ECOLOGY

Tree mycorrhizal association types control biodiversity-productivity relationship in a subtropical forest

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Mycorrhizae are symbiotic associations between terrestrial plants and fungi in which fungi obtain nutrients in exchange for plant photosynthates. However, it remains unclear how different types of mycorrhizae affect their host interactions and productivity. Using a long-term experiment with a diversity gradient of arbuscular (AM) and ectomycorrhizal (EcM) tree species, we show that the type of mycorrhizae critically controls the effect of diversity on productivity. With increasing diversity, the net primary production of AM trees increased, but EcM trees decreased, largely because AM trees are more effective in acquiring nitrogen and phosphorus. Specifically, with diversity increase, AM trees enhance both nutrient resorption and litter decomposition, while there was a trade-off between litter decomposability and nutrient resorption in EcM trees. These results provide a mechanistic understanding of why AM trees using a different nutrient acquisition strategy from EcM trees can dominate in subtropical forests and at the same time their diversity enhances productivity.

INTRODUCTION

High plant diversity often promotes primary productivity (*1*, *2*). To maintain their growth and productivity and thus coexist, different species in plant communities often have complementary resource acquisition strategies (*3*, *4*). One of the most critical acquisition strategies for soil resources is mycorrhizal symbiosis, which can expand plant root surface area and thus plant access to nutrients (*5*, *6*). Nutrient resorption and litter decomposition provide ~90% of the annual nitrogen (N) and phosphate (P) needs for tree growth (*7*, *8*). However, how mycorrhizal plants balance or coordinate these two pathways to optimize their nutrient acquisition in high-diversity ecosystems is still unknown.

There are two dominant mycorrhizal types associated with trees, arbuscular mycorrhizae (AM) and ectomycorrhizae (EcM) (*9*), which may regulate plant-soil feedbacks and drive plant diversity (*10*, *11*). While AM tree species generally experience negative feedback and dominate in high-diversity ecosystems, EcM tree species often exhibit positive feedback and promote monodominance or familial dominance (*12*). This difference has largely been attributed to different types of mycorrhizae. While AM fungi offer low root protection against soilborne pathogens and AM trees exhibit conspecific inhibition (*10*–*12*), EcM fungi form a mantle around tree roots that better protects against pathogens and facilitates conspecific species growth (*10*–*12*). At the same time, AM fungi have low host specificity and complement each other spatially during nutrient foraging in soils, thereby promoting plant coexistence and productivity (*13*, *14*). In contrast, EcM fungi have high host specificity and could establish a common fungal network to transfer nutrients and signals between conspecific trees, which usually promotes their dominance (*15*, *16*). Thus, plant-soil feedback theory may explain why AM trees are more diverse than EcM trees, but not why AM trees with lower resistance to pathogens should be more competitive than EcM trees in mixed subtropical forest (*10*, *12*). Our understanding of the drivers of AM trees' competitive advantage is still inadequate.

The contrasting nutrient acquisition strategies of AM and EcM plants may play important roles in regulating the relationship between plant diversity and productivity (*4*, *9*, *17*–*19*). Compared to AM plants, EcM plants supposedly favor a more conservative nutrient strategy and are often associated with higher resorption efficiency but lower litter decomposition rate (*8*, *20*, *21*). This difference may stem from the coevolutionary history of plants with fungi (*22*). The evolution from AM to EcM symbioses was accompanied by an increase in plant lignification and of symbiosis with lignin-degrading fungi such as Agaricomycetes (*22*–*24*). Therefore, EcM trees often have higher lignin concentrations and produce more recalcitrant litter than AM trees, resulting in slower litter decomposition and nutrient mineralization but higher soil organic matter accumulation (*20*, *25*). In a high-diverse ecosystem where nutrient competition intensifies, AM trees may rely more on rapid litter decomposition to gain inorganic nutrients (*9*, *25*). In contrast, EcM trees may be dependent more on EcM fungi to mine and absorb nutrients directly from the organic matter because EcM fungi retain degradative enzymes from their saprotrophic ancestors (*9*, *26*). Also, as the decomposition capacity of EcM fungi is lower than that of saprotrophic fungi (*27*), EcM plants may have to rely on other nutrient conservation strategies, such as nutrient resorption, to ensure their nutrient needs (*7*).

When productivity increases with diversity, plant communities likely adjust their nutrient acquisition strategies via either physiological plasticity or species reordering (*28*, *29*). However, there is a lack of experimental evidence regarding how trees with different mycorrhizal symbioses regulate their nutrient resorption and litter

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decomposition for optimizing nutrient acquisition in high-diversity ecosystems, as AM and EcM trees rarely are planted together at the same site in subtropical areas. We used a controlled biodiversity-ecosystem functioning (BEF) experiment in a subtropical forest in Southeast China to study these issues. We hypothesized that as plant nutrient demand increases with diversity, AM and EcM trees use different strategies to increase their nutrient supply. More specifically, the acquisitive AM trees would mainly rely on inorganic nutrient supply to meet their growing nutrient demands via litter decomposition, while the conservative EcM trees would enhance aboveground nutrient resorption to alleviate their nutrient limitation.

RESULTS

Biodiversity effects on net primary productivity controlled by mycorrhizal types

Tree species richness positively affected the net primary productivity (NPP) of the experimental forest communities (Fig. 1A and fig. S2A). However, after dividing the community by mycorrhizal type, tree species richness had a positive effect on NPP of AM tree subcommunities (Fig. 1B and fig. S2B), while it had a negative effect on NPP of EcM tree subcommunities (Fig. 1C and fig. S2C). After 9 years, the communities initially evenly planted with AM and EcM trees, shifted to communities dominated by AM tree biomass, accounting for 57, 79, 90, and 99% of the total biomass in the 2-, 4-, 8-, and 16-species mixtures, respectively (figs. S3 and fig. S4). NPP of the experimental forest communities and AM subcommunities were negatively correlated with tree species evenness (fig. S5, A and B), while NPP of EcM subcommunities were positively correlated with tree species evenness (fig. S5C).

