Mycorrhizal evolution restructures forest ecosystems

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Running title | Ecosystem Regime Restructuring by Mycorrhizal Symbiosis

Abstract

Mutualisms are key drivers of species diversification and biodiversity, yet their comprehensive role in shaping contemporary ecosystems remains poorly understood. Mycorrhizal symbioses (Arbuscular mycorrhiza [AM] and Ectomycorrhizal [EcM]) are among the most ecologically important interactions on Earth, driving the origin and maintenance of terrestrial biodiversity. Nearly all tree species associate with these fungi; AM symbiosis, the ancient form, dominates tropical forests, while the later-emerging EcM symbiosis, though taxonomically narrow, primarily influences temperate forests. Previous studies have shown that mycorrhizal type is associated with both tree population density and forest spatial organization. At the population level, EcM trees tend to attain higher local densities than AM trees. At the forest-community level, EcM-rich forests exhibit stronger spatial structuring, characterized by greater conspecific aggregation than the dispersed distributions typically observed in AM-dominated forests. In this paper, we propose the Ecosystem Regime Restructuring by Mycorrhizal Symbiosis (ERRM) hypothesis. Here, we defome am ecosystem regime as the large-scale organization of ecosystems characterized by dominant spatial structures, trophic interactions, and trait syndromes. This hypothesis posits that the evolutionary shifts in mycorrhizal type from AM to EcM have widely altered ecosystem spatial structure, thereby reshaping tree macroevolutionary patterns, driving large-scale ecosystem reorganization, and creating distinct ecological and evolutionary contexts. Dispersed AM trees typically favor long-range biotic seed dispersal and biotic pollination. Clustered EcM trees, conversely, favor wind pollination and short-range wind dispersal. This suggests joint evolution between mycorrhizal type and reproductive/dispersal modes. Spatial structure also influences plant defense strategies: clustered EcM trees

may tend to display a higher carbon-to-nitrogen ratio and carbon-based quantitative defenses. AM trees may be associated with higher nutrient content and qualitative chemical defenses like alkaloids. These contrasting defense strategies may reflect differences in herbivore encounter rates determined by the spatial structure of AM and EcM communities. Furthermore, the dense, stable resource environment provided by EcM clusters facilitates the evolution of specialized herbivores. We present this novel hypothesis with an empirical dataset partially supporting it. Finally, we argue that the ERRM hypothesis provides the fundamental framework toward a new understanding of the present ecosystem regime with an integrative approach combining phylogenetic analysis, macroecology, and experimental studies.

Keywords | aboveground and belowground interactions, ecological network, ecosystem evolution, plant-soil feedback, spatial and temporal structure, trophic interactions

Introduction

Mycorrhizal symbioses are widespread mutualisms that mediate plant nutrient acquisition and influence plant community dynamics across terrestrial ecosystems, with important consequences for terrestrial biodiversity. For more than 400 million years, these mutualisms have supported the diversification of land plants by enabling nutrient exchange between fungi and their hosts, and have influenced plant community dynamics across terrestrial ecosystems (Tedersoo et al., 2020; Benton et al., 2022). Moreover, the mycorrhizal symbiosis had impacts on decomposition processes and soil nutrient cycling (e.g., Phillips et al., 2013; Steidinger et al., 2019). Yet, the consequences of the evolution of mycorrhizal symbiosis for the ecological and evolutionary dynamics of terrestrial forest ecosystems, particularly aboveground, remain an area of research that has not yet been extensively explored (Yamawo & Ohno 2024; Moora et al., 2025).

Nearly all tree species associate with mycorrhizal fungi: the majority form arbuscular mycorrhizal (AM) symbioses, while approximately 2% form ectomycorrhizal (EcM) associations (Steidinger *et al*., 2019; Brundrett & Tedersoo, 2020; Tedersoo *et al*., 2020). Despite their relatively narrow taxonomic distribution, EcM associations dominate temperate forests, whereas AM associations prevail in tropical forests. Importantly, AM and EcM symbioses differ fundamentally in spatial population structures in forest ecosystems (Bennett et al., 2017; Delavaux et al., 2023). Specifically, mycorrhizal type is associated with tree recruitment, local density, and forest spatial organization across multiple scales. EcM trees experience weaker negative conspecific density dependence than AM trees across global forest plots (Delavaux et al., 2023), EcM-rich forest communities show stronger spatial structuring (Bennet et al.,

2017; Shinohara et al., 2024), and contrasting spatial associations between AM and EcM trees have been reported in temperate forest megaplots (Mao et al., 2024). Although EcM symbiosis evolved independently in multiple plant lineages, this structural pattern is universal and manifests across broad spatial scales (Bennett et al., 2017; Tedersoo et al., 2020; Delavaux et al., 2023; Shinohara et al., 2024), inevitably exerting macro-level influences on interspecific interactions and the organization of terrestrial communities. Indeed, accumulating evidence indicates that key functional traits, including those of leaves, flowers, and fruits, differ systematically among mycorrhizal association types (AM or EcM), reflecting the broad ecological and evolutionary consequences of population structure (Tedersoo et al., 2020; Yamawo & Ohno, 2024).

In this Perspective, we illustrate how the contrasting spatial population structures driven by different mycorrhizal symbioses may influence the evolutionary trajectories of tree species (Tedersoo et al., 2020; Yamawo & Ohno, 2024). Theoretical and empirical studies suggest that differences in plant population density can alter interactions with herbivores through changes in resource concentration, plant apparency, and plant–plant interactions (Root, 1973; Agrawal et al., 2006; Underwood et al., 2020; Ohsaki et al., 2022). Plant population density can also influence interactions with pollinators, with consequences for visitation and reproductive success (Mustajärvi et al., 2001). Therefore, we hypothesize that density-driven effects shaped by the evolutionary history of mycorrhizal associations can, in turn, influence the evolution of both plants and their associated biota, ultimately shaping patterns of coevolution and diversification across trophic networks.

