

Joint evolution of mutualistic interactions, pollination, seed dispersal mutualism, and mycorrhizal symbiosis in trees

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Summary

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Key words: arbuscular mycorrhizal (AM), biotic pollination, ectomycorrhizal (EcM), endozoochory, plant–soil feedback, tree diversity.

- Mycorrhizal symbiosis, seed dispersal, and pollination are recognized as the most prominent mutualistic interactions in terrestrial ecosystems. However, it remains unclear how these symbiotic relationships have interacted to contribute to current plant diversity.
- We analyzed evolutionary relationships among mycorrhizal type, seed dispersal mode, and pollination mode in two global databases of 699 (database I) and 10 475 (database II) tree species. Although database II had been estimated from phylogenetic patterns and therefore had lower certainty of the mycorrhizal type than database I, whose mycorrhizal type was determined by direct observation, database II allowed analysis of many more taxa from more regions than database I.
- We found evidence of joint evolution of all three features in both databases. This result is robust to the effects of both sampling bias and missing taxa. Most arbuscular mycorrhizal-associated trees had endozoochorous (biotic) seed dispersal and biotic pollination, with long dispersal distances, whereas most ectomycorrhizal-associated trees had anemochorous (abiotic) seed dispersal and wind (abiotic) pollination mode, with shorter dispersal distances.
- These results provide a novel scenario in mutualistic interactions, seed dispersal, pollination, and mycorrhizal symbiosis types, which have jointly evolved and shaped current tree diversity and forest ecosystem world-wide.

Introduction

Mutualistic interactions are critical in promoting diversification across various taxa and have played a significant role in shaping current biodiversity and ecosystem (Heckman *et al.*, 2001; Steidinger *et al.*, 2019; Brundrett & Tedersoo, 2020; Tedersoo *et al.*, 2020). Pollination, seed dispersal, and mycorrhizal symbiosis are recognized as the most dominant mutualistic interactions involving plants in terrestrial ecosystems and are essential constituents of current ecosystems. Mycorrhizal symbiosis is the oldest known biological interaction in plants: Plants have lived closely with mycorrhizal fungi for over 400 million years, and most tree species in the world rely on mycorrhizas (Steidinger *et al.*, 2019; Brundrett & Tedersoo, 2020). Trees have evolved several types of mycorrhizal symbioses, notably arbuscular mycorrhizal (AM), ectomycorrhizal (EcM), and ericoid. Fossils of the earliest land plants provide evidence that fungi morphologically similar to the extant Glomeromycotina (AM mycorrhizal) lived within their cells (Remy *et al.*, 1994; Heckman *et al.*, 2001). The association of Endogonales with liverworts and hornworts has recently been proposed to be among the earliest forms of mycorrhizal symbiosis, possibly as old as or older than Glomeromycotina (Hoysted *et al.*, 2018). Ectomycorrhizal-type trees evolved in the

Cretaceous era (Tedersoo *et al.*, 2020). Arbuscular mycorrhizal is widespread, and almost 80% of plants have an AM symbiosis. By contrast, EcM are less common (*c.* 2% of plants) and are more associated with trees (Tedersoo *et al.*, 2020). Mycorrhizal symbiosis is recognized as an important factor in growth and survival of trees and maintaining the diversity of tree species in forest ecosystems (Teste *et al.*, 2017; Tedersoo *et al.*, 2020). Mycorrhizal fungi provide their host plants with nutrients from the soil or aid in defense against insects and antagonistic microbes and enhance the survival rate, growth, flower production, and fitness of their host plants (Tedersoo *et al.*, 2020). Pollination and seed dispersal have sometimes been considered key characteristics that led to the evolutionary success of the angiosperms (Regal, 1977; Crepet, 1984; Pellmyr, 1992). Pollination modes include biotic and wind (Wang *et al.*, 2019). Biotic pollination depends on other organisms such as insects, bats, and birds, whereas wind pollination depends primarily on wind. Seed dispersal modes categorized by Heleno & Vargas (2015) include biotic (e.g. endozoochory), wind (anemochory), and gravity (unspecialized). Endozoochory depends on a wide taxonomic variety of organisms, such as mammals, birds, and insects. Although there are several studies of the relationships between mycorrhizal symbiosis and pollination, most studies are limited to experimental

approaches focused on ecological effects in a few species (Wolfe *et al.*, 2005; Wang *et al.*, 2019), and their evolutionary relations have not been elucidated.

The pollination, seed dispersal, and mycorrhizal symbiosis may have jointly evolved, because they each interact in ways that are mediated by the spatial structure of tree populations. For example, trees associated with different mycorrhizal types should favor different seed dispersal and pollination modes, because different mycorrhizal types promote different tree population densities in each species. Several studies reported low population densities in AM-type trees and high densities in EcM-type trees world-wide (Bennett *et al.*, 2017; Delavaux *et al.*, 2023; Kalyuzhny *et al.*, 2023) and suggested that the difference is due to differences in within-species plant–soil feedbacks (PSFs) between AM- and EcM-type trees (Bennett *et al.*, 2017; Tedersoo *et al.*, 2020). In EcM-associated trees, PSFs are positive within species: Growth and survival rate are increased in soil in which conspecifics grow (Bennett *et al.*, 2017), because association with EcMs often protects the seedlings of their host plant from host-specific pathogens better than in an AM association (Tedersoo *et al.*, 2020). Conversely, in AM-type trees, PSFs are negative within species: Growth and survival rate are reduced in soil in which conspecifics grow (Bennett *et al.*, 2017). These contrasting effects may promote low and high population densities in AM- and EcM-type trees, respectively (Bennett *et al.*, 2017).

Biotic (animal) pollen and seed dispersal may permit greater dispersal distances than wind or unspecialized (abiotic) dispersal (Pellmyr, 1992; Mustajärvi *et al.*, 2001; Seidler & Plotkin, 2006; Hesse & Pannell, 2011). Thus, negative PSFs, which promote low population density in trees, may favor long-range biotic seed dispersal in AM-associated trees, and positive PSFs in EcM trees, which may favor shorter range wind or unspecialized seed dispersal more than biotic seed dispersal. Trees at high population densities do not require animal pollination because there are enough individuals to make wind effective. AM- and EcM-associated trees are expected to favor biotic pollination, enabling dispersal over long distances (Pellmyr, 1992), and wind pollination, effective over short distances (Mustajärvi *et al.*, 2001; Hesse & Pannell, 2011), respectively. If our hypothesis is supported by evolutionary patterns, we might find evolutionary correlations among them: AM-associated trees may have endozoochorous (biotic) seed dispersal and biotic pollination, whereas EcM-associated trees may have anemochorous (abiotic) seed dispersal and wind (abiotic) pollination mode.

First, we compared seed and pollen dispersal distances in each mode to examine the general differences in dispersal distance among dispersal modes. Next, we constructed and investigated the evolutionary relationships among mycorrhizal type (AM, EcM, and both AM + EcM), seed dispersal (by animals: endozoochorous; by wind: anemochorous; and unspecialized), and pollination mode (biotic and wind) in 699 tree species (database I) whose mycorrhizal type is recorded from direct observation of trees in Asia, the Americas, Africa, Europe, and Oceania, in tropical, subtropical, and temperate regions (Harley & Harley, 1987, 1990; Wang & Qiu, 2006; Akhmetzhanova *et al.*, 2012; Hempel *et al.*, 2013; Soudzilovskaia *et al.*, 2020) (Supporting Information

Fig. S1a,c), based on log-linear analysis and Bayesian-trait analysis. To get more robust evidence, we investigated the evolutionary relationships among mycorrhizal type, seed dispersal, and pollination mode in 10 475 tree species from Eurasia (2616 species from 499 genera in 165 families), North America (1113 species from 377 genera in 142 families), South America (4661 species from 566 genera in 168 families), Africa (1513 species from 448 genera in 128 families), and Oceania (1275 species from 353 genera in 137 families), whose mycorrhizal type (AM or EcM) has been predicted (Steidinger *et al.*, 2019) (database II) (Fig. S1b,d). Although database II had lower certainty of mycorrhizal type than database I, being estimated from phylogenetic patterns, it allows analysis of many more taxa from more regions than database I. Based on these results, we discuss the potential for joint evolution among mycorrhizal symbiosis, seed dispersal, and pollination mode, and explore the underlying evolutionary processes.

Materials and Methods

Phylogenetic relations among mycorrhizal type, pollination, and seed dispersal mode

We collected information on mycorrhizal type, seed dispersal mode, and pollination mode of trees defined by Beech *et al.* (2017) from multiple databases and constructed databases I and II for this study (Dataset S1). Database I was based on direct observation of mycorrhizal types. Database II was based on predictions of the mycorrhizal type from phylogenetic patterns.