Nutrient acquisition strategies of AM and EcM trees

Community-level nitrogen resorption efficiency (NRE_c) and phosphorus resorption efficiency (PRE_c) positively correlated with tree species richness (Fig. 2, A and D). Linear mixed-effect models (LMMs) showed that the effects of tree species richness on species-level NRE_i and PRE_i varied depending on plant mycorrhizal type (Table 1 and table S4). NRE_i and PRE_i increased with tree species richness for AM trees (Fig. 2, B and E; figs. S6 and S7; and table S4) but decreased with tree species richness for EcM trees (Fig. 2, C and F; figs. S6 and S7; and table S4).

Community-level litter decomposition rate (k_c) positively correlated with tree species richness (Fig. 2G and fig. S8). Similarly, AM and EcM litter decomposition rates (k_i) at the species level were also positively correlated with tree diversity (Fig. 2, H and I). LMMs showed that the positive effect of tree species richness on litter decomposition rates was still significant, even after accounting for variations in mycorrhizal type, litter traits, and soil microbial community (table S3). The results of phylogenetic LMMs for resorption and decomposition were in broad agreement with the results derived from LMMs (tables S6 and S7 and Supplementary Result).

The net biodiversity effect on NRE_c and PRE_c increased with tree species richness, mainly driven by a positive selection effect (Fig. 3, A and B), as diverse plant communities contained competitive species that had high NRE_i and PRE_i and thus became dominant (figs. S3 and S4). When considering how species diversity affects the litter decomposition rate, we found that the increase of the selection effect was greater than the decrease of complementarity effects (CEs); thereby, the net biodiversity effect also increased with tree species richness (Fig. 3C).

Functional differences between AM and EcM trees

AM trees had significantly higher NRE_i than EcM trees (Fig. 2 and Table 1). Tree species richness had a negative correlation with litter N, P, and lignin concentrations of AM trees but had a positive correlation with litter N concentration and did not alter litter P and lignin concentrations of EcM trees (fig. S9).

Soil microbial community abundance and composition

Tree species richness did not affect the microbial abundance, as indicated by total phospholipid fatty acids (PLFAs; fig. S10A), but it significantly altered soil microbial community structure. The ratio of soil fungi (F) to soil bacteria (B) was positively correlated with tree species richness (fig. S10B). Tree species richness altered the relative abundance of symbiotrophs and pathotrophs but not the relative abundance of saprotrophs (Fig. 4A) or the unclassified group (fig. S11). The increase in tree species richness caused a decrease in the relative abundance of EcM fungi but had no effects on that of AM fungi (Fig. 4A and fig. S12). The relative abundance of

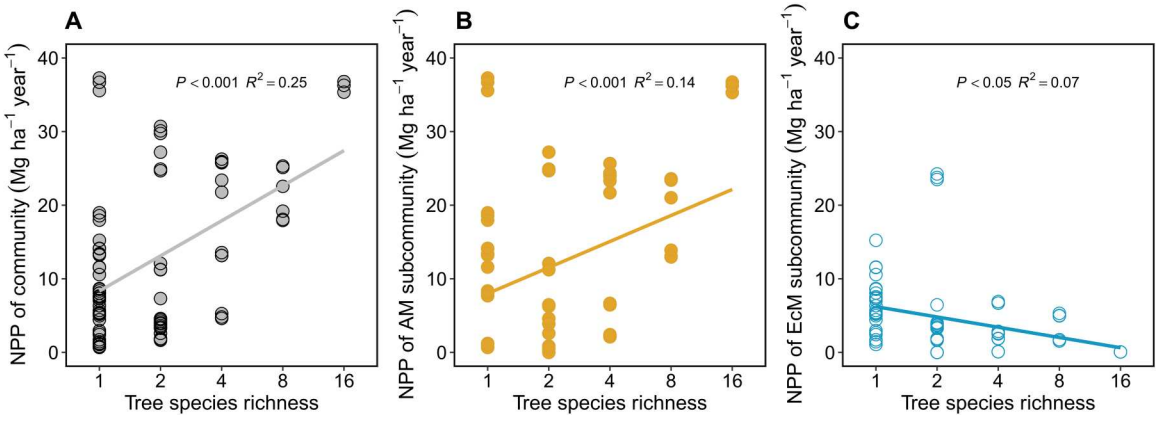

Fig. 1. Effects of tree species richness on NPP. NPP as a function of species tree richness at community level (**A**), at AM subcommunity level (**B**), and at EcM subcommunity level (**C**). Solid lines indicate significant regression lines. Levels of significance and coefficient of determination (R^2) for all lines are shown in plots.