Here, we propose the Ecosystem Regime Restructuring by Mycorrhizal

Symbiosis (ERRM) hypothesis, which links the evolutionary history of mycorrhizal associations to the evolution of aboveground traits and species interactions through changes in the spatial organization of tree populations (Figure 1; Table 1). The central premise of ERRM is that evolutionary transitions in mycorrhizal associations can alter the ecological processes governing conspecific recruitment and population persistence, thereby modifying the spatial and temporal distribution of host resources. These changes, in turn, may reshape the selective environments experienced by trees and their associated organisms, influencing the evolution of reproductive strategies, plant defenses, and herbivore specialization. ERRM proposes a critical causal pathway through which mycorrhizal evolution can shape evolutionary trajectories by modifying spatially structured ecological interactions. To address ERRM, we synthesize the existing literature and present new analyses, including forest inventory data from Japan, to examine how mycorrhizal type is associated with spatial organization of tree populations and to evaluate empirical patterns relevant to broader ERRM predictions concerning plant traits, species diversity, and associated biotic interactions. We distinguish well-supported empirical patterns from hypothesized mechanisms and novel ERRM predictions, highlighting where direct evidence is still lacking.

Mycorrhizal associations, plant–soil feedbacks, and tree spatial structure

Plant–soil feedback and spatial structures of AM- and EcM-trees

Multiple lines evidence show association with mycorrhizal type to tree recruitment, local population density, and forest spatial organization (Bennet et al., 2017; Johnson et al., 2017; Sasaki et al., 2019; Delavaux et al., 2023; Shinohara et al., 2024; Mao et al., 2024). Our analysis using Japanese forest dataset also show that the EcM tree species

exhibited, on average, several-fold higher population densities than AM tree species (Figure 2). The key unresolved question is which mechanisms generate them and how general they are across forest systems. Plant–soil feedbacks (PSFs) are one leading candidate mechanism. (Bennett *et al*., 2017; Kadowaki 2024). PSFs represent the net effects of plant-induced changes in the biotic and abiotic soil environment on subsequent plant performance, and their direction may arise through multiple mechanisms. Negative PSFs can arise through several mechanisms, including the accumulation of host-specific pathogens around adult trees, nutrient depletion, or changes in mycorrhizal communities themselves (Bennett *et al*., 2017; Bever, 2002; Kadowaki 2024; Tedersoo *et al*., 2020). These processes facilitate local species turnover and may lead to spatially variable species composition, especially when seed dispersal is sufficiently long-distance and effective. Consequently, negative PSFs may contribute to lower local conspecific recruitment and greater spatial and temporal turnover in conspecific host availability. By contrast, positive PSFs occur when plant-induced changes in soil conditions enhance subsequent conspecific performance. Such effects may involve the accumulation of mutualistic organisms, changes in nutrient availability, or reduced effects of antagonists, enhancing the establishment of conspecific seedlings and may promoting the persistence of monodominant forest stands (McGuire, 2007; Tedersoo *et al*., 2020). Thus, positive PSFs may contribute to spatially concentrated and persistent conspecific populations (Shan *et al*., 2025). The contrasting PSF effects between AM and EcM trees may stem partly from differences in their ability to protect seedlings from host-specific pathogens: EcM associations may reduce pathogen effects on seedlings more strongly than AM associations (Tedersoo *et al*., 2020).

Shifts of tree distributional patterns over evolutionary time scales

EcM symbiosis evolved repeatedly and independently in multiple plant lineages, substantially later than the origin of AM symbiosis. These independent transitions provide a natural comparative framework for investigating whether changes in mycorrhizal associations have repeatedly altered the ecological processes governing tree spatial structure (Figure 1). A critical prediction of ERRM is that evolutionary transitions in mycorrhizal associations should be associated with repeated changes in recruitment processes and spatial population structure across independent plant lineages. For example, spatial distribution patterns are phylogenetically conserved in tropical forests, with closely related species tending to show similar spatial structures (Réjou-Méchain *et al*., 2011; Martins *et al*., 2018), consistent with the ERRM prediction that tree spatial structure changes over evolutionary time. Similarly, meta-analyses of PSF experiments show that phylogenetically related species tend to have more similar PSF responses (Crawford *et al*., 2019; Wandrag *et al*., 2020), suggesting that PSF itself has an evolutionary component. Because plant pathogens have existed since early in plant evolution (Strullu-Derrien *et al*., 2018; Morris & Moury, 2019), AM-associated tree lineages may have long experienced negative PSFs and relatively dispersed spatial distributions. Independent transitions to EcM symbiosis may have weakened these negative PSFs or, in some cases, shifted them toward positive feedbacks, promoting greater local aggregation and monodominance (Figure 1, Event 1).

How does the spatial structure of a tree population affect the evolution of other tree traits?

Reproductive and dispersal characteristics

Given that different mycorrhizal types promote contrasting tree population densities (Tedersoo et al., 2020), we posit that trees associated with different mycorrhizal types exhibit preferences for distinct seed dispersal and pollination modes (Figure 1). Biotic pollen and seed dispersal permit greater dispersal distances than wind or unspecialized dispersal in trees (Pellmyr 1992; Hesse & Pannell 2011; Mustajärvi et al. 2001; Yamawo & Ohno 2024). Specifically, negative plant-soil feedbacks (PSFs) in AM trees, may favor long-range biotic seed dispersal. Conversely, positive PSFs in EcM trees, may favor short-range wind or unspecialized seed dispersal. Furthermore, while animal pollination may be unnecessary for EcM trees due to the high density of conspecifics facilitating adequate wind pollination, AM trees are expected to favor biotic pollination to achieve dispersal over longer distances (Pellmyr, 1992; Yamawo & Ohno, 2024). In fact, using global tree databases, Yamawo & Ohno (2024) show the evolutionary relationships among mycorrhizal type, seed dispersal mode, and pollination mode. Most AM trees had endozoochorous seed dispersal and biotic pollination, whereas most EcM trees had anemochorous seed dispersal and wind pollination. These results suggest that the ecological factors relation to mycorrhizal types including contrast PSF effects influence the evolution of pollination and seed dispersal modes.

Independent ecological evidence provides a plausible basis for this proposed mechanism. Janzen–Connell effects generate distance- and density-dependent variation in seed and seedling survival around conspecific adults (Janzen, 1970; Connell, 1971), and soil fungal communities can contribute to interspecific variation in conspecific negative density dependence (Chen et al., 2019). These processes could create selection favoring seed dispersal away from conspecific adults. Comparative analyses linking PSF strength, seed dispersal and pollination modes, realized seed-dispersal and

pollination distance, and conspecific density across taxa would provide a direct test of this proposed pathway. In addition to mycorrhizal type, understanding how seed dispersal and pollination modes interact to shape tree spatial structure represents another important avenue for future research under the ERRM hypothesis (Figure1, Event 1).

