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2 Rethinking angiosperm diversification through the functional integration of mutualisms
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Summary

Flowering plants have generated and maintained exceptional diversity for over 100 million years despite repeated environmental change and mass extinction events. Explaining this evolutionary success requires understanding not only how new lineages arise, but also how they persist after divergence. Although multiple ecological traits and interactions are known to influence angiosperm diversification, less attention has been paid to whether different interactions contribute asymmetrically to lineage generation and lineage persistence. Here, I develop the Functionally Integrated Symbiotic System (FISS) as an organizational and testable hypothesis in which ecological interactions are functionally integrated when they make distinct and 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 may contribute more strongly to persistence-related processes by promoting spatial expansion, successful recruitment, and environmental buffering. These three mutualisms are treated as an illustrative set spanning reproductive, dispersal, and establishment stages rather than as an exhaustive set of interactions affecting diversification. FISS therefore predicts that mutualistic traits should show asymmetric associations with lineage generation and persistence, and that their joint functional configuration should provide greater explanatory or predictive information about long-term diversification than individual interactions alone. FISS provides a basis for testing how the functional organization of ecological interactions may shape macroevolutionary dynamics.

- 34 Keywords: biological interactions, diversification, macroevolution, mycorrhizal
- 35 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 two components need not respond to ecological processes in the same way. 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). Consequently, elevated rates of lineage formation do not necessarily lead to sustained lineage accumulation. Identifying processes that influence the balance between lineage generation and persistence is therefore central to understanding long-term diversification.

Angiosperm diversification has been attributed to morphological and genomic innovations, environmental change, ecological opportunity, and combinations of these factors (Donoghue & Sanderson, 2015; Helmstetter et al., 2023; Ding et al., 2025). Frameworks such as confluence and synnovation have emphasized that diversification can result from combinations of traits and innovations rather than from single key innovations acting independently (Donoghue & Sanderson, 2015). Mutualistic interactions have likewise been implicated in angiosperm diversification. Pollination can alter reproductive isolation and floral divergence, seed dispersal can influence

colonization and spatial connectivity, and mycorrhizal symbioses can affect establishment, resource acquisition, and environmental tolerance (Hodges & Arnold, 1995; Tiffney & Mazer, 1995; Tedersoo et al., 2020; Peris et al., 2025). The unresolved issue, however, is not simply whether multiple interactions contribute jointly to diversification. Rather, it is whether different interactions make systematically different contributions to the distinct processes that generate and maintain lineages. Existing multi-factor approaches generally ask which combinations of traits or ecological conditions are associated with diversification, but have less often explicitly distinguished how different factors contribute to lineage generation and lineage persistence.

Pollination, seed dispersal, and mycorrhizal symbioses provide a useful system in which to develop this idea because they influence 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. These three mutualisms are therefore considered here not because they represent all interactions relevant to angiosperm diversification, but because together they span reproductive, dispersal, and establishment bottlenecks through which newly formed lineages must pass. Other mutualisms, including defensive and nitrogen-fixing symbioses, as well as antagonistic interactions and intrinsic life-history traits, may influence the same or additional bottlenecks and could be incorporated into the same framework where appropriate.

Available evidence suggests that these three mutualisms may differ in their predominant contributions to diversification. Pollination-related traits can 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 strongly influence ecological processes expected to enhance 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). These associations are not exclusive: dispersal and mycorrhizal symbioses can also contribute to divergence, whereas pollination can affect persistence. Moreover, much of the evidence linking dispersal and mycorrhizal symbioses to persistence derives from population- and ecological-level processes rather than direct estimates of macroevolutionary extinction rates. The proposed asymmetry should therefore be treated as a hypothesis about predominant functional tendencies that requires explicit comparative testing, rather than as an established partitioning of mutualistic effects.

