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2 # Rethinking angiosperm diversification through functionally integrated mutualisms

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Summary

Flowering plants have generated and maintained exceptional diversity for over 100 million years. Explaining this macroevolutionary success requires understanding not only how new lineages arise, but also how they persist after divergence. Although multiple interactions influence angiosperm diversification, their relative contributions to lineage generation and persistence remain poorly resolved, and their joint effects have rarely been evaluated. Here, I develop the Functionally Integrated Symbiotic System (FISS) as a testable hypothesis: mutualistic interactions are functionally integrated when they make distinct but complementary contributions across demographic and evolutionary bottlenecks. Pollination is expected to contribute disproportionately to lineage generation through reproductive isolation, whereas seed dispersal and mycorrhizal symbioses are expected to contribute more strongly to establishment and persistence by facilitating range expansion, recruitment, and environmental buffering. Climatic change may alter these contributions by changing whether dispersal, establishment, or reproduction limits lineage persistence. FISS proposes that mutualistic traits should show asymmetric associations with lineage generation and persistence, and that considering these interactions together should explain or predict long-term diversification better than considering individual interactions alone.

Keywords: biological interactions, diversification, macroevolution, mycorrhizal symbiosis, pollination, seed dispersal

Introduction

Flowering plants (angiosperms) dominate terrestrial ecosystems and have generated and maintained exceptional species diversity for more than 100 million years, representing one of the most consequential macroevolutionary radiations in the history of life (Benton et al., 2022; Ding et al., 2025). Understanding this evolutionary success requires explaining both the repeated generation of new lineages and their persistence over evolutionary time. These components can respond differently to ecological processes. Processes that promote lineage splitting, including ecological specialization, assortative mating, population subdivision, and geographic isolation, can also increase demographic or environmental vulnerability, particularly during the early stages of lineage formation (Van Valen, 1976; Bell, 1982; Lancaster, 2010; Rabosky, 2013). Elevated rates of lineage formation can occur without sustained lineage accumulation. The problem is to identify how ecological processes contribute to these two components of long-term diversification.

Angiosperm diversification has been attributed to morphological and genomic innovations, environmental change, ecological opportunity, and their combinations (Donoghue & Sanderson, 2015; Helmstetter et al., 2023; Ding et al., 2025). Recent large-scale analyses further indicate that diversification has unfolded within strongly changing geographic and climatic settings (Dimitrov et al., 2023; Zuntini et al., 2024). Climate and geography shape the conditions under which lineages arise and disappear, whereas ecological interactions may influence how lineages respond within those conditions. Mutualistic interactions may also influence these components through reproductive isolation, colonization, spatial connectivity, and environmental tolerance

(Hodges & Arnold, 1995; Tiffney & Mazer, 1995; Tedersoo et al., 2020; Peris et al., 2025). Frameworks such as confluence and synnovation emphasize combinations of traits and innovations rather than single key innovations (Donoghue & Sanderson, 2015). However, whether different interactions contribute asymmetrically to lineage generation and persistence remains unclear. Net diversification cannot resolve this distinction because similar rates can arise from different combinations of lineage formation and loss.

Pollination, seed dispersal, and mycorrhizal symbioses provide a useful system because they act at different major stages of the angiosperm life cycle. Pollination directly affects mating, gene flow, and reproductive isolation; seed dispersal determines the spatial redistribution of offspring, colonization, and connectivity among populations; and mycorrhizal symbioses strongly influence establishment, nutrient acquisition, stress tolerance, and plant–soil interactions. Together they span reproductive, dispersal, and establishment bottlenecks that newly formed lineages must pass. Available evidence suggests that these three mutualisms may primarily differ in their predominant contributions to diversification. Pollination-related traits can primarily promote reproductive isolation and lineage splitting through pollinator shifts, assortative pollen transfer, and floral divergence (Grant & Grant, 1965; Kay & Sargent, 2009; van der Niet et al., 2014; Serrano-Serrano et al., 2017; Dorey & Schiestl, 2024). , In contrast, seed dispersal and mycorrhizal symbioses primarily influence ecological processes associated more directly with persistence, including successful recruitment, geographic expansion, demographic connectivity, resource acquisition, and

environmental buffering (Levin et al., 2003; Peay, 2016; Tedersoo et al., 2020; Beckman & Sullivan, 2023).

