A Functionally Integrated Symbiotic System as a Mechanism for Angiosperm Diversification

Akira Yamawo

Affiliation: Center for Ecological Research, Kyoto University, 2-509-3 Hirano, Otsu, Shiga 520-2113, Japan

Author for correspondence: Akira Yamawo: yamawo.aki@gmail.com

Abstract

Flowering plants have maintained exceptionally high diversity for over 100 million years, yet the mechanisms enabling sustained macroevolutionary diversification remain unresolved. Classical theory predicts a trade-off between speciation and extinction, but angiosperms have repeatedly diversified while persisting across heterogeneous environments. Mutualistic interactions, pollination, seed dispersal, and mycorrhizal symbioses, are widely recognized as key drivers of plant evolution. However, their macroevolutionary roles have largely been examined in isolation, limiting our understanding of how diversification emerges from their combined effects. Here, I propose that angiosperm diversification is better understood as an emergent property of a Functionally Integrated Symbiotic System (FISS), in which multiple mutualisms are organized into a coordinated but functionally asymmetric system. Within this framework, pollination primarily promotes reproductive isolation and lineage splitting, whereas seed dispersal and mycorrhizal symbioses enhance lineage persistence by improving establishment, spatial spread, and tolerance to environmental variability. This functional differentiation effectively decouples processes that promote speciation from those that buffer extinction risk, allowing lineages to both originate and persist. The coordinated action of these mutualisms therefore relaxes the speciation–extinction trade-off and generates positive net diversification over macroevolutionary timescales. By shifting the focus from individual interactions to their configurational integration, this perspective provides a testable framework for understanding angiosperm diversification as a system-level process and highlights the role of ecological interactions as macroevolutionary engines.

Keywords: emergent properties, macroevolution, mutualism, symbiosis, ecological interactions, speciation–extinction decoupling, interaction networks

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). Classical evolutionary theory predicts a fundamental trade-off: 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). Yet throughout their evolutionary history, angiosperms have repeatedly diversified while persisting across heterogeneous and fluctuating environments. How angiosperms relaxed the speciation–extinction trade-off to achieve long-term persistence remains a central and unresolved problem in evolutionary biology.

Angiosperm diversification has traditionally been explained by morphological key innovations, environmental change, and ecological opportunity (Donoghue & Sanderson, 2015; Helmstetter et al., 2023; Ding et al., 2025). In particular, studies recognize that the emergence and expansion of mutualistic interactions, such as pollination, seed dispersal, and mycorrhizal symbioses, have been a key factor promoting angiosperm diversification by reshaping ecological opportunities (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, and these interactions are increasingly recognized as evolutionarily and ecologically interdependent rather than operating in isolation (Tedersoo et al., 2020; Carvalheiro et al., 2021; Benton et al., 2022; Yamawo & Ohno, 2024). In addition, increasing evidence indicates that mutualistic interactions, including pollination, seed dispersal, and mycorrhizal associations, play a central role not only in facilitating speciation but also in buffering extinction risk by enhancing reproduction, dispersal, and stress tolerance (Hodges et al., 1995; Tiffney & Mazer, 1995; Benton et al., 2022; Peris et al., 2025). These observations suggest that angiosperm diversification may be facilitated by the coordinated action of multiple mutualistic interactions, which can mitigate or relax trade-offs between speciation and extinction that would constrain diversification under any single innovation or mutualism alone.

This Review synthesizes evidence suggesting that major angiosperm mutualisms differentially influence speciation and lineage persistence. It also suggests that long-term diversification is unlikely to be fully explained by any single interaction alone. Instead, diversification may have been promoted by a set of functionally distinct mutualistic interactions acting in concert. These interactions form a Functionally Integrated Symbiotic System (FISS), a macroevolutionary system in which interdependent mutualisms fulfill distinct evolutionary roles. In its simplest form, the FISS consists of pollination, seed dispersal, and mycorrhizal symbioses. Within this framework, available evidence indicates that these interactions may contribute asymmetrically to diversification. Pollination is often associated with reproductive isolation and lineage splitting, but may also increase extinction risk. In contrast, seed dispersal and mycorrhizal associations are thought to mitigate this risk by enhancing establishment, spatial spread, and tolerance to environmental variability. As a result, their combined effects could accelerate effective diversification by increasing the likelihood that newly formed lineages persist through vulnerable stages. By shifting the focus from isolated key innovations to the organization and evolutionary dynamics of interacting mutualisms, this framework provides a testable basis for understanding how angiosperm lineages may escape the specialization–extinction trade-off and achieve sustained diversification.

Pollination Systems: Drivers of Reproductive Isolation and Speciation

Most flowering plants, approximately 90% of all angiosperm species, depend on animal-mediated pollination for reproduction (Ollerton, 2017; Stephens et al., 2023; Tong et al., 2023; Peris et al., 2025). Palaeobotanical and phylogenetic evidence indicate that biotic pollination systems originated from abiotic pollination systems before the emergence of angiosperms, during the gymnosperm-dominated phase of seed plant evolution (Brundrett, 2002; Peris et al., 2025; Negri & Toledo, 2025). Early angiosperms were therefore likely pre-adapted to animal pollination, suggesting that biotic pollination constituted a pre-existing ecological context rather than a late-derived innovation during angiosperm radiation (Stephens et al., 2023; Valencia-Montoya et al., 2025).

A large body of empirical and comparative studies showed that pollination-related traits can promote reproductive isolation and speciation, particularly through shifts in pollinator assemblages and divergence of floral traits (Grant & Grant, 1965; van der Niet et al., 2014; Serrano-Serrano et al., 2017; Barreto et al., 2024; Dorey & Schiestl, 2024). Most angiosperms interact with multiple pollinators within generalized and nested pollination networks (Waser et al., 1996; Bascompte & Jordano, 2007), where pollinator behavior, learning, and flower constancy can still generate non-random mating and effective reproductive isolation (Chittka et al., 1999; Kay, 2006; Kay & Sargent, 2009; Hopkins & Rausher, 2014; Hopkins, 2022). Floral divergence in morphology and chemistry further reinforces isolation by altering pollen placement and reducing heterospecific pollen transfer (Muchhala & Potts, 2007). The modular genetic architecture of floral traits, including partially independent regulatory networks such as CYC/TB1-like transcription factors, enhances floral evolvability and enables repeated shifts among pollination syndromes (Whittall & Hodges, 2007; Hileman, 2014).

Despite these strong effects on speciation, evidence that pollination alone consistently increases net diversification remains mixed (Sargent, 2004; O'Meara et al., 2016; Peris et al., 2025). This pattern likely reflects the dual role of pollination mutualisms, which can promote lineage splitting while also increasing extinction risk under certain ecological conditions. Pollination mutualisms often have weaker and context-dependent effects on extinction. High specialization can increase sensitivity to partner loss and environmental variability, elevating extinction risk and generating high lineage turnover rather than sustained diversification (Janzen, 1979; Herre et al., 2008; Nee, 2001). In generalized systems, functional redundancy among pollinators can stabilize reproduction (Waser et al., 1996; Memmott et al., 2004). However, shared pollinators may also impose reproductive interference and minority disadvantage, favoring rapid floral divergence through character displacement (Levin & Anderson, 1970; Waser, 1978; Morales & Traveset, 2008; Pauw, 2013; Johnson et al., 2022). Empirical studies indicate that these outcomes depend strongly on ecological context, including pollinator availability, adaptive foraging, and demographic structure (Lanuza et al., 2018; Bergamo et al., 2020; Valdovinos et al., 2025). These findings indicate that pollination mutualisms can facilitate lineage splitting but do not consistently buffer lineages against extinction. Accordingly, focusing on pollination alone may not capture effective diversification, as gains in speciation can be offset by elevated extinction risk. Their macroevolutionary consequences, therefore, depend on ecological and demographic context and are unlikely to be sufficient in isolation to explain long-term angiosperm diversification.

Seed Dispersal: Contributions to Lineage Persistence

Recent global estimates indicate that approximately 60% of angiosperm species, and the vast majority of woody taxa, depend on biotic seed dispersal (Jin et al., 2026). Extensive ecological research demonstrates that seed-dispersal mutualisms influence plant population dynamics by shaping recruitment, spatial structure, and gene flow. Although extreme long-distance dispersal can, under certain conditions, increase extinction risk, for example via demographic sinks or maladaptation (Chen et al., 2023), dispersal mutualisms more commonly enhance population persistence through spatial spread, recolonization, and the maintenance of genetic diversity (Vamosi et al., 2018; Beckman & Sullivan, 2023; Wu et al., 2023).

The most basic function of animal-mediated dispersal is the alleviation of density-dependent mortality near conspecific adults. Host-specific enemies, including seed predators, herbivores, and soil-borne pathogens such as *Pythium* spp., accumulate around parent plants, causing high seed and seedling mortality when dispersal is limited (the Janzen–Connell effect) (Janzen, 1970; Connell, 1971; García & Martínez, 2012). By relocating propagules to low-density microsites, animal dispersers consistently reduce these constraints across both tropical and temperate forests (Comita et al., 2010, 2014). In communities with diverse disperser assemblages, variation in dispersal distances, deposition sites, and movement patterns further partitions recruitment niches among plant species, reducing competitive overlap and promoting stable coexistence (Kakishima et al., 2015; Dehling et al., 2016; Fricke et al., 2025; Inoue et al., 2025). At broader scales, such niche partitioning limits dominance and competitive exclusion, thereby lowering extinction risk in demographically vulnerable lineages (Wiegand et al., 2025).

