



Global imprint of mycorrhizal fungi on whole-plant nutrient economics

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Edited by Sarah E. Hobbie, University of Minnesota, St. Paul, MN, and approved October 4, 2019 (received for review May 15, 2019)

Mycorrhizal fungi are critical members of the plant microbiome, forming a symbiosis with the roots of most plants on Earth. Most plant species partner with either arbuscular or ectomycorrhizal fungi, and these symbioses are thought to represent plant adaptations to fast and slow soil nutrient cycling rates. This generates a second hypothesis, that arbuscular and ectomycorrhizal plant species traits complement and reinforce these fungal strategies, resulting in nutrient acquisitive vs. conservative plant trait profiles. Here we analyzed 17,764 species level trait observations from 2,940 woody plant species to show that mycorrhizal plants differ systematically in nitrogen and phosphorus economic traits. Differences were clearest in temperate latitudes, where ectomycorrhizal plant species are more nitrogen use- and phosphorus use-conservative than arbuscular mycorrhizal species. This difference is reflected in both aboveground and belowground plant traits and is robust to controlling for evolutionary history, nitrogen fixation ability, deciduousness, latitude, and species climate niche. Furthermore, mycorrhizal effects are large and frequently similar to or greater in magnitude than the influence of plant nitrogen fixation ability or deciduous vs. evergreen leaf habit. Ectomycorrhizal plants are also more nitrogen conservative than arbuscular plants in boreal and tropical ecosystems, although differences in phosphorus use are less apparent outside temperate latitudes. Our findings bolster current theories of ecosystems rooted in mycorrhizal ecology and support the hypothesis that plant mycorrhizal association is linked to the evolution of plant nutrient economic strategies.

mycorrhizal fungi | plant traits | plant nutrition | nutrient limitation | plant economics

Mycorrhizal fungi are critical members of the plant microbiome, enhancing plant access to soil nutrients and water (1). Among mycorrhizal fungi, there are 2 predominant functional types, arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi, which form symbioses with the roots of most plants on Earth (2). A long-standing hypothesis in ecosystem ecology is that AM and EM associations represent contrasting nutrient acquisition strategies (3, 4). Specifically, AM-associated plants rely on inorganic soil nitrogen (N) resources and dominate “fast” N cycling ecosystems with high soil N mineralization rates, while EM-associated plants thrive in “slow” N cycling ecosystems with low soil N mineralization rates, enabled by the ability of EM fungi to degrade and take up organic N from soil (5–8). In support of this idea, anthropogenic inorganic N pollution in North America is associated with a shift in forest composition from EM- to AM-associated tree species (9, 10). While these arguments generally focus on plant N nutrition, in principle this dichotomy may also extend to plant phosphorus (P) acquisition strategies if EM fungi invest more than AM fungi in extracellular P acquisition (8, 11, 12).

Systematic differences in soil nutrient cycling rates between AM and EM ecosystems (13) generate a second hypothesis, that a plant’s mycorrhizal association is correlated with plant nutrient economic traits: specifically, AM fungal-associated plants may be selected to have nutrient acquisitive traits, and EM fungal-associated plants may be selected to have nutrient conservative

traits (3). Such a dichotomy would represent an eco-evolutionary feedback between plants and the soil nutrient environment, mediated by mycorrhizal fungi, selecting for plant traits that reinforce fast or slow nutrient cycling within AM and EM ecosystems.

Despite the hypothesized correlations between mycorrhizal association and plant nutrient economic trait profiles (3), there is conflicting evidence that AM- and EM-associated plant species systematically differ in these traits. Regional and global sampling of thousands of plant species have shown no difference in green foliar N or P concentrations between AM fungal- and EM fungal-associated plants (14, 15). A more recent analysis has shown idiosyncratic variation in foliar nutrient resorption, with AM plants resorbing more N within tropical latitudes and EM plants resorbing more P within boreal latitudes (16). However, plant traits, plant mycorrhizal associations, and plant evolutionary history are not independent (17–19). Given that most studies of EM plants are focused within either the Pinaceae or Fagales lineages (15, 17), it is difficult to determine whether these findings truly emerge due to differences in mycorrhizal habit or whether mycorrhizal association is a proxy for strong correlations between plant traits and plant evolutionary history. The systematic differences observed may reflect traits common among a few plant clades arising independently of plant mycorrhizal association, coupled with nonrandom sampling of plant clades across the plant phylogeny. Understanding whether groups of species differ

