frontiers in Ecology and Evolution

TYPE Review
PUBLISHED 22 September 2026
DOI 10.3389/fevo.2026.1932299

Check for updates

OPEN ACCESS

EDITED BY
Tao Feng,
Yangzhou University, China

REVIEWED BY
Lifeng Zhou,
Henan University, China
Min Su,
Hefei University of Technology, China
Deivid Almeida de Jesus,
Federal University of Rio de Janeiro, Brazil

*CORRESPONDENCE
Ioan Valentin Petrescu-Mag
ioan.mag@usamvcluj.ro

RECEIVED 08 July 2026
REVISED 26 August 2026
ACCEPTED 09 September 2026
PUBLISHED 22 September 2026

CITATION
Pandey P, Tripathi A, Bora F-D and Petrescu-Mag IV (2026) How animals shape plant evolution: an ecological and evolutionary synthesis. *Front. Ecol. Evol.* 14:1932299. doi: 10.3389/fevo.2026.1932299

COPYRIGHT
© 2026 Pandey, Tripathi, Bora and Petrescu-Mag. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

How animals shape plant evolution: an ecological and evolutionary synthesis

Praveen Pandey[1], Arpita Tripathi[2], Florin-Dumitru Bora[3] and Ioan Valentin Petrescu-Mag[4,5]*

[1]Division of Plant Breeding and Genetic Resource Conservation, CSIR-Central Institute of Medicinal and Aromatic Plants, Lucknow, India, [2]Faculty of Education, Teerthanker Mahaveer University, Moradabad, India, [3]Faculty of Horticulture and Business for Rural Development, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Cluj-Napoca, Romania, [4]Department of Environmental Engineering and Protection, Faculty of Agriculture, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Cluj-Napoca, Romania, [5]Doctoral School of Engineering Science, University of Oradea, Oradea, Romania

This review synthesizes current knowledge on how animals shape plant evolution through a complex network of mutualistic and antagonistic interactions operating across ecological and evolutionary timescales. Plant–animal interactions, ranging from pollination and seed dispersal to herbivory and parasitism, generate reciprocal selective pressures that drive diversification in plant reproductive, defensive, and dispersal traits. Coevolutionary dynamics are increasingly understood within a network framework, where indirect interactions and community structure play a critical role in shaping adaptive landscapes. Animal pollinators have been central to the evolution of floral traits, including morphology, color, scent, and phenology, while herbivores impose selection on plant defenses, often leading to trade-offs between reproduction and resistance. Similarly, frugivores influence the evolution of fruit and seed traits, contributing to the emergence of dispersal syndromes and large-scale diversification patterns in angiosperms. Interactions such as synzoochory highlight the continuum between mutualism and antagonism, emphasizing context dependency in ecological outcomes. Recent advances extend classical coevolutionary frameworks to include microbiome-mediated interactions, revealing that plant–animal relationships are frequently embedded within tripartite systems involving microbial communities that modulate signals, rewards, and defenses. Additionally, phenotypic plasticity emerges as a key mechanism enabling rapid plant responses to fluctuating biotic and abiotic environments, often preceding longer-term genetic adaptation. The review also integrates spatial and temporal perspectives, including the geographic mosaic of coevolution, eco-evolutionary feedbacks, and the persistence of evolutionary anachronisms resulting from past interactions. Anthropogenic pressures—such as climate change, habitat fragmentation, and species invasions—are profoundly reshaping plant–animal interactions, altering selection regimes and driving rapid evolutionary responses. Overall, this synthesis highlights that plant evolution cannot be fully understood without considering the dynamic, multi-layered, and context-dependent influences of animal interactions, which operate across scales from genes to ecosystems and from historical legacies to contemporary global change.

KEYWORDS
antagonism, anthropogenic change, coevolution, mutualism, phenotypic plasticity, pollination, seed dispersal

1 Introduction

The evolution of plants has traditionally been interpreted through the lens of adaptation to abiotic constraints, including light availability, water limitation, temperature regimes, and soil chemistry (Bora et al., 2025; Li et al., 2024; Pandey et al., 2026; Popescu and Tripathi, 2026; Tripathi et al., 2026; Bordea and Popescu, 2023). While these factors undoubtedly influence plant physiology, morphology, and fitness, they do not fully capture the selective environments in which plants evolve. In natural communities, plants are embedded within complex biotic systems in which interactions with organisms ranging from microorganisms to large vertebrates can alter survival, reproduction, dispersal, and ultimately evolutionary trajectories (Azis et al., 2025; Del-Claro and Torezan-Silingardi, 2021; Guimarães et al., 2017; Hu et al., 2023; Farooq et al., 2026).

In this review, we define animal-mediated plant evolution as the process by which interactions with animals generate sustained changes in plant phenotypic distributions across generations through natural selection, genetic adaptation, or their interaction with phenotypic plasticity, when these changes are causally linked to animal presence, abundance, behavior, or traits. This definition deliberately distinguishes (i) immediate ecological effects of animals on plant fitness, (ii) reversible plastic responses within a generation, (iii) directional or diversifying selection on heritable variation, (iv) reciprocal coevolution between plants and animals, (v) macroevolutionary patterns of diversification, and (vi) historical legacies of past interactions (evolutionary anachronisms). While these processes frequently co-occur and interact, they are not interchangeable: only those pathways that alter allele frequencies or the genetic architecture of plastic responses constitute evolutionary change in the strict sense. Throughout the manuscript we therefore specify, wherever possible, whether an observed pattern reflects short-term ecological filtering, plastic adjustment, contemporary selection, reciprocal coevolution, or the lingering imprint of extinct interactions.

Plants should therefore be viewed as participants in dynamic multispecies systems rather than as isolated entities responding independently to environmental filters. Their phenotypes are shaped by reciprocal interactions, feedbacks, and context-dependent selection, while the ecological effects of plant traits can in turn modify the abundance, behavior, and distribution of interacting animals (Azis et al., 2025; Guimarães et al., 2017; Petrescu-Mag, 2025; Petrescu-Mag et al., 2008). Unlike abiotic factors such as temperature or precipitation, animal partners can themselves evolve in response to plant phenotypes, generating reciprocal selective pressures and potentially accelerating evolutionary change (Del-Claro and Torezan-Silingardi, 2021; Hu et al., 2023).