Here, I develop this hypothesis as the Functionally Integrated Symbiotic System (FISS). In FISS, interactions are functionally integrated when they act on distinguishable demographic or evolutionary bottlenecks, make complementary contributions across them, and together predict macroevolutionary outcomes better than any single interaction alone. This use of integration does not require obligate coevolution, physical coupling, or a discrete interaction network. Within FISS, pollination is expected to contribute disproportionately to lineage generation, whereas seed dispersal and mycorrhizal symbioses are expected to contribute more strongly to processes associated with establishment and persistence. Mutualistic traits are not necessarily independent: mycorrhizal status is associated with seed-dispersal syndromes (Correia et al., 2018), and pollination, seed dispersal, and mycorrhizal associations show correlated evolutionary patterns (Yamawo & Ohno, 2024). FISS therefore focuses on biotic interactions as proximate ecological pathways linking lineage generation and persistence. Environmental change can alter these effects by shifting which bottleneck is most limiting. FISS asks whether the ecological functions of these interactions are asymmetrically distributed across lineage generation and persistence and whether considering them together improves explanations or predictions of long-term diversification.

Lineage generation and persistence as distinct components of diversification

Long-term diversification depends on both the generation of new lineages and their persistence after divergence. These components can respond differently to ecological processes. Newly diverged lineages are often geographically restricted, demographically small, or ecologically specialized, conditions that can increase vulnerability to environmental variation and lineage loss (Futuyma & Moreno, 1988; Dynesius & Jansson, 2000; Davies et al., 2004; Vamosi & Vamosi, 2010). High rates of lineage formation can fail to translate into sustained lineage accumulation over macroevolutionary timescales (Ricklefs, 2007; Rabosky, 2013). Rapid lineage formation can then generate high turnover when newly formed lineages fail to establish or persist. Many angiosperm clades nevertheless combine repeated lineage formation with long-term persistence across heterogeneous and fluctuating environments (Crepet & Niklas, 2009; Sauquet & Magallón, 2018). This combination suggests that ecological processes acting after divergence can modify the relationship between lineage generation and extinction vulnerability. This raises a more specific question: which processes promote lineage splitting, and which help newly formed lineages establish and persist?

Pollination as a divergence-promoting mutualism

Lineage splitting in angiosperms arises through multiple ecological and evolutionary processes, including habitat specialization, geographic isolation, polyploidization, and biotic interactions (Benton et al., 2022; Ding et al., 2025). Among these processes, pollination mutualisms are particularly relevant to lineage divergence because they directly affect mating patterns and gene flow. A large proportion of angiosperm species are associated with animal-mediated pollination (Ollerton, 2017; Stephens et al., 2023; Tong et al., 2023; Peris et al., 2025), and palaeontological evidence shows that insect-

mediated pollination predates angiosperms (Peris et al., 2025; Negri & Toledo, 2026), while phylogenetic reconstruction suggests that early angiosperms were ancestrally insect-pollinated (Stephens et al., 2023).

Empirical and comparative studies show that pollination-related traits can promote reproductive isolation through pollinator shifts, floral divergence, and assortative pollen transfer (Grant & Grant, 1965; Kay & Sargent, 2009; van der Niet et al., 2014; Serrano-Serrano et al., 2017; Barreto et al., 2024; Dorey & Schiestl, 2024). Changes in pollinator behaviour or floral phenotype can reduce gene flow among populations and thereby facilitate reproductive divergence (Waser et al., 1996; Chittka et al., 1999; Muchhala & Potts, 2007). Pollination can also contribute to lineage persistence after divergence by sustaining reproduction, but because it directly modifies mating patterns and gene flow, its effects may more often generate opportunities for lineage splitting.

However, enhanced reproductive divergence can occur without sustained lineage accumulation. Evidence that pollination-related specialization consistently increases long-term net diversification remains mixed across clades and ecological contexts (Sargent, 2004; O'Meara et al., 2016; Peris et al., 2025). Mixed effects on net diversification do not rule out a stronger role in lineage generation, because net diversification combines lineage formation and lineage loss, and the macroevolutionary consequences of floral specialization may vary among clades and ecological contexts (Armbruster, 2014). Specialized pollination systems may also increase dependence on particular partners and thereby heighten sensitivity to partner loss or environmental fluctuations (Janzen, 1979; Herre et al., 2008).

Dispersal and mycorrhiza as persistence-related mutualisms

Seed dispersal and mycorrhizal symbioses primarily affect offspring redistribution, establishment, resource acquisition, demographic connectivity, and environmental buffering. At the population level, these processes can increase persistence and may help newly formed lineages establish and persist after divergence.

