Rethinking angiosperm diversification through the functional integration of mutualisms

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Abstract

Flowering plants have maintained exceptional diversity for over 100 million years despite repeated environmental change and mass extinction events. A central challenge in plant macroevolution is understanding how lineages achieve both extensive diversification and long-term persistence. While pollination, seed dispersal, and mycorrhizal symbioses are recognized as key drivers of plant evolution, they are typically studied in isolation, limiting our understanding of how their combined effects influence diversification dynamics. Here, I propose that angiosperm diversification may be better understood through a framework that considers the functional integration of multiple mutualisms operating across the plant life cycle. Within this framework, pollination is expected to contribute disproportionately to lineage divergence through reproductive isolation, whereas seed dispersal and mycorrhizal symbioses may contribute more strongly to lineage persistence by enhancing establishment success, spatial expansion, environmental buffering, and recovery from disturbance. Importantly, these mutualisms are unlikely to act independently; instead, their interactions may generate functional complementarity across life-history stages, potentially coupling processes of diversification and persistence. I term this organizational hypothesis a Functionally Integrated Symbiotic System (FISS), a conceptual framework for understanding how multiple mutualisms may collectively influence lineage divergence and persistence across evolutionary timescales. By shifting attention from pairwise interactions to the higher-order organization of symbiotic systems, FISS generates testable predictions regarding how alternative mutualistic configurations may influence diversification and persistence in angiosperms. More broadly, this framework suggests that large-scale evolutionary dynamics may emerge from the hierarchical integration of ecological interactions into coordinated functional systems, and provides an organizational perspective for interpreting how multiple mutualisms may jointly shape macroevolutionary patterns.

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

Introduction

Flowering plants (angiosperms) dominate terrestrial ecosystems and have sustained extraordinary species diversity for over 100 million years, marking one of the most consequential macroevolutionary transitions in the history of life (Benton et al., 2022; Ding et al., 2025). Throughout their evolutionary history, angiosperms repeatedly diversified while persisting across heterogeneous and fluctuating environments, despite classical evolutionary theory predicting a fundamental trade-off between speciation and extinction. Processes that promote speciation, such as ecological specialization and population subdivision, also tend to increase extinction risk (Van Valen, 1976; Bell, 1982; Lancaster, 2010; Rabosky, 2013). How angiosperms have been able to relax this trade-off and maintain long-term diversification dynamics remains a central and unresolved problem in evolutionary biology.

Angiosperm diversification has traditionally been explained by morphological key innovations, environmental change, and ecological opportunity, often considered independently or in combination (Donoghue & Sanderson, 2015; Helmstetter et al., 2023; Ding et al., 2025). Increasing evidence indicates that mutualistic interactions, including pollination, seed dispersal, and mycorrhizal symbioses, have also played important roles by reshaping ecological opportunities and influencing lineage persistence (Hodges et al., 1995; Tiffney & Mazer, 1995; Benton et al., 2022; Peris et al., 2025). Most angiosperms engage in multiple mutualisms across their life cycle, yet empirical studies have typically examined these interactions in isolation, limiting our ability to understand their combined macroevolutionary consequences. This is particularly relevant because diversification depends not only on lineage splitting, but also on the persistence of newly formed lineages through post-divergence stages, which are likely influenced by different mutualistic processes. Accumulating evidence suggests that mutualisms can affect both reproduction and establishment, as well as dispersal and stress tolerance, indicating that their effects may be complementary across different stages of lineage formation and persistence. This motivates a conceptual framework that explicitly links multiple mutualistic interactions to the coupled processes of lineage divergence and persistence over macroevolutionary timescales.

Existing studies have largely evaluated pollination, seed dispersal, and mycorrhizal symbioses as independent drivers of diversification. However, diversification is ultimately a demographic process requiring both lineage divergence and persistence through vulnerable post-divergence stages. A framework focusing on individual mutualisms alone may therefore overlook how different interactions contribute to distinct components of diversification dynamics.

This Review synthesizes evidence that major angiosperm mutualisms differentially influence lineage divergence and persistence. These interactions are integrated in the Functionally Integrated Symbiotic System (FISS), a conceptual framework describing how multiple mutualisms jointly shape lineage formation and long-term persistence. Here, “integration” is used in a functional sense, referring to complementary effects across ecological and evolutionary scales, rather than tightly coevolved or obligatorily coordinated networks. Diversification and persistence are fundamentally asymmetric outcomes of mutualistic interactions. Diversification reflects contingent lineage-splitting processes associated with reproductive isolation and trait divergence, whereas persistence reflects cumulative, state-dependent processes governing long-term lineage survival. Because these processes differ in their temporal and spatial scales and are underpinned by partially distinct ecological mechanisms, the same mutualistic interactions cannot be assumed to exert equivalent or predictably coupled effects on both outcomes. This asymmetry implies that macroevolutionary success cannot be inferred from diversification processes alone, but instead emerges from their interaction with persistence filters. Within this framework, pollination is primarily associated with lineage divergence, whereas seed dispersal and mycorrhizal symbioses more often may contribute to persistence through establishment, spatial expansion, and environmental buffering. Rather than contributing additively to a single adaptive outcome, these mutualisms structure a post-diversification filtering process in which only a subset of diverged lineages transitions into long-term persistence. Their combined effects therefore link, but do not equate, diversification and persistence, generating an inherent asymmetry in how mutualistic interactions scale from lineage formation to macroevolutionary success.