Seed dispersal can also contribute to lineage persistence by shaping geographic range size, spatial population structure, and genetic connectivity. Narrow geographic distributions are associated with elevated extinction risk due to sensitivity to localized disturbances (Jablonski, 2008; Larson-Johnson, 2016), whereas animal-mediated dispersal can increase the number and spatial arrangement of populations and facilitating range shifts under climatic change, particularly during the Cenozoic (Bolmgren & Eriksson, 2005; Beckman & Sullivan, 2023). However, broad geographic ranges are better interpreted as correlates of reduced extinction risk rather than direct outcomes of dispersal, given their strong dependence on dispersal mode, landscape structure, and habitat availability (Levey et al., 2005; Wu et al., 2023; Fricke et al., 2025). Beyond spatial effects, dispersal maintains genetic connectivity, reducing inbreeding depression, limiting genetic drift, and preserving adaptive potential in small or fragmented populations (Levin et al., 2003, 2005; Caughlin et al., 2015), although the macroevolutionary consequences of these processes remain uncertain (Beckman & Sullivan, 2023; Wu et al., 2023).

Seed-dispersal mutualisms have therefore been proposed as contributors to angiosperm diversification, with support reported in some clades (Lagomarsino et al., 2016; Larson-Johnson, 2016; Simpson et al., 2022; Chen et al., 2023). However, angiosperm-wide analyses detect no consistent association between dispersal mode and diversification rates (Jin et al., 2026), consistent with earlier studies showing no systematic richness differences between biotically and abiotically dispersed taxa (Eriksson & Bremer, 1991; Ricklefs & Renner, 1994; Reginato et al., 2020). Instead, current evidence suggests that seed-dispersal mutualisms primarily promote lineage persistence rather than speciation, with effects contingent on lineage traits, ecological context, and interactions with other evolutionary processes. Although extinction-rate estimates from molecular phylogenies should be interpreted with caution (Rabosky, 2010), several studies nonetheless infer lower extinction rates in animal-dispersed lineages (Reginato et al., 2020; Chen et al., 2023). Overall, seed-dispersal mutualisms chiefly contribute to the maintenance of lineages after origination by enhancing population persistence, spatial stability, and ecological resilience in context-dependent ways.

Mycorrhizal Symbioses: Supporting Lineage Persistence

Mycorrhizal symbioses influence plant performance by mediating resource acquisition, stress tolerance, and population-level processes (Tedersoo et al., 2020). Here, I focus on arbuscular mycorrhizal (AM) fungi, the earliest-evolving and most widespread mycorrhizal associations among land plants. Given their antiquity and prevalence, AM symbioses provide a baseline ecological context within which many angiosperm lineages diversified; other mycorrhizal types are considered in the Synthesis.

Approximately 72% of angiosperm species maintain ancestral mutualisms with AM fungi (Tedersoo et al., 2020). By enhancing access to belowground resources, particularly phosphorus and nitrogen, AM fungi buffer spatial and temporal heterogeneity in soil nutrient availability. At ecological timescales, this buffering stabilizes plant growth and reproductive output, especially under fluctuating environmental conditions, resulting in more consistent recruitment across years (Koide, 2010; Hyjazie & Sargent, 2024; Kumari et al., 2025). By jointly stabilizing resource acquisition and reproduction, AM fungi can sustain viable populations in environments where establishment would otherwise be sporadic or unreliable (Peay, 2016; Tedersoo et al., 2020).

Beyond demographic stabilization, mycorrhizal symbioses enhance tolerance to abiotic stress, including drought, salinity, nutrient limitation, and heavy-metal exposure, through improved physiological regulation and resource uptake (Tedersoo et al., 2020). These benefits are often strongest during establishment and early life stages, which represent critical bottlenecks for population persistence, although their long-term evolutionary effects remain context dependent, varying with environmental conditions, host specificity, and interactions with other ecological processes. At the community level, mycorrhizal networks redistribute nutrients among plants and microsites, buffering spatial heterogeneity and weakening priority effects. Through plant–soil feedbacks and density-dependent processes, AM fungi frequently suppress conspecific recruitment relative to heterospecifics, reducing competitive exclusion and promoting stable coexistence, particularly in nutrient-poor or highly competitive environments (Mangan et al., 2010; Tedersoo et al., 2020).

Mycorrhizal symbioses have been proposed as direct drivers of plant diversification by influencing resource allocation or reproductive timing, potentially facilitating reproductive isolation (Savolainen et al., 2006). Empirical support for this hypothesis, however, remains limited. Comparative analyses have not identified particular mycorrhizal types as consistent predictors of elevated diversification rates or as key innovations (Feijen et al., 2018). Instead, available evidence suggests that lineages capable of associating with multiple mycorrhizal types may exhibit higher net diversification, pointing to symbiotic flexibility rather than any single mycorrhizal strategy as the relevant macroevolutionary factor. Overall, mycorrhizal symbioses appear to influence angiosperm diversification primarily by enhancing lineage persistence through improved resource acquisition, ecological tolerance, and demographic stability, rather than by consistently promoting lineage splitting.

Integrative effects of different mutualisms on plant diversification

Pollination, seed dispersal, and mycorrhizal symbioses have often been studied independently, yet this perspective is insufficient to fully explain angiosperm diversification. Rather than acting in isolation, these interactions appear to form a coordinated system in which different mutualisms contribute asymmetrically to lineage diversification and persistence (Yamawo & Ohno, 2024). Comparative, phylogenetic, and ecological studies suggest that these interactions influence distinct components of angiosperm diversification (Table S1), and that their combined effects give rise to emergent ecological processes that are not readily inferred from any single mutualism in isolation.

Pollination-related traits primarily promote reproductive isolation and biased lineage splitting, acting as speciation-promoting processes. In contrast, seed dispersal and mycorrhizal associations mainly enhance mitigation negative density dependence, geographic spread, and tolerance to environmental variability, acting as persistence-promoting processes. Populations isolated through specialized or biased pollination often have smaller effective population sizes and higher extinction risk. Seed dispersal reduces this risk by moving offspring away from parent plants, lowering density-dependent mortality, and maintaining connectivity, while mycorrhizal symbioses improve nutrient acquisition and stress tolerance during establishment. The combined action of seed dispersal and mycorrhizal associations connects the spatial movement of propagules with successful establishment, thereby enabling dispersed propagules to become demographically effective individuals. Evidence for the joint dispersal of mycorrhizal fungi and plant diaspores by birds indicates that seed dispersal and mycorrhizal associations may be even more tightly integrated than previously assumed, further reinforcing their combined effects on establishment and persistence (Correia et al., 2019). Together, these persistence-promoting mutualisms allow lineages generated by pollination-driven divergence to survive early vulnerable stages and complete lineage formation (Comita et al., 2014; Peay, 2016; Tedersoo et al., 2020).

At the community level, functional differences among mutualisms are reflected in network structures. Pollination networks typically show high nestedness and local modularity, forming semi-independent plant–pollinator modules within a cohesive web (Bascompte & Jordano, 2007; Olesen et al., 2007). This structure allows localized interaction specificity and assortative mating without breaking overall connectivity, promoting reproductive isolation and lineage splitting (speciation-promoting). Seed-dispersal networks are generally highly nested, weakly modular, and functionally redundant, dominated by generalist animal vectors (Bascompte et al., 2003; Donatti et al., 2011). They decouple recruitment from local demographic failures and increase robustness across heterogeneous landscapes. Importantly, seed dispersal promotes the coexistence of multiple plant species. By mediating spatial niche separation and reducing competitive clustering, seed dispersal contributes to lineage persistence within complex communities (persistence-promoting). Mycorrhizal networks, especially those involving arbuscular fungi, exhibit high connectome and extensive host sharing, redistributing resources and buffering demographic stochasticity at the community level (van der Heijden et al., 2015; Tedersoo et al., 2020). By mediating resource-based coexistence and reducing fitness inequalities among co-occurring species, mycorrhizal symbioses further stabilize lineage persistence within diverse communities. Thus, seed dispersal and mycorrhizal symbioses jointly contribute to lineage persistence by mediating multi-species coexistence.

At ecosystem and landscape scales, seed dispersal and mycorrhizal symbioses determine whether newly differentiated lineages persist beyond initial divergence through facilitating spatial expansion. Seed dispersal moves propagules across heterogeneous landscapes and increases spatial coupling among local populations (Frick et al., 2025). Mycorrhizal symbioses improve establishment and survival in stressful or variable new habitats through enhanced nutrient uptake and physiological tolerance. Together, these mutualisms provide complementary spatial and physiological insurance against environmental variability, allowing lineages to persist across space and time. Without these persistence-promoting processes, many lineages generated by pollination-driven divergence would remain confined to isolated populations and face higher extinction risk. Seed dispersal and mycorrhizal associations therefore facilitate metapopulation persistence, stabilize plant recruitment and biomass accumulation, and enable newly formed lineages to become embedded within ecosystem-level processes, contributing to long-term lineage persistence and ecosystem structure (van der Heijden et al., 2015; Tedersoo et al., 2020).