Animal-mediated seed dispersal is widespread among angiosperms and many woody lineages (Yamawo & Ohno, 2024; Jin et al., 2026). Animal-mediated dispersal can reduce density-dependent mortality near conspecific adults (Janzen, 1970; Connell, 1971; Comita et al., 2014), increase spatial spread and recolonization, and maintain genetic connectivity among populations (Levin et al., 2003; Beckman & Sullivan, 2023). By facilitating colonization and connectivity across heterogeneous landscapes, dispersal may also enhance metapopulation persistence and environmental tracking under changing conditions (Snäll et al., 2005; Sexton et al., 2009; Thompson et al., 2017). Because larger and more connected geographic ranges are generally associated with lower extinction vulnerability, these effects provide a potential ecological pathway linking dispersal to long-term lineage persistence (Sheth et al., 2020).

Mycorrhizal symbioses can support persistence by improving nutrient acquisition and seedling performance while increasing tolerance to stress and pathogens. Arbuscular mycorrhizal symbioses are widespread among angiosperms (Tedersoo et al., 2020) and can modify resource acquisition and plant–soil interactions in ways that buffer environmental variability (Peay, 2016; Tedersoo et al., 2020). At broader biogeographic scales, mycorrhizal type can also influence plant colonization

and establishment. A global analysis of island floras found that arbuscular mycorrhizal plants experience a stronger colonization filter than plants with other mycorrhizal types, particularly on more isolated islands (Delavaux et al., 2021). Such buffering may stabilize populations under stochastic environmental conditions, where variation in recruitment and survival can strongly influence persistence (Morris et al., 2008; Koons et al., 2009). In short, pollination can affect persistence by altering reproductive limitation and plant coexistence (Johnson et al., 2022), whereas seed dispersal and mycorrhizal symbioses can contribute to divergence through spatial isolation, ecological differentiation, niche expansion, or local adaptation (Onstein et al., 2017).

Comparative analyses have often detected weak or inconsistent associations between dispersal mode, mycorrhizal type, and overall diversification rates (Feijen et al., 2018; Reginato et al., 2020; Jin et al., 2026). A synthesis of phylogenetic comparative datasets across mutualistic systems found no consistent association between mutualism and diversification, with effects varying among interaction types and clades (Kaur & Pennell, 2023). For example, a global analysis of 35,131 angiosperm species found no significant association between seed-dispersal mode and diversification rate (Jin et al., 2026). Mutualistic interactions may affect lineage generation and persistence differently. Net diversification combines lineage formation and lineage loss and can therefore obscure such differences. Testing these components separately provides a more direct way to evaluate the predictions of FISS. For seed dispersal and mycorrhizal symbioses, evidence for effects on persistence comes mainly from ecological and population-level studies of recruitment, range dynamics, demographic buffering, and environmental tolerance. Whether these processes translate

into long-term lineage persistence remains to be tested.

Functionally Integrated Symbiotic System: integration across lineage bottlenecks

I use FISS to formalize these contrasting tendencies as complementary and asymmetric effects across different stages of lineage generation and persistence (Fig. 1). Functionally integrated interactions act on distinguishable demographic or evolutionary bottlenecks, make complementary contributions across them, and together support lineage-level predictions that no interaction considered separately can provide. Co-occurrence of multiple mutualisms within a lineage is insufficient by itself; coordinated coevolution, obligate interactions, and a discrete biological system are outside the definition. The key criterion is whether the interactions affect different stages of lineage generation and persistence, not taxonomic identity or physical coupling among interacting partners. Environmental conditions may alter these associations by changing which bottleneck is most important for lineage generation or persistence. The relative contributions of different mutualisms are therefore expected to vary among lineages and environments. At ecological scales, multiple mutualists can have non-additive effects on host performance and selection, including both synergistic and antagonistic effects (Afkhami et al., 2014, 2021).

Within FISS, pollination is expected to contribute disproportionately to lineage generation through effects on mating, gene flow, and reproductive isolation. Seed dispersal and mycorrhizal symbioses are expected to contribute more strongly to post-divergence establishment and persistence through spatial expansion, demographic

connectivity, resource acquisition, and environmental buffering. Seed dispersal and mycorrhizal symbioses may also contribute to divergence, and pollination may influence persistence under some ecological conditions. Seed dispersal and mycorrhizal symbioses may complement one another during establishment and persistence. Successful establishment requires propagules to reach suitable sites and recruits to obtain the resources and belowground associations necessary for survival. Seed dispersal and mycorrhizal symbioses may therefore affect different requirements for successful establishment after divergence. The joint dispersal of plant diaspores and mycorrhizal fungal propagules by birds illustrates one way these pathways can become ecologically coupled (Correia et al., 2019). This ecological coupling provides a way to test whether complementary effects on establishment and persistence are associated with macroevolutionary differences. The predicted asymmetry concerns the relative contributions of different interaction classes to lineage generation and persistence.

