Alternative stable states of the forest mycobiome are maintained through positive feedbacks

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Most trees on Earth form a symbiosis with either arbuscular mycorrhizal or ectomycorrhizal fungi. By forming common mycorrhizal networks, actively modifying the soil environment and other ecological mechanisms, these contrasting symbioses may generate positive feedbacks that favour their own mycorrhizal strategy (that is, the con-mycorrhizal strategy) at the expense of the alternative strategy. Positive con-mycorrhizal feedbacks set the stage for alternative stable states of forests and their fungi, where the presence of different forest mycorrhizal strategies is determined not only by external environmental conditions but also mycorrhiza-mediated feedbacks embedded within the forest ecosystem. Here, we test this hypothesis using thousands of US forest inventory sites to show that arbuscular and ectomycorrhizal tree recruitment and survival exhibit positive con-mycorrhizal density dependence. Data-driven simulations show that these positive feedbacks are sufficient in magnitude to generate and maintain alternative stable states of the forest mycobiome. Given the links between forest mycorrhizal strategy and carbon sequestration potential, the presence of mycorrhiza-mediated alternative stable states affects how we forecast forest composition, carbon sequestration and terrestrial climate feedbacks.

Most trees on Earth form belowground networks with symbiotic mycorrhizal fungi, which in turn can connect different tree stems and species within a forest. Yet, the vast majority of tree species can only form one of two predominant functional types of mycorrhizal symbiosis, arbuscular mycorrhizal or ectomycorrhizal (AM or EM), each of which may set in motion processes that favour the establishment and persistence of one mycorrhizal network over the other. For example, common mycorrhizal networks may facilitate resource transfers which favour the recruitment and survival of their own mycorrhizal strategy (the con-mycorrhizal strategy) at the expense of the alternative strategy. Furthermore, once established, AM and EM forests may engineer soil nutrient cycling conditions, further reinforcing positive con-mycorrhizal feedbacks to favour their own mycorrhizal strategy. Additionally, establishment of either strategy can lead to an accumulation of con-mycorrhizal spores and mycelium, which may further strengthen positive feedbacks, as could potentially other yet-to-be-discovered ecological phenomena. If such positive feedbacks exist across a wide range of forests they may, in time, generate alternative stable states of forested biomes, mediated by interactions between trees and the forest fungal microbiome. As a result, forest mycorrhizal type may act as a filter on forest biodiversity, restricting community membership as a function of mycorrhizal compatibility, which may be further reinforced by soil nutrient cycle feedbacks, compatible symbiont density and more. Given the links between forest mycorrhizal status and carbon sequestration potential, the presence of mycorrhiza-mediated alternate stable states would affect how we forecast forest composition and emergent ecosystem carbon balance.

The potential for positive feedbacks to drive alternative stable states in AM and EM symbioses at continental scale was originally hypothesized three decades ago, yet empirically testing this hypothesis at large spatial scale remains a challenge. Recent work lends support to this idea, showing that mixed mycorrhizal forests are far rarer than expected by chance. While this co-occurrence pattern is consistent with the presence of alternative mycorrhizal stable states, there remain numerous other possible explanations for this pattern, including environmental filtering and dispersal limitation, which can also lead to the clumping of similar species. Demonstrating that patterns in AM versus EM forests reflect mycorrhiza-induced alternative stable states requires evidence that (1) bimodality exists in the frequency distribution of forest mycorrhizal types, (2) positive community feedbacks in time could give rise to alternative stable states and (3) observed feedbacks are strong enough to generate and maintain alternative stable states in the face of environmental heterogeneity and demographic stochasticity. Importantly, each of these criteria must consider and account for many potential nonlinear controls of the environment on tree species’ demographic rates and spatial distributions, as well as signatures of dispersal limitation in recruitment dynamics. These challenges have prevented previous work from disentangling the effects of mycorrhizal community feedbacks from environmental filtering and dispersal limitation. As a result, the generality of potential mycorrhizal feedbacks in shaping forest distributions at large spatial scales remains unknown.

Results
Clear bimodality in forest mycorrhizal strategies. Here, we use long-term forest inventory data across the United States to show that AM versus EM forests probably coexist at a landscape scale as alternative stable states and that these findings cannot be explained by confounding with the environment or dispersal limitation. First, we identify clear bimodality in AM versus EM tree relative abundances, with two distinct frequency peaks at 100% AM and 100% EM dominance across the Eastern United States (Fig. 1a,b). Importantly, this signature persists even after controlling for environmental filtering.

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by accounting for over 200 potential environmental drivers of tree species composition (Fig. 1c). This was accomplished by fitting statistical models to forest mycorrhizal composition data, accounting for linear and nonlinear community–environment relationships and then adjusting relative abundance values to remove observed environmental signatures (Methods; additional visualization of how each environmental driver influences the balance of AM versus EM tree species can be found at https://hooge104.shinyapps.io/alt_stable_states_env_conditions/).

The bimodal distribution of forest types is consistent with the presence of alternative stable states fundamentally structuring the distribution of forest symbioses across North America, similar to previous analyses15. Importantly, however, we also find that this bimodal distribution remains after removing the signal of environmental filtering on the distribution of AM versus EM tree species (Fig. 1c), demonstrating that this pattern cannot be explained solely by differing habitat preferences between AM and EM trees. Additional analysis showed that stand age (a proxy for successional stage) had a very small effect on AM versus EM balance and could not explain the observed bimodal distribution (Extended Data Fig. 1).