All trees (699 plant species from 338 genera in 95 families) in database I were assigned to one of three mycorrhizal types: AM (475 species from 290 genera in 89 families: 68%), AM + EcM (62 species from 35 genera in 20 families: 8.9%), or EcM (162 species from 53 genera in 18 families: 23%). Association with AM fungi was widespread across the phylogenetic tree, being present in 96.8% of all families and 90.5% of genera (Figs 1, S2). Both angiosperm and gymnosperm clades were present. Tree species of all three mycorrhizal types were present in both clades. Similarly, seed dispersal modes (endozoochorous, 328 species from 182 genera in 76 families; anemochorous, 213 species from 78 genera in 30 families; and unspecialized, 158 species from 88 genera in 23 families; Figs 1, S2) and pollination modes (wind, 217 species from 65 genera in 24 families) were scattered across the phylogenetic tree. Biotic pollination modes (482 species from 276 genera in 79 families) were found in only angiosperms. In this database, species for which all three data were not available were excluded.

Database II (Steidinger *et al.*, 2019) included 10 475 plant species from 1340 genera in 170 families, assigned to either AM (9447 species from 1266 genera in 159 families) or EcM (1028 species from 74 genera in 17 families). Association with AM fungi was widespread across the phylogenetic tree, being present in 90.19% of families and 94.5% of genera. Seed dispersal modes (endozoochory, 8342 species from 988 genera in 149 families; anemochory, 1070 species from 186 genera in 46 families; and unspecialized, 1063 species from 175 genera in 49 families;

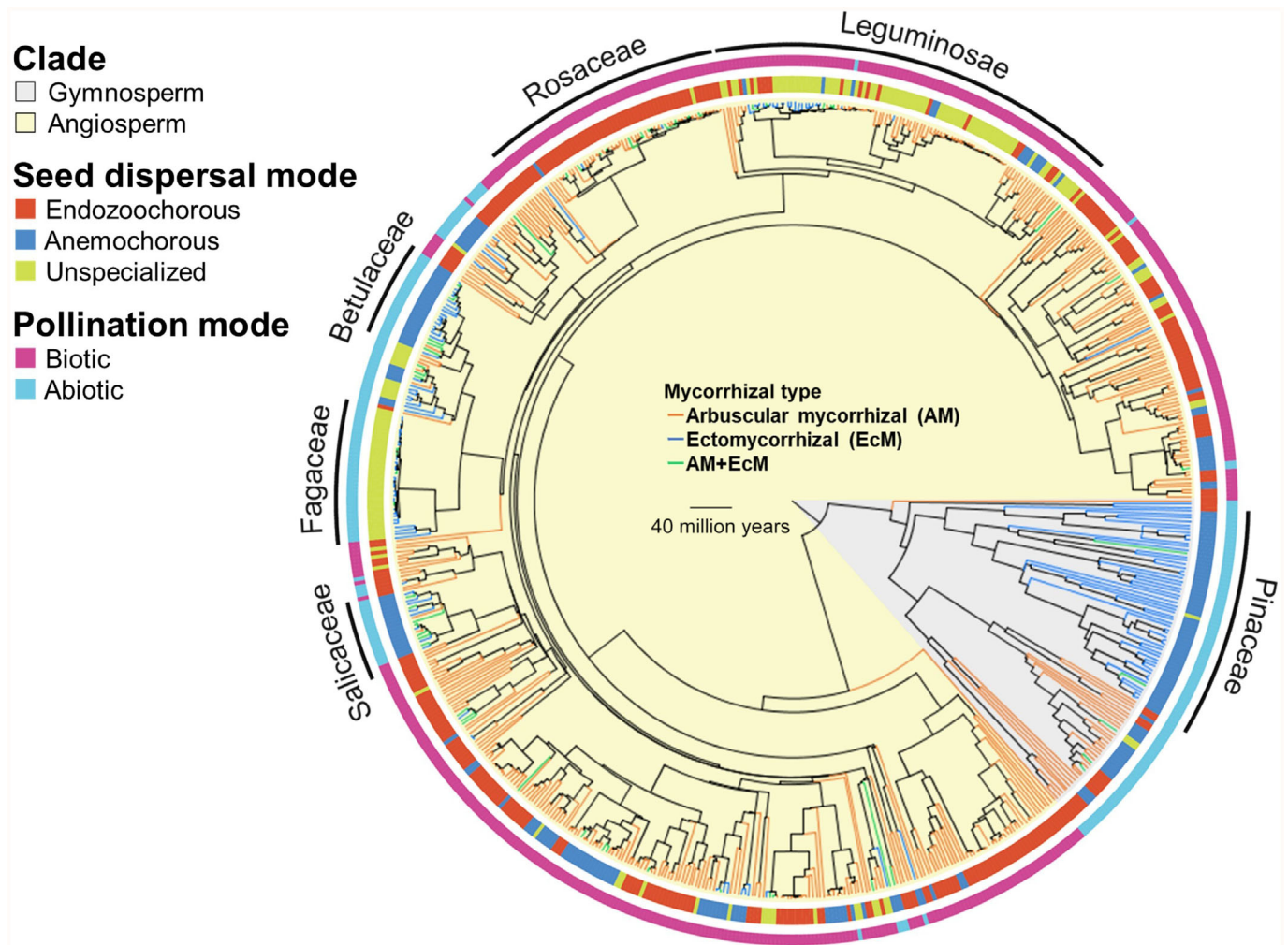


Fig. 1 Time-calibrated phylogeny of the 699 tree species (database I) used in this study provided by Scenario 3 of S.PhyloMaker. Branch color denotes mycorrhizal type (orange, AM; blue, EcM; green, AM + EcM). Colors of inner and outer labels ringing the tree indicate seed dispersal mode (red, endozoochorous; blue, anemochorous; yellow, unspecialized) and pollination mode (pink, biotic; blue, abiotic). The bar represents 40 million years.

Fig. S3) and pollination modes (wind, 1086 species from 107 genera in 29 families; biotic, 9389 species from 1233 genera in 157 families only in angiosperms) were scattered across the phylogenetic tree. The details of data collection are described below under ‘Mycorrhizal types’ and ‘Primary seed dispersal and pollination modes’ in the Materials and Methods section.

Mycorrhizal types Five main sources were used to compile information on tree mycorrhizal type (AM, EcM, or AM + EcM): (1) Mycoflor, a database that lists the mycorrhizal types of tree species (Hempel *et al.*, 2013); (2) an updated checklist of mycorrhizas of land plants (Wang & Qiu, 2006); (3) a checklist of mycorrhizas of the flora of Britain (Harley & Harley, 1987, 1990); (4) a database documenting mycorrhizal associations in 3000 vascular plant species from the former Soviet Union (Akhmetzhanova *et al.*, 2012); and (5) a dataset from the Global Biodiversity Information Facility (<https://www.gbif.org>) (Soudzilovskaia *et al.*, 2020). Other sources of information on

mycorrhizal type are included in the [Supporting Information](#). To minimize errors, these data were individually checked in multiple databases and their cited references. This became database I.

Database II (Steidinger *et al.*, 2019) lists the estimated mycorrhizal types of 28 000 tree species. It is the largest such database currently available. We selected tree species estimated as having either AM or EcM mycorrhizal types for our analysis.

Primary seed dispersal and pollination modes Primary seed dispersal and pollination modes were collected at the species level in database I and at the family level in database II. Data on seed features were collected from the list compiled by Heleno & Vargas (2015), the Plants of the World Online (POWO; <http://www.plantsoftheworldonline.org/>), and the Global Biodiversity Information Facility (Edwards *et al.*, 2000) (Supporting data list). The list compiled by Heleno & Vargas (2015) includes the long-distance dispersal characteristics of 10 792 species from 142 families in the Flora Europaea (Tutin *et al.*, 1980). The POWO

is a Web portal that makes available scientific data collected at the Royal Botanical Gardens, Kew, including the names of over a million plants from around the globe, plus images and detailed descriptions of many. Seeds with characteristics that promote wind dispersal, such as wings or a pappus (e.g. achene, follicle, and samara), were classified as anemochorous; seeds with tissues that attract animals, such as fleshy or nutritious tissues such as berry and drupe, were classified as endozoochorous (Vargas *et al.*, 2012). Other types such as capsule, pod, pyxis, and silique were classified as unspecialized. Unspecialized seeds may use various types of dispersal such as synzoochory, ectozoochory, and hydrochory. However, the distance of secondary seed dispersal, including by synzoochory or ectozoochory, is similar to that by unspecialized or wind (Table S1). Although some tree species depend on water streams, long dispersal depends on ocean currents (Nathan *et al.*, 2008). Therefore, the simplification of the seed dispersal mode is considered appropriate in terms of dispersal distance. Epizoochorous seeds were not included in our database.