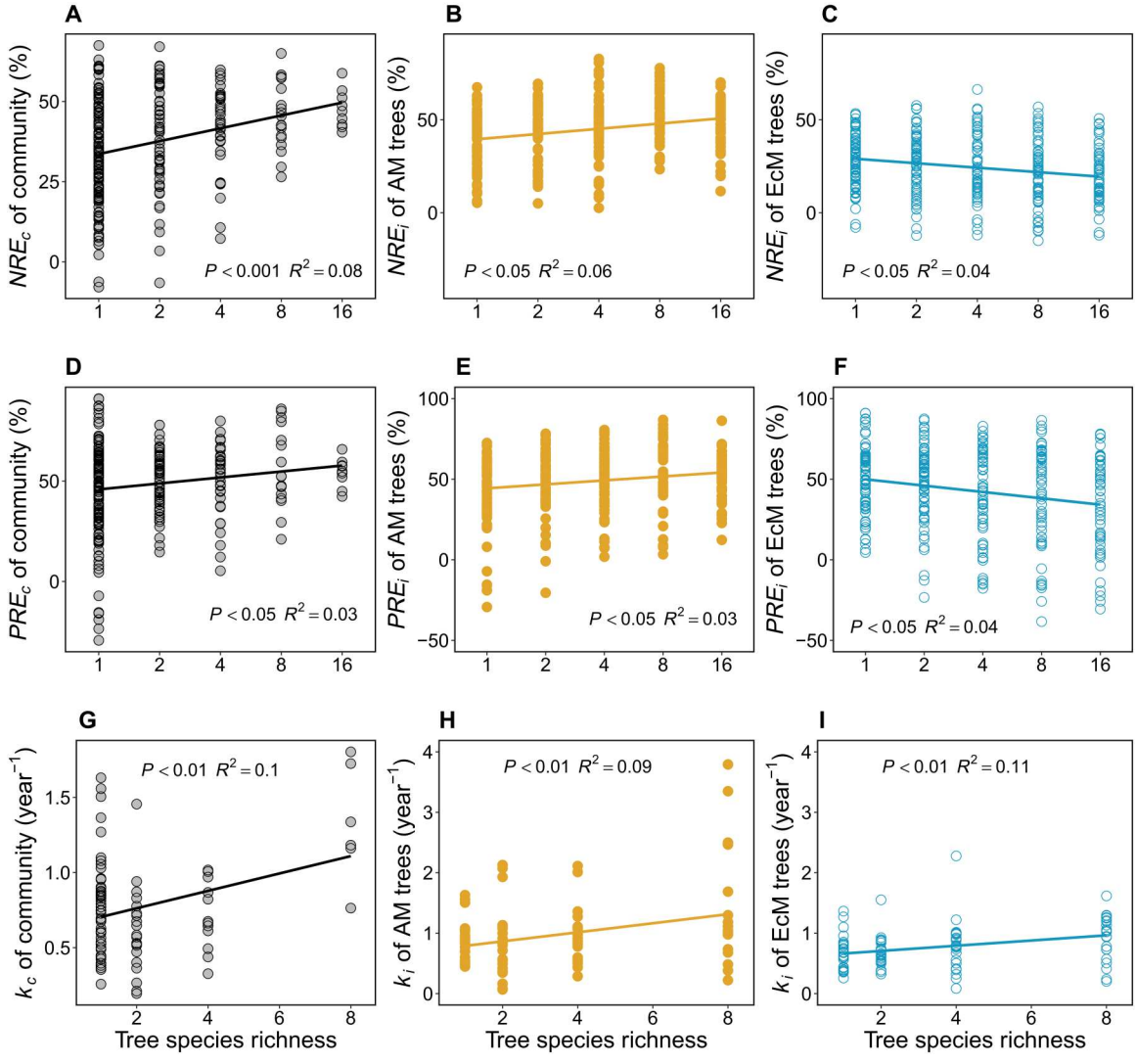

Fig. 2. Effects of tree species richness on *NRE*, *PRE*, and litter decomposition rate (*k*). *NRE* as a function of species tree richness at the community level (**A**) and at species level for AM trees (**B**) and EcM trees (**C**). *PRE* as a function of species tree richness at the community level (**D**) and at species level for AM trees (**E**) and EcM trees (**F**). *k* as a function of species tree richness at the community level (**G**) and at species level for AM trees (**H**) and EcM trees (**I**). Solid lines indicate significant regression lines. Levels of significance and R^2 for all lines are shown in plots.

symbiotrophs in EcM monoculture soils was much higher than that in AM monoculture soils (Fig. 4B); the relative abundances of saprotrophs in EcM monoculture soils were lower than those in AM monoculture soils (Fig. 4B).

Canonical correspondence analysis (CCA) further showed that soil fungal community composition varied with tree species richness (Fig. 4, C and D, and table S8). Tree species richness had a positive effect on AM fungal diversity and a negative effect on saprotrophic fungal diversity (Fig. 4, C and D, and fig. S12). Saprotrophic and pathogenic fungi were dominated in AM tree–dominated communities (Fig. 4, C and D). In addition, litter decomposition rate was positively correlated with saprotrophic fungal diversity and with AM fungal diversity (Fig. 4D and fig. S12).

Relationships between microbial composition, litter decomposition, and NPP

Litter decomposition rate of AM trees was negatively correlated with litter lignin concentration (fig. S13C). However, litter decomposition rate of EcM trees was positively correlated with litter N and P concentrations (fig. S13, D and E) but not with litter lignin concentration (fig. S13C).

NPP of AM-subcommunity was positively associated with total PLFAs, fungal diversity, and AM fungal diversity but was negatively associated with the relative abundance of Agaricomycetes; the opposite associations were observed for NPP of EcM subcommunity (Fig. 4D and fig. S14).

Table 1. Linear mixed-effect models for studying effects of tree species richness [log_2(SR)] and other factors on species-level NRE_i and PRE_i. The factors shown in the table are fixed factors (type I sum of squares). ddf, denominator degrees of freedom. F and *P* represent F-ratios and *P* values of the significance tests, respectively. $P < 0.05$ are in bold. MT, mycorrhizal type of plant species; SR, species richness.

	NRE_i			PRE_i		
Factor	**ddf**	**F**	***P***	**ddf**	**F**	***P***
MT	13.82	20.37	**<0.001**	12.25	0.26	0.622
Year	29.37	3.50	0.071	43.62	8.62	**<0.01**
Log_2(SR)	17.72	0.05	0.818	52.12	1.02	0.318
MT × year	424.95	16.99	**<0.001**	23.08	0.01	0.914
MT × log_2(SR)	107.67	18.57	**<0.001**	351.15	17.92	**<0.001**
Log_2(SR) × year	34.32	0.00	0.947	51.79	0.00	0.966

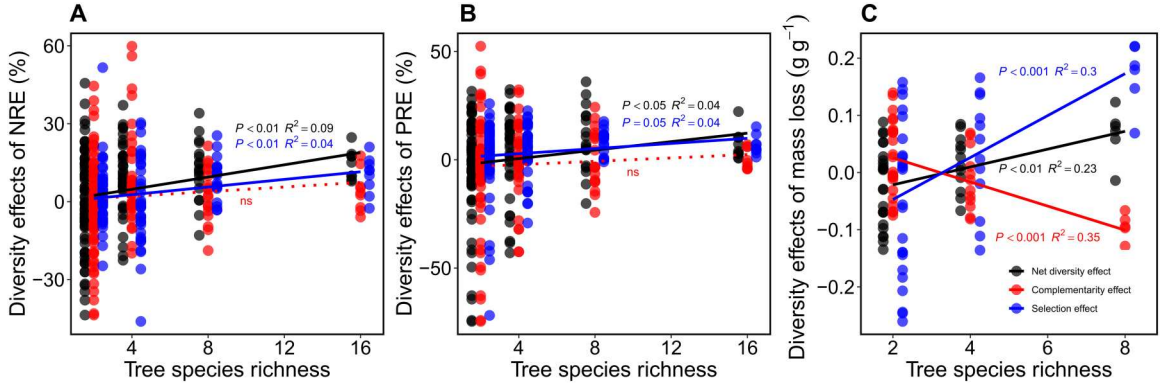

Fig. 3. Net diversity, complementarity, and selection effects of tree species richness on nutrient resorption efficiency and litter mass loss. NREc (**A**), PREc (**B**), and litter mass loss (**C**). Solid lines and dotted lines indicate significant and non-significant relationships, respectively. Levels of significance and R2 for all lines are shown in plots.