Defense against herbivores

Contrasting spatial and temporal population structures (dispersion versus clustering) are likely to impose different selective pressures for plant defense mechanisms, mediated through varying herbivore encounter rates. A review by Agrawal *et al*. (2006) provides a comprehensive overview of how plant community structure influences plant–animal interactions. Here, we focus on how spatial structure associated with mycorrhizal type may influence plant defense.

In general, herbivores are more abundant and inflict greater damage in areas where host plants are concentrated, due to high plant density or low species diversity (Root, 1973; Rhainds & English-Loeb, 2003; Jactel et al., 2021; Ohsaki et al., 2022; Yuan & Wang, 2025). Because EcM trees tend to attain higher local densities and show stronger spatial structuring than AM trees, they may experience higher herbivore encounter rates and stronger selection for defense. Conversely, the lower local densities and more dispersed spatial distributions associated with AM trees may expose them to different herbivore encounter regimes, potentially favoring different defensive strategies.

Another major prediction in plant defense theory is that long-lived, dominant trees in late-successional communities tend to invest heavily in quantitative chemical defenses (e.g., tannins, phenolics) (Feeny 1975, 1976; Rhoades & Cates, 1976). In

contrast, fast-growing, early-successional plants allocate more resources to toxic, qualitative defenses (e.g., alkaloids, amines). Although this prediction, Plant Apparency Hypothesis (PAH), has been criticized for oversimplifying plant defense strategies (Price *et al*., 1980; Bernays & Graham, 1988), it remains a foundational concept in explaining herbivory patterns within forest ecosystems (Yuan & Wang, 2025; Jactel *et al*., 2021; Zhou *et al*., 2024). In short, the mechanism underlying these predictions suggests that differences in the frequency and predictability of herbivore encounters can favor different defense strategies.

Based on these mechanisms, the contrasting spatial structures associated with AM and EcM trees, together with potential differences in temporal persistence, may generate systematic differences in herbivore encounter regimes. Because AM and EcM trees differ in local density and spatial structure, they may also differ in their rates of encounter with herbivores. The higher local densities of EcM trees may favor greater investment in quantitative defenses, whereas the lower densities and more dispersed distributions of AM trees may favor qualitative defenses (Figure 1, Event 2). Conversely, the lower local densities and more dispersed spatial distributions associated with AM trees may result in less consistent herbivore encounters, potentially favoring qualitative defenses. Comparison of defenses among mycorrhizal types in trees therefore provides an opportunity to examine the evolution of plant defenses in relation to spatial and temporal population structure, while reducing some of the major life-history differences that complicate comparisons between herbs and trees.

Several pioneering studies have reported that the chemical composition of fresh leaves and leaf litter differs between EcM- and AM trees (e.g. Seyfried *et al*. 2021; Jantzen *et al.* 2023). For instance, EcM tree species often exhibit higher lignin content

than AM species. Additionally, our analysis based on the Plant Trait Database indicates that the fresh leaves of AM tree species tend to have higher nutrient and chlorophyll content (Figure 3A and B). Conversely, EcM species display a higher carbon-to-nitrogen ratio, as shown in Figure 3C, a pattern that is consistent with, greater investment in carbon-based quantitative defenses. Furthermore, Wink (2020) pointed out that alkaloid production, a form of qualitative chemical defense that often functions as a neurotoxin against insects and vertebrates, is more common among biotically pollinated plant species, while biotic pollination is more frequent among AM-associated trees (Yamawo & Ohno, 2024). These findings suggest that mycorrhizal associations are linked to broader differences in leaf resource-use strategies, which may influence the costs and benefits of alternative defense strategies. Thus, evolutionary transitions in mycorrhizal association, through their effects on plant spatial structure and herbivore encounter rates, may be associated with shifts in defensive strategies from greater reliance on qualitative toward greater reliance on quantitative defenses (Figure 1, Event 2). This prediction can be tested by examining whether tree spatial structure and herbivore interactions mediate the relationship between mycorrhizal type and plant defense traits. Integrating metabolomics with phylogenetic comparative analyses could help clarify these relationships.

Effects of the spatial population structure of trees on the species evolution of associated organisms

Theoretically, intense competition can favor the evolution of broader diet breadths in herbivores through negative density-dependent selection, particularly in variable environments (Smith & Hoekstra, 1980; Futuyma & Moreno, 1988; Hardy *et al*., 2020).

Generalists may be favored in heterogeneous environments, whereas specialists should evolve in more homogeneous settings. Broad niches can also be advantageous even in the absence of intense competition, particularly when environmental uncertainty is high. While acknowledging that several constraints may influence this relationship between diet breadth and environmental factors (Hardy *et al*., 2020), we apply this framework to investigate how mycorrhizal types influence the evolution of tree-associated herbivores as a fundamental hypothesis. As discussed above, EcM tree species tend to form aggregations, creating dense patches of conspecifics. Such arrangements produce spatially homogeneous resource environments for herbivores both above and below ground, including insects and arthropods. Furthermore, colonization of new seedlings of the same species in EcM-dominated forests suggests that these patches also provide a high temporal certainty of habitat, enabling herbivore populations or demes to encounter the same host species with high probability across generations. Consequently, EcM species may facilitate the evolution of herbivore specialization. In contrast, the sparse distribution of AM species creates resource environments that are spatially heterogeneous and temporally uncertain, potentially promoting the evolution of generalist herbivores (Figure 1, Event 3).

We examined whether herbivore specialization was associated with the mycorrhizal type of host trees (Supplementary methods). In Cerambycidae, host-use patterns differed significantly from random expectations, with specialists disproportionately associated with EcM hosts (Figure 4). Lepidoptera showed a similar tendency, and Heteroptera also exhibited an excess of EcM-associated specialists, although the overall pattern was not statistically significant. These findings support the ERRM hypothesis that mycorrhizal associations may influence the evolution of

herbivore specialization, potentially contributing to the diversification of specialist herbivores.