FISS does not require reciprocal diversification between plants and their mutualistic partners. However, angiosperm diversification may create new ecological opportunities for mutualistic partners, whose subsequent diversification could expand the interaction opportunities available to plants (Grimaldi & Engel, 2005; Condamine et al., 2016; Gómez & Verdú, 2012; Onstein et al., 2017; Peris & Condamine, 2024). Such feedback could reinforce the functional integration proposed by FISS.

The three mutualisms emphasized here provide a starting framework. Other biotic interactions may also affect speciation and extinction, either directly or indirectly. Pathogen-related immune evolution can contribute to reproductive incompatibility (Alcázar et al., 2014), whereas beneficial microbial associations can buffer

environmental stress and support population persistence (Compant et al., 2019; Li et al., 2026). In some cases, herbivory can also promote lineage splitting (Maron et al., 2019) or reducing population growth and potentially persistence (Maron & Crone, 2006). These effects may operate together with, or independently of, pollination, seed dispersal, and mycorrhizal symbioses. FISS can therefore be expanded to test how multiple biotic interactions jointly shape speciation, extinction, and net diversification.

Predictions and tests of FISS

FISS predicts asymmetric associations between ecological interactions and lineage generation and persistence. Pollination-related traits are predicted to be more strongly associated with reproductive isolation and lineage splitting, whereas seed-dispersal and mycorrhizal traits are predicted to be more strongly associated with establishment, range expansion, demographic stability, and environmental tolerance. Individual interactions may affect both components of diversification; the predicted difference lies in the relative strength of these associations. Because these strengths may vary among lineages and environments, comparative analyses should ask whether the same functional asymmetries recur across contexts. Comparative analyses that distinguish lineage-generation processes from persistence-related outcomes provide the most direct test. FISS would be supported if interaction classes show reproducible functional asymmetries, models that consider these interactions together predict lineage patterns better than models based on individual interactions, and transitions among interaction states are associated with corresponding changes in lineage accumulation or persistence.

Considering ecological interactions together should explain or predict long-term lineage accumulation better than considering each interaction separately. If different interactions affect different stages of lineage generation and persistence in complementary ways, their effects on lineage accumulation should depend partly on whether processes that generate new lineages occur together with those that support establishment and persistence. Lineages experiencing frequent reproductive divergence may not accumulate diversity if newly generated lineages repeatedly fail to establish or persist. Processes that enhance persistence can influence long-term diversity without directly increasing lineage generation. Models that include the joint states of pollination, seed dispersal, and mycorrhizal associations should provide greater explanatory or predictive performance than models based on individual interactions alone. If complementarity matters, models allowing interactions among these states should also outperform purely additive models. Environmental and geographic variables can be included as covariates or interaction terms to test whether the predicted complementarity recurs across contexts.

Evolutionary transitions in pollination mode, dispersal strategy, or mycorrhizal association provide another test. Such transitions can change the balance between lineage-generation and persistence-related processes and may be followed by changes in lineage accumulation or evolutionary turnover. Testing this prediction requires distinguishing the effects of individual transitions from those of the broader set of interactions while accounting for phylogenetic history, environmental context, and other traits that influence diversification. Transitions among arbuscular mycorrhizal (AM), ectomycorrhizal (EcM), ericoid mycorrhizal (ErM), and orchid mycorrhizal (OM)

systems provide potential starting points for such analyses (Cairney & Meharg, 2003; Tedersoo & Smith, 2013; Givnish et al., 2015; Fig. 2). The prediction is a shift in the relative contributions of lineage-generation and persistence-related processes following changes in interaction state.

Hidden-state models can account statistically for variation associated with unobserved factors, but they do not directly test a priori predictions about which ecological functions are more strongly associated with lineage generation or persistence. When biologically motivated interaction data are available, explicit multi-trait models provide a more direct test of the functional asymmetry and complementarity predicted by FISS. Comparing models that incorporate observed interaction states, their combinations, and hidden sources of heterogeneity can help determine whether the observed interactions explain diversification beyond unmeasured background variation.

