M., Selosse, M.-A. & Sanders, I. R. Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytol.* **205**, 1406–1423 (2015).
10. Burrill, E. A. et al. *The Forest Inventory and Analysis Database: Database Description and User Guide Version 8.0 for Phase 2* (U.S. Department of Agriculture, Forest Service, 2018).
11. Jo, I., Fei, S., Oswalt, C. M., Domke, G. M. & Phillips, R. P. Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts. *Sci. Adv.* **5**, eaav6358 (2019).
12. Jo, I. & Fei, S. *Responses of Dominant Tree-Mycorrhizal Associations to Anthropogenic Impacts in the USA* (Purdue Univ. Research Repository, 2019).
13. Read, D. J. Mycorrhizas in ecosystems. *Experientia* **47**, 376–391 (1991).
14. Laliberté, E., Zemunik, G. & Turner, B. L. Environmental filtering explains variation in plant diversity along resource gradients. *Science* **345**, 1602–1605 (2014).
15. Ricklefs, R. E. Community diversity: relative roles of local and regional processes. *Science* **235**, 167–171 (1987).
16. Cleland, D. T. et al. *Ecological Subregions: Sections and Subsections for the Conterminous United States. General Technical Report WO-76D* (U.S. Department of Agriculture, 2007).
17. Tedersoo, L. & Bahram, M. Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biol. Rev. Camb. Philos. Soc.* **94**, 1857–1880 (2019).
18. Taylor, D. L. et al. A first comprehensive census of fungi in soil reveals both hyperdiversity and fine-scale niche partitioning. *Ecol. Monogr.* **84**, 3–20 (2014).
19. Mariotte, P. et al. Plant–soil feedback: bridging natural and agricultural sciences. *Trends Ecol. Evol.* **33**, 129–142 (2018).
20. Zemunik, G., Turner, B. L., Lambers, H. & Laliberté, E. Diversity of plant nutrient-acquisition strategies increases during long-term ecosystem development. *Nat. Plants* **1**, 15050 (2015).
21. van der Heijden, M. G. A. et al. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69–72 (1998).
22. Maherali, H. & Klironomos, J. N. Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* **316**, 1746–1748 (2007).
23. Lin, G., McCormack, M. L. & Guo, D. Arbuscular mycorrhizal fungal effects on plant competition and community structure. *J. Ecol.* **103**, 1224–1232 (2015).
24. Hartnett, D. C. & Wilson, G. W. T. The role of mycorrhizas in plant community structure and dynamics: lessons from grasslands. *Plant Soil* **244**, 319–331 (2002).
25. Mangan, S. A. et al. Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466**, 752–755 (2010).
26. Peh, K. S.-H., Lewis, S. L. & Lloyd, J. Mechanisms of monodominance in diverse tropical tree-dominated systems. *J. Ecol.* **99**, 891–898 (2011).
27. ter Steege, H. et al. Hyperdominance in the Amazonian tree flora. *Science* **342**, 1243092 (2013).
28. Newman, E. I. & Reddell, P. Relationship between mycorrhizal infection and diversity in vegetation: evidence from the Great Smoky Mountains. *Funct. Ecol.* **2**, 259–262 (1988).
29. Bahram, M. et al. Plant nutrient-acquisition strategies drive topsoil microbiome structure and function. *New Phytol.* **227**, 1189–1199 (2020).
30. Beisner, B. E., Haydon, D. T. & Cuddington, K. Alternative stable states in ecology. *Front. Ecol. Environ.* **1**, 376–382 (2003).
31. Zhu, K., Woodall, C. W. & Clark, J. S. Failure to migrate: lack of tree range expansion in response to climate change. *Glob. Change Biol.* **18**, 1042–1052 (2012).
32. Phillips, R. P., Brzostek, E. & Midgley, M. G. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytol.* **199**, 41–51 (2013).
33. Jenkins, C. N., Van Houtan, K. S., Pimm, S. L. & Sexton, J. O. US protected lands mismatch biodiversity priorities. *Proc. Natl Acad. Sci. USA* **112**, 5081–5086 (2015).
34. Chao, A., Chiu, C.-H. & Jost, L. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annu. Rev. Ecol. Evol. Syst.* **45**, 297–324 (2014).
35. R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2018).
36. Bürkner, P.-C. brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).
37. Dowle, M. & Srinivasan, A. data.table: Extension of ‘data.frame’ R package version 1.14.0 <https://CRAN.R-project.org/package=data.table> (2017).
38. Wickham, H., Francois, R., Henry, L. & Müller, K. dplyr: A grammar of data manipulation. R package version 1.0.2 <https://CRAN.R-project.org/package=dplyr> (2017).
39. Wickham, H. ggplot2: *Elegant Graphics for Data Analysis* (Springer-Verlag, 2016).
40. Kassambara, A. ggpubr: ‘ggplot2’ Based Publication Ready Plots. R package version 3.3.3 <https://CRAN.R-project.org/package=ggpubr> (2018).
41. Dunnington, D. ggspatial: Spatial Data Framework for ggplot2. R package version 1.1.1 <https://CRAN.R-project.org/package=ggspatial> (2018).
42. Hijmans, R. J. raster: Geographic Data Analysis and Modeling. R package version 3.4-5 <https://CRAN.R-project.org/package=raster> (2019).
43. Wickham, H. Reshaping data with the reshape Package. *J. Stat. Softw.* **21**, 1–20 (2007).
44. Pebesma, E. Simple features for R: standardized support for spatial vector data. *R. J.* **10**, 439–446 (2018).
45. Wickham, H. & Henry, L. tidy: Tidy messy data. R package version 1.1.0 <https://CRAN.R-project.org/package=tidy> (2019).
46. Oksanen, J. et al. vegan: Community ecology package. R package version 2.5-6 <https://cran.r-project.org/web/packages/vegan/index.html> (2017).
47. Forest Inventory and Analysis; <https://apps.fs.usda.gov/fia/datamart/CSV/ENTIRE.zip>
48. Carteron, A. alexiscarter/mycorrhiza_tree_diversity: custom code <https://doi.org/10.5281/ZENODO.5713273> (2021).