This pattern is also consistent with independent observations from a temperate deciduous forest, where leaf miners associated with AM maple trees used a broad range of plant families, whereas a substantial proportion of those associated with EcM oak trees were restricted to a single host species (Hirao & Murakami, 2008).Top-down regulation by predators is strong, while competition among herbivores is not a primary limiting factor (Hariston *et al*., 1960). However, negative indirect interactions among herbivores for host resources—mediated by induced plant defenses and shared natural enemies—are also significant (Ohgushi, 2005; Denno et al., 2007). Therefore, our assumption of competition, specifically negative interactions between herbivores, remains reasonable within the context of the specialist and generalist evolution scenario in plant-herbivore systems. Furthermore, it is important to note that the direction of evolution favoring specialists or generalists, driven by resource uncertainty in space and time associated with EcM and AM tree species, is consistent with scenarios involving intense competition, despite the absence of direct competitive interactions.

Indeed, researchers have long recognized that the evolution of herbivore specialization is influenced by the relative abundance of plant species (Jaenike, 1990; Bernays, 1998; Kuussaari *et al*., 2000; Utsumi *et al*., 2009; Ohsaki *et al*., 2025). Polyphagous insect species often forage on rare or unpredictable hosts, which are difficult to locate, whereas more specialized species utilize abundant and readily available plants (Jaenike, 1990). Additionally, Jaenike (1990) discussed that the unpredictability of host occurrence can favor polyphagy, and similarly, the unpredictability of host suitability should promote risk spreading behavior. For

example, females may lay eggs on multiple host species, ensuring that at least some offspring survive. Such a strategy can lead to a broader acceptance of various host species for oviposition.

The higher local densities associated with EcM trees could also influence herbivore specialization indirectly through predators. Higher local tree density may increase herbivore abundance or biomass and thereby support greater predator abundance through bottom-up trophic effects. Increased predation pressure may, in turn, favor particular forms of host or resources specialization in herbivores, such as preferences for specific plant tissues, limited phenological windows, or behaviors to avoid predation. For example, gall formation is a herbivore anti-predator strategy, and most gall-inducing species tend to be specialists. The diversification rate of gall-inducing insects is notably high among Eurina sawflies on Salicaceae and Apiomorpha scale insects on Myrtaceae (Hardy & Cook, 2010). Both families are dominated by EcM species (Hardy & Cook, 2010). In addition, the number of gall midge species in Japan is remarkably high within Salicaceae and Fagaceae, which are EcM-dominant families, compared to the number of plant genera (Yukawa *et al*., 2005).

The evolution of herbivore diet breadth has been extensively discussed (Futuyma & Moreno, 1988; Jaenike, 1990; Poisot *et al*., 2011; Forister *et al*., 2015). Hardy et al. (2020) comprehensively summarize the various causes of diet expansion and contraction. In addition to plant densities, numerous factors such as genetic architecture, information processing, and natural enemies influence dietary specialization. Although these factors can direct the evolution of diet breadth in different contexts, we hypothesize that the observed differences in plant density, together with the proposed differences in defense traits and predator interactions, may

348 act together to influence selection toward broader or narrower host use.

349 Evolutionary changes in herbivore diet breadth may also have broader
350 consequences for the organization of ecological interaction networks. Under ERRM, the
351 spatial concentration and temporal persistence of host resources associated with EcM
352 trees are predicted to favor greater host specialization in herbivores. Such specialization
353 could reduce the number of plant species used by individual herbivores and alter the
354 structure of plant–herbivore interaction networks. In contrast, more spatially
355 heterogeneous and temporally unpredictable host environments associated with AM
356 trees may favor broader host use and more generalized interactions. Additionally, the
357 evolution of herbivore specialization or generalization may cascade to predators because
358 herbivore diet breadths can generate similar patterns of spatial resource distribution for
359 predators. Consequently, an ecological network with greater modularity may be
360 observed in EcM-associated plant–herbivore networks specifically when increased host
361 specialization produces relatively distinct groups of interacting species. For example,
362 greater compartmentalization (i.e., greater modularity) has been reported in a food web
363 involving an EcM-associated willows than in one involving an AM-associated box
364 elders (Barbosa *et al*. 2007). Although this observation is consistent with the ERRM
365 prediction, broader replicated comparisons are needed to determine whether
366 mycorrhizal associations systematically influence multitrophic network organization.
367

368 **Future directions**

369 Testing ERRM requires linking the ecological processes that shape tree spatial structure
370 to their evolutionary consequences. **One central question is whether plant–soil**
371 **feedbacks (PSFs) generate these contrasting spatial distributions, which may be**

further reinforced by pollination and seed dispersal modes. In spatially mapped forest plots, pollen movement, seed production and dispersal, and seedling recruitment could be measured alongside experimental estimates of PSFs. Spatially explicit demographic models could then examine how these processes jointly influence conspecific density and aggregation across generations. This would clarify how differences in reproductive processes and soil-mediated recruitment combine to generate and maintain the spatial structures associated with each mycorrhizal type.

A second question concerns the evolutionary consequences of these spatial structures for plants and their associated organisms. Our analyses revealed differences in leaf functional traits among mycorrhizal types (Figure 3) and patterns of herbivore host use consistent with ERRM predictions, particularly in Cerambycidae (Figure 4). Combining broader forest inventory data with reproductive traits, defense chemistry, and herbivore host-use records would allow these associations to be examined across a wider range of species and environments. Comparisons across independent evolutionary origins of EcM symbiosis could then determine whether changes in tree spatial structure have repeatedly accompanied shifts in plant traits and herbivore specialization. Evidence of such repeated changes would suggest that the evolutionary relationships proposed by ERRM extend beyond particular plant lineages.

The role of spatial structure in shaping natural selection on plant defense can be examined experimentally. Manipulating conspecific density and spatial aggregation, together with herbivore access, would allow selection on defensive traits to be measured under different spatial conditions. Metabolomic analyses, combined with measurements of plant fitness, could identify defensive compounds favored under different levels of host aggregation. Tree species capable of forming both AM and EcM associations offer

a useful experimental system because mycorrhizal type and spatial arrangement can be varied within the same host species. Such experiments could distinguish the effects of mycorrhizal associations on plant defense from those mediated by tree spatial structure and establish whether differences in spatial structure alter the direction or strength of selection on defensive traits. These studies could establish whether the spatial changes associated with mycorrhizal evolution have contributed to repeated evolutionary shifts in plant traits and interactions with associated organisms, as proposed by ERRM (Table 1).