Orchids offer a concrete test case. Specialized pollination, highly dispersible seeds, and dependence on mycorrhizal fungi during germination and establishment span processes associated with reproductive divergence, dispersal, and establishment, and these components vary substantially among orchid lineages and habitats. Epiphytic lineages, for example, have experienced rapid diversification and high evolutionary turnover in association with ecological specialization and distinctive pollination and mycorrhizal systems (Gamisch & Comes, 2019; Pérez-Escobar et al., 2024). FISS predicts that lineage accumulation should depend on how processes promoting reproductive divergence are combined with those supporting dispersal, establishment, and persistence. Variation among orchid lineages and habitats therefore provides a useful system for testing whether complementary mutualisms contribute to sustained

diversification.

Evolutionary assembly and temporal dynamics of FISS

The major mutualisms considered in FISS arose at different stages of plant evolution, raising the possibility that their macroevolutionary effects assembled sequentially (Fig. 2). Arbuscular mycorrhizal symbioses originated early during land-plant evolution (Remy et al., 1994; Strullu-Derrien et al., 2018), whereas early angiosperms were already associated with biotic pollination (Stephens et al., 2023). Animal-mediated seed dispersal expanded later alongside the increasing prevalence of fleshy fruits and frugivory (Tiffney & Mazer, 1995; Eriksson et al., 2000; Jin et al., 2026). These temporal differences suggest that interactions affecting belowground resource acquisition, reproduction, and dispersal accumulated progressively during angiosperm evolution.

The macroevolutionary effects of mutualisms may have changed as interactions affecting different stages of the plant life cycle accumulated over evolutionary time. Biotic pollination originated before major increases in angiosperm diversification rates (Benton et al., 2022; Ding et al., 2025). If pollination primarily promotes lineage generation, its early presence alone need not have produced sustained lineage accumulation. The later expansion of dispersal and other interactions that support establishment and persistence may have increased the probability that newly generated lineages established, expanded, and persisted across heterogeneous environments. Under this interpretation, long-term diversification should be associated with shifts in

combinations of pollination, dispersal, and mycorrhizal interactions, not simply with the origin of individual mutualisms.

These temporal associations are correlational. The temporal associations among mutualisms and angiosperm diversification are largely correlational and do not demonstrate that complementary interactions caused major radiations. Testing this prediction will require fossil evidence together with phylogenetic reconstructions of interaction states to ask whether interactions promoting reproductive divergence and those supporting establishment and persistence preceded shifts in lineage accumulation. Changes in interaction configurations after their initial assembly provide another test of FISS. Transitions among combinations of pollination, seed dispersal, and mycorrhizal associations should be associated with changes in lineage generation, persistence, or turnover if these interactions make complementary contributions to diversification. Recurrent associations between particular configurations and diversification dynamics across independent lineages may therefore help explain heterogeneity in trait-dependent diversification across angiosperms (Helmstetter et al., 2023; Table 1; Fig. 2).

Environmental modulation of FISS under climatic change

Recent studies indicate that Cenozoic climate change was associated with major changes in plant diversification. A phylogenomic analysis of nearly 8,000 angiosperm genera detected a second increase in diversification during the Cenozoic, coincident with global cooling (Zuntini et al., 2024). Diversification also increased after the Cretaceous in a global analysis of 14,244 angiosperm genera, with young and rapidly

diversifying genera concentrated in temperate and dry regions (Dimitrov et al., 2023), and rosids showed pronounced diversification during the last 15 million years of global cooling (Sun et al., 2020). Climate change was also associated with lineage loss. Late Cenozoic cooling was associated with the selective loss of cold-sensitive woody lineages and shifts in the distributions of surviving genera (Eiserhardt et al., 2015; Shiono et al., 2018). In Western and Central Europe, tree genus richness declined by about 75% from its Miocene maximum to the present (Wilkens et al., 2026). Thus, present-day plant diversity reflects not only the generation of new lineages but also their differential persistence and loss through time. How much of the remaining variation in lineage fate is stochastic, and how much reflects ecological differences in the ability to persist or track suitable environments?