Decoupling of Speciation and Persistence

Macroevolutionary theory has long recognized a frequently discussed tension between speciation and extinction dynamics (Stanley 1979; Rabosky 2010). Processes that promote lineage splitting, such as ecological specialization, assortative mating, habitat subdivision, and geographic isolation, often simultaneously increase extinction risk because newly diverged lineages tend to occur as small, spatially restricted, and demographically vulnerable populations (Futuyma & Moreno 1988; Owens & Bennett

2000; Dynesius & Jansson 2000). In many cases, divergence is associated with reduced geographic ranges, increased habitat specialization, and heightened sensitivity to environmental variability and disturbance, all of which can elevate the probability of lineage loss before long-term establishment (Davies et al. 2004; Vamosi & Vamosi 2010). As a consequence, elevated speciation rates do not necessarily translate into long-term diversification dynamics over macroevolutionary timescales (Ricklefs 2007; Rabosky 2013). Rapid lineage formation may instead generate high lineage turnover if newly formed populations fail to persist through ecological or demographic bottlenecks. Long-term diversification dynamics therefore depend not only on the generation of new lineages, but also on the ecological and demographic processes that govern their persistence after divergence.

However, this classical view assumes a relatively tight coupling between speciation and extinction processes that may not hold universally across lineages. Yet angiosperm lineages frequently exhibit both rapid lineage formation and long-term persistence across highly heterogeneous and fluctuating environments (Crepet & Niklas 2009; Sauquet & Magallón 2018). This pattern suggests that certain ecological processes may decouple the relationship between lineage splitting and extinction risk in angiosperms, thereby supporting sustained diversification over evolutionary timescales. Identifying the mechanisms that relax this coupling is therefore essential for understanding long-term macroevolutionary dynamics.

Pollination as divergence mechanism

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, pollination mutualisms are considered major drivers of reproductive isolation and floral diversification. Most angiosperms depend on animal-mediated pollination for reproduction (Ollerton, 2017; Stephens et al., 2023; Tong et al., 2023; Peris et al., 2025), and palaeobotanical evidence suggests that early flowering plants were likely already associated with biotic pollination systems (Brundrett, 2002; Peris et al., 2025; Negri & Toledo, 2025).

Empirical and comparative studies have shown that pollination-related traits can promote reproductive isolation and lineage splitting through pollinator shifts and floral divergence (Grant & Grant, 1965; van der Niet et al., 2014; Serrano-Serrano et al., 2017; Barreto et al., 2024; Dorey & Schiestl, 2024). Changes in pollinator behavior and floral traits can generate assortative pollen transfer and reduce gene flow among populations, thereby facilitating reproductive divergence (Waser et al., 1996; Chittka et al., 1999; Muchhala & Potts, 2007; Kay & Sargent, 2009). However, evidence that pollination alone consistently leads to elevated long-term net diversification remains mixed (Sargent, 2004; O'Meara et al., 2016; Peris et al., 2025). While pollination mutualisms can promote lineage splitting, their effects on long-term diversification may vary depending on ecological context and the degree of specialization. Highly specialized pollination systems may become sensitive to partner loss and environmental fluctuations, and may in some cases be associated with elevated lineage turnover rather than sustained net diversification (Janzen, 1979; Herre et al., 2008; Nee, 2001). Thus, associations between pollination specialization and diversification remain heterogeneous across clades and ecological contexts. These findings suggest that pollination mutualisms are often more directly associated with lineage splitting, but are unlikely to fully explain long-term angiosperm diversification in isolation.

Dispersal and Mycorrhiza as persistence mechanisms

In contrast to pollination mutualisms, which are more consistently associated with lineage splitting, seed-dispersal and mycorrhizal mutualisms appear to influence angiosperm diversification mainly by contributing to persistence-related processes. Approximately 60% of angiosperm species, and most woody plants, depend on biotic seed dispersal (Yamawo & Ohno, 2024; Jin et al., 2026). Animal-mediated dispersal promotes persistence by reducing density-dependent mortality near conspecific adults (Janzen, 1970; Connell, 1971; Comita et al., 2014), increasing spatial spread and recolonization, and maintaining genetic connectivity among populations (Levin et al., 2003, 2005; Beckman & Sullivan, 2023). By increasing colonization success and demographic connectivity across heterogeneous landscapes, dispersal may also facilitate metapopulation persistence and environmental tracking under fluctuating conditions (Snäll et al., 2005; Sexton et al., 2009; Thompson et al., 2017). Larger and more connected geographic ranges are generally associated with reduced extinction risk, suggesting that dispersal-mediated range dynamics can substantially influence long-term lineage survival (Sheth et al., 2020).