Conclusion

Mycorrhizal symbiosis research has primarily focused on the functions of mycorrhizae, such as the acquisition of nutrients and resistance to stress, as well as the effects on the coexistence of different species and the nutrient cycle in the ecosystem. We provide a novel perspective proposing that different types of mycorrhizal symbiosis may influence the biological interactions between tree species and other organisms and their evolutionary trajectories, such as leaf traits and diet breadth of herbivores. Differences in the spatial population structure of tree species may mediate the effects of different types of mycorrhizal symbiosis. Mycorrhizal symbiosis is an ancient and widespread biological interaction that has accompanied land plants since their early evolution: plants have lived closely with mycorrhizal fungi for over 400 million years (Tedersoo & Bahram, 2020), and most tree species in the world rely on mycorrhizae (Brundrett & Tedersoo, 2020). EcM symbiosis evolved repeatedly and independently in multiple plant lineages, substantially later than the origin of AM symbiosis (Tedersoo & Bahram, 2020). Therefore, considering the evolutionary history of mycorrhizal symbiosis from a

tree perspective may provide new insights into the evolutionary history of trees and forest ecosystems, as proposed by the ERRM hypothesis. In future research, ERRM can be tested through an integrative approach combining phylogenetic analysis, biodiversity information, mesocosm experiments, plant physiology, and macroecology; in particular, evaluating the effects of spatial structure using dual mycorrhizal tree species will provide a valuable opportunity to investigate ERRM experimentally. Comparisons across independent evolutionary origins of EcM symbiosis may provide an additional powerful test of whether the ecological and evolutionary changes predicted by ERRM have repeatedly evolved.

Acknowledgments

We thank Dr. Evan Fricke for providing valuable comments on an earlier draft of this manuscript, which significantly improved its clarity and content. We thank Yuichiro Kanzaki for his support in creating the illustrations. We are also profoundly grateful to Misuzu Ohno for discussing the early ideas that shaped this review. AY, KK, YT, NS, and SU were supported by the Japan Society for the Promotion of Science (JSPS) KAKENHI Grants-in-Aid for Scientific Research: grant numbers 25H01003 (AY), 23K21214 (KK), 24K18191 (NS), and 24H00507 (SU).

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626

627 **Figure legends**

628 Figure 1 Conceptual diagram of the Ecosystem Regime Restructuring by Mycorrhizal
629 Symbiosis (ERRM) hypothesis. Early forests are depicted as being dominated by
630 arbuscular mycorrhizal (AM) trees, followed by repeated independent origins of
631 ectomycorrhizal (EcM) associations and potential shifts in plant–soil feedbacks (PSFs)
632 and tree spatial structure. ERRM proposes three major evolutionary consequences of
633 these shifts: Event 1, changes in spatial population structure associated with more
634 negative PSFs in AM trees and weaker negative or positive PSFs in EcM trees. The
635 evolution of seed dispersal and pollination modes may also act in concert with PSFs to
636 shape these spatial patterns. Event 2, shifts in plant defense strategies, with greater
637 reliance on qualitative defenses predicted for AM trees and quantitative defenses for
638 EcM trees. Event 3, changes in associated organisms, with greater herbivore
639 generalization predicted for AM-associated systems and greater specialization for EcM-
640 associated systems. Purple arrows indicate the proposed temporal sequence from early
641 forests to modern ecosystems, and E1–E3 mark the three hypothesized evolutionary
642 consequences.

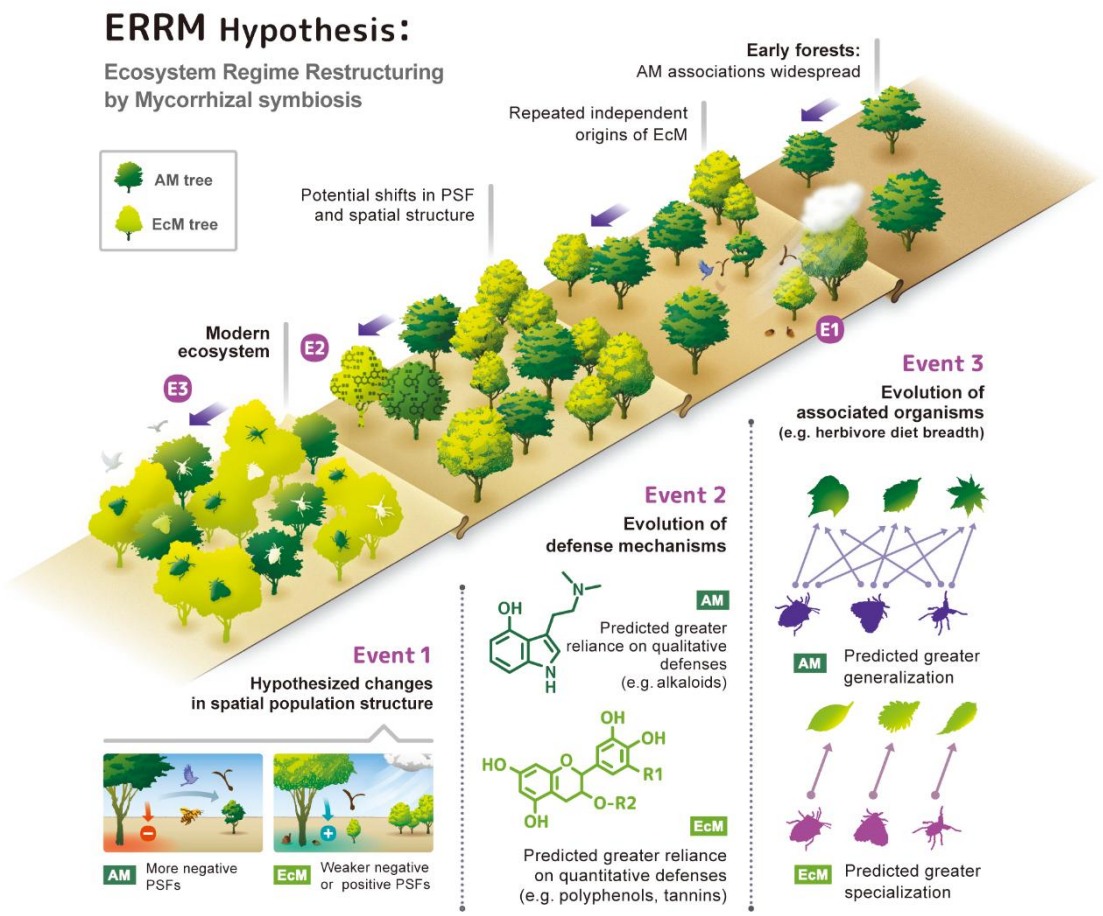
643

644 Figure 2 Population density of tree species associated with arbuscular mycorrhizal
645 (AM) or ectomycorrhizal (EcM) fungi. Population density was expressed as the number
646 of individuals per hectare. An asterisk indicates a significant difference between AM
647 and EcM species (Gamma GLM with a log link, $P < 0.05$). Data were obtained from the
648 nationwide Monitoring Sites 1000 forest-monitoring program in Japan (Ishihara et al.,
649 2010).