Significance

Most plants on Earth form a symbiosis with root-associated (i.e., mycorrhizal) fungi, trading plant photosynthate for fungal-acquired soil nutrients. Ecologists have long thought that different types of mycorrhizal fungi—arbuscular vs. ectomycorrhizal—represent adaptations to high vs. low soil nutrient availability. Here we show that these different mycorrhizal associations are linked to differences in a suite of plant traits related to nutrient economic strategies. Ectomycorrhizal plant species are more nutrient use-conservative than arbuscular mycorrhizal plant species, an effect that is robust to controlling for plant growth form and evolutionary history. These findings bolster emerging theories in ecosystem ecology that leverage the ecology of mycorrhizal fungi to better predict ecosystem carbon-nutrient cycle interactions.

Author contributions: C.A. and S.N.K. designed research; C.A., W.D.P., and S.N.K. performed research; C.A., W.D.P., and S.N.K. analyzed data; and C.A., J.M.B., M.C.D., W.D.P., and S.N.K. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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Data deposition: All code to replicate analyses and figures can be found at github.com/colinaverill/Averill_et_al_2019_myco_traits.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1906655116/-DCSupplemental.

First published October 28, 2019.

systematically in a given trait requires accounting for evolutionary history (20, 21).

Moreover, the analyses reported to date have focused on foliar nutrient concentrations, although differences between AM and EM plant nutritional strategies may be more related to below-ground traits than to aboveground traits, consistent with slower root litter decomposition of EM compared with AM plant species (22, 23). Plants can invest as much or more carbon in fine roots as in aboveground foliage (24), and systematic differences in plant nutrient economic traits may manifest in root nutrient concentrations rather than in green or senescent foliar nutrient concentrations.

Finally, in addition to nutritional strategy differences between mycorrhizal types, biogeochemical theory predicts that plants shift from N to P limitation from the poles to the tropics (25). Plants within high-latitude boreal-arctic ecosystems on younger soils are predicted to be primarily N-limited, while low-latitude tropical forests on old, highly weathered soils are predicted to be P-limited (25, 26). If EM plants are inherently more nutrient use-conservative than AM plants, and if the primary element limiting plant growth shifts from N to P from the poles to the tropics, then we may predict EM plants to be more N use-conservative compared with AM plants at high latitudes and more P use-conservative at low latitudes. Alternatively, if N and P strategies are fundamentally linked to an overall plant nutritional strategy, then we predict EM plants to be more N and P use-conservative than AM plants across all latitudes.

Here we analyzed 17,764 species-level observations of mycorrhizal association, N fixation status, plant growth form, deciduous vs. evergreen leaf habit, green foliage, senescent foliage, and root element concentrations across 2,940 woody plant species (Fig. 1 and *SI Appendix, Table S1*). First, we used these data to test the hypothesis that AM- and EM-associated plants differ systematically in plant nutrient economic traits and to determine whether this effect is independent of climate, plant growth form, N fixation ability, deciduous vs. evergreen leaf habit, and evolutionary history by including all these predictors in a single statistical model. Second, we tested for interactions between mycorrhizal associations and latitudinal zone (boreal, temperate, tropical), to understand how correlations between mycorrhizal association and nutrient use may change across latitudes. Because data coverage is heterogeneous across mycorrhizal associations and latitudinal zones, we assessed our ability to detect significant differences in plant nutrient economic traits between mycorrhizal associations, given our sample size and phylogenetic autocorrelation