Similarly, arbuscular mycorrhizal (AM) symbioses, which occur in approximately 72% of angiosperm species (Tedersoo et al., 2020), enhance resource acquisition, stress tolerance, and seedling establishment, thereby buffering environmental variability and demographic instability (Peay, 2016; Tedersoo et al., 2020). Such buffering effects may be particularly important in stochastic environments, where demographic stability and stress tolerance can strongly influence persistence probabilities over long timescales (Morris et al., 2008; Koons et al., 2009).

Although pollination mutualisms may also contribute to persistence under some ecological contexts (Johnson et al., 2022), these effects appear highly context dependent and are often counterbalanced by demographic vulnerability associated with specialization. In contrast, seed dispersal and mycorrhizal symbioses more consistently influence processes directly associated with lineage persistence, including establishment success, spatial stability, and population maintenance.

Evidence that seed dispersal and mycorrhizal mutualisms independently increase speciation remains limited. Comparative analyses often detect weak or inconsistent associations between dispersal mode, mycorrhizal type, and diversification rates across angiosperms (Reginato et al., 2020; Feijen et al., 2018; Jin et al., 2026). Instead, available evidence suggests that these mutualisms primarily reduce extinction risk and stabilize lineages after origination rather than directly driving lineage splitting. Their macroevolutionary significance may therefore lie in maintaining newly diverged lineages long enough for diversification to accumulate over evolutionary timescales. Because extinction disproportionately removes newly originated, geographically restricted, and demographically unstable lineages, even modest increases in persistence may substantially alter long-term net diversification trajectories. Comparative and theoretical studies increasingly suggest that lineage persistence depends strongly on geographic range dynamics, demographic buffering, and the capacity to track environmental change across heterogeneous landscapes (Sexton et al., 2009; Hagen et al., 2018; Sheth et al., 2020). Although most available evidence concerns population-level persistence, these processes are hypothesized to scale up to lineage persistence over macroevolutionary timescales.

Integration across lineage bottlenecks

Why individual mutualisms may be insufficient

Diversification depends not only on lineage divergence, but also on lineage persistence. However, most mutualism-based hypotheses have focused on individual interactions in isolation. Pollination is often associated with reproductive divergence, whereas seed dispersal and mycorrhizal symbioses are more frequently linked to establishment success and persistence. Because different mutualisms influence different components of diversification, their macroevolutionary consequences cannot be fully understood when considered separately. This motivates a framework that explicitly links multiple mutualisms to both lineage divergence and persistence.

Integration across demographic bottlenecks

Rather than forming a tightly coevolved or discrete biological system, integration arises because different mutualisms act on successive ecological and demographic bottlenecks that jointly determine lineage outcomes. Comparative and phylogenetic evidence suggests that pollination, seed dispersal, and mycorrhizal symbioses influence distinct components of angiosperm diversification (Table S1), generating effects that are not predictable from any single interaction in isolation.

Although pollination, seed dispersal, and mycorrhizal symbioses are discussed here in terms of their predominant functional roles in lineage divergence and persistence, we acknowledge that these interactions are not strictly partitioned. Seed dispersal and mycorrhizal symbioses can also contribute to speciation through processes such as range fragmentation, ecological differentiation, and local adaptation, whereas pollination systems may in some cases enhance persistence by stabilizing reproductive success and buffering demographic stochasticity. However, these effects are generally context-dependent and appear secondary to their primary roles in shaping diversification dynamics across successive demographic bottlenecks. This conceptual simplification is adopted to clarify the predominant functional contributions of each mutualism to different stages of diversification.

Pollination is primarily associated with reproductive isolation and lineage splitting through floral divergence and pollinator-mediated assortative mating (Grant & Grant, 1965; van der Niet et al., 2014; Serrano-Serrano et al., 2017; Barreto et al., 2024; Dorey & Schiestl, 2024). In contrast, seed dispersal and mycorrhizal symbioses more strongly influence post-divergence persistence by enhancing spatial expansion, establishment success, and demographic stability. Seed dispersal reduces extinction risk by facilitating colonization and metapopulation connectivity (Janzen, 1970; Connell, 1971; Levin et al., 2003; Beckman & Sullivan, 2023), whereas mycorrhizal symbioses buffer environmental stress and improve recruitment and survival (Peay, 2016; Tedersoo et al., 2020). Because establishment success depends on both dispersal and belowground symbiosis, these interactions jointly stabilize newly diverged lineages during vulnerable post-divergence stages. Evidence that birds can collectively disperse plant diaspores and mycorrhizal fungal propagules further suggests that these interactions may sometimes operate in coordinated persistence systems (Correia et al., 2019).