The pollination mode was classified as either biotic or wind (Wang *et al.*, 2019), and our classification scheme did not include other categories, such as self-pollination. In angiosperms, flowers with typically developed petals (i.e. flowers with a perianth) were classified as having a biotic pollination mode. Flowers without a perianth were classified as wind-pollinated (abiotic), which mostly often used indicator for prediction of pollination mode (e.g. Wang *et al.*, 2019; Stephens *et al.*, 2023). All gymnosperms were classified as wind, because they lack petals and sepals. Information on the classification of pollination modes was collected from the above databases (Dataset S1).

Phylogenetic tree Plant List 1.1 was used to standardize species names, and membership in higher taxonomic groups was standardized against Angiosperm Phylogeny Group IV (2016). Database I contains information on the mycorrhizal types, seed dispersal, and pollination modes of 699 plant species from 338 genera in 95 families. The most represented families in our study were the Leguminosae (14.6%), Rosaceae (8.6%), Pinaceae (8.0%), Fagaceae (5.0%), and Betulaceae (3.3%). Database I contains families, which hold 81.0% of tree species around the world (Beech *et al.*, 2017). Moreover, the proportions of tree species in large families (> 100 tree species) did not differ between our database I and a world database of tree species (Beech *et al.*, 2017) (world, 93.5%; database I, 86.8%; $\chi^2 = 1.74$, $P = 0.19$).

Database II contains information on the mycorrhizal types, seed dispersal, and pollination modes of 10 475 plant species from 1340 genera in 170 families. The most represented families in our study were the Myrtaceae (6.8%), Lauraceae (6.6%), Rubiaceae (5.5%), Annonaceae (3.7%), and Sapindaceae (3.5%). Database II hold 82.5% of tree families around the world (Beech *et al.*, 2017). Between the two databases, the mycorrhizal types, pollination modes, and seed dispersal modes roughly matched within each plant family. Therefore, our databases reflect the trends of traits of trees around the world.

We used the PHYTOPHYLO tree software (Qian & Jin, 2016) to construct a phylogenetic tree based on the phylogeny generated

by Zanne *et al.* (2014) and updated by Qian & Jin (2016). Then, we reconstructed this tree by using the 'S.PhyloMaker' function implemented in R. The final phylogenetic tree for database I had 699 tip labels, and 671 internal nodes in Scenario 1, which added genera or species as basal polytomies within their families or genera; the number was 672 in Scenario 3 (Figs 1, S2). The accuracy of these scenarios has been verified in Qian & Jin (2016). The final phylogenetic tree for database II had 10 475 tip labels, and 3484 internal nodes in Scenario 1 and 3598 in Scenario 3, the accuracy of which has been verified (Fig. S3). All phylogenetic trees include only tree species.

Data collection of seed and pollen dispersal distances

We searched the Web of Science (<http://apps.webofknowledge.com>) for articles in English and Google Scholar (<https://scholar.google.com/>) for papers in English and Japanese that included 'tree', 'woody plant', 'seed dispersal distance', or 'pollination distance' in the title, abstract, or keywords. All peer-reviewed papers published between 1970 and 2020 that investigated maximum, mean, and/or minimum value of seed dispersal distance or pollination distance were selected and examined. We inspected their references and added studies not found in the initial search. Dispersal modes were divided based on information in each article. The details of the methods are provided in the [Supporting Information](#). In the final constructed database, the taxa that were common to both databases were 87 genera 71 species for database I, and 135 genera 187 species for database II in seed dispersal, and 44 genera 29 species for database I and 56 genera 49 species for database II in pollen dispersal.

Statistical analyses

Phylogenetic relations among mycorrhizal type, pollination mode, and seed dispersal mode We used two statistical analyses, log-linear analysis and the Markov chain Monte Carlo (MCMC) method, to examine the phylogenetic relations among mycorrhizal type, pollination mode, and seed dispersal mode. For these analysis, we used both Scenarios 1 and 3 of phylogenetic trees. Log-linear analysis tests the correlations among three or more categorical data. The reversible-jump (rj) MCMC method accounts for uncertainty arising from phylogenetic and posterior distribution errors and provides a statistical significance test of the null hypothesis that traits are associated randomly with phylogeny tips.

Log-linear analysis Log-linear analysis with maximum likelihood chi-squared and *post hoc* Freeman–Tukey deviation tests, with Bonferroni's correction, was used to test for univariate relationships between mycorrhizal type, seed dispersal, and pollination modes (Legendre & Legendre, 1998).

In all analyses, a phylogenetic species richness (PSR) index was used to correct for phylogenetic relatedness (Helmus *et al.*, 2007). To calculate PSR, the number of species in a sample is multiplied by the phylogenetic species variability, a term that describes how the variance of a trait is decreased by the

phylogenetic relatedness of the species being studied (Helmus *et al.*, 2007). Phylogenetic species richness thus represents the species richness of a sample after species relatedness has been discounted, making it more appropriate than uncorrected species richness for use in the contingency table. Phylogenetic species richness values decrease as species relatedness increases, approaching zero (Helmus *et al.*, 2007).

First, mycorrhizal type (AM, AM + EcM, and EcM) was tested against the proportion of seed dispersal mode (anemochorous, endozoochorous, and unspecialized) or pollination mode (biotic and wind), respectively. Seed dispersal mode was also tested against the proportion of pollination mode. For each pair of mycorrhizal type and/or dispersal mode, PSR was calculated in the R package PICANTE (Kembel *et al.*, 2010); these values were used in the contingency tables as described (Sokal & Rohlf, 1995; Pyšek *et al.*, 2011).

Contingency tables were used to check for differences between categories by the use of log-linear models with maximum likelihood chi-squared analysis. *Post hoc* Freeman–Tukey deviation tests (Sokal & Rohlf, 1995) with Bonferroni's correction were used for two-way or multiway contingency tables. In the Freeman–Tukey test, the observed and expected counts were used to calculate an approximately normalized estimate of how far each observed frequency deviates from the null hypothesis (Freeman–Tukey deviate: $\sqrt{(O)} + \sqrt{(O + 1)} - \sqrt{(4E + 1)}$). We also used the approach described by Sokal & Rohlf (1995) to calculate a critical value for the Freeman–Tukey deviates ($\sqrt{(v \times (1, \infty)^2)} / (\text{no. cells})$).

Markov chain Monte Carlo analysis by BayesTraits To test for correlated character evolution as evidence of adaptive or functional relationships among mycorrhizal types, seed dispersal, and pollination modes, we used MCMC approaches implemented in BayesTraits. In this analysis, we used only database I, because of the limitations of our computing power computers. In particular, we tested the hypothesis that an evolutionary change in mycorrhizal symbiosis (AM, ECM, and AM + ECM) causes an evolutionary change in seed dispersal or pollination modes, or vice versa. We also tested the hypothesis that an evolutionary change in pollination mode causes an evolutionary change in seed dispersal mode or mycorrhizal type, or vice versa, among angiosperms, because gymnosperms did not develop flower petals. BayesTraits compares an independent model (i.e. the evolution of one trait does not depend on the other trait) and a dependent model (i.e. the evolutionary transitions of each trait depend on the state of the other trait, suggesting correlated evolution), of discrete trait evolution for a pair of binary traits and a given phylogenetic tree. To binarize the data, we combined the categories of mycorrhizal symbiosis as AM and ECM (ECM and AM + ECM), or AM (AM and AM + ECM) and ECM; and the categories of seed dispersal modes as biotic (endozoochorous) and abiotic (anemochorous and unspecialized).

Pagel & Meade's (2006) Bayesian approach for testing correlated evolution of pairs of binary traits in phylogenetic trees was implemented via the Discrete module in BAYES TRAITs v. 3.0.5 software (Pagel *et al.*, 2004). This calculates the likelihoods of

two models applied to the data: one that allows the traits to evolve independently and the other that assumes correlated evolution between the two traits. It also uses the rj-MCMC procedure, which samples the posterior probability distributions of the parameter values of the model of trait evolution within a sample of phylogenetic trees that estimates the posterior probability of phylogenies (Pagel, 1994, 1997, 1999; Pagel & Meade, 2006), thus accounting for uncertainty in both the model of trait evolution and the phylogeny.