FISS predicts that mutualistic interactions contribute to these differences by affecting dispersal, establishment, and reproduction. Animal-mediated seed dispersal can help propagules reach newly suitable habitats (Corlett & Westcott, 2013; Nuñez et al., 2023), whereas mycorrhizal symbioses can promote establishment and stress tolerance after arrival, although dependence on compatible fungal partners may also restrict colonization (Lankau et al., 2015; Segal & Kivlin, 2025; Li et al., 2026). Pollination can further influence persistence when reproduction limits small or isolated populations, particularly when plant and pollinator ranges shift at different rates (Moeller et al., 2012; Richman et al., 2020). Where suitable habitats remain geographically accessible, these interactions may also allow lineages to continue diverging while tracking climatic change through latitudinal or elevational range shifts. Therefore, FISS predicts that functional integration among pollination, seed dispersal,

and mycorrhizal symbioses can support continued lineage generation and persistence during climatic change, with pollination contributing more strongly to lineage generation and seed dispersal and mycorrhiza to persistence. These effects may remain detectable after climatic tolerance, geography, and phylogenetic history are taken into account.

Conclusion

The evolutionary success of angiosperms depends on both lineage generation and persistence. FISS predicts that mutualistic interactions contribute differently to these components: pollination more directly to reproductive isolation and lineage generation, and seed dispersal and mycorrhizal symbioses more strongly to establishment, range expansion, and persistence. Climatic change may shift which of these processes limits persistence and thereby alter the relative contribution of each interaction. Long-term lineage accumulation should therefore depend not only on individual mutualisms but also on how their functions combine across lineage generation and persistence. Support for FISS would require reproducible asymmetries among interaction classes and additional explanatory or predictive information from joint models; failure to detect these patterns would weaken the hypothesis. More broadly, FISS links ecological interactions acting across the plant life cycle to the long-term generation and persistence of plant diversity.

Author contributions

Akira Yamawo conceived the study, developed the FISS hypothesis, designed the manuscript, interpreted the literature, and wrote the manuscript.

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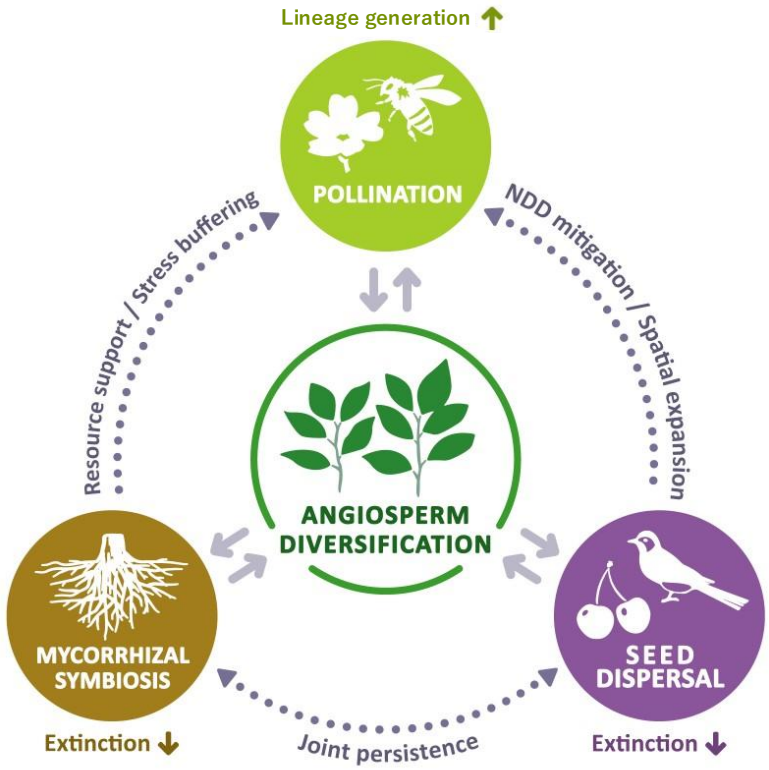

Figure 1. The Functionally Integrated Symbiotic System (FISS) Hypothesis: asymmetric and complementary contributions of ecological interactions to lineage generation and persistence

Solid arrows indicate hypothesized associations between major mutualisms and diversification-related processes; dashed arrows indicate potential ecological linkages among interactions. Labels on dashed arrows identify representative processes such as environmental buffering, establishment facilitation, and negative density dependence (NDD). The arrows represent hypothesized tendencies, not demonstrated causal effects.