Positive feedbacks in mycorrhizal recruitment and survival. To examine the potential role of positive feedbacks in driving this observed bimodality within the forest mycorrhizal system over time, we analysed tree recruitment and mortality across 6,965 repeatedly measured forest inventory plots. Our analysis revealed strong positive con-mycorrhizal feedbacks across the Eastern United States (Fig. 2). After controlling for tree size, environmental factors and stand conditions, an individual EM tree is more likely to die in an AM forest than an individual AM tree and AM trees are more likely to die in EM forests than EM trees (Fig. 2a). Recruitment patterns were similar to mortality, with con-mycorrhizal relative abundance having a positive effect on con-mycorrhizal recruitment. Holding all else constant, EM tree recruitment is greater than AM recruitment in EM forests and vice versa (Fig. 2c). These findings were robust to spatially subsetting the dataset across geographically defined ecoregions (Extended Data Fig. 2). Furthermore, finer-scale spatial-subsetting and refitting of models revealed that the strength of con-mycorrhizal survival advantage was a strong predictor of the degree of mycorrhizal monodominance at the subregional level (Extended Data Fig. 3). In other words, the larger the benefit of con-mycorrhizal neighbours for tree survival, the more bimodal the distribution of AM versus EM trees within a subregion. Finally, while we observed spatial autocorrelation in raw recruitment observations, consistent with dispersal limitation that could drive clustering of individual species and therefore mycorrhizal types, final statistical models were able to capture and account for this autocorrelation and therefore separate local community feedbacks from the potential influence of dispersal limitation (Extended Data Fig. 4).

The observed patterns of recruitment and mortality were also apparent at the species level. Among the 22 most abundant AM and EM tree species, individual tree species are more likely to
recruit and survive if their neighbours are of the same mycorrhizal type, a pattern that appears to be independent of hardwood versus coniferous life history and the basal area of conspecific trees (Fig. 2b,d). Individual AM trees also grew more slowly around EM neighbours, yet no tree species grew faster in EM relative to AM. Plotted values are estimates based on the full model, holding environmental conditions and stand structure constant and drawn from the model 95% CI. Positive feedbacks observed in tree recruitment and survival.

**Fig. 2 | Positive con-mycorrhizal feedbacks observed in tree recruitment and survival.** a, Survival probability of an individual AM tree (green) or EM tree (purple) within a forest stand where all other trees are either AM or EM. Plotted values are estimates based on the full model, holding environmental conditions and stand structure constant and drawn from the model 95% CI. b, Difference in survival probability of individual tree species under EM relative to AM conditions. Differences are calculated on the log-linear scale of the model. Positive values indicate that an individual of a given tree species is more likely to survive within an EM-dominated forest and negative values indicate that an individual is more likely to survive within an AM forest. Error bars represent the 95% CI of the difference in means. c, Recruitment rate of new AM and EM trees into a forest already dominated by AM or EM trees. Plotted values are estimates based on the full model, holding environmental conditions and stand structure constant, and drawn from the model 95% CI. d, Difference in recruitment rates of individual tree species under EM relative to AM conditions. Differences are calculated on the log-log scale of the model. Positive values indicate that an individual of a given tree species is more likely to recruit within an EM forest and negative values indicate that an individual is more likely to recruit within an AM forest. Error bars represent the 95% CI of the difference in means.

Positive feedbacks are necessary and sufficient to maintain alternative stable states. To test if positive con-mycorrhizal feedbacks in recruitment and mortality observed over a short time-scale are strong enough to generate and maintain alternative mycorrhizal stable states over longer time-scales, we ran a series of demographic simulations, driven by empirically fitted statistical models of growth, recruitment and mortality. We initialized 1,000 forest plots with varying AM versus EM composition and allowed them to grow for 200 years. We incorporated environmental heterogeneity by drawing plot-scale environmental conditions randomly from observed values across forests used to fit statistical models. We ran two sets of simulations, both of which used the same empirical demographic models of growth, mortality and recruitment described above but the 'null' model excluded con-mycorrhizal predictors.

We found that simulations driven by demographic models fit without con-mycorrhizal predictors could not generate a bimodal distribution of AM versus EM forests, while simulations driven by models fit with con-mycorrhizal predictors recovered the observed
bimodal distribution of AM versus EM forests (Fig. 3). These findings suggest that observed con-mycorrhizal recruitment and mortality feedbacks are both necessary and sufficient in magnitude to generate and maintain alternative mycorrhizal stable states of the forest biome in the face of environmental heterogeneity, demographic stochasticity and changes in forest structure over time. We note that simulation results are more bimodal than observed empirical patterns and this probably reflects our choice of initial conditions—most forests in simulations are ~200 years old and all started from either an AM- or EM-dominated state (which gave our null simulation the best chance of reproducing bimodality and therefore disproving our hypothesis). Relaxing these assumptions may improve the match between the simulation and empirical data.