We tested for correlated evolution between a pair of discrete binary traits by comparing fits (logarithm of the marginal likelihood values) of the discrete trait data to independent and dependent models of evolution. The first model assumes that two traits, such as mycorrhizal type (AM vs EcM) and seed dispersal mode (biotic vs abiotic), evolve independently on the tree, hence creating two rate coefficients per trait (a four-rate model). The second model allows traits to evolve in a correlated fashion, such that the rate of change in one trait depends on the background state of the other; this creates four states, one for each combination of the two binary traits, and thus eight-rate coefficients (an eight-rate model). To determine whether a character (e.g. mycorrhizal type) shows correlated evolution with another trait (e.g. seed dispersal mode), we compared the logarithm of the marginal likelihood values for these two models (determined with rj-MCMC analyses), using the Bayes factor (BF) test statistic: 2 (log marginal likelihood (dependent model) – log marginal likelihood (independent model)). The Bayes factor allows us to infer the strength of the evidence for or against correlated evolution: BF > 2 is interpreted as positive evidence that the dependent model is favored, BF > 5 as strong evidence, and BF > 10 as very strong evidence, whereas BF < 0 is evidence in favor of the independent model (Pagel & Meade, 2006).

All results were integrated over a sample of two phylogenetic trees, Scenarios 1 and 3 of S.PhyloMaker, particularly those seeking patterns of phylogenetic properties, chosen randomly (Alejandro *et al.*, 2008). To explore the influence of the priors on estimated evolutionary transition rates, we used both uniform priors drawn from a distribution of 0–100 and a hyper-prior approach using a uniform distribution of 0–100 to seed an exponential prior. The results for both sets of priors were similar, so we report only values derived from the uniform approach. Final BayesTraits analyses were conducted with the following settings: 10 100 000 generations, with 100 000 generations as burn-in and sampling every 5000th generation. Three identical runs for each analysis allowed us to assess the stability of the logarithm of the harmonic mean of the likelihood value. Marginal likelihoods were calculated using stepping-stone sampling with 100 samples and 1000 iterations per sample. The stepping-stone sampler estimates the marginal likelihood by placing a number of 'stones', which link the posterior with the prior; the stones are successively 'heated', forcing the chain from the posterior toward the prior.

Having discerned which tree features evolved in a correlated fashion with mycorrhizal types, seed dispersal modes, and pollination modes, we examined these associations further and determined the evolutionary pathways and the order of transitions underlying the correlated evolution. To assess the probability that

the values of each of the eight transition rate parameters of the dependent model are non-zero, we used the posterior probability distribution of the proportion of evolutionary models visited by the rj-MCMC chain in which the evolutionary model for each transition rate was assigned a value of 0 (*Z*-score) (Alejandro *et al.*, 2008). Transitions that have a high probability of being non-zero have a *Z*-score < 0.05.

To evaluate the effects of sampling bias on our results, we repeated the analysis using subsampled datasets. Using database I, we assessed the potential sampling bias in specific plant families by randomly resampling one species from each family 10 times (sub-dataset I). Using database II, we replicated the differences in species counts by plant family from the global tree list (60 065 species; Beech *et al.*, 2017) at the same proportions as in the population in 10 subsamples (sub-dataset II). These sub-datasets allowed us to investigate the effects of varying sample sizes among plant families.

Next, we assessed the effect of a large number of missing taxa. First, we randomly generated 10 subsamples (sub-dataset III) including 70 plant families from database I. Then, we randomly generated 10 subsamples (sub-dataset IV) with the same proportion of species as in our dataset from the global database of tree species in database II (Beech *et al.*, 2017). The 10 475 species in database II represent 17.4% of described tree species (Beech *et al.*, 2017). As above, we ran BayesTraits analysis for each subsample.

Phylogenetic comparison of seed and pollen dispersal distances All data were \log_{10} -transformed to a normal distribution. Maximum and mean dispersal distance of seed or pollen among the dispersal modes were compared using a phylogenetic generalized least squares analysis (pGLS) (Paradis, 2011) by the *gl* function in the nlme package to account for evolutionary history of the species (Felsenstein, 1985). To test the effects of outliers, we conducted the pGLS that used maximum and minimum values in each species, which had multiple data in addition to average values for each analysis in maximum and mean seed or pollen dispersal distance, because the pGLS could not use multiple data in each species (see the Supporting Information for details). All analyses were performed in the R v. 4.1.0 software (R Development Core Team, 2021).

Results

Dispersal distance and the pollination and seed dispersal modes

Our comparative analysis of seed dispersal distances revealed that the mean dispersal distances of endozoochorous seeds was longer than those of anemochorous seeds and unspecialized seeds (Fig. 2b; Table S2). However, the maximum distance did not differ significantly between endozoochorous and anemochorous seeds (Fig. 2a; Table S2). The secondary seed dispersal distances were shorter than the endozoochorous and anemochorous dispersal distances, and did not differ from the dispersal distances of unspecialized seeds (Table S1). The maximum pollen dispersal

distance by biotic pollination was longer than those of abiotic pollination (Fig. 2c) but did not differ mean pollen dispersal (Fig. 2d; Table S3). These results were robust in all analyses including outlier (Tables S2, S3).

Phylogenetic relations among mycorrhizal type, pollination, and seed dispersal mode

The phylogenetically corrected log-linear analysis revealed that mycorrhizal type and seed dispersal mode were significantly linked in both databases (Tables 1, S4). BayesTraits analysis also provided strong evidence for correlated evolution between mycorrhizal type and seed dispersal mode (Tables S5, S6). More specifically, of the AM-associated trees, a greater proportion produced endozoochorous seeds and a lower proportion produced anemochorous seeds than expected by the phylogenetically corrected log-linear model (Fig. 3a,d; Table S4). By contrast, more EcM-associated trees produced anemochorous seeds and a lower proportion produced endozoochorous seeds compared with number of species than expected by the phylogenetically corrected log-linear model (Fig. 3a,d; Table S4).

Pollination mode was also associated with mycorrhizal type (Fig. 3b,e; Tables 1, S7) and seed dispersal mode (Fig. 3c,f; Tables 1, S8). BayesTraits analysis also provided strong evidence for correlated evolution between pollination mode and mycorrhizal type, and seed dispersal mode (Table S5). These results were robust to the effects of both sampling bias and missing taxa (Table S6). Approximately 76% of AM-type trees are biotically pollinated, whereas > 91% of EcM-type trees are wind-pollinated (Fig. 3b). Approximately 82% of endozoochorous seed type trees are biotically pollinated, whereas > 80% of anemochorous seed type trees are wind-pollinated (Fig. 3c). Similar results were found in the analysis based on 10 475 tree species (Fig. 3e,f).

Estimating the evolutionary process of the mycorrhizal type and the seed dispersal and pollination modes We used flow-loop diagrams to illustrate the evolutionary process (Figs 4, 5, S4) based on the results of the BayesTraits analysis. The transitions between the different character pairs under a model of dependent evolution are shown as vectors with different magnitudes (rates) and directions. Each estimated transition rate is reported beside the arrow to indicate the direction of evolution between two characters. Because transitions between two-character states can be contingent on the state of one of the characters, the rates can be different.

A flow-loop diagram indicates that EcM-associated trees that use biotic seed dispersal are more likely to evolve abiotic seed dispersal (anemochorous and unspecialized) than the reverse, regardless of database (Figs 4a, 5a, S4a). On the other hand, AM-associated trees that use abiotic seed dispersal are more likely to evolve biotic seed dispersal than the reverse (Fig. 5a, but it similar in Figs 4a, S4a).

Mycorrhizal type affects the evolution of pollination mode. Arbuscular mycorrhizal tree species, which developed biotic seed dispersal mode (Fig. 3a,e), are more likely to drive from abiotic