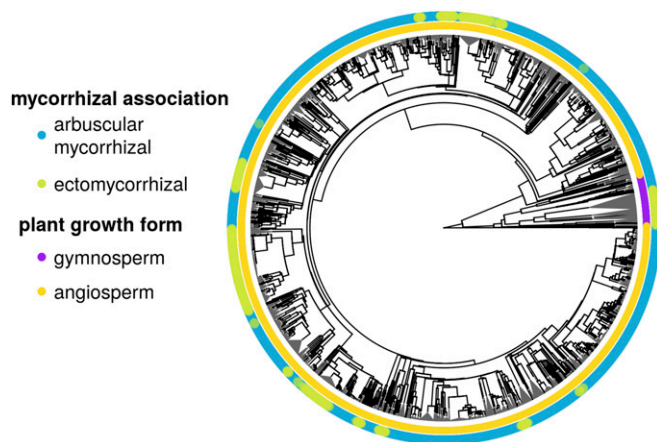


Fig. 1. Phylogeny of all plant species used in this analysis. The inner ring identifies which species are angiosperms (orange) vs. gymnosperms (purple); the outer ring, which species are arbuscular (blue) vs. ectomycorrhizal (green).

structure, by comparing posterior distributions of mycorrhizal trait estimates relative to biologically meaningful effect sizes.

Results

EM plant species traits were systematically more nutrient use-conservative across most traits measured, and the effects were clearest for N traits across all latitudes. EM plants also had more conservative P traits in temperate latitudes, where data were most abundant (Fig. 2). Green foliar N correlations with mycorrhizal association were strong and independent of latitudinal zone. EM green foliar N values were ~10–14% lower than AM values in all latitudinal zones, although the difference was significant only in temperate and tropical latitudes (Bayesian P values <0.05 ; Fig. 2A). We emphasize that even when latitudinal zone main effects and interactions are not significant, they can still drive insignificant AM-EM contrasts within latitudinal zones, as these terms also propagate uncertainty associated with differences in sample sizes across latitudinal zones. This generally occurs when a small sample size within a latitudinal zone drives large latitudinal parameter uncertainty, which propagates through to latitude-specific mycorrhizal trait estimates. Senescent foliar N values varied by latitudinal zone and mycorrhizal type. Senescent foliar N values were 35% to 48% lower in EM plants compared to AM plants within boreal and temperate latitudes (Bayesian P values <0.05) but were similar between mycorrhizal associations within tropical latitudes (Fig. 2B). Root N values differed by mycorrhizal association independent of latitudinal zone, with EM plants having 19% to 32% less N in roots compared to AM plants across all latitudes (Bayesian P values <0.05 ; Fig. 2C).

Differences in P traits between mycorrhizal types were more complex than differences in N traits. Green foliar P concentrations were affected by mycorrhizal association and latitudinal zone (Bayesian P value <0.05). Green foliar P concentrations were 18% to 26% lower in EM plants compared with AM plants in temperate and boreal latitudes (Fig. 2D) and ~8% lower in tropical latitudes, although the difference within tropical latitudes was not significant (Bayesian P value >0.05). Senescent foliar P responses were also affected by latitudinal zone but were more variable, likely due to smaller sample size. Differences in senescent foliar P between AM and EM mycorrhizal types were never significant (Fig. 2E). Root P concentrations were dependent on latitudinal zone. Mycorrhizal fungal association was an important predictor in models of root P concentrations; however, posterior contrasts showed a significant difference between plant mycorrhizal associations only within temperate latitudes, where EM root P concentrations were ~32% lower than AM root P concentrations (Bayesian P value = 0.03; Fig. 2F). EM root P concentrations were 19% and 32% lower in tropical and boreal latitudes, respectively; however, these differences were not significant.

We found that phylogeny alone could explain a substantial amount of trait variation for several traits. Analysis of plant traits as a function of phylogenetic distance alone (without environmental and ecological covariates) showed a substantial phylogenetic signal in plant traits (Pagel's $\lambda = 0.40$ to 0.81). Phylogeny alone explained 15% to 38% of the variation in plant trait values, depending on the trait (Fig. 3). When we visualized AM-EM contrasts for all traits within temperate latitudes before and after accounting for phylogeny (*SI Appendix, Fig. S2*), the magnitude of trait values between mycorrhizal associations often changed substantially, although qualitative differences between AM and EM plant traits did not change. Incorporating phylogeny generally increased parameter uncertainty, as phylogenetic residual autocorrelation reduced statistical power. However, this increased parameter uncertainty was not large enough to mask significant differences between EM and AM plants in nutrient economic traits within temperate latitudes.