Here, I develop this hypothesis as the Functionally Integrated Symbiotic System (FISS). In FISS, “integration” does not imply obligate coevolution, physical coupling, or the evolution of a discrete interaction network. Instead, interactions are considered functionally integrated when they (i) influence distinguishable demographic or evolutionary bottlenecks, (ii) make complementary rather than fully redundant contributions across those bottlenecks, and (iii) generate joint predictions about lineage outcomes that cannot be inferred from individual interactions alone. 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. Yamawo and Ohno (2024) showed that pollination, seed dispersal, and mycorrhizal associations can exhibit non-independent evolutionary relationships. FISS addresses a different question: whether the ecological functions of such interactions are asymmetrically organized across lineage generation and persistence, and whether this organization helps explain long-term diversification. This Viewpoint first evaluates the evidence for these contrasting functional tendencies, then develops FISS as an organizational and testable hypothesis, and finally outlines predictions for determining whether interaction configurations influence diversification beyond the effects of individual mutualisms.

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 need not respond similarly 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). Consequently, elevated rates of lineage formation do not necessarily translate into sustained lineage accumulation over macroevolutionary timescales (Ricklefs, 2007; Rabosky, 2013). Rapid lineage formation may instead generate high turnover when newly formed

lineages fail to pass through ecological or demographic bottlenecks.

Many angiosperm clades nevertheless combine repeated lineage formation with long-term persistence across heterogeneous and fluctuating environments (Crepet & Niklas, 2009; Sauquet & Magallón, 2018). This pattern raises the possibility that ecological processes acting after divergence can modify the relationship between lineage generation and extinction vulnerability. From this perspective, understanding angiosperm diversification requires identifying not only mechanisms that promote lineage splitting, but also processes that increase the probability that 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 palaeobotanical evidence suggests that biotic pollination was already widespread early in angiosperm evolution (Peris et al., 2025; Negri & Toledo, 2026).

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). These mechanisms provide a direct functional
link between pollination and lineage generation.

However, enhanced reproductive divergence does not necessarily lead to
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). This
inconsistency does not necessarily contradict a predominant role of pollination in
lineage generation, because net diversification integrates both 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 influence different ecological
processes from those most directly affected by pollination. Their primary effects are
often expressed through offspring redistribution, establishment, resource acquisition,
demographic connectivity, and environmental buffering. These processes can increase
population-level persistence and therefore provide plausible mechanisms through which

newly formed lineages may survive post-divergence bottlenecks.

Approximately 60% of angiosperm species, and most woody plants, depend on biotic seed dispersal (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 similarly influence persistence-related processes by enhancing nutrient acquisition, stress tolerance, pathogen protection, and seedling performance. Arbuscular mycorrhizal symbioses, which occur in approximately 72% of angiosperm species (Tedersoo et al., 2020), are particularly widespread and can modify resource acquisition and plant–soil interactions in ways that buffer environmental variability (Peay, 2016; Tedersoo et al., 2020). At a broader biogeographic scale, 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, with subsequent consequences for patterns of diversification (Delavaux

et al., 2021). Such buffering may increase demographic stability under stochastic environmental conditions, where variation in recruitment and survival can strongly influence population persistence (Morris et al., 2008; Koons et al., 2009).

These functional tendencies are not exclusive. Pollination can also influence 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). The distinction proposed here therefore concerns predominant functional pathways rather than fixed categories of interaction effects.

Importantly, the evidence for persistence-related effects differs in scale from much of the evidence linking pollination to reproductive divergence. 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). More broadly, 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). Such results do not necessarily exclude effects on lineage persistence, because net diversification may obscure distinct or context-dependent effects on lineage generation and lineage loss. Moreover, most evidence that dispersal and mycorrhizal symbioses enhance persistence comes from ecological and population-level processes, including recruitment, range dynamics, demographic buffering, and environmental

tolerance, rather than from direct estimates of macroevolutionary extinction rates. FISS therefore does not assume that these mutualisms have already been demonstrated to reduce extinction rates. Instead, it generates the hypothesis that their effects on persistence-related ecological processes can scale up to influence lineage persistence over macroevolutionary timescales. Testing this scaling relationship is a central empirical challenge for FISS.