Together, these mutualisms define a sequential filtering process in which pollination generates lineage divergence, while seed dispersal and mycorrhizal symbioses determine whether diverged lineages persist. Without these persistence-enhancing processes, many newly formed lineages would remain demographically fragile and prone to extinction despite successful divergence.

Functionally Integrated Symbiotic System hypothesis

The evidence above indicates that angiosperm diversification cannot be fully explained by any single mutualism in isolation. Instead, diversification dynamics emerge from how multiple mutualisms influence distinct stages of lineage formation and persistence across ecological scales.

Here, I propose the Functionally Integrated Symbiotic System (FISS) hypothesis as a conceptual framework describing how multiple mutualisms may collectively contribute to lineage divergence and persistence across ecological scales.

FISS is not a hypothesis about individual mutualisms, but about the organization of multiple mutualisms across successive stages of lineage formation and persistence. Importantly, FISS is not simply the co-occurrence of multiple mutualisms within a lineage, nor is it a coordinated interaction network in which mutualisms evolve as a single integrated unit. Instead, FISS refers to a functional organization in which different mutualisms disproportionately influence different stages of lineage formation and persistence. FISS does not assume coordinated coevolution, obligate interactions, or a discrete biological system. Rather, it describes a functional organization in which distinct mutualisms operate across successive demographic and ecological bottlenecks associated with lineage divergence and persistence. Within this framework, mutualisms are defined by their functional contributions to diversification dynamics rather than by their taxonomic identity. Pollination is more frequently associated with lineage splitting through reproductive isolation, whereas seed dispersal and mycorrhizal symbioses primarily enhance persistence by stabilizing establishment, survival, and spatial expansion. Diversification may therefore reflect not only lineage generation but also the filtering of lineages through persistence constraints. The central premise of FISS is that diversification outcomes depend not only on the presence of multiple mutualisms, but also on how their functions are organized across successive stages of lineage formation and persistence. FISS does not require either specialized or obligate interactions. Both specialized and generalized interactions may contribute when they influence distinct demographic or ecological bottlenecks associated with lineage divergence and persistence. These differences should therefore be viewed as variations in degree rather than discrete categories.

The influence of FISS is expected to vary among clades and environments, depending on ecological context and evolutionary history. Fossil and phylogenetic evidence suggests that diversification in pollinating insects, seed-dispersing animals, and mycorrhizal fungi broadly coincided with angiosperm diversification (Grimaldi & Engel, 2005; Condamine et al., 2016; Gómez & Verdú, 2012; Onstein et al., 2017; Peris & Condamine, 2024), consistent with long-term reciprocal diversification dynamics. Although largely correlational, these patterns provide a plausible evolutionary context for interaction-mediated macroevolutionary processes. These processes operate alongside abiotic change, genomic innovation, and ecological opportunity. However, their key role is to reduce the coupling between lineage divergence and extinction vulnerability. By increasing the probability that newly diverged lineages persist through post-divergence bottlenecks, FISS provides a conceptual framework linking multiple mutualisms to long-term macroevolutionary diversification (Figure 1: Box 1). FISS should therefore be viewed primarily as an organizational hypothesis that provides a framework for interpreting how multiple mutualisms may collectively influence diversification-related processes, rather than as a discrete evolutionary mechanism or a self-contained causal explanation of diversification.

Predictions and Future Directions

If diversification depends on passage through successive lineage bottlenecks, several testable predictions follow.

First, diversification may be better explained by configurations of mutualistic interactions than by any single mutualism alone. Because pollination, seed dispersal, and mycorrhizal symbioses influence different components of diversification, models incorporating combinations of these interactions are expected to show higher explanatory performance than single-mutualism models in accounting for angiosperm diversification patterns (Hodges et al., 1995; Tiffney & Mazer, 1995; Tedersoo et al., 2020; Benton et al., 2022). This reflects their distinct roles in reproductive divergence, establishment success, and lineage persistence.

Second, diversification may be higher when divergence-promoting and persistence-promoting mutualisms co-occur. Pollination-driven lineage splitting alone may not consistently lead to elevated long-term diversification unless accompanied by mechanisms that enhance persistence. In contrast, lineages combining reproductive isolation with effective seed dispersal and mycorrhizal symbioses are expected to show higher net diversification over macroevolutionary timescales (Levin et al., 2003; Beckman & Sullivan, 2023; Peay, 2016; Tedersoo et al., 2020). Such lineages lacking persistence-promoting mutualisms are instead expected to experience higher extinction risk and evolutionary turnover (Howe & Smallwood, 1982).