665 The figure asks whether complementary functions across lineage generation and
666 persistence provide information beyond the effects of individual mutualisms (Box 1).
667

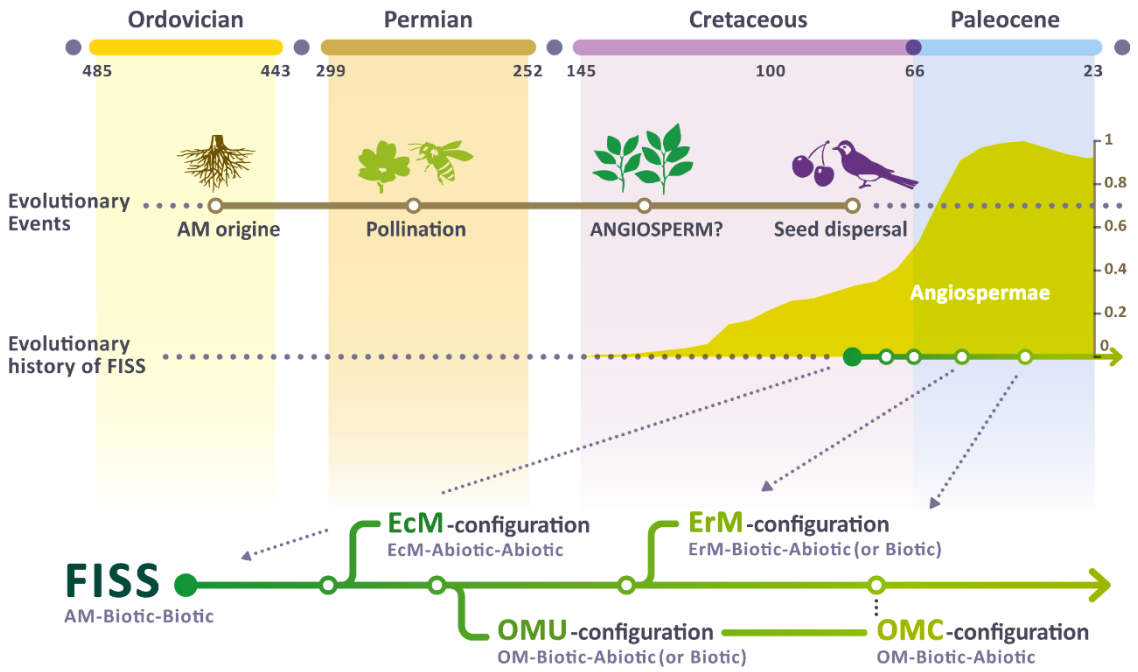

Figure 2. Hypothesized temporal assembly of alternative interaction configurations under FISS.

Combinations of mycorrhizal symbioses, pollination, and seed-dispersal mutualisms may contribute to complementary processes of lineage divergence and persistence during angiosperm evolution. Configurations are listed as mycorrhizal association, pollination mode, and seed-dispersal mode. The AM–biotic pollination–biotic seed dispersal configuration is shown as a representative mutualistic configuration; EcM-, ErM-, and OM-dominated configurations illustrate alternatives that may differ in the relative contributions of lineage-generation and persistence-related processes (Table 1). Orchid OMF- and OMC-dominated configurations represent conceptual understory and canopy orchid systems. Connections indicate potential transitions among configurations and do not represent reconstructed evolutionary pathways or direct evidence of historical relationships.

682 Table 1. Hypothetical contributions of alternative interaction configurations to lineage generation and persistence under FISS

683 Alternative combinations of pollination mode, seed-dispersal mode, and mycorrhizal association may make different contributions to
684 lineage generation and persistence. These are conceptual examples rather than empirical categories or quantitative predictions. No
685 configuration is assumed to be universally optimal; relative contributions are expected to vary among lineages and environments.

Illustrative interaction configuration	Primary pollination mode	Seed-dispersal mode	Mycorrhizal association	Hypothesized contribution to lineage generation	Hypothesized contribution to persistence
AM–biotic pollination–animal dispersal configuration	Biotic pollination	Animal-mediated	Arbuscular mycorrhiza (AM)	Biotic pollination may promote reproductive isolation through pollinator shifts, assortative pollen transfer, and floral divergence.	Animal-mediated dispersal and AM symbiosis may facilitate recruitment, spatial expansion, demographic connectivity, resource acquisition, and environmental buffering.
EcM-dominated configuration	Predominantly wind pollination	Gravity and wind	Ectomycorrhiza (EcM)	Pollination-mediated lineage generation may be relatively weak, although geographic or ecological differentiation	EcM associations may enhance resource acquisition and environmental tolerance, potentially strengthening