The presence of alternative mycorrhizal stable states may fundamentally change temporal predictions of forest mycorrhizal composition over environmental gradients. If alternative stable states are present, then forest mycorrhizal transitions should exhibit hysteresis in response to N pollution, an environmental change driver known to shift forests from EM to AM states\textsuperscript{21}. If positive feedbacks are strong, then the relative abundance of AM versus EM trees in a forest will depend on not just the environment but also the initial distribution of these forest types (Fig. 4a versus b). To understand the potential magnitude of hysteresis in forest mycorrhizal transitions under N pollution, we ran a second set of simulations, growing forests across a N deposition gradient, initializing 1,000 regenerating forests at the beginning of the simulation as either mostly EM dominated (80% of stands initialized with only EM trees, the remainder AM) or mostly AM dominated (80% of stands initialized with only AM trees, the remainder EM). Forest simulations were run for 400 years to minimize the influence of demographic lags on model outcomes. Remarkably, our simulations accurately reproduced the known relationship between a decline in EM forest dominance and N deposition\textsuperscript{21}. Furthermore, we observed substantial hysteresis across the N deposition gradient, where the relative abundance of EM trees across all forest plots strongly depended on the initial community state of the simulation (Fig. 4c). For the same environmental conditions, the relative abundance of EM trees was much greater if the set of forest plots was initially dominated by EM trees rather than if they were initially dominated by AM trees. Null simulations show that the magnitude of observed hysteresis cannot be explained in the absence of mycorrhizal feedbacks (Extended Data Fig. 6). While we have focused on N deposition here, it is directly linked to one potential mechanism of positive feedback and can be easily incorporated into your model framework, this finding probably extends to other global change drivers that affect AM versus EM dominance in forests, particularly fire frequency.

Discussion
Researchers have long suspected that contrasting forest mycorrhizal strategies may generate feedbacks that reinforce the establishment and persistence of con-mycorrhizal strategies among trees\textsuperscript{1}. However, only recently has sufficient data accrued to understand forest mycorrhizal composition and turnover at massive spatial scale, allowing us to empirically test this hypothesis. Here, we show that the distribution of AM versus EM trees is bimodal across the Eastern United States, probably maintained by strong positive recruitment and survival feedbacks within AM and EM forests, consistent with the presence of alternative mycorrhizal stable states. Our findings are consistent with foundational work on alternative ecosystem stable states of eastern hemlock (EM associated) and sugar maple (AM associated) forests in northern Michigan, United States\textsuperscript{12,23}. Findings from this previous work are likely to be a specific example of a more general and widespread phenomenon. Given the prominent role of mycorrhizal fungi in shaping the biogeochernistry of their ecosystems\textsuperscript{14,15}, it is unsurprising that mycorrhizal feedbacks extend across multiple tree species and larger spatial scales. Indeed, previous work on common mycorrhizal networks has shown positive associations between con-mycorrhizal but not hetero-mycorrhizal tree species\textsuperscript{14,15}. We hypothesize that both N-cycle feedbacks and common mycorrhizal networks within mycorrhizal types may act in concert to mediate positive feedbacks that generate and maintain alternative mycorrhizal stable states.

We focus on the potential roles of common mycorrhizal networks and soil nutrient cycle feedbacks, as there is substantial empirical evidence from many different studies to support these positive feedback mechanisms\textsuperscript{14,15}, yet other mechanisms remain plausible. For example, forests dominated by a particular mycorrhizal strategy may harbour a greater abundance of compatible mycorrhizal mutualists or may be more likely to harbour exceptionally beneficial mutualists, both of which could also explain observed positive feedbacks, as could other yet-to-be-discovered ecological phenomena. Regardless of the particular mechanism, the importance of positive con-mycorrhizal feedbacks demonstrated here calls for more intensive empirical study to decompose the relative importance of

![Fig. 3 | Simulating forest feedbacks](image-url)
different positive feedback mechanisms that give rise to alternative mycorrhizal stable states. Identifying the dominant drivers will probably affect how we understand and manage these fundamentally different symbiont strategies.

It is important to recognize that the presence of con-mycorrhizal feedbacks does not negate the role of environmental filtering in structuring the distribution of AM versus EM forest symbioses at broad spatial scales11,21. In particular, climate is a strong predictor of AM versus EM dominance within our study region22. However, within a continental-scale envelope of environmental conditions, prediction of AM versus EM forests can only be made probabilistically, due to the presence of strong positive con-mycorrhizal feedbacks, which give rise to priority effects and alternative stable states23. This is analogous to how high versus low rainfall is linked to the presence of savannah versus forest but, at intermediate rainfall, alternative stable states of forest versus savannah emerge due to positive feedbacks linked to fire24. It is also likely that different environmental drivers modulate the strength of con-mycorrhizal feedbacks, which may further explain environmental dependencies and should be a focus of future work. Nevertheless, our findings help to provide mechanism behind sharp transitions in the spatial distribution of AM versus EM ecosystem types observed at global scale11. Past analysis of the global distribution of mycorrhizal strategies reveals clear bimodality at the plot scale25, suggesting that the feedbacks observed here may extend beyond North America, consistent with positive mycorrhizal feedbacks observed in this study and within forest plots outside of North America26,27. Our analysis has also lumped incredible taxonomic and functional diversity of both plants and fungi into AM versus EM functional groups. We recognize that different tree species and different mycorrhizal fungi have diverse and complex ecological strategies28 and that these strategies may modify the strength of con-mycorrhizal density dependence and its environmental sensitivity (Fig. 2). We see exploring this diversity as the next frontier in understanding how the predominant form of tree mycorrhizal symbiosis shapes the biogeography and function of the forest macrosystem.