Third, specific combinations of pollination mode, seed dispersal strategy, and mycorrhizal association may be overrepresented among species-rich angiosperm clades. Interaction architectures that jointly enhance reproductive isolation, colonization capacity, and environmental buffering are expected to shape extant diversity patterns. This expectation is consistent with evidence that biotic pollination, biotic seed dispersal, and arbuscular mycorrhizal associations are common among extant tree species and become increasingly dominant toward lower latitudes (Yamawo & Ohno, 2024).

These predictions can be evaluated by examining whether transitions among alternative interaction-system architectures are associated with shifts in diversification dynamics. Comparative analyses suggest that transitions among arbuscular (AM), ectomycorrhizal (EcM), ericoid (ErM), and orchid mycorrhizal (OM) systems may correspond to distinct diversification trajectories (Cairney & Meharg, 2003; Tedersoo & Smith, 2013; Givnish et al., 2015).

Orchids may provide a clear illustrative example, as their combination of specialized pollination, wind dispersal, and orchid mycorrhizal symbioses is associated with rapid diversification and elevated turnover in epiphytic lineages (Gamisch & Comes, 2019; Pérez-Escobar et al., 2024). By framing diversification as the outcome of multiple mutualisms operating across successive demographic and ecological bottlenecks, the FISS hypothesis provides a structured framework for evaluating how interaction-system architectures may shape macroevolutionary dynamics across angiosperms.

Evolutionary assembly and temporal dynamics of FISS

Growing evidence suggests that major plant mutualisms have not evolved independently but are instead linked through recurrent evolutionary associations among belowground and aboveground interactions. From the perspective of the Functionally Integrated Symbiotic System (FISS) framework, the evolutionary history of angiosperms can therefore be viewed not as a sequence of independent mutualistic innovations, but as a process shaped by the progressive accumulation and functional complementarity of multiple mutualisms (Figure 2).

Arbuscular mycorrhizal symbioses originated early in land plant evolution, likely during initial terrestrialization (Remy et al., 1994; Brundrett, 2002; Strullu-Derrien et al., 2018). Angiosperms later emerged and early lineages were already associated with biotic pollination (Stephens et al., 2023). Subsequently, animal-mediated seed dispersal expanded, accompanied by increased prevalence of fleshy fruits and frugivory (Tiffney & Mazer, 1995; Eriksson et al., 2000; Jin et al., 2026). This stepwise accumulation of mutualisms may have progressively expanded the ecological and evolutionary conditions under which angiosperm lineages could persist and diversify.

This framework may also help explain the decoupling between the origin of biotic pollination and the later rise in angiosperm diversification rates (Benton et al., 2022; Ding et al., 2025). Although pollination mutualisms originated early, elevated net diversification is mainly observed later in angiosperm evolution (Benton et al., 2022; Ding et al., 2025). Pollination alone may therefore not have been sufficient to sustain long-term diversification unless coupled with mutualisms associated with persistence-related processes operating across later lineage bottlenecks. The subsequent expansion of seed dispersal mechanisms may have increased the probability that newly diverged lineages persisted across heterogeneous and fluctuating environments.

Major phases of angiosperm radiation can thus be interpreted not as outcomes of isolated innovations, but as the result of increasingly complementary mutualistic interactions acting across lineage formation and persistence. This interpretation remains provisional, yet it provides a broader organizational perspective for understanding long-term diversification dynamics in angiosperms. These historical associations remain largely correlational and do not demonstrate coordinated macroevolutionary dynamics. Future work integrating phylogenetic comparative methods and fossil evidence will be necessary to test whether and how mutualistic interactions have shaped diversification and persistence across macroevolutionary timescales.

Conclusion

The extraordinary diversification of angiosperms remains one of the central questions in evolutionary biology. While pollination, seed dispersal, and mycorrhizal symbiosis have each been linked to diversification, their evolutionary consequences are typically considered independently. Here, we propose the Functionally Integrated Symbiotic System (FISS) hypothesis, which suggests that diversification may depend on the complementary effects of multiple mutualisms acting across different stages of lineage formation and persistence.

Within this framework, pollination is more frequently associated with lineage divergence, whereas seed dispersal and mycorrhizal symbiosis are more often associated with establishment success, environmental tolerance, and lineage persistence. The FISS framework proposes that functional integration may arise because these interactions influence different demographic and ecological bottlenecks across the plant life cycle, collectively reducing the coupling between lineage divergence and extinction vulnerability. The value of the FISS framework lies not in identifying additional mutualisms, but in providing an organizational perspective that links complementary mutualistic functions to distinct stages of lineage divergence and persistence. Testing this hypothesis may provide a new perspective on the evolutionary success of flowering plants and the broader role of ecological interactions in macroevolution. More broadly, the FISS framework suggests that diversification may emerge from the functional organization of interactions acting across successive stages of lineage formation and persistence, a possibility that could extend beyond plant mutualisms to other complex ecological systems. Future comparative analyses of mutualistic configurations across lineages may help determine whether diversification is better explained by individual mutualisms or by their functional organization within lineages.