Overall, angiosperm diversification reflects the coordinated action of multiple mutualisms across population, community, and ecosystem levels. Pollination, seed dispersal, and mycorrhizal associations influence different components of diversification, and their interactions generate ecological outcomes such as enhanced reproductive isolation, biased lineage splitting, conversion of nascent lineages into persistent populations, and long-term lineage persistence. Although maintaining multiple mutualists can involve costs or trade-offs, certain configurations of multi-mutualist associations provide substantial net benefits (Afkhami et al., 2014, 2021). These effects at the ecological scale suggest that pollination drives reproductive isolation and lineage splitting, while seed dispersal and mycorrhizal associations enhance survival, establishment, and range expansion of newly diverged lineages

(Figure 1). By acting together, these mutualisms ensure that nascent lineages persist through vulnerable early stages and ecosystems over long evolutionary timescales. Thus, it is not simply the presence of multiple mutualisms, but rather their coordinated organization and complementary functions across population, community, and ecosystem levels that *may* shape long-term diversification patterns.

Synthesis

A Functionally Integrated Symbiotic System (FISS): *a configuration-based framework for plant diversification*

In mentioned above, the evidence suggests that the diversification of angiosperms cannot be explained by single interactions alone. Rather, it arises from the way multiple mutualisms are organized and interact across population, community, and ecosystem scales. This perspective calls for a move away from each biological interaction analyses toward integrative frameworks that explicitly examine how configurations of interactions are structured and maintained over evolutionary time.

I propose that certain configurations of interacting mutualisms can give rise to an emergent macroevolutionary system; *A Functionally Integrated Symbiotic System* (FISS). In macroevolutionary studies, diversification-promoting processes are often described metaphorically as “engines,” and in this sense, the coordinated system of interacting mutualisms described here may be termed a *Symbiotic Engine*. This concept refers to a dynamic macroevolutionary system in which different mutualisms play complementary but unequal roles, and together promote both lineage formation and long-term persistence (Box 1; Figure 1). The FISS does not imply that any single mutualism alone drives diversification. It describes how different mutualisms work together. One mutualism might speed up speciation, while another reduces extinction risk. Under specific conditions, these combined effects drive a positive net diversification. Under this view, interactions need not be universally strong or directly integrated; even weak or context-dependent links can contribute to diversification when complementary interactions act on different macroevolutionary constraints.

In addition, as plant diversity accumulates, diversification dynamics may become increasingly shaped by mutualistic interactions rather than by external environmental factors alone. Fossil and phylogenetic evidence suggest that during early angiosperm radiations, reduced extinction risk and expanded ecological opportunities increased diversity in both plants and pollinating insect lineages. Later, lineages with persistent floral associations, such as bees and some lepidopterans, showed elevated speciation rates, reflecting the growing importance of interaction-dependent evolutionary dynamics (Grimaldi & Engel, 2005; Condamine et al., 2016; Schuldt et al., 2018; Peris & Condamine, 2024). Similar patterns are observed in seed dispersal animals and fungi. Frugivorous vertebrates and other seed dispersers tend to diversify in response to plant trait diversification, spatial and temporal variation in resources, and increased ecological opportunity (Dumont et al., 2012; Gómez & Verdú, 2012; Onstein et al., 2017; Burin et al., 2021; Wang et al., 2024). Arbuscular mycorrhizal fungi generally show broad geographic distributions and low endemism, consistent with extensive partner sharing and long-term persistence, while ectomycorrhizal fungi exhibit higher host specificity and regional diversification that coincides with radiation in plant lineages such as Fagaceae and Betulaceae (Angelard et al., 2014; Davison et al., 2015; Sato et al., 2017). Although this reciprocal diversification feedback between plants and mutualists does not directly establish a self-sustaining diversification mechanism, they provide a plausible ecological context in which coordinated mutualistic interactions can reinforce long-term diversification (Figure 1).

Evolutionary Emergence of FISS

The evolutionary assembly of the proposed FISS appears to have proceeded in a broadly stepwise manner (Figure 2), although the timing and impact of each step remain uncertain. Arbuscular mycorrhizal associations were established early in land plant evolution, likely around 460 million years ago during the initial colonization of terrestrial environments (Remy et al., 1994; Brundrett, 2002; Strullu-Derrien et al., 2018). Angiosperms originated later, in the Early Cretaceous (approximately 130–100 Ma), and phylogenetic and palaeobotanical evidence suggests that many early angiosperm lineages were already associated with biotic pollination (Stephens et al., 2023). Subsequently, animal-mediated seed dispersal increased dispersal distances and reshaped spatial patterns of recruitment. Fossil and phylogenetic evidence indicates that fleshy fruits and frugivore-mediated dispersal became increasingly common from the Late Cretaceous to the early Paleogene (approximately 100–60 Ma) (Tiffney & Mazer, 1995; Eriksson et al., 2000; Jin et al., 2026). Rather than representing a deterministic pathway to diversification, this stepwise assembly suggests that the gradual addition of mutualisms expanded the range of ecological conditions under which angiosperm lineages could persist and diversify.

This sequential integration provides a mechanistic explanation for the long-recognized temporal gap between the early origin of biotic pollination and the later major radiation of angiosperms (Benton et al., 2022; Ding et al., 2025). Although biotic pollination is inferred to have originated by the Early Cretaceous (Stephens et al., 2023; Peris & Condamine, 2024; Ding et al., 2025), elevated net diversification rates in angiosperms are mainly detected from the mid- to Late Cretaceous (approximately 100–60 Ma), with further radiations continuing into the Paleogene (Benton et al., 2022; Ding et al., 2025). This period broadly coincides with the ecological expansion and increasing dominance of angiosperms in terrestrial ecosystems (Ding et al., 2025; Jin et al., 2026), during which mycorrhizal symbiosis, pollination, and seed dispersal likely acted in concert to sustain an integrated diversification system. Together, these patterns suggest that sustained angiosperm radiations may have emerged through the progressive and coordinated integration of multiple functionally distinct mutualisms, including mycorrhizal associations, pollination, and seed-dispersal interactions.

Predicted Macroevolutionary Signatures of the FISS

The FISS generates a set of testable macroevolutionary predictions that distinguish interaction-based diversification regimes from trait-based or single-interaction models. These predictions follow from two core properties of the system: (i) the partial decoupling of processes that promote lineage splitting and those that enhance persistence, and (ii) the asymmetric contributions of different mutualisms to these processes.

Angiosperms commonly engage in mycorrhizal symbioses, pollination mutualisms, and seed-dispersal mutualisms, but not all lineages maintain all of these interactions. Some species rely on abiotic agents such as wind or gravity for pollination or seed dispersal (Stephens et al., 2023; Yamawo & Ohno, 2024), and mycorrhizal associations themselves are diverse (Tedersoo et al., 2020). As a result, lineages differ in the configurations of biotic and abiotic interactions they maintain. Such variation provides a natural basis for testing the predictions of the FISS, as different configurations reflect alternative ways in which lineages balance processes that promote speciation and those that buffer extinction under heterogeneous environmental conditions.

(1) Configuration-dependent diversification

Lineages characterized by specific combinations of mutualistic interactions are expected to exhibit distinct diversification dynamics because different combinations integrate processes that promote lineage splitting and those that enhance persistence in different ways.

A representative example is a configuration integrating biotic pollination, animal-mediated seed dispersal, and arbuscular mycorrhizal (AM) symbiosis. This configuration, common among many tree lineages, predictably promotes lineage splitting through pollinator-mediated reproductive isolation while simultaneously enhancing persistence via effective dispersal and efficient belowground resource acquisition. This pattern can be empirically tested and is inferred to have been most prominent during periods of rapid angiosperm expansion, coinciding with the establishment and ecological consolidation of tropical and subtropical forests (Ding et al., 2025).

By contrast, alternative configurations that rely predominantly on abiotic pollination and seed dispersal, together with ectomycorrhizal (EcM) associations, are expected to produce different diversification dynamics. Under such configurations, diversification is predicted to rely less on specialization on animal mutualists and more on physiological tolerance, geographic expansion, and environmental isolation, resulting in slower, weaker, or more context-dependent diversification patterns. These configurations are inferred to have become more influential during later stages of angiosperm diversification, associated with the expansion of temperate forest biomes (Ding et al., 2025).

Highly specialized combinations of mutualistic interactions can promote diversification even under harsh conditions by relaxing constraints on key life-history stages (Figure 2; Table 1). Orchids illustrate this pattern: strong reproductive isolation, specialized pollination, and orchid-specific mycorrhizal associations generate high speciation rates but also elevated extinction risk. In epiphytic orchids, the combination of specialized pollination, wind-mediated seed dispersal, and orchid mycorrhizae is predictably associated with rapid lineage turnover (Gamisch & Comes, 2019; Pérez-Escobar et al., 2024). These predictions can be empirically tested.

Then, such variation in the configuration of the interactions may therefore help explain the heterogeneity in trait-dependent diversification observed across angiosperms (Helmstetter et al., 2023). By framing these patterns as testable predictions, the FISS provides a structured framework for evaluating how specific configurations of mutualistic interactions and abiotic processes shape macroevolutionary dynamics under changing environments. Table 1 summarizes explicit hypotheses regarding the expected macroevolutionary outcomes associated with each configuration of the interaction. These predictions can be tested using comparative, phylogenetic, or ecological approaches.

(2) Emergent effects among mutualisms

The joint effects of multiple mutualisms on diversification are expected to be non-linear (Afkhami et al., 2014, 2021). In particular, extinction-buffering interactions such as seed dispersal and mycorrhizal symbioses are predicted to disproportionately amplify the macroevolutionary success of speciation-prone lineages, such as pollinator-specialized lineages, rather than contributing additively to diversification rates. Orchids may illustrate this pattern: strong reproductive isolation, specialized pollination, and orchid-specific mycorrhizal associations generate high speciation rates but also elevated extinction risk. In epiphytic orchids, the configuration of specialized pollination, wind-mediated seed dispersal, and orchid mycorrhizae is predictably associated with rapid lineage turnover (Gamisch & Comes, 2019; Pérez-Escobar et al., 2024).