This reciprocity makes plant–animal interactions fundamentally different from adaptation to nonliving environmental conditions. Selection operates within ecological networks in which the fitness consequences of a plant trait depend not only on the focal animal but also on the identity, abundance, behavior, and traits of other interacting species. Mutualistic and antagonistic interactions therefore cannot always be treated as discrete categories; rather, their outcomes may shift along a continuum according to environmental conditions, resource availability, population densities, and community composition (CaraDonna et al., 2020; Van Leeuwen et al., 2022). Such context dependence can continuously reshape the selective landscape and generate divergent evolutionary trajectories among populations and species.

Animals influence plant evolution through multiple functional pathways, including pollination, herbivory, seed dispersal, seed predation, habitat modification, and the movement of genes and propagules (Del-Claro and Torezan-Silingardi, 2021; Gómez et al., 2018; Kooi et al., 2020; Van Leeuwen et al., 2022). Importantly, these effects are not restricted to direct pairwise interactions. Animals can modify competitive environments, alter microhabitats, redistribute resources, and restructure interaction networks, thereby generating indirect and higher-order effects on plant fitness. Consequently, the evolutionary consequences of animal-mediated selection may emerge from the collective structure of ecological communities rather than from any single interaction.

The evolutionary significance of these processes becomes particularly apparent when interaction networks change through time. Variation in animal abundance, behavior, phenology, or geographic distribution can modify the intensity and direction of selection acting on plant traits. Plants may initially respond through phenotypic plasticity, while persistent changes can subsequently alter the strength and direction of genetic selection. Conversely, evolutionary changes in plant traits can feed back on animal interactions, potentially reinforcing, weakening, or redirecting existing ecological relationships. Plant evolution is therefore embedded within coupled ecological and evolutionary processes that operate across multiple temporal and spatial scales.

Against this background, a central challenge is to understand how the different mechanisms through which animals influence plants are integrated across scales. Pollination and seed dispersal affect reproductive traits; herbivory shapes defense and life-history strategies; microbiome-mediated interactions modify the expression of rewards and defenses; and changing animal communities can alter both the direction and magnitude of selection. These processes are further modified by spatial heterogeneity, historical legacies, phenotypic plasticity, and contemporary anthropogenic change.

The primary objective of this review is therefore to synthesize the ecological and evolutionary mechanisms through which animal interactions shape plant trait evolution, diversification, and adaptive dynamics. Particular emphasis is placed on the interplay between mutualistic and antagonistic interactions, network-level effects, microbiome mediation, phenotypic plasticity, eco-evolutionary feedbacks, historical contingencies, and contemporary changes in animal communities. By integrating these perspectives, we aim to clarify how animal-mediated selection operates from individual traits and molecular responses to populations, interaction networks, and broader evolutionary patterns.

2 Literature selection methodology

The literature survey underlying this narrative review was conducted through a carefully designed search strategy across

multiple major scientific databases, including Google Scholar, CABI, Scopus, and Web of Science. These platforms were selected to ensure comprehensive coverage of both peer-reviewed journal articles and relevant gray literature, thereby minimizing database-specific bias and enhancing the robustness of the bibliographic corpus.

Search queries were constructed using combinations of domain-specific keywords and Boolean operators, tailored to capture the breadth of topics relevant to plant–animal interactions and their evolutionary and ecological dimensions. The search process was iterative, allowing refinement of keywords and inclusion criteria as thematic patterns emerged from the initial results. Particular attention was given to high-impact journals, recent publications, and frequently cited works to ensure both temporal relevance and scientific rigor.

Inclusion criteria focused on studies that provided empirical data, theoretical frameworks, or comprehensive reviews directly related to the subject matter. Articles were screened based on title, abstract, and, where necessary, full-text evaluation. Preference was given to peer-reviewed sources, while non-peer-reviewed materials were considered only when they contributed unique or otherwise unavailable insights. Redundant, marginally relevant, or methodologically weak studies were excluded to maintain analytical clarity and coherence.

To further ensure quality and relevance, backward and forward citation tracking was employed. This approach facilitated the identification of seminal works and emerging research trends not immediately captured through keyword-based searches. The final selection represents a curated synthesis of the most pertinent and methodologically sound contributions within the field.

3 Coevolutionary foundations of plant – animal interactions

Plant-animal interactions span a continuum from strongly positive (pollination, seed dispersal, defensive mutualisms) to negative (herbivory, seed predation, parasitism), with many relationships occupying intermediate positions on a mutualism–antagonism gradient (Del-Claro and Torezan-Silingardi, 2021; Gómez et al., 2018; Kooi et al., 2020; Van Leeuwen et al., 2022). This continuum is inherently dynamic, as the net outcome of interactions often depends on ecological context, species identity, and environmental conditions, leading to temporal and spatial shifts in interaction outcomes. Such context dependency challenges binary classifications and underscores the importance of viewing plant–animal relationships as fluid components of adaptive systems.

Coevolution should be distinguished from the broader set of evolutionary processes through which animal interactions can influence plant traits. Reciprocal selection refers to a process in which traits expressed by one partner alter the selective environment experienced by the other, whereas coevolution denotes reciprocal evolutionary change in which such selection is sufficiently persistent and causally linked to produce correlated changes in the interacting lineages (Păsărin et al., 2025). Adaptation, in contrast, refers to heritable changes that increase fitness under a particular selective regime and does not necessarily require reciprocal selection between interacting species. Similarly, correlated evolutionary change does not by itself demonstrate coevolution, because trait correlations may also arise from shared ecological conditions, common selective agents, phylogenetic constraints, or correlated responses to other traits. Ecological fitting represents a further distinction: organisms may interact successfully by using pre-existing traits without a prior history of reciprocal evolutionary adaptation. Thus, plant-animal interactions may generate selection, adaptation, correlated evolution, ecological fitting, or true coevolution, depending on the persistence, reciprocity, heritability, and ecological context of the interaction (Rehling et al., 2021; Del-Claro and Torezan-Silingardi, 2021; Guimarães et al., 2017; Hu et al., 2023). These reciprocal dynamics are rarely symmetrical; instead, they often involve diffuse coevolution, where multiple species impose overlapping selective pressures on shared traits. As a result, plant phenotypes frequently reflect the integrated outcome of selection imposed by diverse functional groups, rather than pairwise interactions alone.