Alternative stable states of terrestrial ecosystems have long been hypothesized but rarely demonstrated, in part because the empirical evidence needed is notoriously difficult to obtain at sufficient spatial and temporal scales29,30. This is particularly true for belowground microbial systems where it is exceptionally difficult to isolate the drivers of community change. Here, we present multiple lines of evidence, each relying on independent analytical approaches, to provide strong inference for the presence of alternative mycorrhizal stable states within the temperate forests of eastern North America. These alternative stable states probably arise from a combination of divergent plant traits31, interactions between mycorrhizal fungi and free-living soil microbial communities at the molecular scale32,33, common mycorrhizal networks34,35 and potentially additional plant and microbial mechanisms. This combination of plant and microbial feedbacks then ripples through the ecosystem to affect the patterning of forest mycorrhizal symbioses across the continent. By highlighting how the soil microbiome shapes the functioning and responsiveness of entire forests, this work demonstrates the emerging importance of the forest microbiome for understanding the biogeography and function of the forest macrosystem. Given the striking differences in carbon cycling and storage between AM- and EM-dominated systems2,12,36, the presence of alternative mycorrhizal stable states requires a rethinking of how forest composition and function vary across time and space, as well as the implications of these predictions for the global carbon cycle and in turn potential future states of the Earth.

**Methods**

**Data collection for the US Forest Service Forest Inventory Analysis Database.** All data used in this set of analyses come from the US Forest Service’s Forest Inventory and Analysis database v.7 (ref. 30). We further subsetted to sites within the Eastern United States, where re-measurement intervals are standardized, which facilitated fitting of demographic models and demographic simulations, as done in previous analyses4 (Fig. 1). Forest Inventory and Analysis (FIA) plots are comprised of four spatially distinct subplots and so ‘plot-level’ data should be considered a subsampling of the larger area. These data have proven valuable for detecting species interactions in other analyses37 and are therefore well suited to test hypotheses regarding mycorrhizal interactions. We only considered sites where all subplots were in a forested condition and excluded plantations as well as any sites with evidence of active management or harvesting. We also excluded any sites where >50% of trees died between re-census intervals, as these frequently represented sites experiencing major invasive pest outbreaks. Trees were assigned AM or EM association as in previous analyses31. Once mycorrhizal associations were assigned, we further subsetted the dataset to sites where >90% of basal area was associated with either AM or EM associated trees. Therefore, a plot with 50% EM basal area and 50% AM basal area would be included in this analysis, however, any plot with >10% mixed mycorrhizal, arbutoid, ericoid or non-mycorrhizal basal area would...
be excluded. This filter excluded 15% of all forested sites. Further investigation showed that two-thirds of excluded sites (that is 10 of the 15%) were due to a high abundance of *Populus*, a well-known dual AM–EM tree genus. The remainder of exclusions were primarily driven by trees where mycorrhizal strategy was unknown. Our final dataset included 6,965 unique forest sites, re-censused at a 5–yr interval, with complete environmental covariates, comprised of 200,363 trees.

**Environmental covariates.** To control for potential environmental filtering we extracted measures of all environmental variables that could be related to forest and mycorrhizal ecology. These environmental variables captured variation in climatic, soil nutrient, soil chemical, soil physical and vegetative indices, radiation and topographic variables and anthropogenic influence (Supplementary Data File 1). We explicitly did not include the soil chemical factors %C, %N, C:N or soil pH, as these are all hypothesized mechanisms by which tree species modify the soil environment and create alternative stable states. All covariates were resampled and reprojected to a unified pixel resolution in EPSG:4326 (WGS84) at 30 arcsec resolution (~1 km at the estimator). Layers with a higher original pixel resolution were down-sampled using a mean aggregation method; layers with a lower original resolution were resampled using simple up-sampling (that is, without interpolation) to align with the higher resolution grid1. To reduce predictor dimensionality we performed principle component analysis on all environmental predictors and included the first ten principle components which captured ~83% of the variation in the original 204 environmental drivers. These ten environmental predictors were included in all statistical models of tree growth, recruitment and survival, as well as the relative abundance of EM trees within a plot.

In addition to the ten environmental variables we also included a metric of historic N deposition loading. By including this in addition to the above ten environmental principle components, we could ask questions about the direct effect of N deposition, independent of these other environmental factors. The 15-yr mean annual wet and dry N deposition was assigned at 0.25° resolution1. We summed wet and dry N deposition to estimate total N deposition. Previous work has shown that 15- and 30-yr wet N deposition data are strongly correlated and are representative of historical patterns of N deposition loading across the United States11. The FIA does not report site coordinates with exact precision and this affects the accuracy of our environmental drivers. Plot locations are limited in accuracy to ~800 m and then 20% of observations are randomly swapped at the county level. Because variations in environmental factors are much larger across counties than within, this limited spatial precision will increase parameter uncertainty associated with these environmental drivers but does not prevent us from detecting large-scale patterns, the goal of this analysis11.