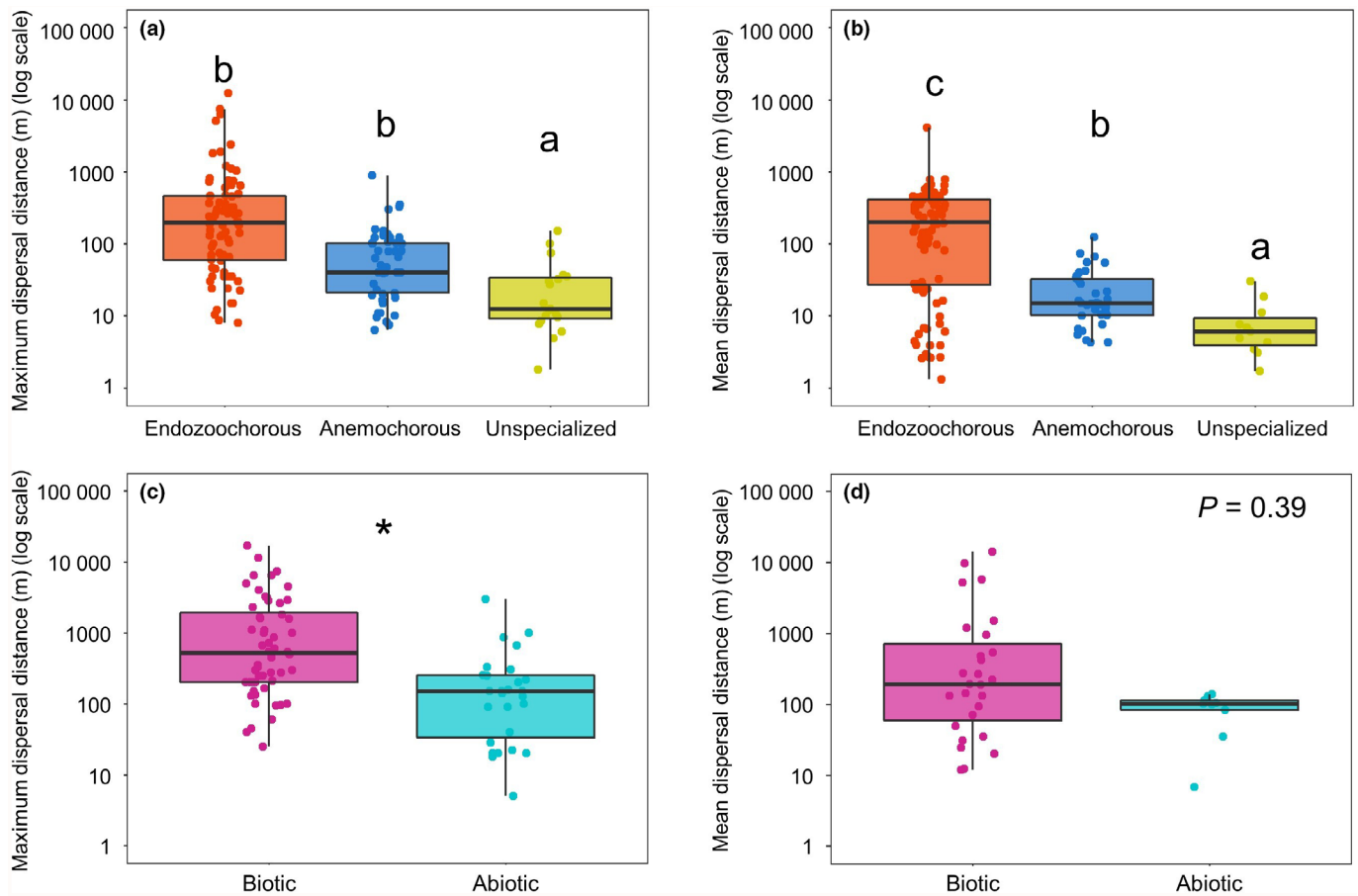


Fig. 2 (a) Maximum and (b) mean seed dispersal distance of each seed dispersal mode. (c) Maximum and (d) mean pollen dispersal distance of each pollination mode. The central black line in the box plots indicates the median, and the box indicates the upper and lower quartiles. Average value of each species and Scenario 3 of phylogenetic tree were used for this analysis. Different letters and asterisks indicate that values differ significantly at $P < 0.05$ (phylogenetic generalized least squares analysis).

Table 1 Results of phylogenetically corrected log-linear analyses examining relationships between mycorrhizal type, seed dispersal, and pollination mode in 699 (database I) and 10 475 (database II) tree species.

	Seed dispersal mode	Pollination mode
Database I		
Mycorrhizal type	$n = 699$, $df = 4$ $\chi^2 = 91.82$, $P < 0.001$	$n = 699$, $df = 2$ $\chi^2 = 127.31$, $P < 0.001$
Seed dispersal mode		$n = 699$, $df = 2$ $\chi^2 = 109.99$, $P < 0.001$
Database II		
Mycorrhizal type	$n = 10\ 475$, $df = 2$ $\chi^2 = 1203.51$, $P < 0.001$	$n = 10\ 475$, $df = 1$ $\chi^2 = 957.75$, $P < 0.001$
Seed dispersal mode		$n = 10\ 475$, $df = 2$ $\chi^2 = 776.21$, $P < 0.001$

Same values were provided by analysis of two phylogenetic trees.

to biotic pollination mode (Figs 4c, 5c). By contrast, EcM species are more likely to drive from biotic to abiotic pollination mode (Fig. 5c; but not Fig. 4).

The flow-loop diagram suggests that seed dispersal and pollination mode can affect the evolution of mycorrhizal type. Ectomycorrhizal-type trees with biotic seed dispersal modes are more likely to evolve to AM-associated trees (Figs 4a, 5a, S4a). Arbuscular mycorrhizal-type trees with abiotic seed dispersal modes are more likely to evolve to EcM-associated trees (Figs 4a, 5a). Ectomycorrhizal-associated trees with biotic pollination mode are more likely to evolve to AM-associated trees, regardless of database (Figs 4b,c, 5b,c, S4b,c).

Angiosperms with biotic seed dispersal are more prone to evolve biotic pollination (Figs 4e, 5e). Additionally, biotic pollination is more likely to develop from trees with biotic seed dispersal mode (Figs 4e, 5e).

Discussion

We found evolutionary correlations among mycorrhizal type, seed dispersal mode, and pollination mode. Most AM trees had endozoochorous (biotic) seed dispersal and biotic pollination, with long dispersal distances, whereas most EcM trees had anemochorous (abiotic) seed dispersal and wind (abiotic) pollination, with shorter dispersal distances. Arbuscular mycorrhizal

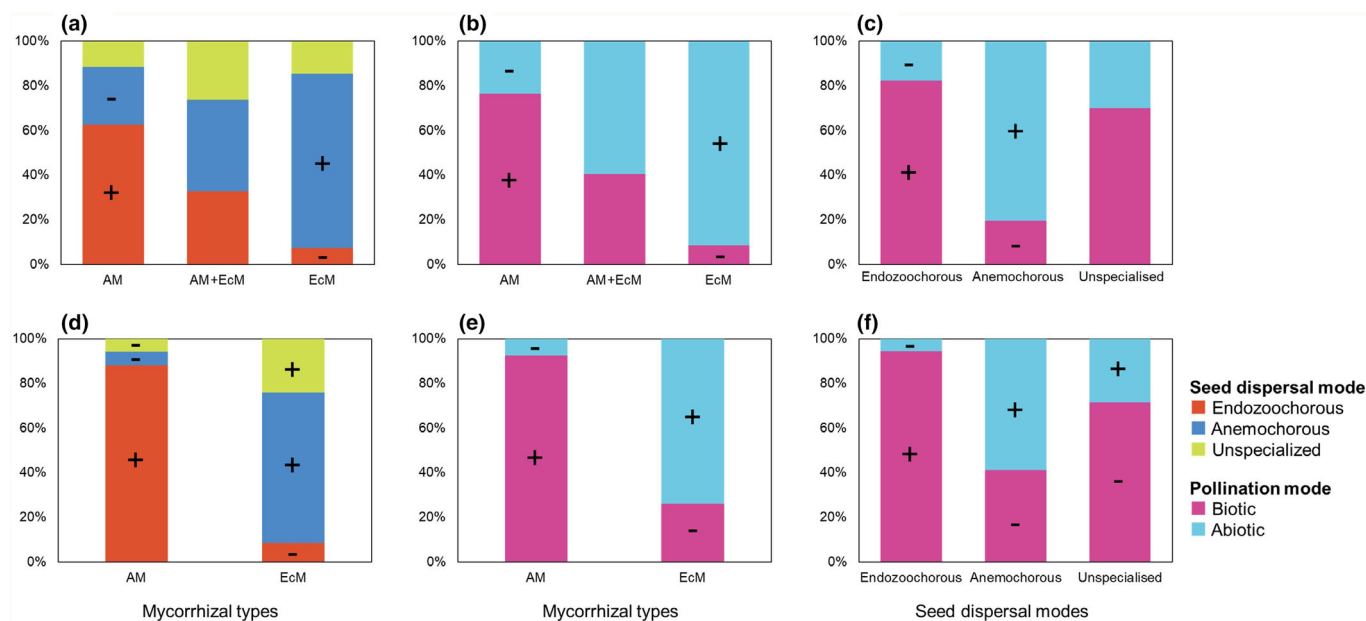


Fig. 3 (a, d) Relative proportions (% of total) of specialized structures for seed dispersal mode in trees with different mycorrhizal types in (a) database I: AM ($n = 475$), AM + EcM ($n = 62$), EcM ($n = 162$); (d) database II: AM ($n = 9447$), EcM ($n = 1028$). (b, e) Relative proportions (% of total) of pollination modes in trees with different mycorrhizal types in (b) database I and (e) database II. (c, f) Relative proportions (% of total) of pollination modes in trees with biotic and abiotic seed dispersal modes in (c) database I and (f) database II. '+' significantly higher and '-' significantly lower percentages than expected by the log-linear model (Freeman–Tukey deviation test, $P < 0.001$).

symbiosis was more likely to drive biotic seed dispersal and pollination modes, whereas EcM symbiosis was more likely to drive abiotic modes. Thus, our results strongly suggest that the three mutualistic interactions – seed dispersal, pollination, and mycorrhizal symbiosis types – have jointly evolved in trees world-wide.