Functionally Integrated Symbiotic System: integration across lineage bottlenecks

The contrasting functional tendencies described above motivate the Functionally Integrated Symbiotic System (FISS), an organizational and testable hypothesis in which ecological interactions make complementary and asymmetric contributions across demographic and evolutionary bottlenecks. FISS does not refer simply to the co-occurrence of multiple mutualisms within a lineage, nor does it require coordinated coevolution, obligate interactions, or the existence of a discrete biological system. Instead, interactions are considered functionally integrated when they (i) influence distinguishable demographic or evolutionary bottlenecks, (ii) make complementary rather than fully redundant contributions across those bottlenecks, and (iii) generate joint predictions about lineage outcomes that cannot be inferred from any single interaction alone. Integration is therefore defined by functional organization rather than by taxonomic identity or physical coupling among interacting partners.

Within FISS, pollination is expected to contribute disproportionately to lineage generation through effects on mating, gene flow, and reproductive isolation, whereas

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. These roles are not exclusive. Seed dispersal and mycorrhizal symbioses may also contribute to divergence, whereas pollination may influence persistence under some ecological conditions. FISS therefore predicts differences in the relative strength of these effects rather than a strict partitioning of mutualistic functions.

Functional complementarity may also occur among interactions acting on persistence-related bottlenecks. Successful establishment requires not only that propagules reach suitable sites, but also that recruits obtain the resources and belowground associations necessary for survival. Seed dispersal and mycorrhizal symbioses may therefore influence different components of the same post-divergence filtering process. The joint dispersal of plant diaspores and mycorrhizal fungal propagules by birds provides an illustrative example of how these pathways can become ecologically coupled (Correia et al., 2019), although direct evidence that such coupling influences macroevolutionary persistence remains limited.

The central premise of FISS is that long-term diversification reflects both the generation of new lineages and their subsequent passage through persistence filters. Macroevolutionary outcomes should therefore depend not simply on the number or presence of mutualisms within a lineage, but on whether their functional effects span complementary bottlenecks associated with lineage generation and persistence. A lineage in which ecological interactions promote reproductive divergence but provide little support for establishment or persistence may experience different long-term

dynamics from one in which divergence-promoting and persistence-related functions occur together. Conversely, interactions that enhance persistence need not increase lineage generation directly to influence long-term lineage accumulation. FISS thus conceptualizes diversification as the combined outcome of lineage generation and subsequent ecological filtering.

The three mutualisms emphasized here provide an illustrative system for developing this hypothesis rather than an exhaustive definition of FISS. Other ecological interactions, including defensive mutualisms, nitrogen-fixing symbioses, antagonistic interactions, and intrinsic life-history traits, could be incorporated when they influence comparable or additional bottlenecks. The relevant unit of comparison is therefore not a fixed set of interaction types, but the functional architecture through which ecological processes affect lineage generation and persistence. The strength and configuration of these effects are expected to vary among clades, environments, and evolutionary histories.

FISS therefore makes two central predictions: ecological interactions should show asymmetric associations with lineage generation and persistence, and their joint functional configuration should provide information about long-term lineage outcomes beyond that provided by individual interactions alone. Testing this hypothesis requires separating processes associated with lineage generation from those associated with persistence and asking whether their functional organization improves explanations and predictions of macroevolutionary diversification.

Predictions and Future Directions

If long-term diversification depends on the passage of newly generated lineages through successive ecological and demographic bottlenecks, FISS generates several testable predictions.

First, ecological interactions should show asymmetric associations with lineage generation and persistence. Pollination-related traits are predicted to be more strongly associated with processes underlying lineage generation, including reproductive isolation and lineage splitting, whereas seed-dispersal and mycorrhizal traits are predicted to be more strongly associated with persistence-related processes, including establishment, spatial expansion, demographic stability, and environmental tolerance. This prediction does not require any interaction to affect only one component of diversification. Rather, FISS predicts differences in the relative strength of these associations. Comparative analyses that distinguish lineage-generation processes from persistence-related outcomes therefore provide the most direct test of the functional asymmetry proposed by FISS.