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Author contributions

E.L., A.C. and M.V. conceived the ideas and designed the methodology. A.C., E.L. and M.V. analysed the data and interpreted the results. A.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41559-021-01634-6>.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41559-021-01634-6>.

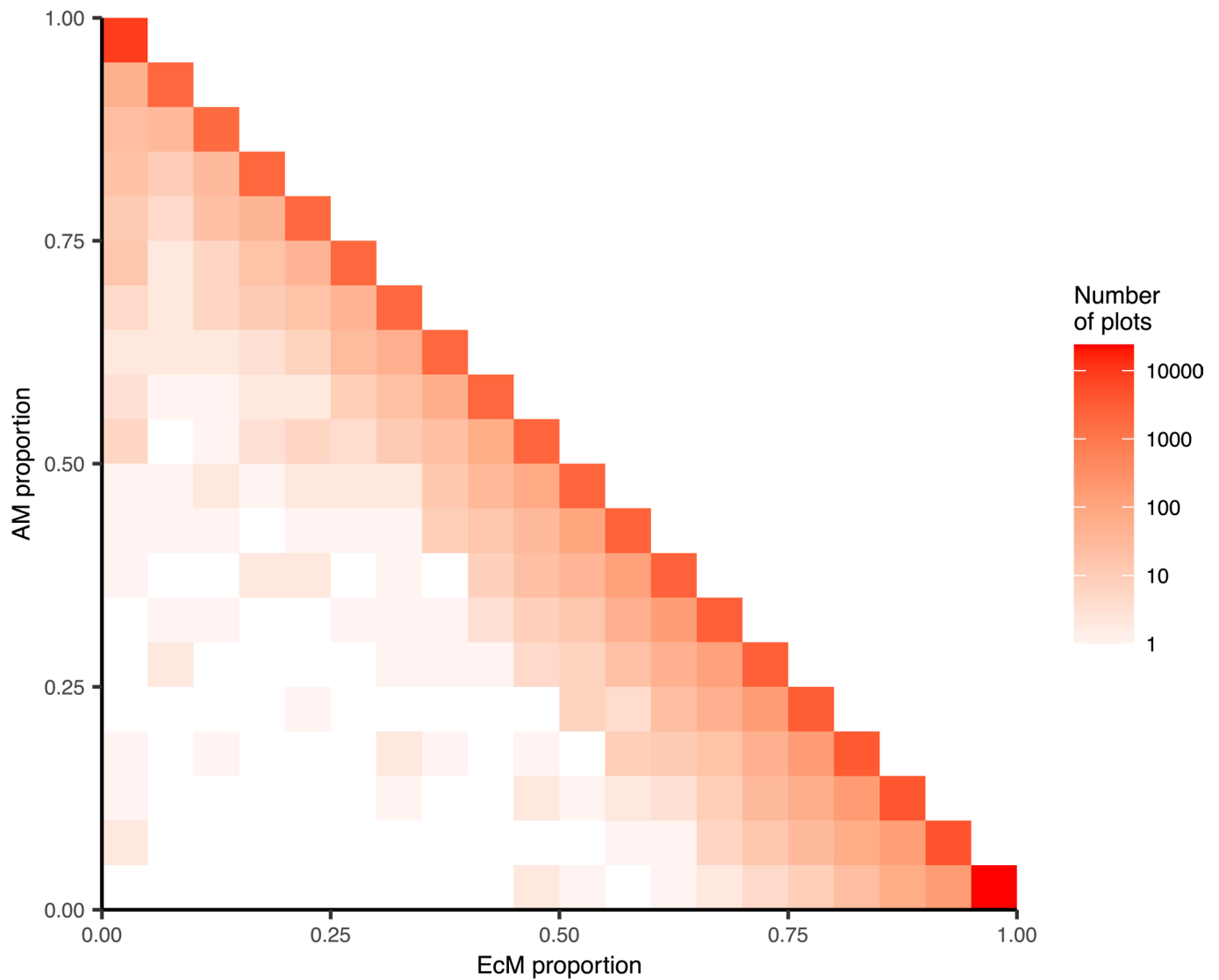
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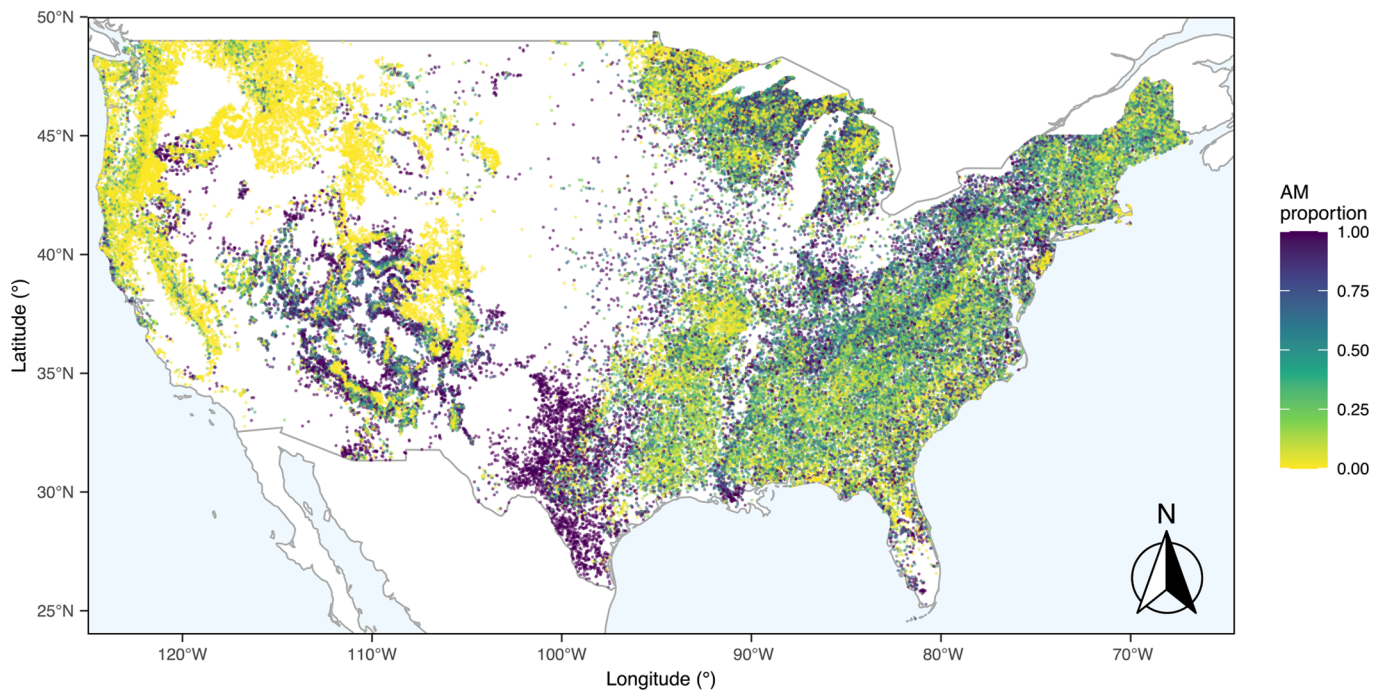
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Extended Data Fig. 1 | Relationship between ectomycorrhizal (EcM) and arbuscular mycorrhizal (AM) proportions in each plot. Relationship between ectomycorrhizal (EcM) and arbuscular mycorrhizal (AM) proportions in each plot. 95 % of the plots have a cumulative sum of AM and EcM proportions > 0.99 (that is, most plots are located on the diagonal). Other plots (that is, below the diagonal) contain ericoid or non-mycorrhizal trees. The number of plots in the legend is presented on a log scale.



Extended Data Fig. 2 | Map of arbuscular mycorrhizal (AM) proportion per plot. Map of arbuscular mycorrhizal (AM) proportion (as the proportion of basal area per plot of tree with DBH > 12.7 cm known to associate with AM fungi).

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Data collection All data were collected using the R platform (R version 3.6.3)

Data analysis All statistical analyses were performed using the R platform (R version 3.6.3)

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Data of Forest Inventory and Analysis (FIA) program are available at <https://apps.fs.usda.gov/fia/datamart/CSV/ENTIRE.zip>. Data for tree mycorrhizal associations are available at <https://doi.org/10.4231/R76D5R7S>.

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Research sample	We used an existing dataset publicly available from the U.S. Department of Agriculture Forest Service, known as the Forest Inventory and Analysis (FIA) program. Data were accessed from https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html on 28 February 2020. All the data information is detailed in Burrill, E. A et al. The Forest inventory and analysis database: database description and user guide version 8.0 for Phase 2. US Department of Agriculture, Forest Service 946p (2018) and available at https://www.fia.fs.fed.us/library/database-documentation/
Sampling strategy	Not applicable
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