N-fixing plant species had greater green foliar N ($P = 0.01$), senescent foliar N ($P = 0.008$), and root N ($P = 0.026$)

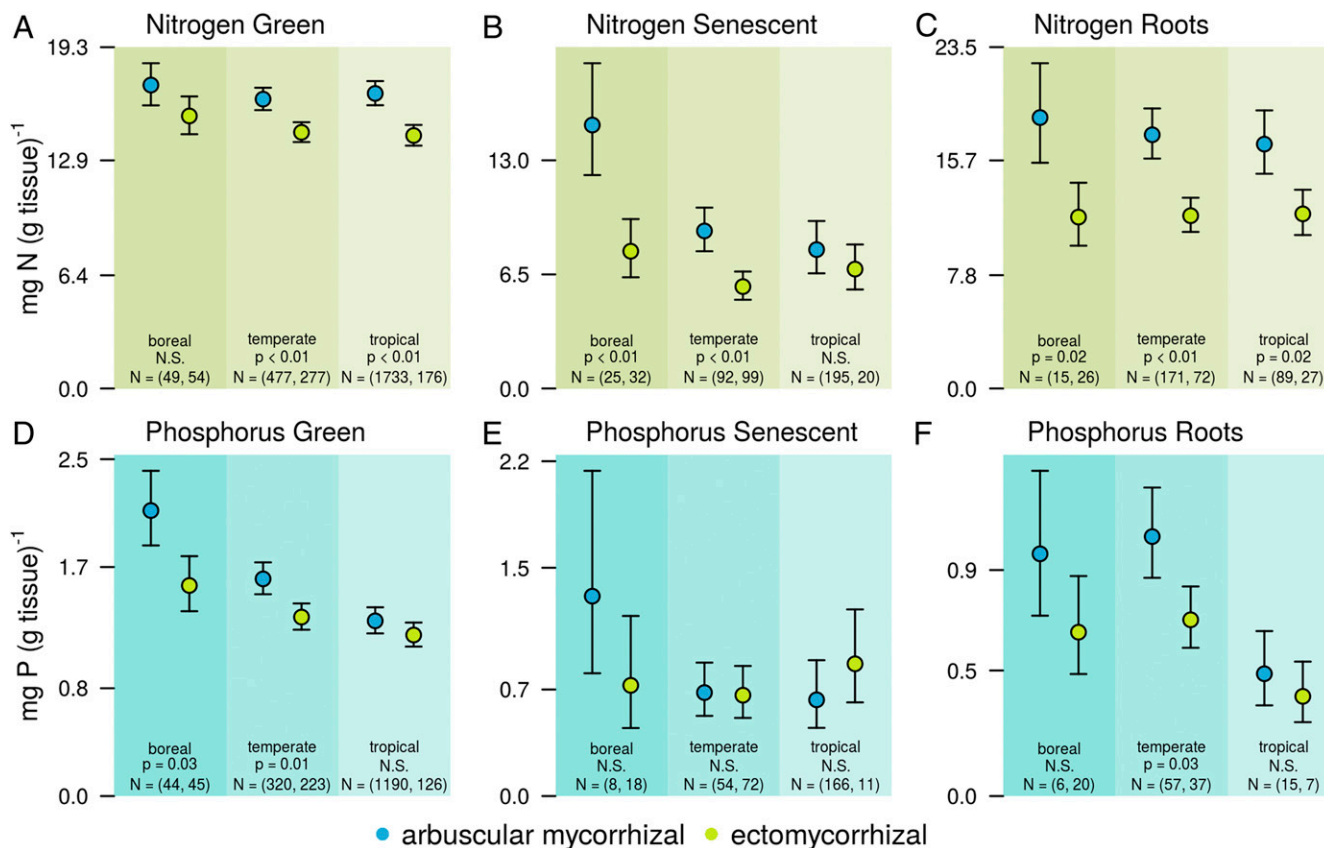


Fig. 2. Arbuscular vs. ectomycorrhizal trait means as estimated by calculating a latitude-specific posterior and its 95% credible interval: N green (A), N senescent (B), N roots (C), P green (D), P senescent (E), P roots (F). Posterior estimates account for differences in mean climate values across latitudes and the effect of climate predictors on trait values. Because N-fixation status, leaf habit, and plant growth form also affect the trait intercept value, all plotted values are normalized to the angiosperm plant growth form, evergreen leaf habit, and non-N-fixing status.

concentrations, but lower green foliar P ($P = 0.001$) and senescent foliar P concentrations ($P = 0.04$). We detected no difference between N-fixing and non-N-fixing plant species in root P concentrations (*SI Appendix, Table S2*).