Second, the functional configuration of ecological interactions should provide information about long-term lineage outcomes beyond that provided by individual interactions alone. If different interactions influence complementary bottlenecks, their macroevolutionary consequences should depend partly on how divergence- and persistence-related functions are combined. Lineages experiencing frequent reproductive divergence may not accumulate diversity if newly generated lineages repeatedly fail during establishment or subsequent ecological filtering. Conversely,

processes that enhance persistence need not directly increase lineage generation to influence long-term diversity. FISS therefore predicts that models incorporating the joint configuration of pollination, seed dispersal, and mycorrhizal states should provide greater explanatory or predictive performance than models based on individual interactions alone. More specifically, models allowing interactions among these states should outperform purely additive models when complementarity across lineage bottlenecks contributes to long-term lineage accumulation.

A further prediction concerns evolutionary transitions in interaction architecture. Such transitions should be associated with predictable changes in the relative contributions of lineage generation and persistence. Transitions in pollination mode, dispersal strategy, or mycorrhizal association can alter the functional configuration through which lineages encounter reproductive, establishment, and persistence bottlenecks. FISS therefore predicts that transitions that modify the balance between divergence- and persistence-related functions 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 interaction architecture 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). These transitions are not expected to imply uniformly higher or lower diversification rates, but rather shifts in the relative contributions of lineage-generation and persistence-related processes.

These predictions also distinguish FISS from approaches that accommodate unmeasured diversification-rate heterogeneity without specifying its biological basis. 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 therefore provide a more direct test of the functional asymmetry and complementarity predicted by FISS. Comparisons between models incorporating observed interaction states, their combinations, and hidden sources of heterogeneity may further help determine whether the proposed functional architecture explains diversification beyond unmeasured background variation.

Orchids provide an illustrative system in which these predictions could be explored. Their combination of specialized pollination, highly dispersible seeds, and dependence on mycorrhizal fungi during germination and establishment spans processes associated with reproductive divergence, dispersal, and establishment, while 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 does not predict a single diversification outcome for such configurations. Instead, it predicts that their macroevolutionary consequences should depend on how divergence-promoting and persistence-related functions are combined and on the ecological contexts in which they operate.

The key empirical challenge is therefore to determine whether ecological interactions influence diversification primarily through independent effects or through a functional architecture spanning lineage generation and persistence. Evidence that different interaction classes show reproducible functional asymmetries, that their joint configurations provide predictive information beyond individual interactions, and that evolutionary transitions in functional architecture are associated with corresponding changes in lineage outcomes would support FISS. Conversely, the absence of consistent functional asymmetry or additional explanatory value of interaction configurations would weaken its central predictions. Together, these predictions make FISS directly falsifiable.

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 were assembled sequentially rather than appearing as a complete interaction architecture from the outset (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 interaction architectures spanning belowground resource acquisition, reproduction, and dispersal may have accumulated progressively

during angiosperm evolution. Such progressive assembly may also have generated self-reinforcing evolutionary dynamics, because diversification of angiosperms could create new ecological opportunities for their mutualistic partners, whose subsequent diversification may in turn expand the interaction opportunities available to plants (Gómez & Verdú, 2012; Peris & Condamine, 2024).

FISS also generates a historical prediction: the macroevolutionary consequences of mutualisms may have changed as complementary functions accumulated across successive lineage bottlenecks. In particular, the early origin of biotic pollination predates 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 persistence-related functions may have increased the probability that newly generated lineages established, expanded, and persisted across heterogeneous environments. Under this interpretation, changes in long-term diversification should be associated not simply with the origin of individual mutualisms, but with transitions in their broader functional configuration.