Network-based models show that in multispecies mutualisms such as pollination and seed dispersal, indirect effects transmitted through non-interacting partners can be as important as direct interactions in shaping trait evolution, particularly in large, nested networks typical of plant–pollinator and plant–frugivore systems (Guimarães et al., 2017). In such networks, the selective pressure experienced by a focal plant is not determined solely by the traits of its immediate partners. Rather, network structure modulates selection through three principal mechanisms. First, nestedness and asymmetric specialization concentrate the influence of a few highly connected animal species; changes in the abundance or preference of these central partners therefore propagate selection across many plant species that never interact with one another directly. Second, modularity partitions selection into relatively independent compartments, allowing divergent trait evolution among modules even when the same animal functional group is present. Third, the density and pattern of indirect pathways create cascading fitness effects: an evolutionary change in one plant's floral or fruit traits can alter the foraging behavior of a shared animal, thereby modifying the selective regime experienced by other plants connected through multi-step paths. These indirect pathways generate cascading effects across interaction networks, altering selection regimes in ways that may not be predictable from pairwise relationships. Consequently, the adaptive landscape experienced by plants is continuously restructured by both direct and indirect interactions, and the strength and direction of selection on any given plant trait become emergent properties of network topology rather than of isolated pairwise encounters.

Over evolutionary timescales, such network-mediated processes contribute to the persistence of trait variation and the maintenance of functional diversity within plant communities (Fontaine et al., 2011; Guimarães et al., 2017; Hoeksema, 2010; Li et al., 2024). By sustaining shifting selective pressures and maintaining multiple potential evolutionary pathways, these dynamics can promote continued trait change and reduce the likelihood of evolutionary stasis, although the realization of evolutionary change will depend

on heritable variation, demographic conditions, and the persistence of the relevant selective regime (Agrawal and Zhang, 2021; Fontaine et al., 2011; Graham et al., 2023; Guimarães et al., 2017; Hoeksema, 2010; Li et al., 2024; Losapio et al., 2019; Segar et al., 2020; Wickman et al., 2023). In this sense, coevolutionary interactions not only drive adaptation but also maintain the conditions necessary for continued evolutionary responsiveness in changing environments (Fontaine et al., 2011; Guimarães et al., 2017; Hoeksema, 2010; Li et al., 2024; Lomáscolo et al., 2019; Losapio et al., 2019).

A comprehensive understanding of how animals shape plant evolution requires bridging the gap between pairwise coevolutionary models and community-level network dynamics (Guimarães et al., 2017). Recent advances in community phylogenetics and trait-based ecology have revealed that the phylogenetic signal in plant-animal interactions is often weaker than expected under strict coevolution, suggesting that ecological fitting and opportunistic partner switching play prominent roles alongside reciprocal selection (Fuzessy et al., 2025; Lomáscolo et al., 2019). This implies that many apparent coevolutionary patterns may arise from the sorting of pre-existing traits within phylogenetically conserved interaction niches rather than *de novo* trait matching. Consequently, the evolutionary trajectory of plant traits is simultaneously constrained by deep phylogenetic history and highly responsive to contemporary community composition (Fuzessy et al., 2025). Integrating phylogenetic comparative methods with network analysis thus offers a powerful framework for disentangling historical contingencies from ongoing selective pressures, allowing researchers to better predict which plant lineages are most likely to exhibit rapid evolutionary responses when animal partners change in abundance or identity.

Animal-mediated selection can also produce repeated or convergent evolutionary outcomes without implying direct coevolution between the same interacting species. When similar ecological functions are imposed by comparable animal guilds or feeding strategies, unrelated plant lineages may independently evolve similar phenotypes, while repeated evolution may occur when comparable traits arise multiple times within related or unrelated lineages under recurrent selective conditions. Such patterns are particularly informative when similar trait–interaction associations occur across independent evolutionary contexts, but phenotypic similarity alone should not be interpreted as evidence of reciprocal coevolution. Instead, convergence and repeated evolution may reflect the recurrence of similar selective regimes, functional constraints, developmental pathways, or ecological opportunities. Animal-mediated selection therefore represents one possible route to evolutionary convergence, alongside phylogenetic constraint and other abiotic and biotic selective pressures.

The evolutionary interpretation of plant–animal interactions also depends on the level of evidence available. Phenotypic associations or differences among populations demonstrate that traits covary with ecological conditions or interaction regimes, but they do not necessarily demonstrate selection. Evidence for selection is stronger when trait variation is associated with differential fitness under controlled or replicated interaction conditions, whereas evidence for evolutionary change additionally requires heritable variation and a change in trait or allele frequencies across generations. At broader phylogenetic scales, correlations between traits and diversification, interaction structure, or lineage richness can reveal macroevolutionary associations, but these patterns do not by themselves establish the underlying selective mechanism. Similarly, theoretical models and adaptive scenarios can predict possible evolutionary trajectories without demonstrating that those trajectories have occurred in nature. Distinguishing these levels of evidence is essential for avoiding the conflation of ecological association, phenotypic selection, contemporary evolution, and macroevolutionary correlation throughout the synthesis.

4 Animal pollinators and the evolution of reproductive traits

Most angiosperms depend on animal pollinators for sexual reproduction, and pollinator-mediated selection has been associated with extensive diversification of floral morphology, color, rewards, and phenology (Byers and Bradshaw, 2021; CaraDonna et al., 2020; Del-Claro and Torezan-Silingardi, 2021; Kooi et al., 2020). Pollinators influence the evolution of plant mating systems (selfing vs. outcrossing), floral display size, nectar and scent chemistry, and sexual specialization (e.g., dioecy) (Johnson et al., 2015). Herbivores simultaneously act on these same traits, either directly (by consuming flowers) or indirectly (through selection on defenses that trade off with floral investment), so reproductive traits and defense traits evolve in an interdependent manner (Johnson et al., 2015).

Recent work emphasizes that plant-pollinator relationships are often asymmetric, with the interests of plants and pollinators only partially aligned. This pattern has been examined across diverse angiosperm-pollinator systems, including interactions involving bee-pollinated plants, hummingbird- and other bird-pollinated plants, moth-pollinated plants, and bat-pollinated tropical plants. Plants may benefit from pollinator fidelity and efficient pollen transfer, whereas pollinators may maximize energetic or nutritional rewards by visiting multiple plant species, generating interaction outcomes that range from mutualism to exploitation (Kooi et al., 2020). The strength and direction of this asymmetry can vary among plant species and populations, pollinator assemblages, and geographic regions, potentially contributing to differences in floral signals, reward quantity and composition, and the degree of pollinator specialization observed across angiosperms (Kooi et al., 2020).

Temporal studies reveal that pollination networks can change substantially over periods ranging from days to years, while retaining characteristic structural features over longer timescales (CaraDonna et al., 2020). Such temporal turnover in pollinator partners can alter the selective environment experienced by plants and may favor generalized floral phenotypes or plasticity in traits such as nectar production and flowering time.