Effects of nutrient strategies on NPP of AM and EcM subcommunities

A structural equation model (SEM) showed that tree species richness directly and positively affected NPP of AM subcommunities. The increasing nutrient resorption and litter decomposition through decreasing litter lignin concentration indirectly mediated the significantly positive associations between tree species richness and NPP of AM subcommunities (Fig. 5A).

In contrast with AM subcommunities, tree species richness directly negatively affected NPP of EcM subcommunities. The decreasing nutrient resorption and changes in microbial community, mainly driven by increasing in fungal diversity and decreasing in Agaricomycetes abundance (fig. S15), indirectly mediated the negative associations between tree species richness and NPP of EcM subcommunities. Tree species richness exerted a positive effect on NPP of EcM subcommunities through increasing litter decomposition rate (Fig. 5B).

DISCUSSION

Results from our long-term field experiment showed that as tree species richness increased, EcM tree biomass rapidly decreased, but AM tree biomass progressively increased, leading to the dominance (>90%) of AM trees in the highest diversity treatment (Fig. 1). This finding is consistent with high dominance of AM trees in diverse tropical and subtropical forests (*25*, *30*) where EcM trees often account for less than 10% of tree stems (*10*, *12*). The high species diversity of AM trees is often attributed to conspecific negative density dependence (CNDD) driven by host-specific pests and pathogens (*10*, *31*). However, CNDD is unable to explain the dominance of AM over EcM trees because EcM fungi often provide better protection against pathogens and have high mycorrhizal abundance (*10*, *12*). Alternative mechanisms may underlie the dominance of AM trees over their EcM counterparts in high-diverse subtropical and tropical forests.

The first and foremost role of mycorrhizal symbioses is to facilitate plant nutrient acquisition (*32*, *33*), which may be key to maintaining high productivity in highly diverse ecosystems (*3*, *33*). AM and EcM fungi have distinct nutrient acquisition strategies: While AM fungi are highly efficient in uptake of inorganic nutrients, EcM fungi evolved a unique capacity to acquire nutrients directly from organic matter (*25*, *34*). This difference may grant competitive advantages of AM trees over EcM trees in mixed forests through several mechanisms.

First, competition for nutrients generally intensifies as the diversity increases, and AM fungi offer a competitive edge for their hosts

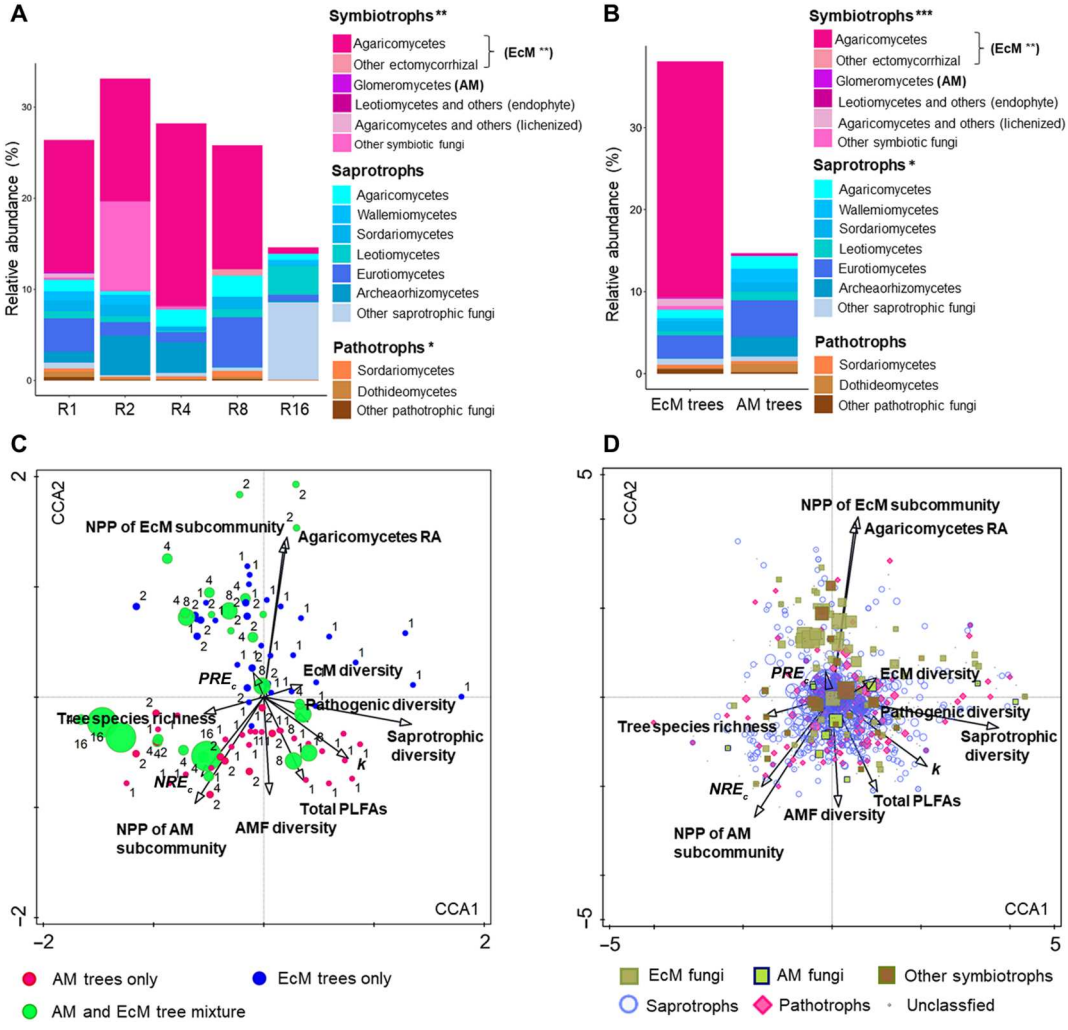

Fig. 4. Changes in three fungi trophic modes including symbiotroph, saprotroph, and pathotroph along tree species richness gradients. The relative abundance of soil fungi taxa under tree species richness levels (**A**) and in AM monoculture and EcM monoculture (**B**). Sample (**C**) and fungal species (**D**) plot of CCA of the three fungi tropic modes across 93 soil samples including 1106 fungal species. CCA axes 1 and 2 account for 17.0 and 12.2%, respectively. Arrows represent explanatory factors, and shape symbols with different colors represent soil samples or fungi species. Symbol size indicates tree species richness (C) and fungi species relative occurrence (D). RA represents relative abundance of Agaricomycetes. R1, R2, R4, R8, and R16 indicate 1, 2, 4, 8, and 16 tree species richness, respectively. *$P \leq 0.05$, **$P \leq 0.01$, and ***$P \leq 0.001$. PLFAs, phospholipid fatty acids.