**Testing for bimodality in the contemporary distribution of AM and EM forests.** Alternative stable state theory predicts that, within some envelope of environmental conditions, ecosystem types should exhibit a bimodal distribution16. However, if exogenous environmental conditions that also affect the abundance of AM versus EM trees within a forest are also bimodal or affect the distribution of trees in nonlinear ways, this may generate bimodality in the distribution of AM versus EM forests17. To control for potential confounding, we fit generalized additive models (GAM) to AM relative abundance to determine the effect of environmental drivers on the distribution of EM versus AM relative abundance. Models were fit using a binomial error distribution and a logit link function via the gamm function within the mgcv package for R statistical software18. Relative abundances were modelled as a function of the ten environmental principle components described above and N deposition. County was included as a random effect to account for potential residual spatial autocorrelation. All predictors, except for county-level random effects, were fit as independent spline terms with a maximum number of potential ‘knots’ set to 5 to account for potential nonlinearities, while avoiding overfitting, using a penalized thin-plate spline regression method18.

In recruitment models, both con-mycorrhizal basal area and con-mycorrhizal relative abundance are included and these predictors are correlated. However, additional analysis shows that this correlation does not prevent including both these predictors in the same statistical model, based on investigation of variance inflation factors (VIFs) and correlation coefficients (R = 0.44–0.69, VIF 1.8–2.5; Extended Data Fig. 7a,b), therefore, it is possible to include both predictors in the same model19. To further address the potential influence of collinearity between con-mycorrhizal basal area and con-mycorrhizal relative abundance on our ability to separate their effects on recruitment, we performed a power analysis. We subsampled our dataset at different levels of sampling effort (preserving the correlation between con-mycorrhizal basal area and relative abundance) and then prespecified effects of SAM versus EM basal area and con-mycorrhizal relative abundance on EM tree recruitment. We show that this correlation does not prevent an unbiased estimate of the con-mycorrhizal relative abundance effect and the sampling effort used in this analysis (>6,000 forest inventory plots) is sufficient to meaningfully constrain the uncertainty of this parameter estimate (Extended Data Fig. 7c).

**Modelling tree mortality (survival).** Tree mortality probability was modelled at the individual level across the most recent 5-yr census interval within the GAM framework using a binomial distribution implemented within the mgcv package for R statistical software18. We fit separate models for AM and EM associated trees. Within each model, tree mortality probability was modelled as a function of an individual tree’s previous diameter, total plot basal area, stem density within a plot, and mortality probability models as above to five regional subsets of the dataset. In each model, current tree diameter was modelled as a function of an individual tree’s previous diameter, total plot basal area, stem density within a plot, all environmental covariates and the relative abundance of EM trees within a plot (that is, the con-mycorrhizal predictor)11. County was included as a random effect to account for potential residual spatial autocorrelation. All predictors, except for county-level random effects, were fit as independent spline terms with a maximum number of potential ‘knots’ set to 5 to account for potential nonlinearities, while avoiding overfitting, using a penalized thin-plate spline regression method18.

**Modelling tree recruitment.** Recruitment of AM and EM trees were modelled separately at the plot level across the most recent 5-yr time interval for each forest site within the GAM framework using a Poisson distribution implemented within the mgcv package for R statistical software18. Recruits are defined as all individuals in the current census >12.7 cm diameter which were not present in the previous census. Recruitment of AM or EM trees was modelled as a function of plot basal area, stem density, basal area of con-mycorrhizal trees, all environmental covariates and the relative abundance of EM trees within a plot (that is, the con-mycorrhizal predictor). The basal area of con-mycorrhizal trees within the plot was included as a term in addition to the con-mycorrhizal predictor to account for the fact that recruitment generally increases with the abundance of a focal species on the con-mycorrhizal functional group within a given site, that is, the apple does not fall far from the tree11. County was included as a random effect to account for potential residual spatial autocorrelation. All predictors, except for county-level random effects, were fit as independent spline terms with a maximum number of potential ‘knots’ set to 5 to account for potential nonlinearities, while avoiding overfitting, using a penalized thin-plate spline regression method18.

**Testing for demographic neighbourhood effects that would reinforce AM versus EM-dominated states.** Changes in the overall relative abundance of AM versus EM trees in a forest are fundamentally driven by differences in AM versus EM forest demographic processes of growth, recruitment and mortality (or survival). We modelled each of these processes as a function of environmental factors, individual tree and stand characteristics (tree size, stand stem density and stand basal area) and the relative abundance of EM trees in the forest (our con-mycorrhizal predictor), to quantify the influence of con-mycorrhizal density dependence. Once models were fit, we held environmental, individual and stand characteristics constant and used the model to understand the sign and magnitude of con-mycorrhizal effects. This allowed us to answer questions like, is an AM tree less likely to die in an AM forest than an EM tree? Or, does an EM tree grow more in an EM forest relative to an AM tree?