Repeated and convergent evolution is particularly relevant to floral traits because similar pollination functions can impose

comparable selective pressures across phylogenetically distant plant lineages. Floral dimensions such as tube length, floral orientation, display size, color, nectar accessibility, scent, and flowering phenology may evolve repeatedly where plants interact with pollinators that impose similar functional demands. Such repeated trait combinations are consistent with the hypothesis that pollinator-mediated selection can favor functional convergence, but they should not automatically be interpreted as evidence of pairwise coevolution. Similar floral phenotypes may instead arise through diffuse selection exerted by multiple pollinators, by correlated selection on several floral traits, or through constraints that limit the number of viable solutions to a particular ecological problem (Byers and Bradshaw, 2021; CaraDonna et al., 2020; Del-Claro and Torezan-Silingardi, 2021; Kooi et al., 2020).

This perspective also places the long-standing concept of pollination syndromes in a broader evolutionary context (Petrescu-Mag et al., 2024). Pollination syndromes describe recurring combinations of floral traits that are associated with particular functional groups of pollinators, such as bees, birds, bats, or moths. These combinations can provide evidence of convergent adaptation when similar trait assemblages repeatedly occur in independent plant lineages exposed to comparable pollinator-mediated selection. However, floral trait combinations do not necessarily correspond to exclusive relationships with a single pollinator group. Generalist plants may interact with multiple pollinators, and the same pollinator functional group may exert different selection pressures depending on geographic location, community composition, resource availability, and the relative abundance of alternative floral resources. Consequently, some floral syndromes may represent broad functional convergence, whereas others may reflect diffuse, context-dependent selection rather than strict specialization. Recognizing this distinction is important because observed associations between floral traits and pollinator groups provide evidence of ecological matching, but stronger evidence is required to demonstrate contemporary selection or reciprocal evolutionary change (Byers and Bradshaw, 2021; CaraDonna et al., 2020; Johnson et al., 2015; Kooi et al., 2020).

5 Herbivores, plant defenses, and the joint evolution of reproduction and resistance

Herbivory exerts a pervasive and often multifaceted selective pressure on plants, acting simultaneously on vegetative and reproductive tissues and thereby integrating defense and reproduction into a shared evolutionary framework. Beyond the well-documented evolution of chemical (e.g., secondary metabolites), structural (e.g., lignification, trichomes, spines), and phenological (e.g., timing of leaf flush or flowering) defenses, herbivore pressure frequently induces correlated responses across life-history traits. This integration arises because defense and reproduction are not independent axes of variation, but are linked through resource allocation constraints, hormonal regulation (e.g., jasmonate–salicylate signaling pathways), and pleiotropic genetic architectures (Hu et al., 2023; Johnson et al., 2015; Katz, 2020). As a consequence, investment in defense can directly reduce resources available for reproductive output (flower, pollen, or seed production), while selection for enhanced reproductive assurance can indirectly reshape defense strategies.

Herbivore-mediated selection is nevertheless heterogeneous because different feeding guilds impose distinct forms of damage and encounter plants under different ecological conditions (Endara et al., 2023; Mertens et al., 2021; Vázquez-González et al., 2025). Folivorous insects, including many Lepidoptera and Coleoptera, commonly exert selection through repeated removal of leaf tissue and can favor chemical, structural, or inducible defenses (Ali et al., 2024; Mezzomo et al., 2023; Zhao et al., 2024; War et al., 2012), whereas sap-feeding insects impose different selective pressures by exploiting phloem or xylem resources and by interacting with plant signaling and defense pathways (Ali et al., 2024; Thompson and Goggin, 2006; Twayana et al., 2022). Florivores and seed predators directly target reproductive tissues, potentially altering the balance between investment in attraction, reproduction, and defense (Aguirrebengoa et al., 2025, 2023; McCall and Irwin, 2006), while large mammalian browsers and grazers impose mechanical damage at a different spatial and temporal scale and may favor traits such as toughness, spines, silica accumulation, or phenological escape (Johnson et al., 2024; Coverdale, 2019; Daouda et al., 2025). These contrasts are ecologically important because the selective consequences of herbivory depend not only on the amount of damage but also on the identity, feeding mode, body size, abundance, and persistence of the herbivore assemblage (Mezzomo et al., 2023; Mertens et al., 2021; Aguirrebengoa et al., 2023; Vázquez-González et al., 2025; Daouda et al., 2025).

Importantly, herbivores do not act uniformly across plant ontogeny or tissue types. Differential attack on leaves, stems, flowers, and fruits creates spatially heterogeneous selection within individual plants, favoring tissue-specific defense allocation strategies. For instance, optimal defense theory predicts that plants should preferentially protect tissues with the highest fitness value or likelihood of attack, such as young leaves or reproductive organs. Empirical evidence supports this, showing that flowers and developing fruits can exhibit elevated concentrations of defensive compounds, including phenolic compounds, terpenoids, alkaloids, and other secondary metabolites that can reduce herbivore feeding, impair digestion or detoxification, or deter florivores and seed predators, despite the simultaneous role of these organs in attracting mutualists such as pollinators and dispersers (Johnson et al., 2015). This creates a fundamental evolutionary tension: traits that deter herbivores may simultaneously reduce attractiveness to pollinators, reinforcing trade-offs between defense and reproduction.

Herbivory can also influence reproductive evolution through demographic and ecological pathways. Chronic or intense herbivore pressure can reduce plant size, delay flowering, or decrease floral display, all of which diminish pollinator attraction and mating opportunities. Under such conditions, selection may favor

reproductive strategies that minimize dependence on external agents, such as autonomous self-pollination or cleistogamy (Johnson et al., 2015). In addition, damage to reproductive structures (e.g., florivory or seed predation) can directly reduce fitness returns from outcrossing, further tipping the balance toward selfing as a form of reproductive assurance. These dynamics are particularly pronounced in environments where herbivore pressure is spatially or temporally unpredictable, amplifying the advantage of flexible or insurance-based reproductive systems.

Conversely, evolutionary shifts in mating systems can feed back onto defense evolution in nontrivial ways. High selfing rates tend to reduce effective recombination and genetic diversity, potentially constraining adaptive responses to herbivores. At the same time, selfing lineages may experience relaxed selection for traits associated with pollinator attraction (e.g., large floral displays), freeing resources that can be reallocated toward defense. In dioecious or sexually dimorphic species, differential herbivore pressure on male and female plants can lead to sex-specific defense strategies, further complicating the evolutionary interplay between reproduction and resistance (Johnson et al., 2015). These feedbacks illustrate that plant mating systems and defense traits coevolve within a shared selective landscape shaped by both mutualists and antagonists.