Evergreen vs. deciduous leaf habit frequently affected trait estimates. Compared with evergreen plants, deciduous plant species had greater green foliar N ($P = 0.001$), green foliar P ($P = 0.001$), and senescent P concentrations ($P = 0.004$), but lower root N concentrations ($P = 0.030$) (*SI Appendix, Table S2*).

Gymnosperm plant species trended toward lower N and P concentrations across all plant tissues except root P, although only differences in senescent foliar N values were significant ($P = 0.026$; *SI Appendix, Table S2*). This likely is a result of strong phylogenetic structure in traits and also the fact that angiosperm and gymnosperm plants are distinct phylogenetic clades. As a result, our phylogenetic approach limits our ability to detect significant differences between these clades.

When accounting for climate, mean annual precipitation effects were more common than mean annual temperature effects, likely because the inclusion of latitudinal zone in the model captured some of the potential effects of temperature. On average, greater precipitation was linked to greater green foliar N ($P = 0.001$), lower root N ($P = 0.002$), lower green foliar P ($P = 0.001$), lower senescent foliar P ($P = 0.001$), and lower root P ($P = 0.001$). On average, higher temperatures were linked to lower green foliar P ($P = 0.001$; *SI Appendix, Table S2*). It is important to note that because latitudinal zone is a predictor in the model, these effects must be interpreted with the understanding that the main effects of latitude will affect baseline trait values as well and complicate the relationships between climate and trait values reported here.

Discussion

The idea that AM-associated and EM-associated plants differ in their nutrient acquisition strategies is central to theories of ecosystems rooted in mycorrhizal ecology (1, 3, 4). The systematic differences in AM vs. EM plant economic traits found in this study provide evidence on a global scale that these plant mycorrhizal strategies are associated with nutrient acquisitive vs. nutrient conservative plant economic traits, and that this difference cannot be attributed to shared evolutionary history coupled with historical oversampling of particular plant clades. The difference in nutrient economic strategies was reflected in both N and P traits and could not be explained by confounding differences in plant growth form, deciduous vs. evergreen leaf habit, N fixation status, or climate. Differences were most apparent in temperate latitudes where sample sizes were largest, however, EM plants were more N use-conservative than AM plants in boreal and tropical latitudes as well. P differences did not generalize to tropical latitudes; however, it is possible that the lack of significant contrasts reflects the low numbers of boreal and tropical observations for these traits. The presence of systematic differences in both aboveground and belowground plant traits between EM and AM plants is consistent with the idea that the form of mycorrhizal symbiosis is a major factor in plant trait evolution. These findings bolster current theories of ecosystem ecology that represent AM vs. EM plants as contrasting nutrient acquisition strategies (3, 4) and ecosystem models that leverage the ecology of mycorrhizal symbiosis to better represent ecosystem carbon–nutrient cycle interactions (27–29).