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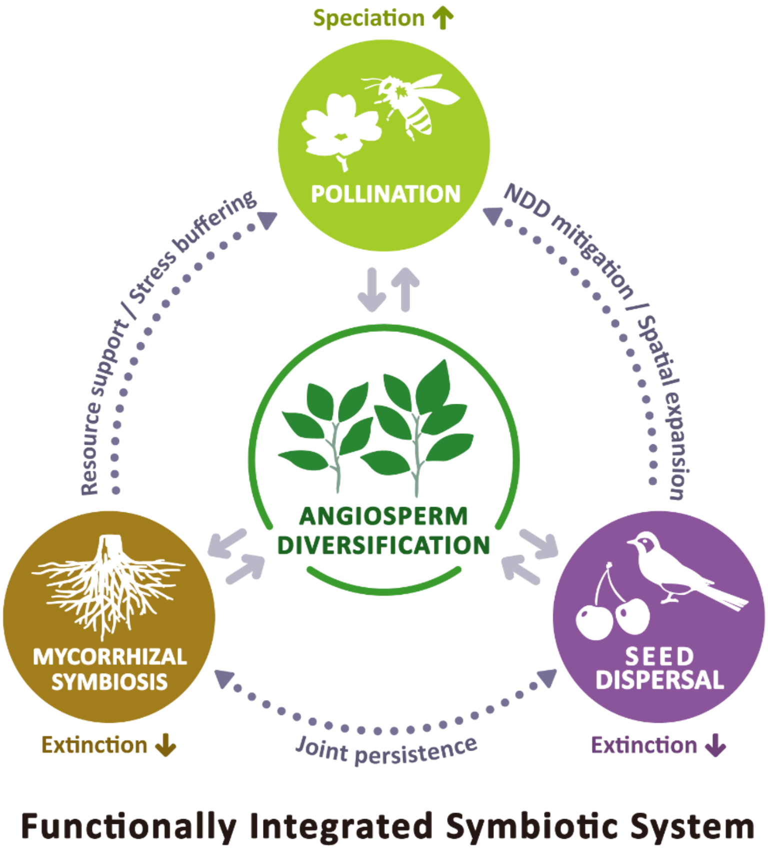

Figure 1. The Functionally Integrated Symbiotic System (FISS) hypothesis as a conceptual framework of complementary mutualisms

Conceptual illustration of the FISS hypothesis, in which angiosperm diversification may reflect the combined and partially complementary influences of mycorrhizal symbioses, pollination, and seed dispersal across different stages of lineage divergence and persistence. Solid arrows represent hypothesized associations between mutualisms and diversification-related processes, whereas dashed arrows indicate potential ecological associations among interactions. These arrows indicate hypothesized tendencies rather than demonstrated causal effects. Labels on dashed arrows denote representative ecological processes (e.g., environmental buffering, establishment facilitation, and negative density dependence, NDD). The framework emphasizes that long-term diversification dynamics may depend on the complementary functions performed by multiple mutualisms rather than on the isolated effects of any single interaction. Unlike ecological syndromes that describe recurring combinations of traits or interactions, the FISS framework focuses on how different mutualisms contribute to distinct but complementary processes of lineage divergence and persistence. Accordingly, FISS is presented as a conceptual framework for organizing potential macroevolutionary influences of multiple mutualisms rather than as a coordinated interaction network, a discrete evolutionary unit, or an independently operating causal mechanism (Box 1).