over EcM fungi in nutrient acquisition. Soils in warm and humid subtropical and tropical regions are highly weathered and thus P limited as most P is bound with iron (Fe) and aluminum (Al) (*32*, *35*). Also, soils in these areas are less N limited because warm and humid climates favor litter decomposition and nutrient mineralization by saprotrophic microbes (*36*) and are conducive to biological N fixation (*37*). Although AM fungi have little saprophytic ability, they are uniquely efficient in obtaining less mobile nutrients such as P and Fe (*32*). For example, AM fungi can promote P-solubilizing bacteria, which release carboxylates and phosphatases to mobilize soil inorganic and organic P as well as micronutrients such as Zinc (Zn), Fe, and manganese (Mn) (*38*). Increased AM fungi diversity in highly diverse ecosystems could enhance nutrient acquisition such as decomposition process, thereby promoting productivity (Fig. 4). In contrast, EcM fungi are able to directly mine nutrients (mainly for N) trapped in organic matter (*39*) but have a low ability to acquire mineral nutrients in soil (*25*). Consequently, P limitation and fast microbial decomposition of litter in high-diverse subtropical and tropical forests favor AM trees over EcM ones (Fig. 2) (*40*).

Second, the positive feedback between plant traits and decomposition rate would benefit AM trees more than EcM trees in the highly diverse subtropical forests (*25*, *41*). Compared with EcM trees, AM trees produce high-quality litter with low concentrations of lignin and secondary metabolites (*30*). With the increase in diversity, lignin concentration of AM litter further decreased, leading to an increase in AM litter decomposition (Fig. 5). The increased litter decomposition promotes a more inorganic nutrient economy, which would benefit AM trees and their diversity more than EcM trees (*9*, *25*). A recent global-scale synthesis identified decomposition rate as the primary driver of the distribution of mycorrhizal symbioses in different climate zones (*40*). Our results provide

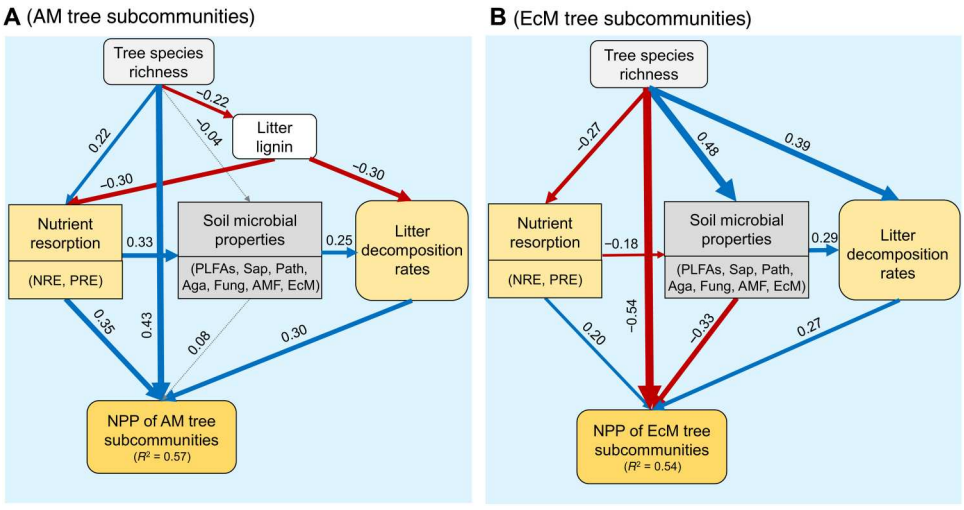

Fig. 5. Generalized multilevel path models indicating the direct and indirect pathways through which tree species richness, nutrient resorption, litter decomposition, litter trait, and soil community drive variations in NPP of AM and EcM tree subcommunities. (**A**) SEMs for AM tree subcommunities, (**B**) SEMs for EcM tree subcommunities. Both models were well supported by the data (A, $\chi^2 = 8.26$, $P = 0.08$, SRMR = 0.06; B, $\chi^2 = 0.52$, $P = 0.47$, SRMR = 0.01). Multiple-layer rectangles represent the first component from principal components analysis conducted for nutrient resorption and soil microbial properties. Nutrient resorption includes N resorption efficiency and P resorption efficiency. Soil microbial properties includes total PLFAs, the relative abundance of Saprotrophs (Sap), pathogen (Path), Agaricomycetes (Aga), fungal diversity (Fung), AMF diversity (AMF), and EcM fungi diversity (EcM). The arrow width is shown proportional to the standardized path coefficient and can be used as the relative importance of each factor. Blue arrows represent positive relationships, red arrows represent negative relationships, and dashed arrows represent nonsignificant relationships.

direct evidence illustrating how microbial decomposition rate is related to mycorrhizal types in (sub)tropical forests.

Another major but often overlooked mechanism affecting plant competition is the ability of competitive species to reuse nutrients via nutrient resorption. Nutrient resorption allows for the conservation of nutrients that may be otherwise returned to the soil via litterfall (*42*). Our results showed that compared with EcM trees, AM trees have higher nutrient resorption efficiency (Fig. 2 and fig. S5). The predicted negative trade-off between litter decomposition and nutrient resorption occurred in EcM trees but not in AM trees. This likely is because AM plant litter decomposition is more affected by litter lignin concentration than by litter N and P concentrations (Fig. 5 and fig. S13). Because leaf cell degradation is a prerequisite for nutrient resorption during leaf senescence (*43*, *44*), the decreased lignin concentration for AM trees not only increases litter decomposition but also weakens the lignin barriers and results in more "complete nutrient resorption" in high-diversity community (*45*). Consequently, high resorption further enhances nutrient reservoirs in AM trees, which allows fast growth and better competition against their EcM counterparts in a diverse community.