Overall, variation in how interactions are combined across lineages provides a practical and testable framework for evaluating the FISS. By comparing these configurations, it becomes possible to assess how different arrangements of mutualistic and abiotic interactions relax evolutionary constraints and generate the heterogeneous patterns of speciation, extinction, and net diversification observed across angiosperms.

Conclusion and Future Perspectives

Importantly, the FISS has not yet been empirically demonstrated, and its validity remains to be tested through integrative comparative and experimental approaches. Rather than proposing a new key innovation, the FISS framework reframes angiosperm diversification as the product of an operational system of coordinated mutualistic interactions, rather than the result of isolated traits. A central prediction is that net diversification depends on specific configurations of pollination, seed dispersal, and mycorrhizal interactions (Box 1). Lineages lacking complementary mechanisms for persistence are expected to experience elevated turnover, whereas configurations that jointly relax constraints on both speciation and extinction may allow long-term lineage accumulation across macroevolutionary timescales.

Although the FISS is defined here as a conceptual diversification regime rather than a specific mechanistic model, its core principles naturally lend themselves to formalization. In particular, the decoupling of speciation and extinction processes, the asymmetric contributions of interactions to speciation rate and extinction rate, and the configurational dependence of diversification outcomes provide a tractable foundation for state-dependent diversification models and network-based theoretical frameworks.

Testing these predictions requires comparative analyses that explicitly model configurations of interactions and their asymmetric effects on speciation and extinction, specifically testing the decoupling of lineage splitting from extinction risk. State-dependent diversification approaches, including SSE-type models such as the Multicharacter Hidden State Speciation and Extinction (Mu-HiSSE; Nakov et al., 2018) and Secondary State-dependent Speciation and Extinction (SecSSE; Herrera-Alsina et al., 2019) framework, provide one promising avenue for this purpose. Crucially, such analyses must account for hidden heterogeneity, regime shifts, and incomplete sampling, all of which can obscure diversification signals over deep time.

Nonetheless, a key limitation of comparative diversification analyses is that associations between interaction configurations and diversification rates do not, by themselves, establish causal direction. Observed correlations may reflect shared environmental regimes, unmeasured trait syndromes, or historical contingencies rather than interaction-driven processes per se. Overcoming these limitations will therefore require explicit integration of ecological data, interaction network structure, environmental reconstructions, and fossil evidence alongside phylogenetic inference.

Although the FISS focuses on mutualistic interactions as its main structural components, explicitly considering other biotic interactions can improve our ability to explain how speciation- and extinction-related processes are shaped across different ecological contexts. Antagonistic interactions, such as herbivory and disease, as well as stress-buffering interactions, including defensive mutualisms and endophytic associations, can affect speciation and extinction in context-dependent and often asymmetric ways (Rooney et al., 2005; Alcázar et al., 2014; Compant et al., 2019). For example, herbivory and disease may indirectly promote speciation by altering interactions with pollinators, but at the same time they can strongly reduce population size and increase extinction risk. In contrast, defensive mutualisms and endophytic associations can reduce damage from herbivores and pathogens and thereby support lineage persistence (Compant et al., 2019; Zhou et al., 2024; Li et al., 2026), often together with seed-dispersal and mycorrhizal mutualisms (Beckman & Sullivan, 2023; Chen et al., 2023). These interactions therefore can act asymmetrically on speciation and extinction rates and are likely to have positive effects on net diversification (e.g. Weber & Agrawal, 2014; Li et al., 2026). By interactively organizing how these interactions influence speciation and extinction rates, either together with or independent of the underlying FISS, they may be incorporated into an expanded FISS that accounts for a broader set of macroevolutionary processes, including lineage persistence, extinction buffering, and variation in diversification rates.

Similarly, the FISS framework provides a platform for integrating key innovations that have often been studied in isolation. Rather than acting independently, traits such as leaf venation, photosynthetic capacity, vascular efficiency, stomatal density, pollen traits, and genome duplication are expected to influence diversification through their combined effects on mutualistic interactions (Donoghue & Sanderson, 2015; Ding et al., 2025). In angiosperms, the integration of these traits, particularly high-efficiency water and resource transport via vessel elements and enhanced carbon gain, may have increased the efficiency with which resources are acquired and allocated, thereby supporting the establishment and persistence of multiple, carbon-intensive mutualistic relationships. Although many gymnosperms also form mycorrhizal associations and some lineages exhibit insect pollination or animal-mediated seed dispersal (Tedersoo et al., 2020; Peris et al., 2025), their generally lower rates of resource acquisition and slower life histories may have constrained the extent to which such interactions could be simultaneously maintained and translated into demographic and evolutionary responses. By reducing the physiological and genomic constraints associated with sustaining pollination, seed dispersal, and mycorrhizal associations together, the angiosperm-specific configuration of traits may have allowed these interacting mutualisms to exert sustained and coordinated effects on speciation and extinction dynamics, contributing to the emergence of the FISS.

In addition to trait-level integration, recurrent whole-genome duplication (polyploidization) may have provided a key genomic foundation for the emergence of the FISS. Whole-genome duplication expands genetic and regulatory diversity, facilitating the evolution of novel traits involved in mutualistic interactions (Van de Peer et al., 2017). Gene duplication can promote functional divergence in pathways related to floral traits, secondary metabolites, and signaling mechanisms, potentially enhancing the ability of plants to interact with a wider range of pollinators, seed dispersers, and symbiotic microbes (Panchy et al., 2016). Polyploidization may also increase phenotypic plasticity and environmental tolerance, allowing plants to maintain multiple mutualistic associations under variable ecological conditions (Van de Peer et al., 2021). In contrast, the more limited incidence and retention of genome duplication in many gymnosperm lineages (Leebens-Mack et al., 2019) may have constrained the diversification of interaction-related traits and their integration. By alleviating genomic constraints on the simultaneous evolution and maintenance of multiple mutualisms, polyploidization may have enabled these interactions to exert sustained and coordinated effects on diversification, thereby contributing to the emergence of the FISS.

More broadly, the FISS is not intended as an angiosperm-specific model, but as a general macroevolutionary principle emphasizing how interactions structure diversification dynamics. Extending this framework to other taxa and ecosystems may clarify how complex biotic networks are assembled, maintained, or constrained over evolutionary time.

Finally, the FISS highlights potential vulnerabilities of diversification systems under contemporary environmental change. Because diversification emerges from the coordinated functioning of multiple interactions, the loss of pollinators, seed dispersers, or mycorrhizal partners may propagate through the system, effectively 'stalling' the *FISS*. Ongoing anthropogenic pressures, including defaunation, habitat fragmentation, and soil degradation, are likely disrupting these co-evolved networks (Caughlin et al., 2015; Sánchez-Bayo & Wyckhuys, 2019; Fricke et al., 2025; Peris et al., 2025). The future diversification and persistence of angiosperms may therefore depend on the maintenance of intact, self-reinforcing interaction networks. If diversification is an emergent property of biological interactions, then the Anthropocene represents the first global-scale experiment in dismantling such biological interactions.

Acknowledgments

I thank Yuuya Tachiki, Haruna Ohsaki, Naoto Shinohara, Kenji Suetsugu, Noboru Katayama and Masato Yamamichi for discussions during the initial stages of this project. I am grateful to Yuichiro Kanzaki for his assistance with the illustrations. I sincerely thank Misuzu Ohno for inspiring the initiation of this project. This work was also supported by Japan Society for the Promotion of Science (JSPS) Grant-in-Aid for Scientific Research (KAKENHI) (grant nos. 25H01003, 23H04970 and 24H00507).

References

Afkhami, M. E., Friesen, M. L., & Stinchcombe, J. R. (2021). Multiple mutualism effects generate synergistic selection and strengthen fitness alignment in the interaction between legumes, rhizobia and mycorrhizal fungi. Ecol. Lett., 24, 1824–1834.

Afkhami, M. E., Rudgers, J. A., & Stachowicz, J. J. (2014). Multiple mutualist effects: conflict and synergy in multispecies mutualisms. Ecology, 95, 833-844.

Alcázar, R., von Reth, M., Bautor, J., Chae, E., Weigel, D., Koornneef, M. & Parker, J.E. (2014). Analysis of a plant complex resistance gene locus underlying immune-related hybrid incompatibility and its occurrence in nature. PLoS Genet., 10, e1004848.

Angelard, C., Tanner, C. J., Fontanillas, P., Niculita-Hirzel, H., Masclaux, F., & Sanders, I. R. (2014). Rapid genotypic change and plasticity in arbuscular mycorrhizal fungi is caused by a host shift and enhanced by segregation. The ISME Journal, 8, 284–294.

Barreto, E., Boehm, M.M.A., Ogutcen, E., Abrahamczyk, S., Kessler, M., Bascompte, J., Dellinger, A.S., Bello, C., Dehling, D.M., Duchenne, F., Kaehler, M., Lagomarsino, L.P., Lohmann, L.G., Maglianesi, M.A., Morlon, H., Muchhala, N., Ornelas, J.F., Perret, M., Salinas, N.R., Smith, S.D., Vamosi, J.C., Varassin, I.G. & Graham, C.H. (2024). Macroevolution of the plant–hummingbird pollination system. Biol. Rev., 99, 1831–1847.