At broader evolutionary scales, plant–herbivore interactions contribute to repeated and sometimes convergent evolution of defensive traits across lineages. Silicon-based defenses exemplify this pattern. The accumulation of silica in plant tissues, often in the form of phytoliths, increases tissue abrasiveness and reduces digestibility, imposing mechanical and physiological costs particularly on mammalian grazers and other herbivores that consume silica-rich grasses and monocots. This defense strategy has evolved multiple times, particularly in grasses and other monocots, and is strongly associated with grazing pressure (Katz, 2020). However, the distribution and intensity of silicon accumulation vary widely among taxa, reflecting differences in evolutionary history, ecological context, and herbivore guild composition.

Crucially, many plant defense traits bear the imprint of past, rather than present, herbivore communities. The concept of evolutionary anachronism is particularly relevant here: traits such as extreme toughness, large spines, or high silica content may have evolved in response to now-extinct megaherbivores and may not be optimally matched to contemporary herbivore assemblages (Katz, 2020). This temporal mismatch implies that current plant–herbivore interactions are shaped not only by ongoing ecological processes but also by historical legacies embedded in plant trait distributions. As a result, modern ecosystems may exhibit "ghosts" of past interactions, where defensive traits persist despite altered or weakened selection pressures.

Taken together, these dynamics highlight that herbivory is not merely a selective force acting on plant defense in isolation, but a central driver of integrated evolutionary change affecting reproduction, life-history strategies, and trait allocation. The joint evolution of resistance and reproduction emerges from a complex web of trade-offs, feedbacks, and historical contingencies, reinforcing the view that plant adaptation must be understood within a multidimensional and temporally layered selective landscape (Hu et al., 2023; Johnson et al., 2015; Katz, 2020).

6 Fruit-frugivore coevolution and seed dispersal syndromes

A major axis along which animals shape plant evolution is seed dispersal. Many angiosperms have evolved fleshy fruits and other traits that encourage consumption and transport by vertebrates; in turn, frugivores depend on these resources for energy and nutrients (Del-Claro and Torezan-Silingardi, 2021; Eriksson, 2016; Fuzessy et al., 2025; Van Leeuwen et al., 2022). Macroevolutionary analyses of Neotropical palms show that fruit color and size have evolved in coordinated fashion consistent with seed-dispersal syndromes shaped by frugivores (Nascimento et al., 2020). Fruit size covaries positively with the presence of spines on leaves, bracts, and stems, suggesting that interactions with large-bodied frugivores and herbivores simultaneously favored large fruits (for dispersal) and structural defenses (against damage), linking mutualistic and antagonistic selection in the same clades (Nascimento et al., 2020).

Comparative data indicate that diversification of angiosperm seed size and fleshy fruits began around 80 million years ago, peaking in the Eocene, coincident with the emergence and expansion of frugivorous mammals and later birds and bats (Eriksson, 2016). Early frugivores such as multituberculates and later primates and rodents likely opened new ecological space for fleshy-fruited plants, while the subsequent evolution of flying frugivores exploited an already diverse flora and may have driven further fruit trait diversification under changing climates and vegetation structures (Eriksson, 2016).

Recent work on primate–plant systems in the Neotropics reveals strong cophylogenetic signals: plant and primate phylogenies are significantly congruent, particularly where highly frugivorous primates interact with plants producing large fruits, implying shared evolutionary histories shaped by seed dispersal interactions (Fuzessy et al., 2021). However, broader analyses across bats, birds and primates suggest that although evolutionary history leaves a detectable imprint on frugivory networks, functional traits - dietary specialization, network connectivity, and fruit characteristics such as husk, color and size - are stronger determinants of who interacts with whom (Fuzessy et al., 2025). Fruit traits are comparatively evolutionarily labile, indicating that plants can respond rapidly to ecological sorting and changes in animal assemblages (Fuzessy et al., 2025).

Seed dispersal effectiveness (SDE) frameworks decompose the contribution of animals to plant fitness into quantitative (number of seeds dispersed) and qualitative (probability of seed survival and recruitment) components, offering mechanistic insight into how different dispersers shape plant demography and trait evolution (Van Leeuwen et al., 2022). An extended SDE framework now incorporates interactions across the mutualism–antagonism continuum, including frugivores, scatter hoarding granivores, folivores, and pure granivores (Van Leeuwen et al., 2022). Early syntheses suggest that scatter hoarders (e.g., rodents and some birds) can be exceptionally effective dispersers because of high removal and caching rates, while classic frugivores provide high deposition but more variable post dispersal survival, and folivores and pure granivores often provide low-quantity but sometimes high-quality dispersal (Van Leeuwen et al., 2022) (Table 1).

TABLE 1 Representative axes of animal-mediated selection on plant seed traits.

Plant traits shaped by animals	Biological context	Dominant animal partners and processes	Evolutionary consequences for plants	References
Fruit size, color, pulp traits	Fleshy-fruited plants in which fruit traits influence animal attraction, fruit removal, and the spatial and temporal distribution of seed dispersal; effects may differ between intact dispersal networks and systems affected by megafaunal loss.	Frugivorous birds, bats, primates, rodents; megaherbivores; attraction, fruit consumption, and seed dispersal.	Diversification of fleshy fruit types and dispersal syndromes; potential expansion of seed-dispersal opportunities across space and time; trait shifts associated with changes in disperser assemblages.	Eriksson, 2016; Fuzessy et al., 2021; Fuzessy et al., 2025; Nascimento et al., 2020; Van Leeuwen et al., 2022; Proorocu and Kovacs, 2023.
Seed size, hardness, nutrient content	Seeds subjected to contrasting fates after removal, including caching, consumption, and predation; selection depends on the relative contribution of dispersal versus seed destruction.	Scatter-hoarding rodents and birds, granivores; caching, transport, consumption, and seed predation.	Evolution of large or protected seeds; dependence on particular disperser or scatter-hoarder assemblages; storage-based recruitment strategies and selection associated with post-dispersal seed fate.	Brehm and Mortelliti, 2022; Gómez et al., 2018; Van Leeuwen et al., 2022.
Defensive structures (spines, toughness) integrated with fruit traits	Plants in which reproductive tissues are simultaneously exposed to dispersers and consumers; particularly relevant where large-bodied herbivores or frugivores impose contrasting selection on fruit and vegetative tissues.	Large herbivores and frugivores; fruit consumption, browsing, tissue damage, and dispersal.	Coupled evolution of defense and dispersal traits; co-shaping of reproductive and defensive life-history strategies.	Johnson et al., 2015; Katz, 2020; Nascimento et al., 2020.