This historical interpretation remains provisional. 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 integrating fossil evidence with phylogenetic reconstructions of interaction states and explicitly asking whether the assembly of divergence- and persistence-related functions preceded shifts in lineage accumulation. Figure 2 should therefore be interpreted as a conceptual illustration of this historical prediction, rather

than as a reconstructed evolutionary pathway.

Conclusion

The evolutionary success of angiosperms cannot be understood solely from the processes that generate new lineages; it also depends on whether those lineages persist. FISS formalizes this distinction by predicting that ecological interactions contribute asymmetrically to lineage generation and persistence. Pollination is expected to be more directly associated with lineage generation through reproductive isolation, whereas seed dispersal and mycorrhizal symbioses may contribute more strongly to persistence-related processes through establishment, spatial expansion, demographic stability, and environmental buffering.

The central proposition of FISS is therefore not simply that multiple mutualisms matter, but that their functional configuration across lineage-generation and persistence bottlenecks provides information that is lost when interactions are considered independently. The three mutualisms emphasized here provide an illustrative rather than exhaustive system for testing this idea. More generally, FISS predicts that long-term lineage accumulation should reflect both functional asymmetry among ecological interactions and complementarity across successive lineage bottlenecks.

Whether this functional organization contributes substantially to macroevolutionary diversification remains an empirical question. Reproducible asymmetries between interactions associated with lineage generation and persistence, together with additional explanatory or predictive information from their joint

configurations, would support FISS; the absence of these patterns would weaken its central predictions. More broadly, FISS provides a testable way to examine how ecological interactions acting at different stages of organismal life cycles combine to shape the long-term generation and maintenance of biological 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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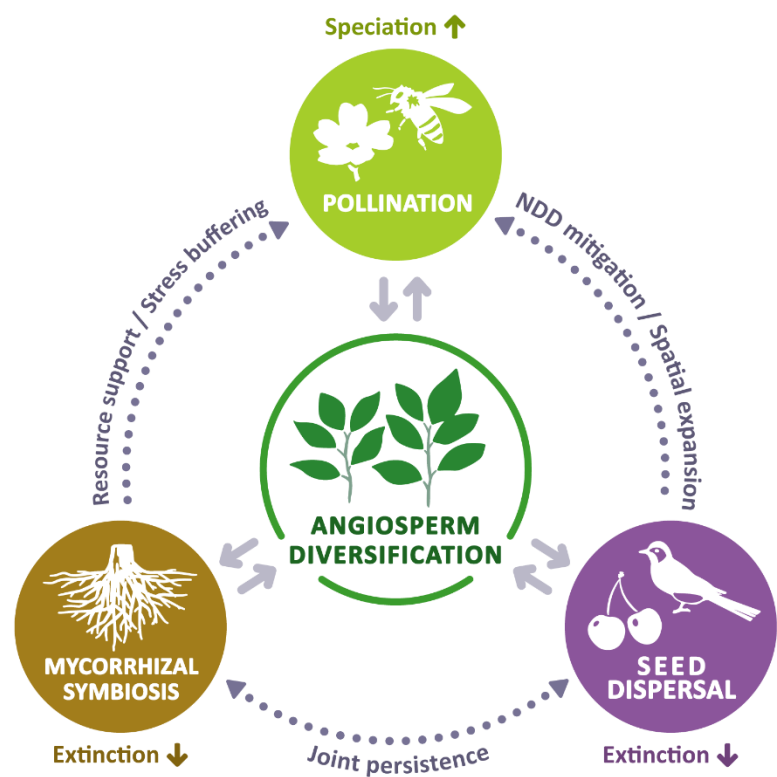
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Functionally Integrated Symbiotic System

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

629 FISS predicts that different ecological interactions contribute asymmetrically across
630 successive lineage bottlenecks. Solid arrows indicate hypothesized associations between
631 major mutualisms and diversification-related processes, whereas dashed arrows indicate
632 potential ecological linkages among interactions. Labels on dashed arrows denote
633 representative ecological processes, including environmental buffering, establishment
634 facilitation, and negative density dependence (NDD). These arrows represent