				may still contribute to lineage generation.	persistence under stressful or seasonal conditions.
ErM-dominated configuration	Biotic pollination, mainly insects	Gravity- or animal-mediated	Ericoid mycorrhiza (ErM)	Biotic pollination and ecological specialization may contribute to reproductive and ecological divergence.	Specialized nutrient acquisition and tolerance of nutrient-poor or stressful environments may facilitate establishment and persistence.
Orchid OMF understory configuration	Reduced or highly specialized biotic pollination, often Hymenoptera	Wind or animal-mediated	Orchid mycorrhiza, often associated with belowground EcM networks	Specialized pollination and ecological specialization may promote reproductive divergence and lineage generation.	Persistence may be strongly context-dependent because mycorrhizal dependence can facilitate establishment while also increasing sensitivity to partner availability and local environmental conditions.
Orchid OMC epiphytic canopy configuration	Highly specialized biotic pollination, often Hymenoptera	Wind dispersal	Orchid mycorrhiza, with weak or no connection to soil EcM networks	Specialized pollination and ecological opportunity may promote reproductive isolation and lineage generation.	Wind dispersal may facilitate colonization, whereas dependence on specialized establishment conditions may increase demographic and environmental vulnerability.

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688 Table S1. Illustrative summary of the hypothesized functional contributions of major plant mutualisms to lineage generation and
689 persistence

690 The table summarizes hypothesized predominant functional tendencies rather than fixed classifications or effect sizes. Each interaction
691 may influence both lineage generation and persistence, with relative contributions expected to vary among lineages and environments.

Mutualistic interaction	Primary ecological function	Hypothesized predominant contribution	Potential contribution to lineage generation	Potential contribution to lineage persistence	Representative mechanisms	Representative references
Polli	Pollen	Linea	Can promote reproductive	Variable and context-	Assortative pollen	Sargent (2004);

nation mutualisms	transfer and mate choice	gene generation	isolation through pollinator shifts, assortative pollen transfer, floral divergence, and reduced gene flow.	dependent; reliable pollination may support reproductive persistence, whereas strong specialization may increase dependence on particular partners.	transfer; pollinator shifts; floral divergence; reduced gene flow; sensory and behavioural specialization	Kay & Sargent (2009); van der Niet et al. (2014); Dorey & Schiestl (2024)
Seed-dispersal mutualisms	Spatial redistribution of offspring	Persistence-related processes	May contribute to divergence through range expansion, spatial isolation, and changes in population connectivity, depending on ecological and geographic context.	May facilitate recruitment, colonization, recolonization, demographic connectivity, environmental tracking, and range expansion.	Reduced density-dependent mortality; colonization; metapopulation connectivity; genetic connectivity; spatial spread	Levin et al. (2003); Reginato et al. (2020); Sheth et al. (2020); Beckman & Sullivan (2023)
Myc	Resourc	Persis	May contribute to	May facilitate seedling	Nutrient acquisition;	Feijen et al.

orrhizal symbioses	e acquisition, establishment, and stress buffering	tence-related processes	ecological divergence through niche expansion, habitat colonization, and local adaptation.	establishment, resource acquisition, stress tolerance, pathogen protection, and demographic buffering under environmental variation.	improved establishment; environmental buffering; stress tolerance; plant–soil interactions; niche expansion	(2018); Peay (2016); Tedersoo et al. (2020)

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Box 1. The Functionally Integrated Symbiotic System (FISS) hypothesis: an organizational framework with testable predictions

FISS asks whether ecological interactions contribute differently to lineage generation and persistence and whether their effects complement one another. Interactions are functionally integrated when they act on distinct demographic or evolutionary bottlenecks, make complementary contributions across them, and together support lineage-level predictions. This definition does not require coordinated coevolution, obligate interactions, or a discrete biological system.

Pollination is expected to contribute more strongly to lineage generation, whereas seed dispersal and mycorrhizal symbioses are expected to contribute more strongly to establishment and persistence. These roles are not exclusive; the prediction concerns differences in their relative contributions. Interactions that promote reproductive divergence may have different long-term consequences depending on whether other processes support establishment and persistence. No combination of interactions is expected to be universally optimal, and their effects may vary among lineages and environments. Pollination, seed dispersal, and mycorrhizal symbioses provide the initial test system, but other interactions can be incorporated when relevant to diversification (Table 1).

FISS differs from ecological or evolutionary syndromes in that it does not require recurrent co-occurrence of particular traits or interactions. It asks instead whether ecological interactions differ reproducibly in their associations with lineage generation and persistence and whether considering them together explains lineage

716 patterns better than considering them separately. Failure to detect either pattern would
717 count against the hypothesis.
718