7 Dual roles: synzoochory and the mutualism-antagonism continuum

Before examining the specific case of synzoochory, it is useful to clarify the conceptual framework of the mutualism–antagonism continuum and the key terms used throughout this section.

Synzoochory complicates the traditional mutualism–antagonism dichotomy by linking two opposing processes - seed survival and seed mortality - within a single interaction pathway. We define the mutualism–antagonism continuum as the continuous range of net fitness outcomes that can arise from a given plant-animal interaction, spanning from strongly positive (net fitness gain for the plant) through neutral to strongly negative (net fitness loss). Position along this continuum is not fixed by interaction type, but is determined by the relative frequencies of beneficial versus detrimental outcomes and by the ecological context in which the interaction occurs. Synzoochory belongs on this continuum because the same animal behaviour (seed removal and handling) simultaneously generates both mutualistic effects (caching and subsequent germination of unrecovered seeds) and antagonistic effects (immediate consumption). The net outcome for the plant is therefore probabilistic and context-dependent rather than categorically mutualistic or antagonistic.

Rather than being defined by a fixed functional outcome, synzoochorous interactions are probabilistic, with plant fitness determined by the relative frequencies of seed caching versus seed consumption. This probabilistic nature implies that selection does not act on discrete interaction categories, but on distributions of outcomes shaped by animal behaviour, environmental conditions, and plant trait expression (Gómez et al., 2018; Van Leeuwen et al., 2022). The resulting net selective pressure - the overall direction and strength of selection experienced by a plant population - is the integrated product of these variable outcomes across individuals, space and time. Because the same plant trait (e.g., seed size or nutrient content) can simultaneously increase both caching probability and consumption risk, the net selective pressure often favours intermediate phenotypes rather than extreme specialization.

A further source of variation arises from the distribution of behavioural types within animal populations. Individuals of the same species frequently differ consistently in traits such as boldness, exploratory tendency or hoarding propensity. This intraspecific behavioural variation means that the balance between mutualistic and antagonistic outcomes is not solely a property of the species, but also of the particular mix of behavioural phenotypes present in the local animal population. Consequently, the net selective pressure experienced by plants can shift even when species composition remains constant, simply because the relative frequencies of caching-prone versus consumption-prone individuals change.

A key consequence of this duality is that plants cannot evolve traits that exclusively maximize dispersal without simultaneously influencing predation risk. Traits such as large seed size, high nutrient content, or protective seed coats can increase attractiveness to scatter-hoarders, thereby enhancing removal rates, but these same traits may also increase the likelihood of immediate consumption rather than caching. This generates a form of antagonistic pleiotropy at the ecological level, where the same trait has both positive and negative fitness effects depending on the behavioral decision of the animal (Gómez et al., 2018). As a result, synzoochorous systems are expected to favor intermediate or "compromise" phenotypes rather than extreme specialization, lim-

iting the emergence of clear-cut dispersal syndromes compared to classical frugivory (Gómez et al., 2018; Green et al., 2022).

The spatial dimension of seed dispersal further modulates these outcomes. Caching behavior typically results in seed burial at varying depths and distances from the parent plant, which can enhance germination probability by reducing density-dependent mortality and escaping pathogens or predators. However, the benefits of dispersal depend critically on cache recovery rates. If animals retrieve a high proportion of cached seeds, the interaction shifts toward antagonism; if many caches are forgotten or abandoned, it becomes more mutualistic. Importantly, these dynamics are influenced by environmental heterogeneity, such as soil conditions, climate variability, and the presence of competing seed predators, all of which affect both caching behavior and seed fate (Gómez et al., 2018; Van Leeuwen et al., 2022).

Temporal variability adds another layer of complexity. In mast-seeding species, for example, synchronous production of large seed crops can temporarily satiate predators, increasing the proportion of seeds that escape consumption and are successfully dispersed. Under low seed production, however, animals may consume a greater fraction of available seeds, reducing the net benefit to plants. Thus, the outcome of synzoochory can fluctuate across years, creating temporally variable selection regimes that may favor plastic or bet-hedging strategies in seed production and traits (Gómez et al., 2018; Van Leeuwen et al., 2022). These dynamics reinforce the idea that plant fitness in synzoochorous systems is not determined by average conditions alone, but by variance in interaction outcomes over time.

At the community level, synzoochory often involves multiple animal species with differing ecological roles and efficiencies, leading to diffuse selection rather than tight pairwise coevolution. Some species act as highly effective dispersers, others as predominantly seed predators, and many occupy intermediate positions. The net selective pressure on plant traits therefore reflects the combined influence of the entire assemblage of interacting animals, weighted by their relative abundance, behavior, and ecological context (Gómez et al., 2018). This diffuse interaction structure can maintain trait diversity within plant populations, as different phenotypes may be favored under different combinations of animal partners.

The context dependency of synzoochory is further reinforced by external ecological factors. Resource availability, for instance, influences whether animals cache or consume seeds: under food scarcity, immediate consumption is favored, whereas surplus conditions promote caching behavior. Similarly, predation risk experienced by the animal can alter foraging strategies, with higher risk often leading to rapid caching to minimize exposure, potentially increasing dispersal effectiveness. Environmental changes, including habitat fragmentation or climate shifts, can therefore indirectly modify plant fitness by altering animal decision-making processes (Brehm and Mortelliti, 2022; Gómez et al., 2018; Van Leeuwen et al., 2022).

Crucially, recent work highlights that intraspecific variation in animal behavior - often described as “animal personality” - can systematically influence the balance between mutualistic and antagonistic outcomes. Individuals within the same species may differ consistently in traits such as boldness, exploratory tendency, or hoarding propensity, leading to predictable differences in seed handling behavior. Experimental studies on scatter-hoarding rodents demonstrate that some individuals preferentially cache seeds (enhancing plant fitness), while others consume them directly, even under similar environmental conditions (Brehm and Mortelliti, 2022). This implies that selection on plant traits may operate not only at the level of species interactions but also through the distribution of behavioral types within animal populations.

From an evolutionary perspective, synzoochory exemplifies how selection can act on interaction variance rather than mean outcomes. Plants may evolve traits that reduce the risk of complete reproductive failure (e.g., by promoting at least partial caching across a range of conditions), rather than maximizing average dispersal success. This risk-sensitive framework aligns with broader theories of bet-hedging, where fitness is optimized over fluctuating environments by minimizing variance in reproductive success. In this context, synzoochorous systems emphasize the role of stochasticity, behavioral heterogeneity, and ecological conditions in driving the evolution of plant traits along the mutualism-antagonism continuum (Brehm and Mortelliti, 2022; Gómez et al., 2018; Van Leeuwen et al., 2022).