How do processes shape the joint evolution of mycorrhizal type, pollination, and seed dispersal mode? Ectomycorrhizal-associated trees that use biotic seed dispersal are more likely to evolve abiotic seed dispersal (anemochorous and unspecialized) than the reverse, regardless of database (Figs 4a, 5a, S4a). The evolution of abiotic seed dispersal in EcM-associated trees allows seedlings to receive positive PSFs from conspecifics (Tedersoo *et al.*, 2020). The evolutionary pattern in EcM tree can also be explained with respect to the ecological characteristics of mycorrhizal types. Mycorrhizal interactions are largely generalist, but EcM fungi are more host-specific than AM fungi (van der Heijden *et al.*, 2015). Thus, short-distance seed dispersal in EcM-type trees may improve encounters with mycorrhizas in the next generation (Wilkinson, 1997). On the other hand, AM-associated trees that use abiotic seed dispersal are more likely to evolve biotic seed dispersal than the reverse (Fig. 5a) and supports our hypothesis that AM mycorrhizal symbiosis promotes the evolution of biotic seed dispersal. The results suggest a effect of negative PSFs by AM mycorrhizal symbiosis on the evolution of seed dispersal mode. Although some studies suggested that the evolution of endozoochory is promoted by other factors such as defense against seed predators (Mack, 2000), environmental changes, and coadaptation traits, along with the evolution of large life forms (Eriksson, 2008), negative interactions with the same species may also be an important factor.

Mycorrhizal type affects the evolution of pollination mode. Arbuscular mycorrhizal tree species, which developed biotic seed dispersal mode (Fig. 3a,d), are more likely to drive from abiotic to biotic pollination mode (Figs 4c, 5c). Long-distance seed dispersal by animals should favor long-distance pollination. The significantly longer maximum pollen dispersal distance by biotic pollination (Fig. 2c) is achieved through the foraging behavior of pollinators (Nason *et al.*, 1998; Kremer *et al.*, 2012) and so may favor low population density tree species. Biotic pollination thus supports effective pollination in tree species with long-distance endozoochorous seed dispersal. In short, long-distance pollination by animals should allow the evolution of long-distance endozoochorous seed dispersal. In fact, biotic seed dispersal angiosperms are more likely to evolve biotic pollination (Figs 4e, 5e), and this process may have led to evolution of the many angiosperm species, which developed biotic seed dispersal and biotic pollination.

By contrast, EcM are more likely to drive from biotic to abiotic pollination mode (Fig. 5c; but not Fig. 4c). Stephens *et al.* (2023) demonstrated evolution of wind (abiotic) pollination links the habitat openness such as dry and low soil fertility regions, using data include all plant life forms. Wind seed dispersal is proportionately more common in more open habitats than in closed habitats (Lorts *et al.*, 2008). Ectomycorrhizal association may favor in the low soil fertility regions (Tedersoo *et al.*, 2020). When the abiotic seed dispersal distance is sufficiently long, low soil fertility may promote joint evolution between wind pollination, wind seed dispersal, and EcM mycorrhizal association through habitat openness. However, it cannot completely explain the joint evolution between wind pollination

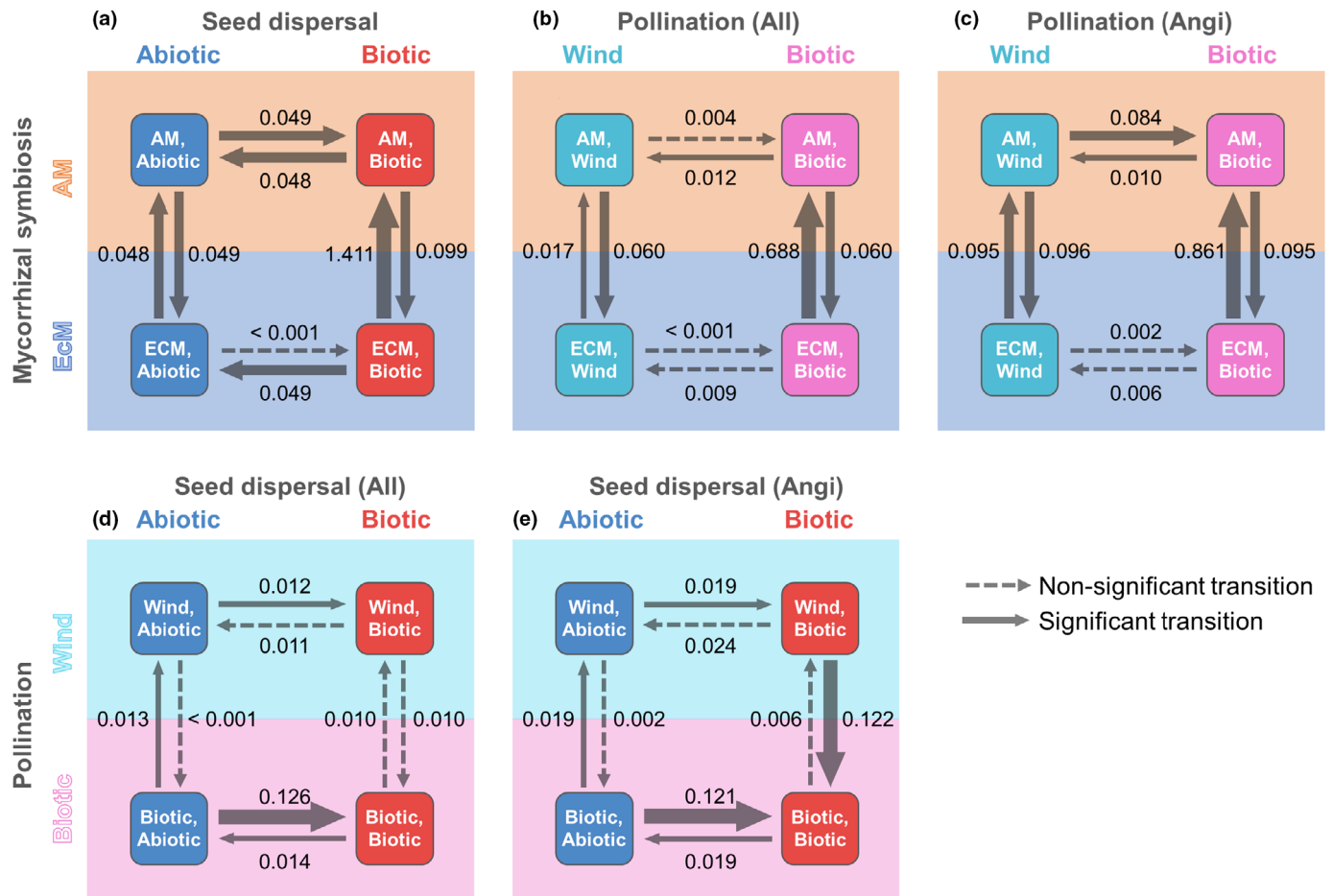


Fig. 4 Flow-loop diagram based on database I showing significant (solid arrows) and non-significant transitions (dashed arrows) in the correlated evolution among mycorrhizal types, seed dispersal modes, and pollination modes, in which the state of one character has a significant influence on the evolution of the other in mycorrhizal types and (a) seed dispersal modes in all species, (b) pollination modes in all species, and (c) pollination modes in angiosperm species; and in pollination modes and seed dispersal modes in (d) all species and (e) angiosperm species. AM + EcM include in EcM type. Values indicate relative transition score. Dashed arrows indicate transition rates that have a high posterior probability of being 0 (Z-score < 95%) and for which alternative model tests failed to reject a hypothesis that a given transition rate has a value of 0 across examined trees. 'All', all species; 'Angi', angiosperms.

and abiotic (include wind) seed dispersal in tree species, because abiotic seed dispersal has short dispersal distance, which may decrease the habitat openness through increase in population density in the future in tree species (Fig. 2a,b).

On the other hand, if population density can cause PSF effects, this could explain the joint evolution between abiotic seed dispersal and pollination in EcM trees. Abiotic seed dispersal trees may directly favor abiotic pollination through this mechanism's effects on the population density of each species or related environmental conditions rather than through the mycorrhizal type. Short-distance seed dispersal by wind should favor short-distance pollination, because wind pollination is more effective when trees have a high population density, and the efficacy decreases as population density decreases because the pollen concentration in the air rapidly decreases with distance from the male tree (Culley *et al.*, 2002). In fact, *Fagus* trees, associated with EcM fungi and high population density, use abiotic pollination, but *Dipterocarpaceae* trees, associated with EcM fungi and low population density, use biotic pollination. The evolution of abiotic pollination mode

appears to be directly linked to other ecological factors such as population density, which depends on mycorrhizal type and seed dispersal modes.