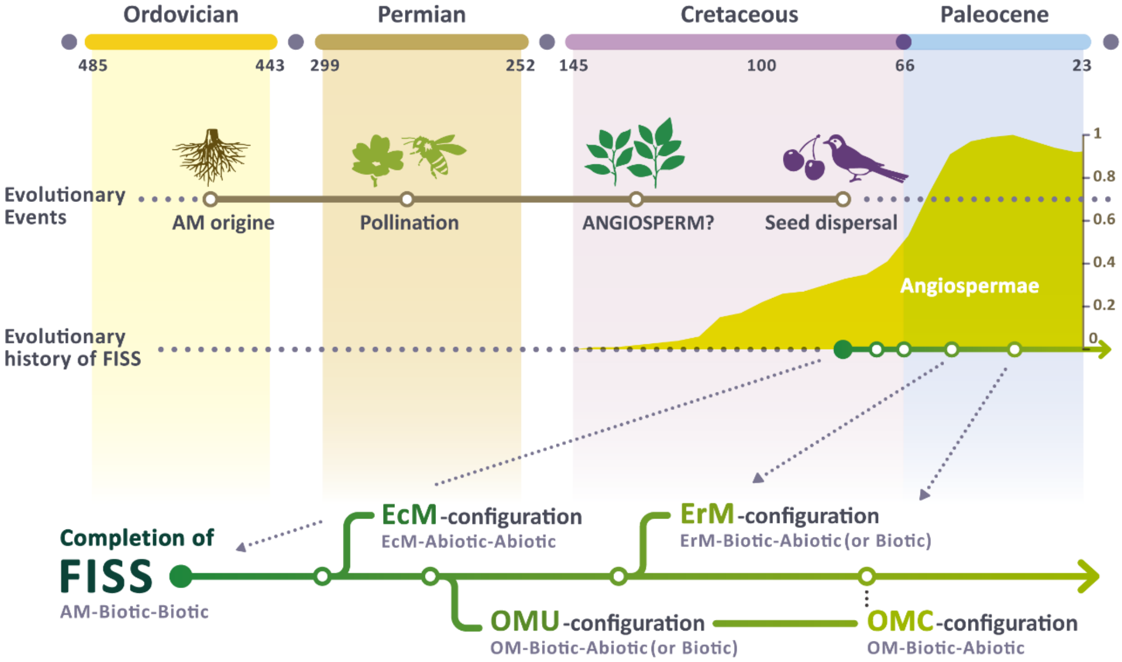

Figure 2. Conceptual illustration of alternative mutualistic configurations within the Functionally Integrated Symbiotic Systems (FISS) framework.

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 example of a mutualistic configuration potentially associated with complementary diversification-related processes, whereas EcM-dominated, ErM-dominated, and orchid mycorrhizal (OM)-dominated configurations represent alternative interaction configurations that may be associated with different diversification tendencies (Table 1). Orchid OMF- and OMC-dominated configurations represent conceptual understory and canopy orchid systems, respectively.

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

Table 1. Hypothetical examples of how alternative combinations of mutualisms may differentially influence lineage divergence and persistence. Interaction combinations shown here are intended as illustrative conceptual hypotheses rather than discrete empirical categories or quantitative predictions. Diversification tendencies are simplified representations of hypothesized ecological and evolutionary tendencies, and substantial variation is expected across lineages and environmental contexts. Interaction contexts are simplified and not mutually exclusive.

Interaction context	**Primary pollination mode**	**Seed dispersal mode**	**Mycorrhizal association**	**Hypothesized macroevolutionary outcome**
Canonical angiosperm mutualism configuration	Biotic pollination	Animal-mediated	Arbuscular mycorrhiza	May promote lineage persistence through enhanced establishment, demographic buffering, and spatial spread.

Interaction context	**Primary pollination mode**	**Seed dispersal mode**	**Mycorrhizal association**	**Hypothesized macroevolutionary outcome**
Ectomycorrhizal (EcM)-dominated configuration	Predominantly wind pollination	Gravity and wind	Ectomycorrhiza	May favor persistence and environmental tolerance more strongly than rapid lineage divergence.
Ericoid mycorrhizal (ErM)-dominated configuration	Biotic pollination (mainly insects)	Gravity- or animal-mediated	Ericoid mycorrhiza	May promote reproductive divergence under strong nutrient limitation, while persistence could be facilitated by specialized nutrient-acquisition strategies and tolerance to stressful environments.
Orchid OMF understory-dominated configuration	Reduced or highly specialized biotic	Wind or animal-mediated	Orchid mycorrhiza (Basidiomycota; often	Specialized pollination and ecological specialization may be associated with elevated lineage divergence, whereas strong symbiotic

Interaction context	Primary pollination mode	Seed dispersal mode	Mycorrhizal association	Hypothesized macroevolutionary outcome
	pollination (often Hymenoptera)		linked to EcM networks)	dependence and demographic sensitivity could increase vulnerability to lineage loss and turnover.
Orchid OMC epiphytic canopy-dominated configuration	Highly specialized biotic pollination (often Hymenoptera)	Wind dispersal	Orchid mycorrhiza (Basidiomycota; weak or no soil EcM connection)	Strong reproductive isolation and ecological opportunity potentially contribute to elevated lineage turnover, although dependence on specialized ecological conditions could also increase environmental and demographic vulnerability.

Table S1. Illustrative conceptual summary of the hypothesized macroevolutionary influences of major plant mutualisms. The relationships summarized here are intended as conceptual syntheses rather than quantitative estimates or discrete empirical classifications. Reported influences are expected to vary substantially across lineages, environments, and interaction contexts.