650

Figure. 3 Leaf functional traits of trees associated with different mycorrhizal types. Fresh-leaf nitrogen concentration (A), chlorophyll concentration (B), and carbon-to-nitrogen (C:N) ratio (C) of tree species associated with arbuscular mycorrhizal (AM), ectomycorrhizal (EcM), or both AM and EcM fungi (AM/EcM). Different lowercase letters indicate significant pairwise differences among mycorrhizal types based on generalized linear models (GLMs) followed by pairwise comparisons, with Benjamini–Hochberg FDR-adjusted $P < 0.05$. Numbers in parentheses indicate the number of tree species. Trait data were obtained from the TRY Plant Trait Database in 2022.

Figure 4 Host breadth of Lepidoptera, Heteroptera, and Cerambycidae (Coleoptera) in Japan in relation to the mycorrhizal type of their host plants. Host breadth was defined as the number of distinct host-plant families recorded for each insect species. Insect species using only arbuscular mycorrhizal (AM) host families were classified as AM users, those using only ectomycorrhizal (EcM) host families as EcM users, and those using both AM and EcM host families as AM/EcM users. The observed joint distribution of host breadth and mycorrhizal category was compared with expectations under weighted randomization using Monte Carlo G-tests. P values are shown in each panel. Numbers in parentheses indicate the number of insect species. Host-use records were obtained from Inoue et al. (1982) and Tomita (1983) for Lepidoptera; Tomokuni et al. (1993), Yasunaga et al. (2001), and Ishikawa et al. (2012) for Heteroptera; and The Japanese Society of Coleopterology (1984) and Ohbayashi and Niisato (2007) for Cerambycidae.

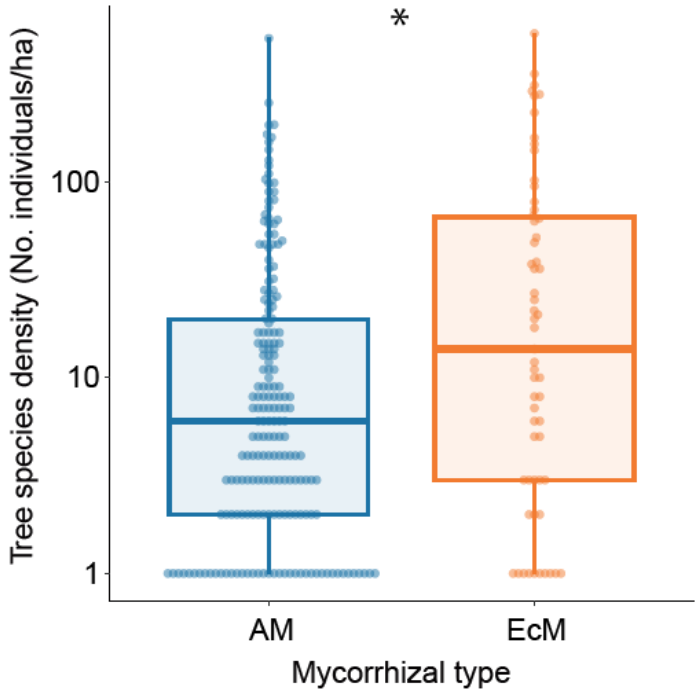


674

675 Figure 1

676 Conceptual diagram of the Ecosystem Regime Restructuring by Mycorrhizal Symbiosis
677 (ERRM) hypothesis. Early forests are depicted as being dominated by arbuscular
678 mycorrhizal (AM) trees, followed by repeated independent origins of ectomycorrhizal
679 (EcM) associations and potential shifts in plant–soil feedbacks (PSFs) and tree spatial
680 structure. ERRM proposes three major evolutionary consequences of these shifts: Event
681 1, changes in spatial population structure associated with more negative PSFs in AM
682 trees and weaker negative or positive PSFs in EcM trees. The evolution of seed
683 dispersal and pollination modes may also act in concert with PSFs to shape these spatial
684 patterns. Event 2, shifts in plant defense strategies, with greater reliance on qualitative
685 defenses predicted for AM trees and quantitative defenses for EcM trees. Event 3,

686 changes in associated organisms, with greater herbivore generalization predicted for
687 AM-associated systems and greater specialization for EcM-associated systems. Purple
688 arrows indicate the proposed temporal sequence from early forests to modern
689 ecosystems, and E1–E3 mark the three hypothesized evolutionary consequences.
690



691

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693 Population density of tree species associated with arbuscular mycorrhizal (AM) or

694 ectomycorrhizal (EcM) fungi. Population density was expressed as the number of

695 individuals per hectare. An asterisk indicates a significant difference between AM and

696 EcM species (Gamma GLM with a log link, $P < 0.05$). Data were obtained from the

697 nationwide Monitoring Sites 1000 forest-monitoring program in Japan (Ishihara et al.,

698 2010).