An unexpected finding was that EcM trees enhanced litter decomposition but not nutrient resorption efficiency with increasing tree species richness. One possible explanation is that, in humid and warm subtropical forests, the decomposition pathway is always more beneficial to plants than the resorption pathway, because resorption requires plants to synthesize enzymes to degrade and remobilize leaf nutrients (*45*). Therefore, as competition increased with tree richness, EcM trees tended to reduce C investment in nutrient resorption, resulting in a lower N and P resorption. A global meta-analysis also showed that, in contrast to boreal and temperate ecosystems, EcM plants resorb less N than AM plants in subtropical and tropical habitats (*46*).

In addition, we observed that EcM tree monoculture communities has a high abundance of symbiotic fungi but low pathogens, whereas AM tree monoculture communities were dominated by saprotrophic and pathogenic fungi (Fig. 4). As tree richness increased, shifts in microbial communities, particularly a decrease in the relative abundances of Agaricomycetes, most of which are EcM fungi, corresponded with a decrease in NPP of EcM subcommunity but have a relatively small impact on NPP of AM subcommunity (Fig. 5B). These results imply that AM trees were less dependent on their fungal partners than EcM trees for nutrient acquisition and that the increasing dominance of AM trees hampered the formation of ectomycorrhizal networks in the mixed forests (*15*, *47*). In addition, the SEM also revealed a direct and positive effect of tree species richness on NPP of AM subcommunities. Compared to EcM subcommunities with the same species diversity, AM subcommunities in this study had a higher phylogenic diversity (table S1). Thus, our results further confirmed the previous finding at this site that tree species richness effects were strongly associated with phylogenic diversity (*1*). Together, our findings suggest that more efficient nutrient-acquiring strategies (Fig. 6), rather than the microbial-mediated negative plant-soil feedback, drive the dominance of AM trees in high-diversity ecosystems. However, as a large proportion of operational taxonomic units (OTUs) were unclassified, better characterization of how mycorrhizal fungi mediate plant-soil feedback still relies on advances in sequencing technologies.

Our study provides direct evidence demonstrating that types of mycorrhizae critically mediate plant interactions and the biodiversity-productivity relationship in diverse forests. Our analyses further reveal that differences in mycorrhizal nutrient acquisition strategies, both nutrient acquisition from soil and nutrient resorption within the plant, contribute to the competitive edge of AM

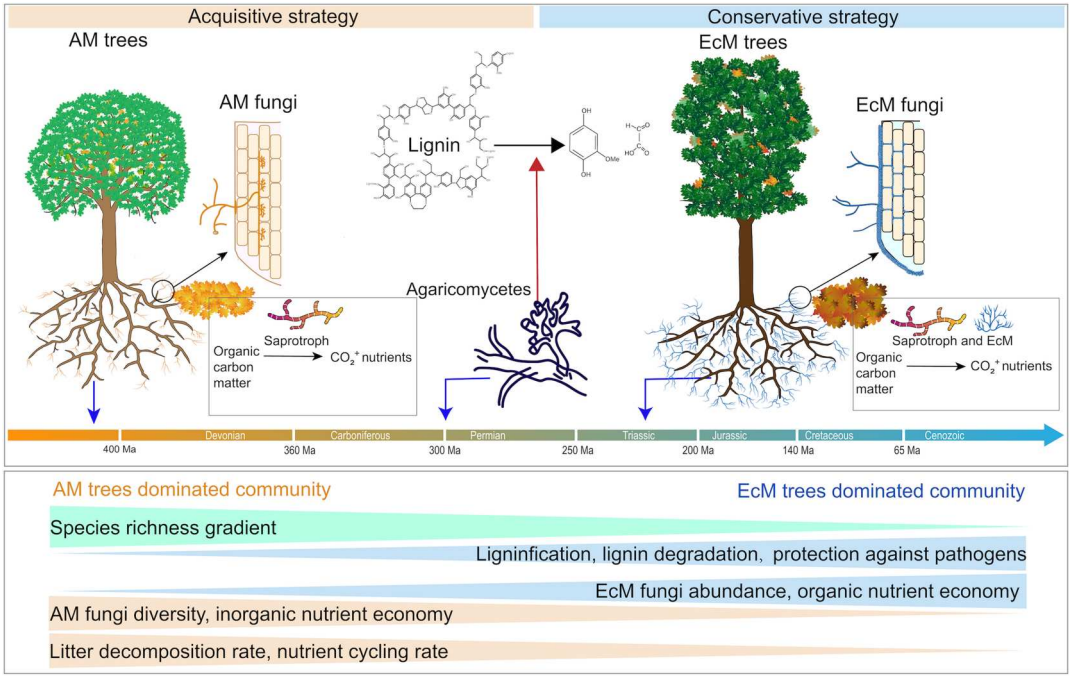

Fig. 6. Conceptual model of nutrient strategies of AM and EcM trees. AM trees with high leaf quality exhibit nutrient acquisition strategies and often dominate in high-diversity communities, whereas EcM trees with low leaf quality show nutrient conservative strategies and generally dominate in monocultures. The differences in nutrient acquiring strategy and diversity pattern between AM and EcM trees could be associated with the coevolution of trees and fungi. The onset of AM-tree symbiotic association occurred before the emergence of lignin-degrading Agaricomycetes, making AM tree nutrient acquisition dependent on saprophytic microbes to degrade lignin. Post-emergence of Agaricomycetes, EcM fungi evolved from humus and wood saprotrophic ancestors and retained part of their enzymatic ability. Thereby, compared to AM trees, EcM trees tend to scavenge N trapped in the organic matter directly. Ma, million years.

trees over EcM ones. These findings provide an alternative mechanism for explaining why and how AM trees usually dominate in high-diversity subtropical forests. Our results also have some implications for predicting the population dynamics and carbon balance of forest ecosystems in subtropical and tropical regions. Deforestation, urbanization, and agricultural practice have resulted in large-scale loss of EcM forests (*48*). Global changes such as N deposition and climate warming also favor AM trees over EcM trees (*40*, *49*). The spread of AM trees in the future would accelerate the nutrient cycle via promoting decomposition, which potentially increases vegetation C sequestration at the cost of soil C stability (*50*, *51*). Together, our findings suggest that mycorrhizal responses to climate change factors need to be considered in forest management, particularly in the selection of tree species for plantation for both timber production and climate change mitigation.