Mutualistic interaction	Primary ecological function	Primary macroevolutionary tendency	Potential influence on lineage divergence	Potential influence on lineage persistence	Representative mechanisms	Representative references
Pollination mutualisms	Pollen transfer and mate choice	Reproductive divergence	Often associated with elevated lineage divergence through pollinator-	Variable and context-dependent	Pollinator-mediated assortative mating; sensory bias; behavioral constancy; floral modularity	Stebbins 1974; Sargent 2004; Van der Niet & Johnson 2014

			mediated assortative mating and floral specialization			
Seed dispersal	Spatial redistribution of offspring	Lineage persistence	May indirectly contribute to divergence through range expansion and spatial isolation	Often associated with enhanced persistence through demographic buffering and reduced density dependence	Reduced density-dependent mortality; range expansion; demographic buffering; genetic connectivity	Seidler & Plotkin 2006; Beckman & Sullivan (2023)

Mycorrhizal symbioses (AM)	Nutrient acquisition and stress buffering	Persistence and ecological expansion	Variable; may facilitate ecological divergence through niche expansion and habitat colonization	Often associated with enhanced establishment, environmental tolerance, and persistence	Improved seedling establishment; resource partitioning; enhanced reproductive allocation; niche expansion	Tedersoo et al. (2020)
Functionally Integrated Symbiotic System	Combined influences of pollination, dispersal, and mycorrhizal	Integrated control of divergence and persistence processes	Complementary influences on reproductive isolation and ecological	Complementary influences on establishment, buffering, and long-term	Functional complementarity across different stages of lineage formation and	This framework

	symbioses		divergence	persistence	persistence	

Box 1. The proposed Functionally Integrated Symbiotic System (FISS): an organizational hypothesis for diversification

Why a new framework?

Existing mutualism research has primarily focused on the evolutionary consequences of individual interaction types. FISS differs by proposing that diversification may depend on the complementary contributions of multiple mutualisms acting across distinct demographic and ecological bottlenecks. The framework therefore shifts the unit of explanation from individual mutualisms to the functional organization of multiple mutualisms within lineages.

Core conceptual features

The Functionally Integrated Symbiotic System (FISS) describes a conceptual framework in which multiple mutualisms influence distinct stages of lineage formation and persistence, thereby decoupling lineage divergence from extinction vulnerability. Rather than arising from individual traits or isolated interactions, diversification is proposed to emerge from the combined effects of pollination, seed dispersal, and mycorrhizal symbioses operating across life-history stages and spatial scales.

Reduced coupling between lineage divergence and persistence processes

Processes promoting lineage divergence and those associated with persistence often operate on different components of the life cycle and across different spatial and temporal scales. Reproductive processes governing mating and gene flow are frequently separated from those controlling establishment, survival, and resource acquisition. This separation may weaken the coupling between lineage splitting and extinction risk, allowing diversification to proceed without a proportional increase in vulnerability.

Asymmetric functional contributions of mutualisms

Within this framework, mutualisms contribute asymmetrically to diversification dynamics. Pollination is more consistently associated with processes promoting lineage divergence, whereas seed dispersal and mycorrhizal symbioses more strongly enhance persistence through demographic buffering, environmental tolerance, and establishment success. This asymmetry reflects functional complementarity among interactions rather than equivalent or additive effects on plant fitness.

Complementary mechanisms of persistence

Persistence over macroevolutionary timescales may be enhanced when multiple mutualisms jointly reduce extinction vulnerability through partially complementary ecological effects. By acting on different demographic and ecological bottlenecks, seed dispersal and mycorrhizal symbioses may promote spatial buffering, demographic stabilization, and environmental tolerance, increasing the likelihood that newly diverged lineages persist through vulnerable post-divergence stages.

Dependence on interaction configuration

Diversification outcomes depend not only on the presence of multiple mutualisms, but also on how they are combined across ecological contexts. Different configurations of pollination, seed dispersal, and mycorrhizal associations may therefore generate distinct macroevolutionary trajectories, suggesting that similar interaction components can yield different outcomes depending on their functional organization (Table 1).

Distinction from ecological syndromes

The FISS framework differs from classical ecological and evolutionary syndromes. Syndromes typically describe recurrent trait or interaction combinations that co-occur within lineages, such as pollination or dispersal syndromes. In contrast, FISS emphasizes the complementary functional roles of mutualisms in shaping macroevolutionary processes. Its central prediction is not the co-occurrence of specific interactions, but that interactions contributing to divergence and those contributing to persistence jointly structure long-term diversification outcomes. FISS is therefore a functional, process-oriented framework rather than a descriptive classification of trait combinations.

Under this perspective, FISS is best understood not as a single mechanism or discrete evolutionary system, but as a conceptual framework describing how multiple mutualisms may collectively contribute to lineage divergence and persistence across stages of lineage formation and diversification.