8 Beyond flowers and fruits: structural and chemical traits

Animals also shape the evolution of plant structural and biochemical traits outside reproductive organs. Silicon accumulation and phytolith formation have likely evolved repeatedly as anti herbivore strategies in grasses and other taxa, with macroevolutionary patterns reflecting past herbivore communities and environmental conditions (Katz, 2020). Likewise, the defensive spines associated with large-fruited Neotropical palms may be legacies of interactions with extinct megafauna that simultaneously dispersed fruits and damaged vegetative tissues, thereby selecting for both large fruits and strong mechanical defenses (Nascimento et al., 2020).

Chemical traits represent another major interface through which animals influence plant fitness and potentially shape evolutionary trajectories. Floral scent and other volatile organic compounds can function as long-distance signals that mediate pollinator attraction, recognition, and behavioral decisions, while variation in nectar chemistry can alter the nutritional and sensory value of floral rewards. The same chemical phenotype can therefore affect both visitation and reproductive success, particularly when animals discriminate among alternative floral resources. In antagonistic interactions, secondary metabolites and other defensive compounds can reduce palatability, interfere with herbivore digestion or detoxification, or deter feeding, thereby generating selection on the expression, composition, and spatial distribution of plant chemical defenses. Because chemical traits simultaneously influence attraction, communication, nutrition, and deterrence, their evolutionary consequences depend strongly on the identity and behavior

of the interacting animal and on the ecological context in which the interaction occurs (Johnson et al., 2015; Hu et al., 2023; Rering et al., 2018).

These chemical effects are also potentially microbiome-mediated: nectar yeasts and bacteria can modify volatile profiles, sugars, amino acids, and pH, whereas endophytic, rhizosphere, and herbivore-associated microbial communities can alter the expression, transformation, or detoxification of defensive compounds. The resulting plant–animal interaction is therefore often mediated by a chemical phenotype that is jointly influenced by plant genotype, microbial community composition, and animal behavior (Ashra and Nair, 2022; Ilyasov et al., 2025; Quevedo-Caraballo et al., 2024; Rering et al., 2018; Vannette, 2020).

At molecular scales, coevolutionary insights extend to gene regulation. Comparative genomic analyses across hundreds of plant and animal species indicate different modes of coevolution between promoters and transcription factors in plants versus animals, with mutualistic coevolution predominating in plants and antagonistic patterns in animals, potentially linked to broader patterns of plant-animal ecological divergence and diversity (Hu et al., 2023; Zhang et al., 2022). Although not specific to particular interaction types, these patterns suggest that long-term biotic interactions have left signatures at regulatory genomic levels.

9 Temporal dynamics and eco evolutionary feedbacks

Mutualistic networks are not static; they fluctuate over days, seasons, years, and centuries. At short temporal scales, pollination, seed dispersal, and ant defense networks show high turnover in interaction identity and frequency, yet many network level metrics remain relatively stable over intermediate timescales (CaraDonna et al., 2020). Over very long periods, however, repeated shifts in interaction partners, extinction of key animals (e.g., megafauna), and environmental change can restructure networks, alter selection pressures, and drive major community reorganization, including loss of interaction functions (CaraDonna et al., 2020; Eriksson, 2016).

Changes in fire regimes offer a clear case in which disturbance regimes alter specialized plant–animal interactions and thus trait evolution. In fire prone ecosystems, specialized pollination, seed dispersal, and herbivory interactions are tightly linked to plant traits such as post fire reproductive mode, morphology, and phenology, and to animal traits related to dispersal, nesting substrates, and feeding behavior (Charles et al., 2025). Altered fire frequency or intensity can disrupt stabilizing feedbacks that previously maintained these interactions and instead trigger abrupt shifts, partner loss, or partner switching, with cascading eco evolutionary consequences (Charles et al., 2025).

At community scales, coevolution in mutualistic networks relies heavily on indirect effects. The structure of networks (nestedness, modularity, degree distributions) determines how selection spreads through communities and whether trait evolution is dominated by direct co-partners or by species connected through multi step pathways (Guimarães et al., 2017). In large, nested pollination and seed dispersal assemblages, indirect effects are often dominant, implying that even species that never directly interact can influence each other's evolution via shared partners (Guimarães et al., 2017).

10 Anthropogenic change and future evolutionary trajectories

Human activities are rapidly modifying the selective landscape in which plant-animal interactions occur (Youngsteadt and Keighron, 2023; Gelmi-Candusso and Hämäläinen, 2019; Molina et al., 2026; Rumengan et al., 2025). A global synthesis of anthropogenic impacts on pollination and seed dispersal highlights pervasive negative effects of agrochemicals, climate change, habitat fragmentation, hunting, non-native species, and urbanization on animal mutualists and their interactions with plants (Youngsteadt and Keighron, 2023). Impacts are unevenly studied, with pollination better documented than seed dispersal and temperate forests better represented than tropical regions, but available evidence consistently indicates declines in mutualist abundance and disruption of interaction networks, particularly through climate-driven phenological mismatches and invasion by non-native frugivores and pollinators (Teixido et al., 2022).

The evolutionary significance of these changes depends not simply on whether an animal partner is lost, but on how the alteration changes the selective regime experienced by plant populations. A reduction in pollinator abundance, for example, can decrease the frequency of successful outcrossing and thereby increase the relative fitness of traits promoting autonomous reproduction. Similarly, the disappearance of effective seed dispersers can alter the demographic value of fruit traits and increase selection for alternative dispersal pathways. Thus, anthropogenic change can modify the relationship between phenotype and fitness by changing the ecological context in which plant traits are expressed.

Loss or functional decline of key animal partners will likely drive rapid evolutionary responses in plants. Potential trajectories include shifts from outcrossing to selfing in response to pollinator declines, evolution of abiotic dispersal or clonality where seed dispersers are extirpated, changes in fruit and seed traits to attract novel dispersers (including humans), and relaxation or redirection of selection on costly defense traits where large herbivores have disappeared (Eriksson, 2016; Johnson et al., 2015; Nascimento et al., 2020; Teixido et al., 2022). These responses need not arise exclusively through immediate changes in allele frequencies. Rapid phenotypic plasticity can provide an initial response to altered animal communities, changing the expression of flowering, nectar production, reproductive allocation, and defense before longer-term genetic responses become detectable. Where altered interaction regimes persist, repeated selection on these phenotypes may promote genetic accommodation or the stabilization of previously plastic responses.