**Species-level growth, recruitment and mortality models.** We fit growth, recruitment and mortality models as above but at the species level for the 11 most abundant AM and 11 most abundant EM tree species on the basis of the number of individual stands within the dataset. Modelling at the species level and controlling for species specific, savannah, for recruitment, where con-mycorrhizal basal area was replaced with the basal area of the particular species being modelled within a plot (that is, conspecific basal area).

**Ecoregion level growth, recruitment and mortality models.** The study region considered here contains multiple ecological subregions with distinct combinations of tree species and interactions between AM and EM associated trees at the functional group level. To understand if our findings across the Eastern United States generalized to ecological subregions, we refit growth, recruitment and mortality probability models as above to five regional subsets of the dataset. Regional subsets were chosen using EPA level 2 ecoregions that contained at least 1,000 unique forest inventory plots15.

**Exploring plot and species-level random effects.** In our full analysis of tree growth and mortality we would ideally account non-independence of individuals
within survey plots as a random effect within statistical models. However, because of computational limitations, we could only include the larger spatial unit of county as a random effect in our analysis. To evaluate the potential influence of this decision, we fit models of mortality to a subregion of the data, the Atlantic Highlands EPA coregion, with either county-level or plot-level random effects and then evaluated how the choice plot versus county random effect influenced the effect on EM tree relative abundance of EM tree mortality probability. The effect of EM tree relative abundance on EM tree mortality probability was nearly indistinguishable among models, with highly overlapping 95% confidence interval (CI) (Extended Data Fig. 8d–f). Therefore, we concluded that the coarser spatial random effect of county was sufficient to account for spatial non-independence within our analysis.

Similarly, different tree species can vary in growth and mortality rates and this may similarly bias our estimates of the role of mycorrhizal strategy. To investigate the relative importance of species effects in our overall analysis, we refit models to a subregion of the data, the Atlantic Highlands EPA coregion, with or without species-level random effects and then evaluated how the choice plot versus county random effect influenced the effect on EM tree relative abundance of EM tree mortality probability. The effect of EM tree relative abundance on EM tree mortality probability was nearly indistinguishable among models, with highly overlapping 95% CI (Extended Data Fig. 8d–f). Therefore, we concluded that species-level random effects were not necessary to understand the continental drivers of positive con-mycorrhizal feedbacks in demographic processes.

Testing relationship between mycorrhizal dominance and con-mycorrhizal feedbacks. To test how observed con-mycorrhizal feedbacks may explain variation in the degree of mycorrhizal monodominance (that is, the prevalence of forest stands comprised of only AM or only EM trees), we repeated our analyses of tree recruitment and survival across 18 hexagonal subregions of our study area, each of which contained at least 150 forest inventory plots. Using these models, we first calculated a metric of AM and EM recruitment and survival advantage—how much more likely it is to recruit or survive if you are surrounded by the same mycorrhizal strategy, compared to when it is surrounded by the alternative mycorrhizal strategy. Specifically, this was calculated by varying the relative abundance of con-mycorrhizal basal area between 0 and 1, while holding all other covariates at their means and then subtracting one score from the other on the original linear scale. We then averaged survival and advantage scores across AM and EM groups. Second, within each subregion, we calculated the proportion of plots where only one mycorrhizal type was present by summing the number of plots with >99% basal area of only AM or only EM trees and then dividing by the total number of plots in the study region. This number was then logit-transformed before analysis to meet the assumptions of linear regression. Finally, we regressed mycorrhizal monodominance scores against average recruitment or survival advantage within a study region using ordinary least squares regression via the lm function within R statistical software13.

Demographic simulation 1: testing if demographic neighbourhood effects are sufficient to maintain alternative stable states. Positive con-mycorrhizal effects in and of themselves are not sufficient to generate and maintain alternative stable states. Positive con-mycorrhizal effects must be sufficient in magnitude to maintain alternative stable states within a dynamic forest, in the face of environmental heterogeneity, demographic stochasticity and changes in stand structure through time. To test if observed con-mycorrhizal effects were sufficient in magnitude to maintain alternative mycorrhizal stable states, we ran a series of demographic simulations driven by empirically fitted demographic models of growth, recruitment and mortality. Simulations are initialized with 1,000 forest plots comprised of 20 trees at 12.7 cm diameter at breast height (the smallest tree measured in FIA surveys) within a plot area identical to that of the FIA and then run for 200 yr. We incorporated stand-replacing disturbance at a probability of 0.36% per year. This number was derived on the basis of the overall North American stand-replacing disturbance probability of 0.9% a year and then reducing this number by 60% to exclude stand replacement associated with human harvest10. When stands were cleared, stem density was reset to 20 trees per plot. Regenerating trees were assigned EM versus AM status using the stands’ prior relative abundance of EM trees as the probability each new regenerating tree being EM versus AM. We incorporated environmental heterogeneity by assigning each plot a set of environmental covariates drawn randomly from the combinations of environmental covariates observed across the forest plots used to fit demographic models. We first asked if empirically fitted demographic models are sufficient to generate bimodality of AM versus EM-dominated forests after 200 yr. We then conducted second simulations with a second set of demographic models which were fit without con-mycorrhizal predictors (the relative abundance EM trees within a plot) to ask if demographic lags or other aspects of our demographic models or simulation could generate bimodality of AM versus EM forests without any feedback mechanism. Half of all forest plots in each simulation were initialized with all AM trees and the other half with all EM trees. This gave our null simulation the best chance to recapitulate bimodality of AM versus EM forests due to demographic lags and therefore disprove our hypothesis.