635 hypothesized tendencies rather than demonstrated causal effects. The framework
636 emphasizes that long-term diversification dynamics may depend on the complementary
637 functions performed by multiple mutualisms, rather than on the isolated effects of any
638 single interaction. Unlike ecological syndromes that describe recurring combinations of
639 traits or interactions, FISS focuses on how different mutualisms contribute to distinct
640 but complementary processes of lineage divergence and persistence. Accordingly, FISS
641 is presented as a conceptual framework for organizing potential macroevolutionary
642 influences of multiple mutualisms, rather than as a coordinated interaction network, a
643 discrete evolutionary unit, or an independently operating causal mechanism (Box 1).

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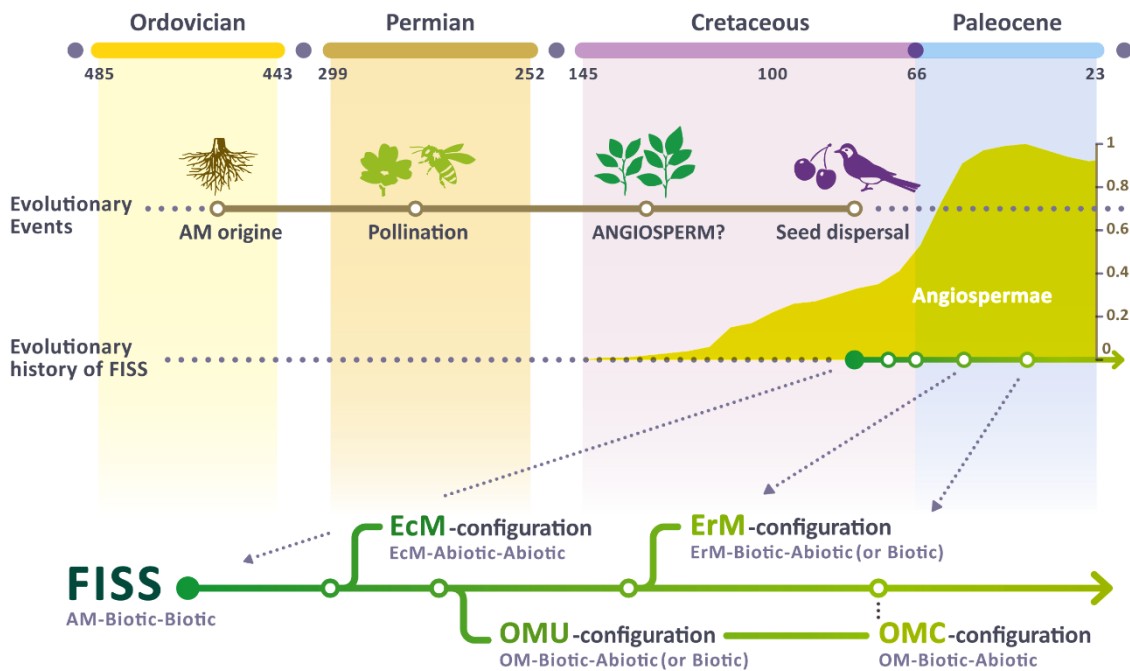


Figure 2. Hypothesized temporal assembly of alternative interaction configurations under FISS.

The figure illustrates how combinations of mycorrhizal symbioses, pollination, and seed-dispersal mutualisms may contribute to complementary processes of lineage divergence and persistence during angiosperm evolution. Interaction configurations are defined by combinations of mycorrhizal association, pollination mode, and seed-dispersal mode, listed in this order. The AM–biotic pollination–biotic seed dispersal configuration is presented as a representative mutualistic configuration potentially associated with complementary diversification-related processes, whereas EcM-, ErM-, and OM-dominated configurations represent alternative interaction architectures 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, respectively. Connections among

659 configurations are included solely to illustrate potential transitions among alternative
660 mutualistic configurations within the FISS framework. They should not be interpreted
661 as reconstructed evolutionary pathways or as direct evidence of historical evolutionary
662 relationships.