On the other hand, our analysis suggests that the seed dispersal mode can also affect evolution of the mycorrhizal type: EcM-type trees with biotic seed dispersal modes are more likely to evolve to AM-associated trees (Figs 4a, 5a, S4a). Arbuscular mycorrhizal fungi are largely generalist (Moora, 2014; van der Heijden *et al.*, 2015). Long-distance seed dispersal may favor symbiosis with generalist AM fungi over that with host-specific EcM fungi through higher encounter rates with generalist AM fungi around them after dispersal. In addition, AM-type trees with abiotic seed dispersal modes are more likely to evolve to EcM-associated trees (Fig. 5a). This result suggests that the abiotic seed dispersal mode promotes a shift in mycorrhizal type from AM to EcM fungi. The latter may provide defense against negative PSF effects, which may promote the shift in mycorrhizal type in species with abiotic seed dispersal.

Similarly, pollination mode also affects the evolution of mycorrhizal types. Ectomycorrhizal-associated trees with biotic

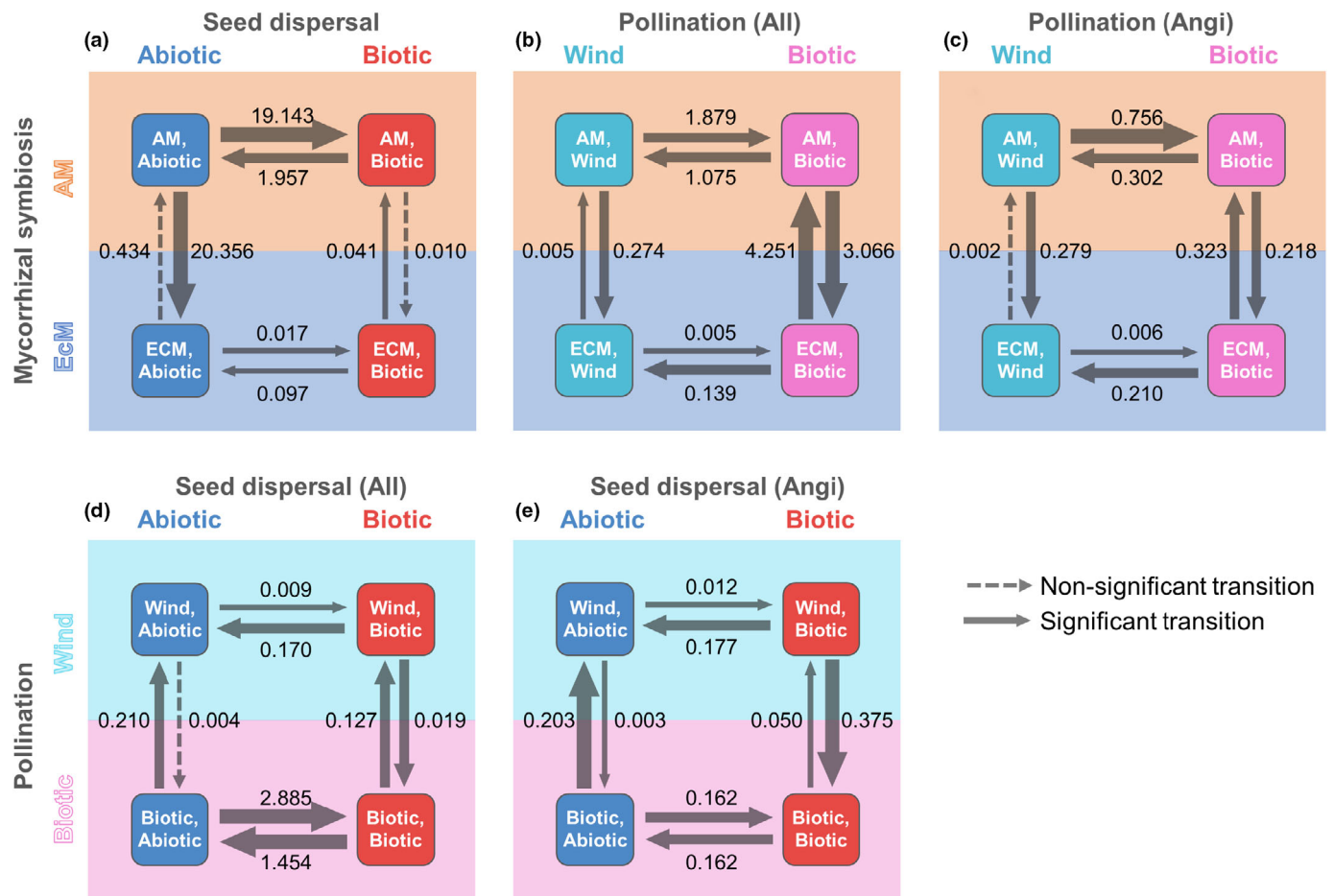


Fig. 5 Flow-loop diagram based on database II showing significant (solid arrows) and non-significant transitions (dashed arrows) in the correlated evolution among mycorrhizal types, seed dispersal modes, and pollination modes, in which the state of one character has a significant influence on the evolution of the other in mycorrhizal types and (a) seed dispersal modes in all species, (b) pollination modes in all species, and (c) pollination modes in angiosperm species; and in pollination modes and seed dispersal modes in (d) all species and (e) angiosperm species. AM + EcM include in EcM type. Values indicate relative transition score. Dashed arrows indicate transition rates that have a high posterior probability of being 0 (Z-score < 95%) and for which alternative model tests failed to reject a hypothesis that a given transition rate has a value of 0 across examined trees. 'All', all species; 'Angi', angiosperms.

pollination mode are more likely to evolve to AM trees, regardless of database (Figs 4b,c, 5b,c, and S4b,c). Because biotic pollination mode is more likely to evolve from biotic-seed-dispersal-mode trees (Figs 4e, 5e), this greater probability may support the shift of mycorrhizal type from EcM to AM. However, despite large transition score in the evolution of EcM-type trees with biotic seed dispersal mode to AM-type trees with biotic seed dispersal mode (1.41, Fig. 4a; 0.041, Fig. 5a) or of EcM-type trees with biotic pollination mode to AM-type trees with biotic pollination mode (0.688, Fig. 4b; 0.861, Fig. 4c; 4.251, Fig. 5b; and 0.323, Fig. 5c), we could not find many EcM-type tree species with biotic seed dispersal or biotic pollination mode, or their shift to AM type within clades of family level (Figs 1, S2, S3). This result suggests that the large transition scores derive more from large-scale phylogenetic patterns than from patterns within families or genera. For example, among rosids, the Fagaceae and Betulaceae, with abiotic seed dispersal and pollination modes, are placed at the

base of the phylogenetic tree, below the Rosaceae, with biotic seed dispersal and pollination modes (Figs 1, S2). This contrast implies that the evolution of biotic seed dispersal and pollination modes produced a large AM clade from EcM clade, and thus wide tree species diversity, and supports the traditional view that the evolution of biotic seed dispersal and pollination modes promoted the diversification of plants (Regal, 1977; Crepet, 1984; Pellmyr, 1992).

Overall, these results suggest a consistent tree evolutionary pattern, namely the existence of a syndrome among mycorrhizal type, seed dispersal mode, and pollination mode. Whether such syndrome are observed throughout the entire plant kingdom or are specific to trees or forest ecosystems is an important and intriguing topic for future investigation. Recently, Stephens *et al.* (2023) confirmed that microbial mutualisms other than mycorrhizal symbiosis can support plant–pollinator mutualisms. The syndrome between microbial organisms and other mutualistic interactions may be found in other mutualistic interactions.

Generality of the evolutionary pattern of trees

Is the evolutionary pattern that we observed in trees prevalent globally? Although our databases encompassed a broad range of tree species distributed from temperate to tropical regions around the world (Fig. S1), our database includes a higher proportion of species from temperate regions of Europe, North America, and Asia, with a smaller proportion of tropical tree species, so our data contain a potentially significant sampling bias (Fig. S1). On the other hand, previous studies suggest that our results are applicable globally (Culley *et al.*, 2002; Wandrag *et al.*, 2017; Stephens *et al.*, 2023). The greater prevalence of endozoochory in tropical regions (Wandrag *et al.*, 2017) and of wind pollination in temperate regions (Culley *et al.*, 2002; Stephens *et al.*, 2023) have been reported or suggested independently of mycorrhizal information. Likewise, AM and EcM trees are more frequently found in tropical and temperate regions, respectively (Gomes *et al.*, 2019; Steidinger *et al.*, 2019). These reports suggest that the joint evolution of pollination, seed dispersal modes, and mycorrhizal symbiosis are globally consistent and drive a latitudinal gradient of these mutualistic interactions. Future research should gather more information on mycorrhizal types and on seed dispersal and pollination modes, particularly for tree species in tropical regions, to provide a more comprehensive understanding of the global prevalence of these evolutionary patterns in trees.