Demographic simulation 2: testing for hysteresis in AM versus EM forest dominance across gradients of N pollution. Hysteresis in community transitions across environmental gradients is a hallmark of alternative stable states22. We ran two sets of demographic simulations described above, across a gradient of N deposition rates from 1 to 14 kg N ha⁻¹ yr⁻¹. In the first set of simulations 800 of 1,000 forest plots were initialized at 100% EM dominance (the remainder initialized as AM) and in the second set of simulations all 800 of 1,000 forest plots were initialized at 100% AM dominance (the remainder initialized as EM). Simulations were run forward for 400 yr to minimize the influence of demographic lags on simulation outcomes. We visualize the relative abundance of EM trees across all plots at the end of the simulation as a function of N deposition.

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

Data availability
All forest data used in this analysis are available from the FIA datamart (https://apps.fs.usda.gov/fia/datamart/). All environmental covariate data sources are publicly available and detailed in the Supplementary Data File.

Code availability
All code used to work up raw data to analysis ready products, analyse data and generate figures can be found at https://github.com/colinaverill/altSS_forest_mycorrhizas12.

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Author contributions

C.A. conceived the study. C.A., C.F. and J.v.d.H. designed and implemented all code and analysis. All authors contributed to interpreting results and writing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Extended Data Fig. 1 | Stand age versus mycorrhizal dominance. (A) Relationship between the relative abundance of Ectomycorrhizal trees and stand age, after controlling for other environmental drivers. There is a weak, positive relationship with EM stands on average 3-years older than AM stands. (B) Histogram of the relative abundance of ectomycorrhizal trees by basal area across North America, after removing environmental and stand age signatures using statistical models. Values of 1 reflect forests with 100% ectomycorrhizal dominance and no arbuscular mycorrhizal trees, while values of 0 reflect forests with 100% arbuscular mycorrhizal dominance and no ectomycorrhizal trees.
Extended Data Fig. 2 | Subregional analysis. Con-mycorrhizal feedbacks in tree recruitment and survival across 5 ecoregions within the larger dataset. Statistical models were fit within all ecoregions that contained at least 1,000 forest inventory plots which passed other filtering criteria (see Methods).
Extended Data Fig. 3 | Survival advantage predicts mycorrhizal monodominance. Mycorrhizal monodominance is plotted within a study subregion as a function of (A) average survival advantage a tree has within a con-mycorrhizal setting compared to a hetero-mycorrhizal setting and (B) average recruitment advantage of trees in a con-mycorrhizal setting compared to a hetero-mycorrhizal setting. Mycorrhizal monodominance is calculated the proportion of plots within a subregion that are >99% AM or EM-dominated by basal area, and then logit-transforming this score for the purposes of analysis via ordinary least squares. Mycorrhizal advantage scores are calculated based on recruitment and survival models fit to regional subsets of the data, and then averaged across AM and EM groups. Additional details are provided in Methods.
Extended Data Fig. 4 | Satisfying assumptions of spatial independence. Residual spatial autocorrelation is visualized as semi-variance as a function of spatial distance in (a.) residuals of arbuscular mycorrhizal tree recruitment modelled with an intercept only (b.) residuals of arbuscular mycorrhizal tree recruitment in the full statistical model (c.) residuals of ectomycorrhizal tree recruitment modelled with an intercept only (d.) residuals of ectomycorrhizal tree recruitment in the full statistical model.
Extended Data Fig. 5 | Mycorrhizal tree growth responses. (A) Estimates of individual arbuscular or ectomycorrhizal tree growth increments when the surrounding forest community is dominated by arbuscular or ectomycorrhizal trees. Plotted values are estimates based on the full model, holding environmental conditions and stand structure constant, and drawn from the predictions 95% confidence interval. (B) Difference in individual tree-level growth increments of particular tree species when the surrounding forest community is dominated by ecto- or arbuscular mycorrhizal trees. Positive values indicate an individual of a given tree species grows faster within an EM-dominated forest, and negative values indicate an individual is grows faster within an AM forest. Error bars represent the 95% confidence interval of the difference in means.
Extended Data Fig. 6 | Hysteresis results. Relative abundance of ectomycorrhizal trees after 400 years within simulations driven by demographic models either (A) fit without con-mycorrhizal feedbacks (that is “null” simulations) or (B) with con-mycorrhizal feedbacks. While some hysteresis is observed in the null simulation due to demographic lags, the difference due to initial conditions is far larger when simulations are driven by models fit with con-mycorrhizal feedbacks.
Extended Data Fig. 7 | Separating basal are vs frequency effects. Correlations between (A) basal area of arbuscular mycorrhizal (AM) trees in a plot versus the relative abundance of ectomycorrhizal (EM) trees, (B) basal area of EM trees versus the relative abundance of EM trees. $R^2$ is the correlation coefficient of the linear fit, and VIF stands for variance inflation factor. To assess how these correlations might influence our ability to detect con-mycorrhizal effects, we simulated ectomycorrhizal recruitment as a function of EM plot basal area and EM relative abundance, with data drawn randomly from the analysis dataset to preserve these correlations. Effects sizes were prescribed so we could assess the ability of the model to detect true effect sizes, given the correlation. Here we present the results of this statistical power analysis (C). The dashed line represents the true parameter estimate, and error bars represent 95% confidence intervals. Despite correlated predictors models recovered unbiased parameter estimates, and the number of plots analysed in this study (>6,000) is sufficient to meaningfully constrain parameter uncertainty.
Extended Data Fig. 8 | Comparing plot versus county-level random effects. Estimated ectomycorrhizal (EM) tree mortality (before inverse logit link function transformation) as a function of the relative abundance of EM trees within the Atlantic Highlands EPA ecoregion. Each panel represents a different random effects scenario. (A) County is included as a random effect, as done in the analysis reported in the main text. (B) Plot is included as a random effect, instead of county. (C) The two curves overlaid to show they are extremely similar. (D) Same as A, County is included as a random effect. (E) Random effects of county and tree species are included. (F) Curves from panel D and E overlaid to show they are extremely similar.
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Data collection