Bascompte, J. & Jordano, P. (2007). Plant–animal mutualistic networks: The architecture of biodiversity. Annu. Rev. Ecol. Evol. Syst., 38, 567–593.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). The nested assembly of plant–animal mutualistic networks. Proc. Natl. Acad. Sci. U.S.A., 100, 9383–9387.

Beckman, N.G. & Sullivan, L.L. (2023). The causes and consequences of seed dispersal. Annu. Rev. Ecol. Evol. Syst., 54, 403–427.

Bell, G. (1982). The masterpiece of nature: The evolution and genetics of sexuality. Berkeley: University of California Press.

Benton, M.J., Wilf, P. & Sauquet, H. (2022). The angiosperm terrestrial revolution and the origins of modern biodiversity. New Phytol., 233, 2017–2035.

Bergamo, P. J., Streher, N. S., Traveset, A., Wolowski, M., & Sazima, M. (2020). Pollination outcomes reveal negative density-dependence coupled with interspecific facilitation among plants. Ecol. Lett., 23, 129-139.

Bolmgren, K. & Eriksson, O. (2005). Fleshy fruits: Origins, niche shifts, and diversification. Oikos, 109, 255–272.

Bosch, J., Martín González, A.M., Rodrigo, A. & Navarro, D. (2009). Plant–pollinator networks: Adding the pollinator's perspective. Ecol. Lett., 12, 409–419.

Brundrett, M.C. (2002). Coevolution of roots and mycorrhizas of land plants. New Phytol., 154, 275–304.

Burin, G., Guimarães Jr., P.R. & Quental, T.B. (2021). Macroevolutionary stability predicts interaction patterns of species in seed dispersal networks. Science, 372, 733–737.

Cairney, J. W., & Meharg, A. A. (2003). Ericoid mycorrhiza: a partnership that exploits harsh edaphic conditions. Eur. J. Soil Sci., 54, 735–740.

Carvalheiro, L. G., Bartomeus, I., Rollin, O., Timóteo, S., & Tinoco, C. F. (2021). The role of soils on pollination and seed dispersal. Philos. Trans. R. Soc. Lond. B Biol. Sci., 376, 20200171.

Caughlin, T.T., Ferguson, J.M., Lichstein, J.W., Zuidema, P.A., Bunyavejchewin, S. & Levey, D.J. (2015). Loss of animal seed dispersal increases extinction risk in a tropical tree species. Proc. R. Soc. B, 282, 20142095.

Chen, Y.S., Muellner-Riehl, A.N., Yang, Y., Liu, J., Dimitrov, D., Luo, A. & Wang, Z.H. (2023). Dispersal modes affect Rhamnaceae diversification rates in a differentiated manner. Proc. R. Soc. B, 290, 20231926.

Chittka, L., Thomson, J.D. & Waser, N.M. (1999). Flower constancy, insect psychology, and plant evolution. Naturwissenschaften, 86, 361–377.

Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., Beckman, N., & Zhu, Y. (2014). Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. J. Ecol., 102, 845–856.

Comita, L.S., Muller-Landau, H.C., Aguilar, S. & Hubbell, S.P. (2010). Asymmetric density dependence shapes species abundances. Science, 329, 330–332.

Compant, S., Samad, A., Faist, H. & Sessitsch, A. (2019). A review on the plant microbiome. Front. Plant Sci., 10, 45.

Condamine, F.L., Clapham, M.E. & Kergoat, G.J. (2016). Global patterns of insect diversification. Sci. Rep., 6, 19208.

Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion. In Dynamics of Populations (pp. 298–312).

Correia, M., Heleno, R., da Silva, L. P., Costa, J. M., & Rodríguez-Echeverría, S. (2019). First evidence for the joint dispersal of mycorrhizal fungi and plant diaspores by birds. New Phytol., 222, 1054–1060.

Davison, J., Moora, M., Öpik, M., Adholeya, A., Ainsaar, L., Bâ, A., Burla, S., Diedhiou, A. G., Hiiesalu, I., Jairus, T., Johnson, N. C., Kane, A., Koorem, K., Kochar, M., Ndiaye, C., Pärtel, M., Reier, Ü., Saks, Ü., Singh, R., Vasar, M., & Zobel, M. (2015). Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism. Science*,* 349, 970–973.

Dehling, D.M., Jordano, P., Schaefer, H.M., Böhning-Gaese, K. & Schleuning, M. (2016). Morphology predicts functional roles in plant–frugivore interactions. Proc. R. Soc. B, 283, 20152444.

Dimitrov, D., Xu, X., Su, X., Shrestha, N., Liu, Y., Kennedy, J.D., Lyu, L., Nogués Bravo, D., Rosindell, J., Yang, Y., Fjeldså, J., Liu, J., Schmid, B., Fang, J., Rahbek, C. & Wang, Z. (2023). Diversification of flowering plants in space and time. Nat. Commun., 14, 7609.

Ding, W., Silvestro, D., Onstein, R.E., Wu, M., Zhou, Z. & Xing, Y. (2025). The stepwise rise of angiosperm-dominated terrestrial ecosystems. Biol. Rev., 100, 2131–2149.

Donatti, C.I., Guimarães, P.R., Galetti, M., Pizo, M.A., Marquitti, F.M.D. & Dirzo, R. (2011). Analysis of a hyperdiverse seed dispersal network: Modularity and underlying mechanisms. Ecol. Lett., 14, 773–781.

Donoghue, M.J. & Sanderson, M.J. (2015). Confluence, synnovation, and depauperons in plant diversification. New Phytol., 207, 260–274.

Dorey, T. & Schiestl, F.P. (2024). Bee-pollination promotes rapid divergent evolution. Nat. Commun., 15, 2703.

Dumont, E. R., Dávalos, L. M., Goldberg, A., Santana, S. E., Rex, K., & Voigt, C. C. (2012). Morphological innovation, diversification and invasion of a new adaptive zone. Proc. R. Soc. B, 279, 1797–1805.

Eriksson O, Bremer B. (1991). Fruit characteristics, life forms, and species richness in the plant family Rubiaceae. Am. Nat., 138, 751–761.

Eriksson, O., Friis, E.M. & Löfgren, P. (2000). Seed size, fruit size, and dispersal systems in angiosperms. Am. Nat., 156, 47–58.

Feijen, F.A., Vos, R.A. & Nuytinck, J., Merckx, V.S. (2018). Evolutionary dynamics of mycorrhizal symbiosis. Sci. Rep., 8, 1–7.

Fricke, E.C., Bello, C., Chaplin-Kramer, R., Dent, D.H., Feeley, K.J., Galetti, M., González-Varo, J.P., Heleno, R. & Reid, J.L. (2025). Drivers and impacts of global seed disperser decline. Nat. Rev. Biodivers., 1, 386–400.

Gamisch, A. & Comes, H.P. (2019). Clade-age-dependent diversification under high species turnover shapes species richness disparities among tropical rainforest lineages of Bulbophyllum (Orchidaceae). BMC Evol. Biol., 19, 93.

García, D. & Martínez, D. (2012). Species richness matters for seed dispersal services. Proc. R. Soc. B, 279, 3106–3113.

Givnish, T. J., Spalink, D., Ames, M., Lyon, S. P., Hunter, S. J., Zuluaga, A., Iles, W. J. D., Clements, M. A., Arroyo, M. T. K., Leebens-Mack, J., & Cameron, K. M. (2015). Orchid phylogenomics and multiple drivers of their extraordinary diversification. Proc. R. Soc. B, 28, 20151553.

Grant, V. & Grant, K.A. (1965). Flower pollination in the Phlox family. Columbia University Press.

Grimaldi, D. & Engel, M.S. (2005). Evolution of the insects. Cambridge University Press.

Gómez-Reyes, J. M., M. Verdú (2012). Mutualism with plants drives primate diversification. Syst. Biol., 61, 567–577 .

Helmstetter, A.J., Zenil-Ferguson, R., Sauquet, H., Otto, S.P., Méndez, M., Vallejo-Marin, M., Kay, K.M., Guignard, M.S., Ruelens, P., Mora, C.V., Saupe, E.E., Sutherland, B.L., Gavazzi, B., Schönenberger, J. & Käfer, J. (2023). Trait-dependent diversification in angiosperms: Patterns, models and data. Ecol. Lett., 26, 640–657.

Herre, E. A., Jandér, K. C., & Machado, C. A. (2008). Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. Annu. Rev. Ecol. Evol. Syst., 39, 439–458.

Herrera-Alsina, L., Van Els, P., & Etienne, R. S. (2019). Detecting the dependence of diversification on multiple traits from phylogenetic trees and trait data. Systematic Biol., 68, 317–328.

Hileman, L.C. (2014). Bilateral flower symmetry—how, when and why? Curr. Opin. Plant Biol., 17, 146–152.

Hodges, S.A. & Arnold, M.L. (1995). Spurring plant diversification. Proc. R. Soc. B, 262, 343–348.

Hopkins, R. & Rausher, M.D. (2014). Pollinator-mediated selection drives reinforcement. Science, 344, 722–726.

Hopkins, R. (2022). Predicting how pollinator behavior causes reproductive isolation. Ecol. Evol., 12, e8847.

Hyjazie, B.F. & Sargent, R.D. (2024). Manipulation of soil mycorrhizal fungi influences floral traits. New Phytol., 242, 675–686.

Inoue T., Okuda K., Sakamoto Y., Miyamoto R., Kobayashi H., Yokoyama M., Yamawo A. (2025) Seed deposition patterns reflect the foraging behavior and food habits of mammalian seed dispersers. Acta Oecologica, 104111.