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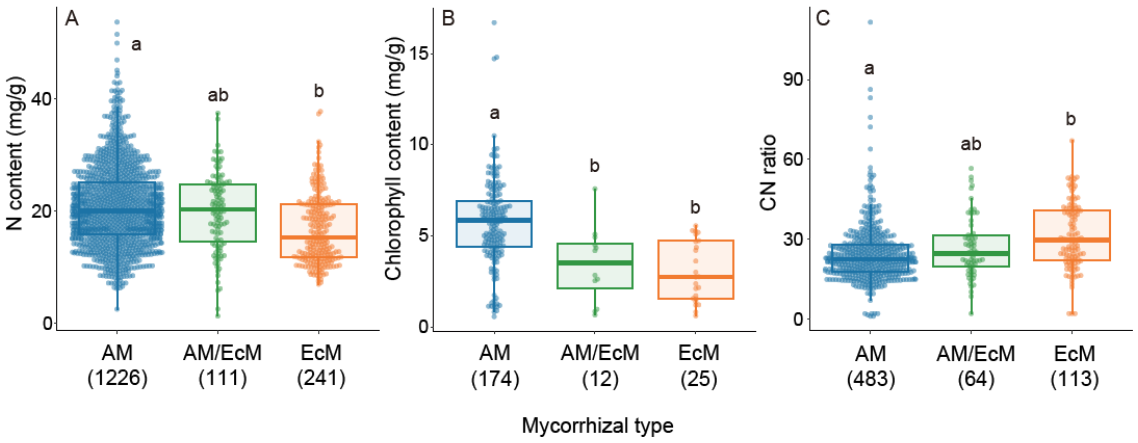
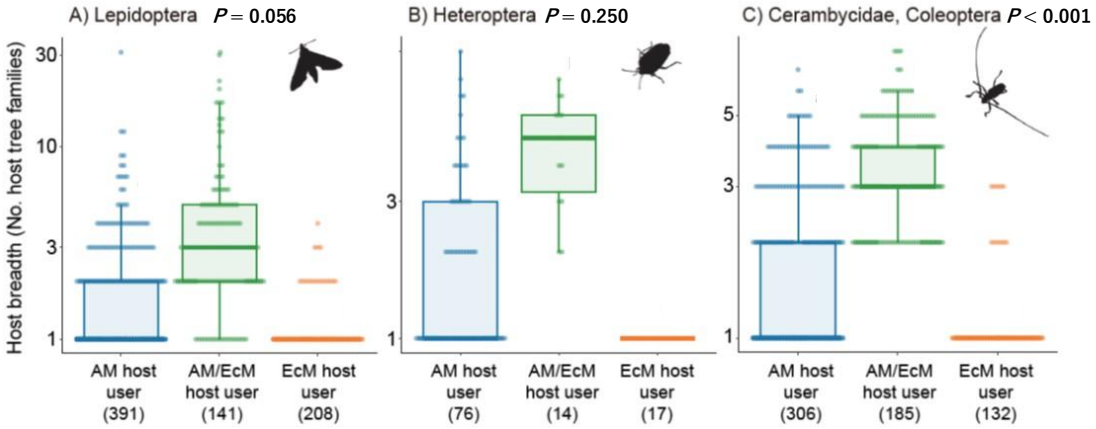


Figure. 3

Leaf functional traits of trees associated with different mycorrhizal types. Fresh-leaf nitrogen concentration (A), chlorophyll concentration (B), and carbon-to-nitrogen (C:N) ratio (C) of tree species associated with arbuscular mycorrhizal (AM), ectomycorrhizal (EcM), or both AM and EcM fungi (AM/EcM). Different lowercase letters indicate significant pairwise differences among mycorrhizal types based on generalized linear models (GLMs) followed by pairwise comparisons, with Benjamini–Hochberg FDR-adjusted $P < 0.05$. Numbers in parentheses indicate the number of tree species. Trait data were obtained from the TRY Plant Trait Database in 2022.



716

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718 Host breadth of Lepidoptera, Heteroptera, and Cerambycidae (Coleoptera) in Japan in
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720 number of distinct host-plant families recorded for each insect species. Insect species
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722 those using only ectomycorrhizal (EcM) host families as EcM users, and those using
723 both AM and EcM host families as AM/EcM users. The observed joint distribution of
724 host breadth and mycorrhizal category was compared with expectations under weighted
725 randomization using Monte Carlo G-tests. P values are shown in each panel. Numbers
726 in parentheses indicate the number of insect species. Host-use records were obtained
727 from Inoue et al. (1982) and Tomita (1983) for Lepidoptera; Tomokuni et al. (1993),
728 Yasunaga et al. (2001), and Ishikawa et al. (2012) for Heteroptera; and The Japanese
729 Society of Coleopterology (1984) and Ohbayashi and Niisato (2007) for Cerambycidae.

730

Table 1. The causal effects underpinning the hypothesis, the mechanisms of these effects, predictions regarding AM and EcM, the empirical approach and available evidence

Predicted causal effects	Relationship or mechanism in ERRM	AM prediction	EcM prediction	Empirical approaches	Evidence status
Plant–soil feedback → Seedling recruitment	Differences in PSF strength influence recruitment and density-dependent processes	More negative PSFs and stronger negative CDD tend to reduce local conspecific recruitment	Weaker negative or occasionally positive PSFs may permit greater local conspecific recruitment	PSF experiments; seedling survival and recruitment analyses	Relatively well supported
Seedling recruitment → Forest structure	Mycorrhizal type is associated with local density and spatial organization; differences in PSF and CDD may contribute to these patterns	Lower local conspecific density and greater dispersion	Higher local conspecific density and greater aggregation	Spatial pattern analysis, long-term population dynamics analysis	Association supported (Bennett et al., 2017; Johnson et al., 2018; Delavaux et al., 2023; Shinohara et al., 2024); PSF/CDD mediation unresolved
Forest structure →	Spatial distribution may alter selection on pollen	Greater reliance on animal pollination and animal-	Greater reliance on wind pollination and	Trait databases, phylogenetic	Association supported (Yamawo & Ohno,

Predicted causal effects	Relationship or mechanism in ERRM	AM prediction	EcM prediction	Empirical approaches	Evidence status
Reproductive traits	and seed dispersal	mediated seed dispersal	wind dispersal	comparative analyses	2024); mechanism hypothesized
Forest structure → Plant defense strategies	Differences in spatial and temporal host concentration may alter the frequency and predictability of herbivore encounters and selection on defense.	Predicted greater reliance on qualitative defenses	Predicted greater reliance on quantitative defenses	Direct defense chemistry and metabolomics; phylogenetic comparative analyses	Novel ERRM prediction / indirect support (Seyfried et al., 2021; Jantzen et al., 2023; Figure 3)
Forest structure → Herbivore diet breadth	Host spatial and temporal predictability is hypothesized to influence herbivore specialization	Predicted greater frequency of generalist herbivores	Predicted higher frequency of specialist herbivores	Host-use datasets and host–herbivore networks; comparative analyses	Novel prediction with preliminary support (Hirao & Murakami, 2008; Figure 4)
Herbivore diet breadth → Food-web	Differences in herbivore specialization may propagate to higher	Predicted lower specialization and weaker compartmentalization.	Predicted higher specialization and modularity	Ecological network analysis; replicated AM–EcM food-	Novel prediction with limited support (Barbosa et al., 2007)