All code used to work up raw data to analysis ready products, analyze data and generate figures can be found at https://github.com/colinaverill/altSS_forest_mycorrhizas.

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All code used to work up raw data to analysis ready products, analyze data and generate figures can be found at https://github.com/colinaverill/altSS_forest_mycorrhizas.

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All forest data used in this analysis are available from the FIA data mart. All code used to work up raw data to analysis ready products, analyze data and generate figures can be found at https://github.com/colinaverill/altSS_forest_mycorrhizas. All forest data used in this analysis are available from the FIA data mart (https://apps.fs.usda.gov/fia/datamart/). All code used to work up raw data to analysis ready products, analyze data and generate figures can be found at https://github.com/colinaverill/altSS_forest_mycorrhizas. All environmental covariate data sources are publicly available, and detailed in Supplementary Data File 1.
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| Study description | This study uses observational data of US forest composition to understand how arbuscular and ectomycorrhizal symbioses influence growth, recruitment and survival of trees. We test for positive con-mycorrhizal feedbacks in these processes. |
|-------------------|-------------------------------------------------------------------------------------------------------------------|
| Research sample   | All data used in this set of analyses comes from the US Forest Service's Forest Inventory and Analysis database, version 728. We further subsetted to sites within the Eastern US where re-measurement intervals are standardized, which facilitated fitting of demographic models and demographic simulations, as done in previous analyses (Figure 1). We only considered sites where all subplots were in a forested condition and excluded plantations as well as any sites with evidence of active management or harvesting. Trees were assigned AM or EM association as in previous analyses. Once mycorrhizal associations were assigned, we further subsetted the data set to sites where >90% of basal area was associated with either AM or EM associated trees. Therefore, a plot with 50% EM basal area and 50% AM basal area would be included in this analysis, however any plot with >10% mixed mycorrhizal, arbutoid, ericoid or non-mycorrhizal basal area would be excluded. This filter excluded 15% of all forested sites. Further investigation showed 2/3 of excluded sites (i.e. 10 of the 15%) were due to a high abundance of Populus, a well-known dual AM-EM tree genus. The remainder of exclusions were primarily driven by trees where mycorrhizal strategy was unknown. Our final dataset included 6,965 unique forest sites, re-censused at a ~5-year interval, with complete environmental covariates, comprised of 200,363 trees. |
| Sampling strategy | The FIA survey is designed as a gridded random sample of US forests. |
| Data collection    | Raw forest inventory data were collected by foresters employed by the U.S. Forest Service. Environmental covariate data were extracted based on latitude/longitude and the geographic data layers described in Supplementary Data File 1. |
| Timing and spatial scale | Forest data were taken from the Eastern US. Plot remeasurement period was standardized to be 4.9-5.1 years apart. |
| Data exclusions    | We further subsetted to sites within the Eastern US where re-measurement intervals are standardized, which facilitated fitting of demographic models and demographic simulations, as done in previous analyses (Figure 1). We only considered sites where all subplots were in a forested condition and excluded plantations as well as any sites with evidence of active management or harvesting. Trees were assigned AM or EM association as in previous analyses. Once mycorrhizal associations were assigned, we further subsetted the data set to sites where >90% of basal area was associated with either AM or EM associated trees. Therefore, a plot with 50% EM basal area and 50% AM basal area would be included in this analysis, however any plot with >10% mixed mycorrhizal, arbutoid, ericoid or non-mycorrhizal basal area would be excluded. This filter excluded 15% of all forested sites. Further investigation showed 2/3 of excluded sites (i.e. 10 of the 15%) were due to a high abundance of Populus, a well-known dual AM-EM tree genus. The remainder of exclusions were primarily driven by trees where mycorrhizal strategy was unknown. Our final dataset included 6,965 unique forest sites, re-censused at a ~5-year interval, with complete environmental covariates, comprised of 200,363 trees. Exclusion criteria were established prior to fitting any statistical models. |
| Reproducibility   | This is an observational study, and therefore no experiments were performed or reproduced. |
| Randomization     | Because this is an observational study, no randomization was performed. |
| Blinding          | Because this is an observational study using data collected by others, no blinding was performed. |
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