Jablonski, D. (2008). Extinction and the spatial dynamics of biodiversity. Proc. Natl. Acad. Sci. U.S.A., 105, 11528–11535.

Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. Am. Nat., 104, 501–528.

Janzen, D.H. (1979). How to be a fig. Annu. Rev. Ecol. Evol. Syst., 10, 13–51.

Jin, Lu, Min Li, Zhi-Heng Wang, Hervé Sauquet, Renske E. Onstein, Dieder de Frens, John T. Clarke, Hai-Fei Yan & Xue-Jun Ge. (2026). Evolutionary history and the global distribution of seed dispersal modes in angiosperms. New Phytol., 250, 1217–1230.

Johnson, C.A., Dutt, P. & Levine, J.M. (2022). Competition for pollinators destabilizes plant coexistence. Nature, 607, 721–725.

Johnson, S.D. & Steiner, K.E. (2000). Generalization versus specialization in pollination systems. Trends Ecol. Evol., 15, 140–143.

Kakishima, S., Morita, S., Yoshida, K., Ishida, A., Hayashi, S., Asami, T., Ito, H., Miller III, D.G., Uehara, T., Mori, S., Hasegawa, E. & Matsuura, K. (2015). Contribution of seed dispersers to tree species diversity. R. Soc. Open Sci., 2, 150079.

Kay, K.M. & Sargent, R.D. (2009). The role of animal pollination in plant speciation: Integrating ecology, geography, and genetics. Annu. Rev. Ecol. Evol. Syst., 40, 637–656.

Kay, K.M. (2006). Reproductive isolation between two closely related hummingbird-pollinated neotropical gingers. Evolution, 60, 538–552.

Koide, R.T. (2010). Mycorrhizal symbiosis and plant reproduction. In Arbuscular Mycorrhizas: Physiology and Function (pp. 297–320). Springer.

Kumari, D., Gupta, N., Sharma, N. & Kumar, V. (2025). From root to fruit: Mycorrhizal impact on fruit crops. In Sustainable Mycorrhizal Cultivation (pp. 147–168). Springer Nature.

Lagomarsino LP, Condamine FL, Antonelli A, Mulch A, Davis CC. (2016). The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). New Phytol., 210, 1430–1442.

Lancaster, L.T. (2010). Molecular evolutionary rates predict both extinction and speciation in temperate angiosperm lineages. BMC Evol. Biol., 10, 162.

Lanuza, J. B., Bartomeus, I., & Godoy, O. (2018). Opposing effects of floral visitors and soil conditions on the determinants of competitive outcomes maintain species diversity in heterogeneous landscapes. Ecol. Lett., 21, 865–874.

Larson-Johnson, K. (2016). Phylogenetic investigation of the complex evolutionary history of dispersal mode and diversification rates across living and fossil Fagales. New Phytol., 209, 418–435.

Leebens-Mack, J.H., Barker, M.S., Carpenter, E.J., Deyholos, M.K., Gitzendanner, M.A., Graham, S.W., et al. (2019). One thousand plant transcriptomes and the phylogenomics of green plants. Nature, 574, 679–685.

Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. & Haddad, N.M. (2005). Effects of landscape corridors on seed dispersal by birds. Science, 309, 146–148.

Levin, D. A., & Anderson, W. W. (1970). Competition for pollinators between simultaneously flowering species. Am. Nat., 104, 455–467.

Levin, S.A., Muller-Landau, H.C., Nathan, R. & Chave, J. (2003). The ecology and evolution of seed dispersal: A theoretical perspective. Annu. Rev. Ecol. Evol. Syst., 34, 575–604.

Li, V.W., Fowler, J.C., David, A.S., Strauss, S.Y., Searcy, C.A. & Afkhami, M.E. (2026). Climate variability disrupts microbial mutualism-driven population persistence. Nat. Ecol. Evol., 10, 1–11.

Mangan, S.A., et al. (2010). Negative plant–soil feedback predicts tree-species relative abundance. Nature, 466, 752–755.

Memmott, J., Waser, N.M. & Price, M.V. (2004). Tolerance of pollination networks to species extinctions. Proc. R. Soc. B, 271, 2605–2611.

Morales, C. L., & Traveset, A. (2008). Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. Critical Reviews in Plant Sciences, 27, 221–238.

Muchhala, N. & Potts, M.D. (2007). Character displacement among bat-pollinated flowers of the genus Burmeistera. Proc. R. Soc. B, 274, 2731–2737.

Nakov, T., Beaulieu, J.M. & Alverson, A.J. (2018). Accelerated diversification is related to life history and locomotion in a hyperdiverse lineage of microbial eukaryotes (Diatoms, Bacillariophyta). New Phytol*.*, 219, 462–473.

Nee, S. (2001). Inferring speciation rates from phylogenies. Evolution, 55, 661–668.

Negri, I. & Toledo, M.E. (2025). Evolution of insect pollination before angiosperms and lessons for modern ecosystems. Insects, 17, 103.

Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. (2007). The modularity of pollination networks. Proc. Natl. Acad. Sci. U.S.A., 104, 19891–19896.

Ollerton, J. (2017). Pollinator diversity: Distribution, ecological function, and conservation. Annu. Rev. Ecol. Evol. Syst., 48, 353–376.

Onstein, R.E., Baker, W.J., Couvreur, T.L.P., Faurby, S., Svenning, J.-C. & Kissling, W.D. (2017). Frugivory-related traits promote speciation of tropical palms. Nat. Ecol. Evol., 1, 1903–1911.

O'Meara, B.C., Smith, S.D., Armbruster, W.S., Harder, L.D., Hardy, C.R., Hileman, L.C., Hufford, L., Litt, A., Magallón, S., Moore, R.G., Psaltis, V.G., Rausher, M.D. & Diggle, P.K. (2016). Non-equilibrium dynamics and floral trait interactions shape extant angiosperm diversity. Proc. R. Soc. B, 283, 20152304.

Panchy, N., Lehti-Shiu, M., & Shiu, S.-H. (2016). Evolution of gene duplication in plants. Plant Physiol., 171, 2294–2316.

Pauw, A. (2013). Can pollination niches facilitate plant coexistence?. Trends Ecol. Evol., 28, 30–37.

Peay, K.G. (2016). The mutualistic niche: Mycorrhizal symbiosis and community dynamics. Annu. Rev. Ecol. Evol. Syst., 47, 143–164.

Peris, D. & Condamine, F.L. (2024). The angiosperm radiation played a dual role in the diversification of insects and insect pollinators. Nat. Commun., 15, 552.

Peris, D., Ollerton, J., Sauquet, H., Hidalgo, O., Peñalver, E., Magrach, A., Delclòs, X., Condamine, F.L., Labandeira, C.C. & Pérez-de la Fuente, R. (2025). Evolutionary implications of a deep-time perspective on insect pollination. Biol. Rev., 100, 1452–1466.

Pérez-Escobar, O.A., Bogarín, D., Przelomska, N.A., Ackerman, J.D., Balbuena, J.A., Bellot, S. & Antonelli, A. (2024). The origin and speciation of orchids. New Phytol., 242, 700–716.

Rabosky, D.L. (2010). Extinction rates should not be estimated from molecular phylogenies. Evolution, 64, 1816–1824.

Rabosky, D.L. (2013). Diversity-dependence, ecological speciation, and the role of competition in macroevolution. Annu. Rev. Ecol. Evol. Syst., 44, 481–502.

Reginato, M., Vasconcelos, T.N., Kriebel, R. & Simões, A.O. (2020). Is dispersal mode a driver of diversification and geographical distribution in the tropical plant family Melastomataceae? Mol. Phylogenet. Evol., 148, 106815.

Remy, W., Taylor, T.N., Hass, H. & Kerp, H. (1994). Four hundred-million-year-old vesicular arbuscular mycorrhizae. Proc. Natl. Acad. Sci. U.S.A., 91, 11841–11843.

Ricklefs RE, Renner SS. (1994). Species richness within families of flowering plants. Evolution, 48, 1619–1636.

Sargent, R.D. (2004). Floral symmetry affects speciation rates in angiosperms. Proc. R. Soc. B, 271, 603–608.

Sato, H., Tanabe, A.S. & Toju, H. (2017). Host shifts enhance diversification of ectomycorrhizal fungi. New Phytol., 214, 443–454.

Savolainen, V., Anstett, M.-C., Lexer, C., Hutton, I., Clarkson, J.J., Norup, M.V., Powell, M.P., Savolainen, D., Salamin, N. & Baker, W.J. (2006). Sympatric speciation in palms on an oceanic island. Nature, 441, 210–213.

Schuldt, A., Assmann, T., Brezzi, M., Buscot, F., Eichenberg, D., Gutknecht, J. et al.

(2018). Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nat. Commun., 9, 2989.

Seidler, T.G. & Plotkin, J.B. (2006). Seed dispersal and spatial pattern in tropical trees. PLoS Biol., 4, e344.

Serrano-Serrano, M.L., Rolland, J., Clark, J.L., Salamin, N. & Perret, M. (2017). Hummingbird pollination and the diversification of angiosperms. Proc. R. Soc. B, 284, 20162816.

Silvestro, D., Cascales-Miñana, B., Bacon, C. D., & Antonelli, A. (2015). Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. New Phytol., 207, 425–436.