Limitations of simplifying assumptions for mycorrhizal types, seed dispersal, and pollination modes on results Overall, our findings suggest that mycorrhizal types and pollination and seed dispersal modes jointly evolved around the world. Despite the robust evidence, our approach makes many simplifying assumptions that were required to enable it. The categorization of seed dispersal and pollination modes was based on seed and flower traits, which might not completely reflect their actual functions. For example, although pollination mode was classified in a binary fashion as either biotic or wind on the sole basis of the presence of petals, certain *Salix*, *Macaranga*, Fagaceae, Gnetales, and gymnosperm species, which do not develop petals, nevertheless depend on insects for pollination (Kato & Inoue, 1994; Manos *et al.*, 2001; Karrenberg *et al.*, 2002; Rydin & Bolinder, 2015; Yamasaki *et al.*, 2015; Gong *et al.*, 2016). However, they also depend partially on wind (Karrenberg *et al.*, 2002; Yamasaki *et al.*, 2015; Gong *et al.*, 2016). Sometimes, unspecialized or wind-dispersed seeds such as those in the Pinaceae and Fagaceae disperse long distances mainly through caching animals, contributing to tree population growth, but the frequency of primary seed dispersal is low and secondary seed dispersal is common (Gómez *et al.*, 2019). In fact, our meta analysis revealed that among species of the Pinaceae, 59% (19/32) were dispersed by wind and 41% (13/32) by animals, among which 94% (12/13) was secondary, which have short dispersal distance than endozoochorous (Table S1). In the Fagaceae, all seed dispersal by animals was secondary (55 studies). This information suggests that seed dispersal through caching animals did not affect the evolution of mycorrhizal types and pollination modes, but it does not deny the

importance of secondary seed dispersal in the development of plant populations. Our results will facilitate our understanding of the relationships among different traits and their evolution, because in many cases, traits reflect pollination and seed dispersal functions (Correia *et al.*, 2018).

Future research on the detailed ecology of species lineages or individual tree species discordant with our findings of evolutionary patterns could improve our understanding of the processes that generate tree diversity. For instance, dispersal distance may differ among dispersal agents. Ideally, using more detailed classifications of pollination and seed dispersal animal species information could reveal clearer trends. Moreover, we found a different combination of seed dispersal and pollination modes in part of the rosids clade. Fabales trees that are AM-type had biotic pollination and unspecialized seed dispersal mode. The latter are associated with N-fixing bacteria. A recent study reported that N-fixing mutualism has a weak negative PSF effect (Png *et al.*, 2019). Such an effect of N-fixing mutualism on PSF may allow the evolution of unspecialized seed dispersal in trees associated with AM mycorrhizal fungi, including those in the Fabales. Although *Salix* and Fagaceae tree species belong to a large EcM-associated clade, some *Salix* and Fagaceae species are associated with AM mycorrhizas (Figs 1, S2). The dependence of some *Salix* tree species on insects for pollination may reflect changes in mycorrhizal types, and it may represent an intermediate stage in the evolution of a new pollination mode in association with changes in mycorrhizal type. In addition, some AM angiosperm, such as *Acers* that do not develop petals, have been shown to undergo biotic pollination. Thus, tree species with mycorrhizal associations that do not fit the patterns shown here may present excellent opportunities for future research to understand tree diversity.

Effects of the evolutionary pattern on adaptation of plant species and ecosystems

The transition from AM trees to EcM trees reflect an adaptation to diverse ecological niches and environmental conditions (Tedersoo & Brundrett, 2017; Cosme, 2023). This evolutionary shift is linked to plant nutrient acquisition strategies through the specific type of mycorrhizal association. Considering previous reports in conjunction with the present results, we hypothesize that external factors such as ecological niches and environmental conditions drive the direction of joint evolution of the mycorrhizal type and of the seed dispersal and pollination modes in trees. In the future, connecting the joint evolutionary patterns to ecological niches or environmental conditions will improve the understanding of the adaptation to new environments during the evolutionary history of trees.

Furthermore, our findings suggest that mycorrhizal symbiosis, seed dispersal, and pollination mutualism have collectively shaped the spatial structure of forest ecosystems. The spatial structure provides a potentially important context in which plant species evolve and interact with other organisms (Underwood *et al.*, 2020; Ohsaki *et al.*, 2022; Leonard *et al.*, 2023). Joint evolution among mycorrhizal type, seed dispersal, and pollination

mode may have influenced ecosystem formation through their effects on spatial structure.

Conclusion

We found the joint evolution of mycorrhizal type, seed dispersal, and pollination mode in tree species. The importance of such interactive effects highlights the need for more integrative studies of mycorrhizal symbiosis, pollination, and seed dispersal to better understand how interactions shape the evolution of diversity in trees. We hypothesized that the PSF effect is a potential mechanism that has driven coevolution of trees and soil microbes. However, the detailed mechanisms and evolutionary history of the microbes involved in this mutualism are not yet clear and must be clarified in future research.

In addition, our results highlight that most AM-associated trees, which are more common globally, are endozoochorous and biotically pollinated, and therefore may depend on mammals, birds, and insects for seed dispersal and pollination. The ‘empty forest syndrome’ describes forests where seed-dispersing animals are absent, their numbers decreased by hunting or human encroachment (Caughlin *et al.*, 2015), and where aggregation of the AM tree species is promoted (Wandrag *et al.*, 2017). The aggregation of conspecific AM-type trees may increase the effects of negative PSFs on seedlings (Bennett *et al.*, 2017; Tedersoo *et al.*, 2020). Moreover, it has been reported that the quantity and species diversity of insects, including pollinators, is decreasing world-wide (Caughlin *et al.*, 2015; Wandrag *et al.*, 2017; Lister & Garcia, 2018; Sánchez-Bayo & Wyckhuys, 2019). Taken together, these facts suggest that mycorrhizal symbiosis, seed and pollination mutualism have interacted during tree evolution, and this emphasizes the comprehensive conservation of mycorrhizal fungus, seed dispersers, and pollinators that is necessary for the conservation of forest ecosystems.

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Competing interests

None declared.

Author contributions

AY and MO developed the core idea, performed the data analyses and wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability

The datasets generated during and/or analyzed during this study are available from [Supporting Information](#) list.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Dataset of database I, database II and seed or pollen dispersal distance.

Fig. S1 Species distribution maps for database I and database II.

Fig. S2 Time-calibrated phylogeny of the 699 tree species (database I) used in this study provided by Scenario 1 of S.PhyloMaker.

Fig. S3 Time-calibrated phylogeny of the 10 475 tree species (database II) used in this study in Scenario 3 in S.PhyloMaker.

Fig. S4 Flow-loop diagram used database I, which AM +EcM include in arbuscular mycorrhizal type showing significant and non-significant transitions in the correlated evolution among mycorrhizal types, seed dispersal modes, and pollination modes, in which the state of one character has a significant influence on the evolution of the other in mycorrhizal types and seed dispersal modes in all species, pollination modes in all species, and pollination modes in angiosperms species.

Table S1 Results of the phylogenetic generalized least squares analysis of secondary seed dispersal distances and endozoochorous, anemochorous, and unspecialized seed dispersal distances.

Table S2 Results of the phylogenetic generalized least squares analysis of endozoochorous, anemochorous, and unspecialized seed dispersal distances.

Table S3 Results of the phylogenetic generalized least squares analysis of biotic and abiotic pollen dispersal distances.

Table S4 Results of the phylogenetically corrected Freeman–Tukey test for relationship between mycorrhizal type and seed dispersal mode in 699 (database I) and 10 475 (database II) tree species.

Table S5 Summary of results from Bayesian correlation tests by mycorrhizal type, seed dispersal mode, and pollination mode using two phylograms from the post-burn-in period of the Bayesian phylogenetic analysis in the BAYESTRAITS software.

Table S6 Summary of results from Bayesian correlation tests by mycorrhizal type, seed dispersal mode, and pollination mode using two phylograms from the post-burn-in period of the Bayesian phylogenetic analysis in the BAYESTRAITS software.

Table S7 Results of the phylogenetically corrected Freeman–Tukey test for relationship between mycorrhizal type and pollination mode in 699 (database I) and 10 475 (database II) tree species.

Table S8 Results of the phylogenetically corrected Freeman–Tukey test for relationship between seed dispersal mode and pollination mode in 699 (database I) and 10 475 (database II) tree species.

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