Predicted causal effects	Relationship or mechanism in ERRM	AM prediction	EcM prediction	Empirical approaches	Evidence status
structure	trophic levels and alter interaction-network structure			web comparisons	
Ecosystem organization	Cascading effects across trophic levels may alter broader ecosystem organization	Predicted more diffuse multitrophic interaction networks	Predicted more structured multi-trophic networks	multitrophic network studies across AM- and EcM-dominated systems	Novel downstream prediction; not yet directly tested

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734

Supplementary Methods for "Mycorrhizal evolution restructures forest ecosystems"

Methods for empirical analyses

To complement the conceptual framework of ERRM, we conducted three empirical analyses examining associations between mycorrhizal type and (1) tree population density, (2) leaf functional traits, and (3) host breadth of tree-associated herbivorous insects. Species were treated as independent observational units in these analyses. All statistical analyses were conducted in R version 4.4.2 (R Core Team, 2024).

Tree population density

To examine whether tree population density differed between mycorrhizal types (Figure 2), we used tree census data from 16 forest sites included in the nationwide Monitoring Sites 1000 program in Japan (Ishihara et al., 2010). Population density at each site was expressed as the number of individuals per hectare. For each tree species, we calculated the mean population density across all sites in which that species was recorded. Sites where the species was absent (density = 0) were excluded from this calculation. Thus, the resulting species-level value represents the mean local abundance of a species where it occurred, rather than its occupancy or overall abundance across the 16 sites.

Mycorrhizal type was assigned at the plant-family level based on published syntheses of plant mycorrhizal associations (Brundrett & Tedersoo, 2018; Steidinger et al., 2019). This family-level classification was used because mycorrhizal association type is phylogenetically conserved across many plant lineages, although variation can occur within some families and genera. Tree species were classified as arbuscular

759 mycorrhizal (AM) or ectomycorrhizal (EcM) according to the assigned status of their
760 family.
761 Differences in mean population density between AM and EcM tree species
762 were evaluated using a generalized linear model with a Gamma error distribution and a
763 log link function. Population density was interpreted as a measure of local abundance
764 and not as a direct measure of spatial aggregation.
765
766 **Leaf functional traits**
767 To examine whether leaf functional traits differed among mycorrhizal types (Figure 3),
768 we used trait data obtained from the TRY Plant Trait Database in 2022 (Kattge et al.,
769 2020). We analyzed leaf nitrogen concentration, leaf chlorophyll content, and leaf
770 carbon-to-nitrogen (C) ratio. For species represented by multiple observations, trait
771 values were averaged to obtain a single species-level value for each trait. Thus, the
772 processed datasets contained one trait value per tree species.
773 Mycorrhizal type was assigned at the plant-family level based on published
774 information on plant mycorrhizal associations (Brundrett & Tedersoo, 2018; Steidinger
775 et al., 2019). Tree species were classified as arbuscular mycorrhizal (AM),
776 ectomycorrhizal (EcM), or dual AM/EcM according to the assigned status of their
777 family. Records with missing trait values or mycorrhizal classifications outside these
778 categories were excluded.
779 Differences among AM, EcM, and AM/EcM tree species were evaluated
780 separately for each trait using generalized linear models (GLMs), with mycorrhizal type
781 as the explanatory variable. Pairwise comparisons among mycorrhizal types were
782 conducted following each model, and P values were adjusted using the Benjamini–

783 Hochberg false discovery rate procedure, with FDR-adjusted $P < 0.05$ considered
784 statistically significant. The C ratio was treated as a leaf functional trait reflecting
785 carbon and nitrogen allocation and was not interpreted as a direct measure of
786 quantitative chemical defense.
787
788 Herbivore host breadth
789 To examine whether herbivore host breadth was associated with host-plant mycorrhizal
790 type (Figure 4), we compiled host-use records for Lepidoptera, Cerambycidae
791 (Coleoptera), and Heteroptera in Japan. Lepidopteran host records were obtained from
792 Inoue et al. (1982) and Tomita (1983), Heteroptera records from Tomokuni et al. (1993),
793 Yasunaga et al. (2001), and Ishikawa et al. (2012), and Cerambycidae records from The
794 Japanese Society of Coleopterology (1984) and Ohbayashi and Niisato (2007).
795 Host plants were standardized at the family level, and each host family was
796 assigned an AM or EcM status based on Steidinger et al. (2019). The complete host-
797 family classifications used in the analyses are provided in the Supplementary Data. For
798 each insect species, host breadth was defined as the number of distinct host-plant
799 families recorded. Insect species using only AM-associated host families were classified
800 as AM users, those using only EcM-associated families as EcM users, and those
801 recorded from both AM and EcM host families as AM/EcM users.
802 Because assignment to the AM/EcM category necessarily requires the use of
803 hosts from both mycorrhizal categories, raw differences in host breadth among AM,
804 EcM, and AM/EcM users can arise mechanically. We therefore conducted a weighted
805 randomization analysis to test whether the observed joint distribution of host breadth
806 and host mycorrhizal category differed from that expected from host breadth and host-

use frequency alone. For each insect species, the observed host breadth was held constant, and the same number of host-plant families was sampled without replacement. Sampling probabilities were weighted according to the observed frequency of use of each host family within the corresponding insect group. Each randomized insect species was then classified as an AM, EcM, or AM/EcM user according to the mycorrhizal types of its sampled host families. Thus, the procedure preserved the number of insect species, the total number of host-use links, and the observed distribution of host breadth, while randomizing the association between host breadth and host mycorrhizal category.

For each randomization, we tabulated the number of insect species in each combination of host breadth and mycorrhizal category. Departure of the observed distribution from the randomized expectation was evaluated using a Monte Carlo likelihood-ratio test (Monte Carlo G-test). The G statistic for the observed data was compared with an empirical null distribution of G statistics generated from the randomized datasets. Randomization was repeated 5,000 times for Cerambycidae and Heteroptera and 50,000 times for Lepidoptera, for which moths and butterflies were pooled. Phylogenetic relationships among insect species were not incorporated in these analyses.

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