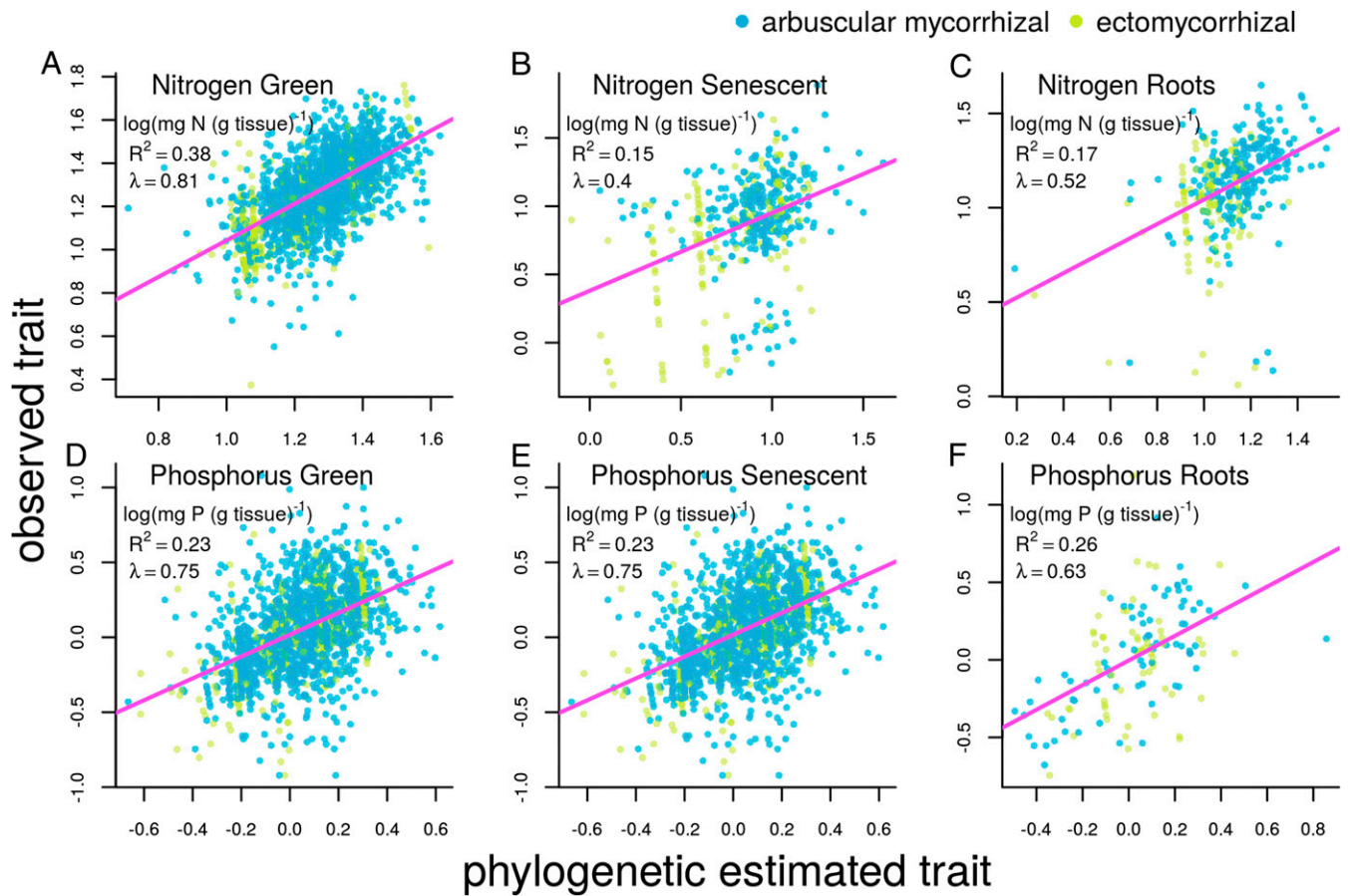


Fig. 3. Phylogenetic estimated vs. observed plant trait values: N green (A), N senescent (B), N roots (C), P green (D), P senescent (E), P roots (F). All values are \log_{10} -transformed. Estimated trait values were generated based on phylogenetic models fit to all data except for the plant species being estimated or leave-one-out cross-validation. Dashed lines indicate nonsignificant relationships between predicted vs. observed values.

EM plant species had significantly lower green foliar N concentrations than AM plant species. This finding is in contrast with the results of previous comparative studies, which detected no difference between mycorrhizal associations, possibly due to a difference in statistical power among analyses. For instance, an analysis of United Kingdom plant N and P concentrations compared 12 EM species and 53 AM species (14) but was unable to definitively identify the influences of mycorrhizal status and deciduousness. A second study examined many more species within a phylogenetic framework, but a lack of phylogenetic resolution necessitated the use of a statistical technique that reduced the dataset to only 17 paired-clade comparisons (15). That test has the advantage of being conservative, but also the disadvantage of reducing statistical power (30) because it cannot make use of all of the species-level data in a single test. Our analysis uses a phylogenetic framework to take information from each species-level observation, increasing the statistical power to more definitively distinguish differences between EM and AM plants hinted at in previous studies. A large phylogenetic analysis of root N concentrations found no difference between AM vs. EM plants, yet most AM observations were nonwoody, potentially reflecting an undersampling of woody plants (31).