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

Alternative combinations of pollination mode, seed-dispersal mode, and mycorrhizal association may make different contributions to lineage generation and persistence. The configurations shown here are illustrative conceptual hypotheses rather than discrete empirical categories or quantitative predictions. No configuration is assumed to be universally optimal, and the relative strength of each contribution is expected to vary among lineages and environmental contexts.

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	EcM associations may enhance resource acquisition and environmental tolerance, potentially strengthening

				ecological differentiation 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.

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

669 persistence

670 The relationships summarized here represent hypothesized predominant functional tendencies rather than fixed classifications or
671 quantitative effect sizes. Each interaction may influence both lineage generation and persistence, and its relative contribution is expected
672 to vary among lineages, environments, and ecological contexts.

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);

nati on mut ualis ms	transfer and mate choice	ge gener ation	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)
See d- disp ersal mut ualis ms	Spatial redistrib ution of offsprin g	Persis tence - relate d proce sses	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.

orrh izal sym bios es	e acquisiti on, establish ment, and stress bufferin g	tence - relate d proce sses	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): an organizational and testable hypothesis

Why FISS?

Multiple ecological interactions can influence diversification, but their effects need not operate through the same processes. FISS focuses on whether different interactions make asymmetric and complementary contributions to lineage generation and persistence. Its novelty therefore lies not in arguing that multiple mutualisms matter, but in organizing their effects according to the demographic and evolutionary bottlenecks through which they act.

Operational definition of functional integration

FISS does not require coordinated coevolution, obligate interactions, or the existence of a discrete biological system. Interactions are considered functionally integrated when they (i) influence distinguishable demographic or evolutionary bottlenecks, (ii) make complementary rather than fully redundant contributions across those bottlenecks, and (iii) generate joint predictions about lineage outcomes that cannot be inferred from any single interaction alone.

Asymmetric functional contributions

FISS predicts differences in the predominant contributions of ecological interactions to diversification. Pollination is expected to contribute more strongly to lineage generation through effects on mating, gene flow, and reproductive isolation, whereas seed dispersal and mycorrhizal symbioses are expected to contribute more strongly to persistence-related processes through establishment, spatial expansion, demographic connectivity, resource acquisition, and environmental buffering. These roles are not exclusive; the hypothesis predicts differences in relative effect strength rather than a strict partitioning of functions.

Functional complementarity across lineage bottlenecks

Long-term diversification depends not only on the generation of new lineages, but also on their passage through subsequent ecological and demographic filters. Interactions promoting reproductive divergence may therefore have different long-term consequences depending on whether other ecological processes facilitate establishment and persistence. Similarly, persistence-related interactions need not directly increase lineage generation to influence long-term lineage accumulation. FISS thus predicts that functional configurations spanning complementary bottlenecks may have macroevolutionary consequences that are not captured by individual interactions alone.

Dependence on interaction configuration

FISS does not predict a universally optimal combination of mutualisms. The consequences of a given configuration should depend on the strength and combination

of divergence- and persistence-related functions, as well as on phylogenetic and environmental context. Pollination, seed dispersal, and mycorrhizal symbioses provide an illustrative system for testing this hypothesis rather than an exhaustive set of interactions relevant to diversification (Table 1).

Distinction from ecological syndromes

Ecological and evolutionary syndromes generally describe recurrent combinations of traits or interactions within lineages. FISS instead concerns the functional distribution of ecological effects across different components of diversification. Its central prediction is therefore not that particular interaction types should repeatedly co-occur, but that interactions associated with lineage generation and those associated with persistence should show reproducible functional asymmetries and complementary effects on long-term lineage outcomes.

How can FISS be tested?

FISS predicts that (i) ecological interactions will differ systematically in the relative strength of their associations with lineage generation and persistence, and (ii) models incorporating their functional configuration will provide greater explanatory or predictive information than models based on individual interactions alone. Failure to detect either pattern would provide evidence against the central predictions of FISS.