MATERIALS AND METHODS

Study site and experimental design

The study was conducted using the BEF-China experiment, established in a subtropical forest near Xingangshan, Jiangxi Province (117°54′E, 29°07′N) in Southeast China (*1*). From 1971 to 2000, the mean annual precipitation at the study site was 1821 mm, while the mean annual temperature was 16.7°C. The BEF-China experiment was implemented at two sites (sites A and B). The current study was conducted in site A, containing 271 randomly distributed plots (25.8 m by 25.8 m). On the basis of a pool of 40 broadleaved tree species occurring in the local forests, the plots were assigned to tree species richness gradients of 1, 2, 4, 8, and 16 species (*1*, *52*). Here, we selected plots with equal representation of eight AM and eight EcM tree species (tables S1 and S2). Each plot had 400 randomly planted saplings in a grid pattern (20 × 20 grid cells) at equal distances of 1.29 m in horizontal projection, in 2009. The number of individuals of all species was equally distributed in all plots, and the understory vegetation between the planted trees was weeded twice a year to remove emerging herbs and woody species that were not part of the planting design.

Plant sampling and chemical analysis

Green leaves and fresh leaf litter were sampled from 2016 to 2018. In August, we sampled three replicates per plot from 2016 to 2018. For each replicate, healthy and fully expanded green leaves of each species were randomly collected from trees near the litterfall traps (fig. S1). In November, fresh leaf litter was collected from the traps and separated by species. Samples from the same plot were pooled by species. The samples of green leaves and fresh leaf litter were oven-dried at 45°C for 48 hours. The N concentration of these samples was analyzed using a CN elemental analyzer (Vario EL III, Elementar Analysensysteme GmbH, Hanau, Germany).

The lignin concentration of litter was estimated using sequential extraction in an acid-detergent solution. First, litter samples were mixed with 72% sulfuric acid and then incubated in a 30°C water bath for 1 hour. The acid mixture was diluted to a 4% concentration and then autoclaved for 1 hour at 121°C. After removing the acid-soluble lignin and carbohydrates, the remaining solids were rinsed

with fresh deionized water and dried at 105°C until constant weight. The dry residue was determined as Klason lignin (*53*).

NPP and nutrient resorption efficiency

NPP was calculated by litterfall and the woody biomass changes between two consecutive years. The woody biomass was estimated with the basal area and height using allometric equations obtained from 154 harvested trees from eight common species near the experiment site (*1*). The N resorption efficiency of individual species (NRE_i) was calculated as the ratio of the difference in N concentrations between the green leaf and the fresh litter using the following formula

$$NRE_i = \left(1 - \frac{N_l}{N_g}\right) \times 100 \quad (1)$$

where N_g and N_l represent the N concentrations of green leaves and fresh litter, respectively.

NRE at the community level (NRE_c) was calculated using the following formula

$$NRE_c = \left(1 - \frac{\sum N_{li} L_c R_i}{\sum N_{gi} G_c R_i}\right) \times 100 \quad (2)$$

where N_{li} and N_{gi} represent N concentrations of fresh leaf litter and green leaves of species *i*, respectively. R_i represents the ratio of the litter biomass of species *i* to that of the community, estimated by using conversion factors obtained from the local allometric equations in Huang *et al.* (*1*) and Ma *et al.* (*54*), $L_c$represents the total leaf litter biomass of the community obtained from Huang *et al.* (*55*). $G_c$represents the total green leaf biomass of the community, which was equal to the annual leaf litter production (*56*). *PRE* was calculated in the same way as *NRE* using Eqs. 1 and 2.

The net biodiversity effect on *NRE* of a tree species mixture was calculated as the difference between the community-level NRE_c of the mixture and the mean *NRE* of the mixture species, when grown in monoculture (here referred to as expected NRE_c of the mixture). The net diversity effect was separated into CEs and selection effects using the additive partitioning method of Loreau and Hector (*57*).

Leaf litter-decomposition experiment

A leaf litter-decomposition experiment was conducted in plots with 1, 2, 4, 8, or 16 tree species (fig. S1). Because the mixed litter in plots of 16 tree species cannot be separated by species after decomposition, these plots were not included in decomposition rate analysis at the species level. The litter samples collected during autumn in 2016 were put in 10 cm–by–20 cm mesh bags with 1-mm mesh size. Each litter bag contained 5 g of oven-dried litter. There were 16 single-species, 8 two-species, 4 four-species, and 2 eight-species combinations. In the multispecies plots, the litter from each species was mixed in equal proportions. The litter bags were placed back on the forest floor in the same plots, from which the litter was sampled in November 2016. The litter bags were retrieved after 61, 122, and 180 days of in situ incubation.

For each litter bag, we first hand removed any dirt on litter surface and then divided the remaining litter by species, resulting in 576 total samples (16 species × 3 replicates × 4 levels of richness × 3 times sampling). The samples were oven-dried at 45°C to constant weight. Subsamples of dried litter were combusted at 500°C in a muffle furnace for 5 hours, to correct for ash content. Litter decomposition rate of individual species was calculated by the exponential decomposition model using the following formula

$$K_i = -ln(M_{it}/M_{io})/t \quad (3)$$

where M_{it} is the litter mass remaining of species *i* at time *t*, M_{io} is the initial litter mass of species *i*, and K_i is the litter decomposition rate of species *i* estimated by a first-order exponential decay model. The community level litter decomposition rate (K_c) was calculated using

$$K_c = -ln\left[\sum (M_{it} R_i / M_{io})\right]/t \quad (4)$$

where M_{it} and M_{io} were previously defined in Eq. 3 and R_i represents the ratio of the litter biomass of species *i* to that of the community. The net biodiversity effect, CE, and selection effects on litter mass loss were also calculated on the basis of the litter mass loss of monocultures and species mixtures (*57*, *58*).