It is important to recognize that many previous analyses comparing AM and EM traits do not account for phylogenetic autocorrelation, especially at the site scale. Indeed, our findings are consistent with previous site-scale studies within geographic regions that found differences in AM and EM nutrient economic traits (32, 33). While controlling for phylogeny may affect parameter estimates substantially, our analysis suggests that previous

conclusions based on AM vs. EM contrasts may be valid; nonetheless, we emphasize that inference may be biased in studies without very large sample sizes (*SI Appendix, Fig. S2*). Furthermore, the goal of the present analysis was to address a question that could be answered only by considering many plant species across the plant phylogeny. Our findings should not be interpreted to suggest that other conclusions based on site-scale studies of fewer species do not have merit.

Green foliar N and root N patterns were similar across latitudes, while past analyses have provided mixed support for coordinated foliar and root nutrient economic strategies (34). Our analysis suggests that some of this discrepancy may be due to a lack of accounting for differences in plant mycorrhizal association in previous analyses, although raw correlations between species level green foliar N and root N are weak in this dataset ($R^2 = 0.04$; $P < 0.001$). It may be that this coordination can be seen only after species are binned into functional groups, as done in this analysis. Future work on aboveground-belowground trait coordination should explore the dominant form of mycorrhizal association as a potential driver, as well as the many other known controls over foliar and root nutrient concentrations described here and in many other analyses (34).

We observed remarkable intraspecific trait variation across traits. Approximately 60% of the variation in senescent foliar N and root N could be attributed to intraspecific variation, although we note that our approach will also combine parameter and observation uncertainty into the estimation of intraspecific variation. Other work has shown that intraspecific trait relationships can substantially deviate from interspecific plant economic relationships

(35). Our analysis focused on mean trait responses; however, large intraspecific variation implies that environmental factors and local adaptation may also play an important role in plant nutrient economic strategies. Furthermore, an analysis of species-level trait variance may add additional nuance to the plant economics spectrum, although such an analysis would require substantially more data.

Overall, foliar N and P concentrations decreased toward the equator, P more so than N, consistent with previous global analyses of foliar nutrient concentrations (25). While EM plants were more N use-conservative than AM plants across latitudes, we did not find statistically significant evidence indicating that EM plants are substantially more P use-conservative in tropical latitudes compared with AM plants. Given strong differences in EM vs. AM P content in temperate and boreal latitudes, this may imply a fundamental difference in mycorrhizal nutrient strategies with regard to P in tropical ecosystems. We also note that there were very few EM plant trait observations from tropical latitudes, which is not likely due to the absence of EM plants in tropical ecosystems. While much of the lowland neotropics is AM-associated, large portions of northeast South America, central Africa, and southeast Asia are dominated by EM forests (36). Greater sampling of EM tropical plant species may help resolve the generality of mycorrhizal differences in plant nutrient acquisition strategies across latitudes.

Our study is consistent with an eco-evolutionary feedback between plants and the soil nutrient environment, mediated by mycorrhizal fungi, selecting for plant traits that reinforce fast or slow nutrient cycling within AM and EM ecosystems. However, other evolutionary scenarios are equally plausible. For instance, it may be that substantial interspecific variation in plant nutrient efficiency traits was already present when EM symbiosis evolved, and that EM symbiosis evolved only in species that were already nutrient use-conservative. While it is also theoretically possible that the evolution of EM symbiosis led to the evolution of fungal organic N and P acquisition traits (e.g., production of organic N-degrading and organic P-degrading extracellular enzymes, organic nutrient uptake transporters), recent ecological and comparative genomics analyses of fungi indicate that these traits were already present in free-living saprotrophic ancestors of ectomycorrhizal fungi (6, 37). Nevertheless, organic N- and P-acquisition traits among EM fungi may have been reinforced or enhanced after the evolution of this particular type of symbiosis. We did not test the order of trait evolution, yet our study provides evidence that plant and mycorrhizal nutrient economic traits may have coevolved through eco-evolutionary feedback.