Simpson, A.G., Wing, S.L. & Fenster, C.B. (2022). Diversification in the Rosales is influenced by dispersal, geographic range size, and pre-existing species richness. Am. J. Bot., 109, 922–938.

Stebbins, G.L. (1974). Flowering Plants: Evolution Above the Species Level. Harvard Univ. Press, Cambridge, MA.

Stephens, R.E., Gallagher, R.V., Dun, L., Cornwell, W. & Sauquet, H. (2023). Insect pollination for most of angiosperm evolutionary history. New Phytol., 240, 880–891.

Strullu-Derrien, C., Selosse, M.-A., Kenrick, P. & Martin, F.M. (2018). The origin and evolution of mycorrhizal symbioses. New Phytol., 220, 1012–1030.

Sánchez-Bayo, F. & Wyckhuys, K.A. (2019). Worldwide decline of the entomofauna: A review of its drivers. Biol. Conserv., 232, 8–27.

Tedersoo, L., & Smith, M. E. (2013). Lineages of ectomycorrhizal fungi revisited: foraging strategies and novel lineages revealed by sequences from belowground. Fungal Biol. Rev., 27, 83–99.

Tedersoo, L., Bahram, M. & Zobel, M. (2020). How mycorrhizal associations drive plant population and community biology. Science, 367, eaba1223.

Tiffney, B.H. & Mazer, S.J. (1995). Angiosperm growth habit, dispersal and diversification reconsidered. Evol. Ecol., 9, 93–117.

Tong, Z. Y., Wu, L. Y., Feng, H. H., Zhang, M., Armbruster, W. S., Renner, S. S., & Huang, S. Q. (2023). New calculations indicate that 90% of flowering plant species are animal-pollinated. Natl. Sci. Rev., 10, nwad219.

Valdovinos, F. S. (2025). Effect of network structure and adaptive foraging on pollination services of species-rich plant-pollinator communities. Integr. Comp. Biol., 65, 981–990.

Valencia-Montoya, W. A., Liénard, M. A., Rosser, N., Calonje, M., Salzman, S., Tsai, C.-C., Yu, N., Carlson, J. R., Cogni, R., Pierce, N. E., & Bellono, N. W. (2025). Infrared radiation is an ancient pollination signal. Science, 390, 1164–1170.

Vamosi, J.C., Magallón, S., Mayrose, I., Otto, S.P. & Sauquet, H. (2018). Macroevolutionary patterns of flowering plant speciation and extinction. Annu. Rev. Plant Biol., 69, 685–706.

Van Valen, L. (1976). The Red Queen lives. Nature, 260, 575.

Van de Peer, Y., Ashman, T.-L., Soltis, P.S., & Soltis, D.E. (2021). Polyploidy: an evolutionary and ecological force in stressful times. The Plant Cell, 33, 11–26.

Van de Peer, Y., Mizrachi, E., & Marchal, K. (2017). The evolutionary significance of polyploidy. Nat. Rev. Genet., 18, 411–424.

Van der Niet, T., Peakall, R. & Johnson, S.D. (2014). Pollinator-driven ecological speciation in plants: New evidence and future perspectives. Ann. Bot., 113, 199–212.

Wang, X., Miao, L., Huang, X., Mao, L., Cai, T., Svenning, J.-C. & Feng, G. (2024). Diversification in birds is promoted by plant diversity, topographic heterogeneity and stable paleoclimate. J. Biogeogr., 51, 2084–2093.

Waser, N. M. (1978). Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology, 59, 934-944.

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. (1996). Generalization in pollination systems, and why it matters. Ecology, 77, 1043–1060.

Weber, M. G., & Agrawal, A. A. (2014). Defense mutualisms enhance plant diversification. Proc. Natl. Acad. Sci. U.S.A., 111, 16442–16447.

Whittall, J.B. & Hodges, S.A. (2007). Pollinator shifts drive increasingly long nectar spurs in columbine flowers. Nature, 447, 706–709.

Wiegand, T., Wang, X., Fischer, S.M., Kraft, N.J.B., Bourg, N.A., Brockelman, W.Y. et al. & Huth, A. (2025). Latitudinal scaling of aggregation with abundance and coexistence in forests. Nature, 640, 967–973.

Wu, Z.Y., Milne, R.I., Liu, J., Nathan, R., Corlett, R.T. & Li, D.Z. (2023). The establishment of plants following long-distance dispersal. Trends Ecol. Evol., 38, 289–300.

Yamawo, A. & Ohno, M. (2024). Joint evolution of pollination, seed dispersal, and mycorrhizal symbioses. New Phytol., 241, 452–463.

Yamawo, A., Tagawa, J., Hada, Y. & Suzuki, N. (2014). Different combinations of multiple defence traits in an extrafloral nectary-bearing plant under varying habitats. J. Ecol., 102, 238–247

Zhou, G., Liu, J.X., Liu, J., Yang, J., Qiao, X., Cao, M. & Jiang, M. (2024). Ants may buffer the Janzen–Connell effect in a tropical forest in Southwest China. Ecology, 105, e4380.

van der Heijden, M.G.A., Martin, F.M., Selosse, M.-A. & Sanders, I.R. (2015). Mycorrhizal ecology and evolution: The past, the present, and the future. New Phytol., 205, 1406–1423.

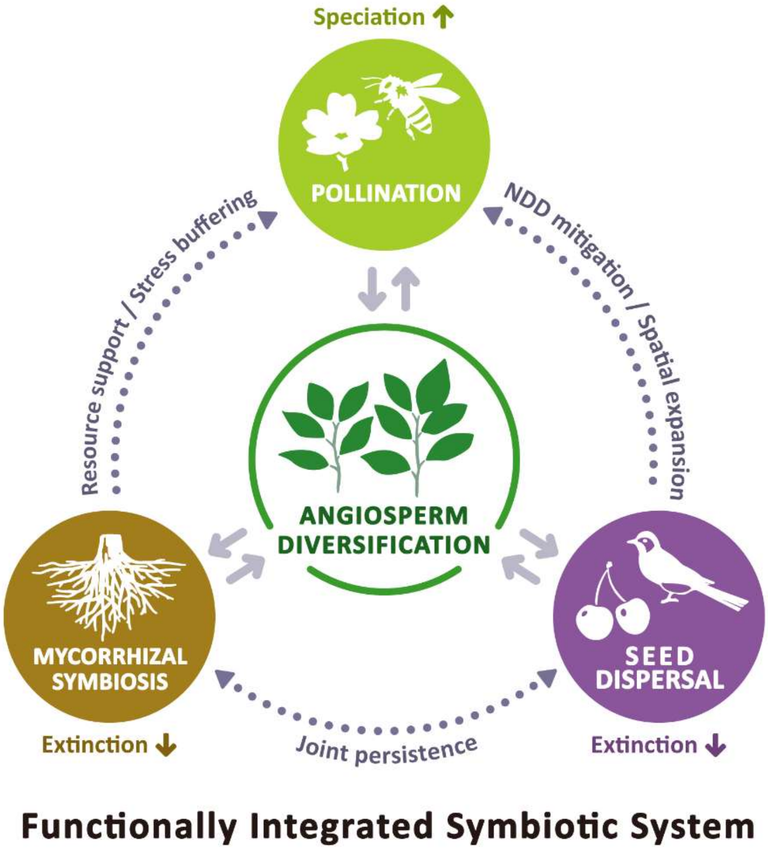

Figure 1. The Functionally Integrated Symbiotic System (FISS) as an emergent outcome of interacting mutualisms

Conceptual illustration of the FISS framework, in which angiosperm diversification emerges from coordinated interactions among mycorrhizal symbiosis, pollination, and seed dispersal. Solid arrows represent direct diversification effects mediated by plant–mutualist interactions, whereas dashed arrows indicate indirect feedbacks among mutualisms. Labels on dashed arrows denote representative underlying processes (e.g., buffering of environmental stress, facilitation of establishment, and negative density dependence, NDD). The framework emphasizes that diversification dynamics arise from the functional coupling of co-occurring mutualisms rather than from the isolated effects of any single interaction. The FISS is presented as a conceptual model describing an emergent diversification regime driven by the decoupling of speciation and extinction, rather than as a single causal mechanism (Box 1).