Soil sampling and soil microbial community

In August 2017, soil samples were collected in triplicates near the place of litter bags at the depth of 0 to 10 cm. After removing stones and roots, soil samples were stored at the laboratory at −80°C for microbial analyses. The fungal DNA from 0.5 g of soil was extracted using the Soil DNA Isolation Kit (Omega Bio-tek, Norcross, GA, USA) following the manufacturer′s protocol. The quality and size of the extracted DNA were checked on agarose gels. For fungi, the internal transcribed spacer (ITS) regions were amplified via polymerase chain reaction (PCR) using the primers ITS1F and ITS2F (GeneAmp 9700, ABI, USA). As ITS region is highly variable for AM fungi, we used primer pair AMV4.5NF-AMDGR, which has high, genus-level resolution for AM fungi communities (*59*), to characterize AM fungi community composition. The PCR products were extracted from agarose gels and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA). The purified amplicons were sent to Majorbio Inc. (Shanghai, China) for analysis on the Illumina′s MiSeq platform (San Diego, CA. USA).

Raw reads were demultiplexed, quality-filtered, and analyzed using Quantitative Insights Into Microbial Ecology. OTUs were clustered with 97% similarity cutoff with UPARSE. The chimeric sequences were identified and removed using UCHIME. In total, 4,263,869 fungal effective sequences were acquired with the ITS1F/ITS2F primer sets, and 4,223,423 AM fungi effective sequences were acquired with the AMV4.5NF-AMDGR primer pair from the 93 soil samples in 31 plots. The taxonomy of each gene sequence was determined on the basis of the UNITE database (UNITE 7.0) for fungi and the Maarjam081 database for AM fungi using a confidence threshold of 70%. We used FUNGuild for assigning fungal sequencing data into three trophic groups, namely, symbiotroph, saprotroph, and pathotroph (*60*). The symbiotroph OTUs were classified into EcM fungi, AM fungi, endophytes, lichenized fungi, and other symbiotic fungi. The saprotroph and pathotroph OTUs were mainly classified into four phyla, namely, Basidiomycota, Ascomycota, Chytridomycota, and Zygomycota. Sequences that were assigned more than one trophic strategy in FUNGuild were excluded from our analysis. For each soil sample, the fungal richness and their relative abundance were calculated for each trophic group, and specialist and generalist sequences were identified within each trophic group. The Shannon-

Wiener index was used to evaluate the diversity of the fungal community of each sample.

We also measured PLFAs in the soil samples using a procedure described by Bååth and Anderson (*61*). Soil samples were extracted in a mixture of chloroform, methanol, and citrate buffer. The phospholipids were separated from the extracted mixture on a silicic acid column, then methylated, and detected with gas chromatography. Bacterial biomass was identified by the fatty acids: i-14:0, i-15:0, a-15:0, i-16:0, 16:1ω9, i-17:0, a-17:0, 17:0-cyclo, 18:1ω9, and 19:0-cyclo. The fatty acids 18:2ω6 were used to represent fungal biomass. The fungal-to-bacterial ratio was calculated as the relative abundance of these two groups.

Statistical analyses

We used LMMs to assess the effects of tree species richness and other variables on N resorption efficiency, considering tree species richness (log_2-transformed), year, mycorrhizal type, and their interactions as fixed effects and tree species identity, plot, and the interaction between plot and year (factor with three levels) as random effects. The litter decomposition rates for each individual species were also analyzed using a mixed-effect framework, considering log_2(tree species richness), mycorrhizal type, litter N concentration, litter lignin concentration, AM fungi diversity, soil saprophytic fungi richness, and interactions as the fixed effects and species identity and plot as random effects. The litter decomposition rate was squared-rooted transformed to improve the normality of model residuals. LMMs were fitted using the *lme4* package. In addition, we tested for phylogenetic signals in *NRE*, *PRE*, and litter decomposition rate of the 16 tree species using Blomberg's *K* and Pagel's λ (*62*). Phylogenetic generalized LMMs were further used to evaluate the response of *NRE*, *PRE*, and litter decomposition rate to tree species richness using the *phyr* package (*63*).

Tukey-Kramer tests were used to compare the mean relative abundances of fungal OTUs among tree species richness levels. Student's *t* tests were used to compare the mean relative abundances of fungal OTUs between AM monocultures and EcM monocultures. To extract the differences between fungal community compositions and evaluate the relationship between three fungi trophic communities (symbiotrophs, saprotrophs, and pathotrophs), nutrient acquiring strategies, and NPP, we also analyzed the fungal community data by ordinations with CCA with CANOCO 5. Variations in fungal community composition were visualized, and the statistical significance of the model was assessed by Monte Carlo permutation tests.

Principal components analyses (PCAs) were conducted with nutrient resorption (*NRE* and *PRE*) and soil microbial properties pooled. The first PCA axis explained 80 and 41% of the total variance for nutrient resorption and soil microbial properties, respectively (fig. S15). Thus, the scores of the first PCA axis were used as a proxy for nutrient resorption and microbial properties in correlation analyses and SEM.

SEM was used to investigate how tree diversity, nutrient resorption, litter chemistry, litter decomposition, and microbial properties influenced NPP of AM and EcM plants. The variables were log-transformed to satisfy normality requirements and linearize relationships between variables when necessary. The *lavaan* package in R software was used for our SEM analyses. We used chi square test and comparative fit index (CFI) (CFI > 0.95) to judge model prediction accuracy. Standardized independent variables and estimated coefficients were used to compare the relative influence of each variable. Statistical tests were defined as significant at $P < 0.05$. All statistical analyses in this study were done with the R statistical software package (version 4.1.2).

Supplementary Materials

This PDF file includes:

Texts S1 and S2
Figs. S1 to S15
Tables S1 to S8

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Acknowledgments: We thank BEF-China staff for measuring biomass data at the field site. We also thank Zhejiang Qianjiangyuan Forest Biodiversity National Observation and Research Station for permission to use the field site. **Funding:** This study was financially supported by the Strategic Priority Research Program of the Chinese Academy of Science(XDA23080301) and the National Natural Science Foundation of China (32125025, 32271625, 31988102, and 31700420). **Author contributions:** L.L. and M.D. conceived the study. M.D. collected and analyzed the data. M.D. and L.L. wrote the manuscript. S.H., L.J., Y.H., and B.S. commented on the details of the manuscript drafts. All authors helped improve the readability of the manuscript drafts. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. The data supporting the findings of this study are available at https://zenodo.org/record/7341024#.Y3tCwnZBy3A.

Submitted 13 June 2022
Accepted 20 December 2022
Published 18 January 2023
10.1126/sciadv.add4468