Few theories of plant and ecosystem ecology consider the form of mycorrhizal symbiosis central to understanding plant nutritional ecology or ecosystem carbon–nutrient cycle interactions (4). Here we show that AM vs. EM symbiosis is indicative of a suite of plant traits linked to acquisitive or conservative nutrient economic strategies. While the potential importance of mycorrhizas was alluded to in the original leaf economic analysis (38), this study provides a demonstration at a scale comparable to that

of the original presentation. Furthermore, while this analysis focuses on plant nutrient concentrations, these traits are linked to broader trait syndromes (34), and so our analysis locates AM and EM plants on the fast and slow ends of the plant economics spectrum, respectively. This has broad implications for ecosystem function; multiple global change factors are changing the distribution of EM vs. AM plant species (9, 10, 39), implying that plant economic trait profiles are also shifting. Future work on plant economic strategies that consider mycorrhizal associations will help us understand plant nutritional biogeography and nutritional constraints of ecosystems under global environmental change and, in turn, potential future states of the Earth.

Methods

We tested whether AM fungal- and EM fungal-associated woody plant species differ systematically in 6 key plant traits linked to whole plant nutrient economics: green foliar N and P concentrations, senescent foliar N and P concentrations, and root N and P concentrations. Our analysis included interactions between mycorrhizal association and latitudinal zones (boreal, temperate, and tropical), to understand how mycorrhizal effects vary across major latitudinal zones, which may serve as a proxy for differences in soil age and, in turn, N vs. P limitation. We focused on woody plant species because nearly all herbaceous plant species are arbuscular mycorrhizal (15). Furthermore, we tested whether this variation was independent of major differences in plant growth form (i.e., woody angiosperms vs. woody gymnosperms, deciduous vs. evergreen) and plant N-fixation status by including these terms as predictors in the full model.

Finally, species are not independent samples from the tree of life, and the evolutionary history that they have in common can bias results if not accounted for (15, 17, 20). To measure and account for this potential bias, we used a Bayesian phylogenetic mixed model (40), which avoids “overcounting” closely related species that differ in a given trait for reasons independent of mycorrhizal association. Furthermore, a Bayesian framework facilitated propagating uncertainty when estimating latitudinal zone-specific mycorrhizal trait values, as well as assessment of statistical power. The spatial distribution of trait observations is plotted in *SI Appendix, Fig. S1*, and the numbers of observations of each trait by mycorrhizal type, N fixation, latitudinal zone, deciduousness, and growth form are reported in *SI Appendix, Table S1*. Complete methodological details are provided in *SI Appendix, Methods*. All code to replicate analyses and figures can be found at github.com/colinaverill/Averill_et_al_2019_myc_traits. Necessary data files are available on request due to data sharing restrictions imposed by some data providers.

ACKNOWLEDGMENTS. C.A. was supported by the National Oceanic and Atmospheric Administration Climate and Global Change Postdoctoral Fellowship Program, administered by Cooperative Programs for the Advancement of Earth System Science, University Corporation for Atmospheric Research, NSF Grant MSB-1638577, and Ambizione Grant PZ00P3_179900 from the Swiss National Science Foundation. M.C.D. was supported by NSF Grants MSB-1318164 and MSB-1638577. J.M.B. was supported by NSF Grant MSB-1638577 and a Peter Paul Professorship at Boston University. W.D.P. was supported by NSF Grants ABI-1759965 and MSB-ECA-1802605 and US Department of Agriculture Forest Service Agreement 18-CS-11046000-041. J. Luecke consulted on figure design. The study has been supported by the TRY initiative on plant traits (<https://www.try-db.org/TryWeb/Home.php>). The TRY initiative and database is hosted, developed, and maintained by J. Kattge and G. Bönisch (Max Planck Institute for Biogeochemistry). TRY is currently supported by DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig.

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