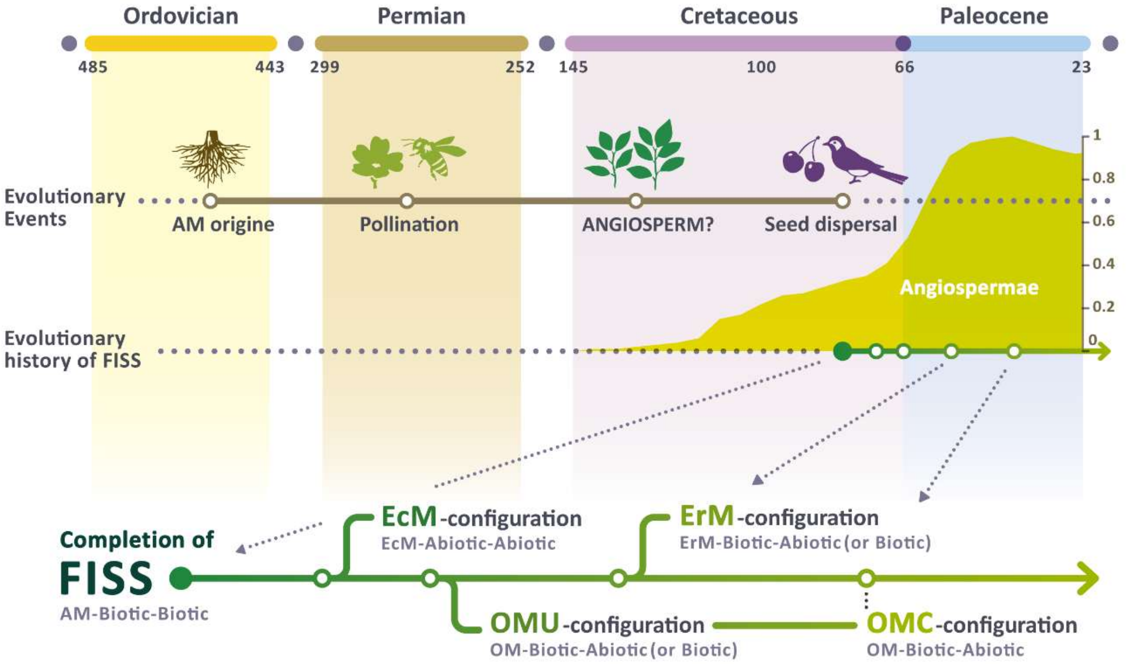

Figure 2. Stepwise assembly of the Functionally Integrated Symbiotic System (FISS) and major configuration of interactions

Conceptual timeline illustrating the sequential emergence of major plant–mutualist interactions and the assembly of Interaction configurations across geological time. Arbuscular mycorrhizal (AM) symbioses were established early in land plant evolution, likely around 460 million years ago during the initial colonization of terrestrial environments (Remy et al., 1994; Brundrett, 2002; Strullu-Derrien et al., 2018). Angiosperms originated later in the Early Cretaceous (approximately 130–100 Ma), and phylogenetic and palaeobotanical evidence indicates that many early angiosperm lineages were already associated with biotic pollination at this time (Stephens et al., 2023). The shaded area labeled ‘Angiospermae’ represents the estimated relative diversity of angiosperms (Silvestro et al., 2015). Subsequently, animal-mediated seed dispersal became increasingly prevalent from the Late Cretaceous to early Paleogene (approximately 100–60 Ma) (Tiffney & Mazer, 1995; Eriksson et al., 2000; Jin et al., 2026). These evolutionary events are shown as the stepwise assembly of enabling structural conditions, defined by specific configurations of mycorrhizal type, pollination mode, and seed dispersal mode (listed in this order). The Baseline configuration of interactions (AM–biotic pollination–biotic seed dispersal) represents the structural foundation that ignites the FISS, whereas alternative configurations involving ectomycorrhizal (EcM; which repeatedly evolved since the Late Cretaceous across multiple plant and fungal lineages, ca. 100–50 Ma; Tedersoo & Smith 2013), ericoid mycorrhizae (ErM; likely originated in the Paleogene, ca. 65–30 Ma; Cairney & Meharg 2003), or orchid mycorrhizal (OM; emerging with the early diversification of orchids in the Late Cretaceous, ca. 100–50 Ma, and involving multiple independent fungal partners; Givnish et al. 2015) associations generate distinct diversification regimes (Table 1). Orchid OMU (forest understory) represents a light-limited escape system enabling persistence under chronically low-light conditions, often via ectomycorrhizal networks, whereas Orchid OMC (canopy epiphyte) represents a canopy escape system exploiting high-light environments with strong dependence on orchid mycorrhizae. The lines connecting FISS to EcM-, ErM-, and OM-based configurations indicate their evolutionary derivation from the ancestral AM symbiosis. They do not imply that these configurations arose directly from FISS itself; rather, they reflect independent reconfigurations of interaction systems built upon an AM-derived symbiotic foundation.

959 Table 1. Interaction configurations and their predicted diversification regimes.

Major configuration category	Primary pollination mode	Seed dispersal mode	Mycorrhizal association	Expected effects on diversification (λ, μ)
Baseline-configuration	Biotic pollination	Animal-mediated	Arbuscular mycorrhiza	Moderate to high λ; low μ – Pollinator-mediated reproductive isolation promotes lineage splitting, while efficient dispersal and AM-mediated nutrient acquisition buffer extinction and support long-term persistence
Ectomycorrhizal (EcM)-configuration	Predominantly wind pollination	Gravity and wind	Ectomycorrhiza	Low to moderate λ; consistently low μ – Diversification driven mainly by physiological tolerance, geographic expansion, and extinction avoidance via

				shared fungal networks rather than partner specialization
Ericoid mycorrhizae (ErM)-configuration	Biotic pollination (mainly insects)	Gravity- or animal-mediated	Ericoid mycorrhiza	Moderate λ; low to moderate μ – Reproductive diversification under strong nutrient limitation; persistence facilitated by highly specialized nutrient acquisition strategies
Orchid OMF (forest understory) - configuration *(light-limited escape system)*	Reduced or highly specialized biotic pollination (often Hymenoptera)	Wind or animal-mediated	Orchid mycorrhiza (Basidiomycota; often linked to EcM networks)	Potentially high λ; high μ – Strong reproductive isolation and niche novelty promote rapid speciation, but extreme symbiotic dependence and demographic sensitivity elevate extinction risk

Orchid OMC (canopy epiphyte)-configuration *(canopy escape system)*	Highly specialized biotic pollination (often Hymenoptera)	Wind dispersal	Orchid mycorrhiza (Basidiomycota; weak or no soil EcM connection)	Moderate to high λ; high μ – Rapid lineage turnover driven by strong reproductive isolation and ecological release, coupled with high environmental and demographic vulnerability

* Expected effects on speciation (λ) and extinction (μ) are comparative and hypothesis-driven, inferred from diversification patterns, ecological persistence, reproductive isolation mechanisms, and symbiotic constraints. These categories represent relative expectations among alternative symbiotic strategies rather than direct rate estimates. Table S1 summarizes predominant tendencies of individual interactions within configurations and does not imply that diversification regimes can be inferred from speciation or extinction components in isolation.

Table S1. Distinct and emergent macroevolutionary roles of major plant mutualisms. Arrows indicate the direction and relative magnitude of effects on diversification components: ↑ and ↓ denote moderate increases or decreases, ↑↑ and ↓↓ denote strong increases or decreases, and ↔ indicates little or no consistent effect. Context-dependent effects reflect variation among taxa or ecological conditions.

Mutualistic interaction	Primary ecological function	Main macroevolutionary effect	Effect on speciation rate (s)	Effect on extinction rate (μ)	Net diversification (λ)	Key mechanisms	Representative references
Pollination	Pollen transfer and mate choice	Lineage splitting	↑↑	↔ / ↑ (context-dependent)	↑	Pollinator-mediated assortative mating; sensory bias; behavioral constancy; floral modularity	Stebbins 1974; Sargent 2004; Van der Niet & Johnson 2014

Seed dispersal	Spatial redistribution of offspring	Lineage persistence	↔ / ↑	↓↓	↔ / ↑	Reduced density-dependent mortality; range expansion; demographic buffering; genetic connectivity	Seidler & Plotkin 2006; Beckman & Sullivan (2023)
Mycorrhizal symbioses (AM)	Nutrient acquisition; stress buffering	Lineage persistence; ecological opportunity	↔ / ↑	↓↓	↔ / ↑	Improved seedling establishment; Resource partitioning; enhanced reproductive allocation; niche	Tedersoo et al. (2020)

						expansion	
Functionally Integrated Symbiotic System (Symbiotic Engine)	Coordinated reproduction, dispersal, and resource acquisition	Sustained net diversification	↑↑	↓↓	↑↑	Resolution of s–μ trade-off through complementary functions; demographic and ecological buffering	

Box 1. The Functionally Integrated Symbiotic System (FISS): Core Features

The Functionally Integrated Symbiotic System (FISS) describes a macroevolutionary system in which multiple mutualistic interactions are organized such that processes promoting lineage splitting and those enhancing lineage persistence are partially decoupled. Rather than arising from individual traits or isolated interactions, this system emerges from the coordinated combination of pollination, seed dispersal, and mycorrhizal symbioses operating across life-history stages and spatial scales.

Functional decoupling

Processes promoting lineage splitting and those enhancing persistence tend to operate on different components of the life cycle and at different spatial and temporal scales. Reproductive processes associated with mating and gene flow are often separated from those governing establishment, survival, and resource acquisition. This separation can allow diversification to proceed without a strict coupling between increased speciation and elevated extinction risk.

Asymmetric contributions of mutualisms

Within this decoupled structure, different mutualisms appear to contribute unequally to speciation and extinction dynamics. Pollination is more consistently associated with processes that promote lineage splitting, whereas seed dispersal and mycorrhizal symbioses tend to enhance persistence by reducing extinction risk. This asymmetry reflects a division of functional roles among interactions, rather than equivalent or additive effects.

System-level buffering

Stability at macroevolutionary timescales may emerge from the combined effects of multiple interactions rather than from the strength of individual pairwise relationships. By operating within multispecies assemblages, persistence-enhancing mutualisms can provide redundancy, spatial buffering, and demographic stabilization, potentially reducing extinction risk even when speciation-promoting processes remain active.

Dependence on the configuration of interactions

Diversification outcomes are expected to depend on how interactions are combined, rather than simply on the presence of multiple mutualisms. Different combinations of pollination, seed dispersal, and mycorrhizal associations can be associated with distinct diversification dynamics, suggesting that similar components may yield different macroevolutionary outcomes depending on their organization (Table 1).

Under these features, the FISS is best understood not as a single mechanism, but as an emergent pattern of diversification arising from the coordinated organization of multiple mutualistic interactions.