At the molecular level, environmentally induced changes in plant defense can also involve epigenetic mechanisms. Herbivory-associated epigenetic changes may contribute to the persistence of

induced phenotypes across generations, potentially allowing plant populations to respond more rapidly to recurring biotic stress than would be possible through changes in allele frequencies alone. Such mechanisms provide a potential link between short-term ecological perturbation and longer-term evolutionary change, although their contribution to adaptation will depend on the stability, heritability, and fitness consequences of the induced phenotype.

Anthropogenic change can also alter the evolutionary potential of populations by changing population size and connectivity. Habitat fragmentation, local extinction, and demographic decline can reduce effective population size and restrict gene flow, potentially increasing the importance of genetic drift and reducing standing genetic variation available for adaptive responses. Under such circumstances, populations exposed to novel animal communities may face a tension between strong directional selection and limited evolutionary capacity. Genetic bottlenecks may therefore influence whether populations can track rapidly changing selective environments or instead experience demographic decline before adaptive evolution can occur.

The evolutionary response is consequently expected to vary among plant lineages according to their standing genetic variation, reproductive system, generation time, degree of phenotypic plasticity, and dependence on particular animal partners. Populations with broad interaction niches or substantial plasticity may be able to buffer initial changes in animal communities, whereas highly specialized plants may experience stronger directional selection and greater demographic vulnerability. These differences may produce divergent evolutionary outcomes even among populations exposed to similar anthropogenic pressures.

Extended SDE frameworks and network-based approaches provide tools to predict which plant lineages are most vulnerable to interaction loss and how trait evolution may proceed under simplified or restructured interaction webs (CaraDonna et al., 2020; Fuzessy et al., 2025; Guimarães et al., 2017; Teixido et al., 2022; Van Leeuwen et al., 2022) (Table 2). Integrating these approaches with information on phenotypic plasticity, population structure, and genetic variation would allow future studies to distinguish demographic consequences of interaction loss from genuine evolutionary responses.

Importantly, anthropogenic change does not merely remove existing selective agents; it can simultaneously introduce new ones (Gelmi-Candusso and Hämäläinen, 2019). Novel pollinators, dispersers, herbivores, and competitors can replace, partially replace, or interact with declining native partners, producing new combinations of selective pressures. Consequently, future plant evolution may increasingly occur within interaction networks characterized by both the loss of historical partners and the emergence of novel ecological relationships. The resulting trajectories are likely to be heterogeneous, contingent, and potentially rapid, particularly where ecological change and evolutionary responses occur on overlapping timescales.

11 Microbiome-mediated plant-animal interactions

Classical plant-animal coevolution has been framed largely as a dyadic process. Growing evidence, however, shows that many of these interactions are embedded in tripartite plant-animal-microbiome systems in which microbes alter the selective environment experienced by both plants and animals (Russell and McFrederick, 2022). Rather than merely describing microbial effects on ecological outcomes, we focus here on the principal mechanisms through which microbiomes modify the strength, direction or targets of selection on plant traits.

Three interrelated mechanisms appear especially important. First, microbes can change the phenotypic interface of the interaction itself. In floral nectar, yeasts and bacteria routinely alter sugar concentration, amino-acid composition, pH and volatile organic compound profiles (Ilyasov et al., 2025; Martin et al., 2022; Quevedo-Caraballo et al., 2024; Rering et al., 2018). Because these chemical shifts modify the attractiveness or nutritional value of the reward, they change the relative fitness of plant genotypes that differ in nectar chemistry or floral morphology. Experimental work demonstrates that honey bees can discriminate among microbial volatiles and preferentially visit flowers colonized by particular taxa such as *Metschnikowia reukaufii* (Deng et al., 2024; Ilyasov et al., 2025; Rering et al., 2018). Consequently, the presence and composition of the nectar microbiome become part of the selective filter acting on floral traits.

Second, microbes can alter the costs and benefits that determine the position of an interaction along the mutualism–antagonism continuum. In *Iris bulleyana*, nectar yeasts increased pollinator

TABLE 2 Examples of anthropogenic drivers altering animal mediated selection on plants.

Anthropogenic factor	Key effects on animal partners	Expected evolutionary responses in plants	References
Climate change and altered phenology	Mismatches in pollinator/fruiting timing, range shifts	Selection on flowering and fruiting phenology; favoring generalist interaction strategies	CaraDonna et al., 2020; Charles et al., 2025; Eriksson, 2016; Teixido et al., 2022.
Hunting and defaunation of large frugivores and herbivores	Loss of long-distance dispersal and browsing pressure	Reduced selection for large fruits and strong structural defenses; shifts to smaller-bodied dispersers or abiotic modes	Eriksson, 2016; Katz, 2020; Nascimento et al., 2020; Teixido et al., 2022.
Agrochemicals and habitat fragmentation	Pollinator and frugivore declines, network simplification	Increased selfing, reduced floral investment, potential evolution toward wind or autonomous self-pollination.	CaraDonna et al., 2020; Johnson et al., 2015; Teixido et al., 2022.

visitation and seed set, partially offsetting the negative effects of floral herbivory (Deng et al., 2024). By changing the net fitness consequences of the same animal visit, microbial partners can shift the selective regime experienced by plants from predominantly antagonistic toward more mutualistic (or vice versa). Similar effects occur in nectar–parasitoid interactions, where microbial modification of sugar and amino-acid profiles influences parasitoid attraction and longevity, thereby reshaping tri-trophic selection on plant defence and reward traits (Cusumano and Lievens, 2023).

Third, microbes can expand or constrain the range of phenotypic variation on which selection acts. Endophytic and rhizosphere microorganisms frequently induce or amplify plant defence responses, while gut microbiomes of herbivores affect the detoxification of secondary metabolites and the induction of plant defences (Ashra and Nair, 2022; Wang et al., 2023). These microbial contributions modify both the expression of plant resistance traits and the counter-adaptations available to herbivores, thereby influencing the evolutionary trajectories of plant–herbivore "arms races." In addition, phenotypic plasticity within nectar-microbe populations themselves (Quevedo-Caraballo and Álvarez-Pérez, 2025) can generate fine-scale spatial and temporal variation in the selective environment, potentially maintaining polymorphism in plant traits that would otherwise be purged.

Field surveys further indicate that plants visited by different pollinator guilds harbour distinct nectar microbiota signatures that transcend geographic distance (De Vega et al., 2021). Pollinators therefore act as vectors that structure microbial communities, while the resulting microbiomes feed back on plant reproductive success. This reciprocal structuring implies that selection on plant traits is often mediated by an intermediate microbial filter whose composition is itself shaped by animal behaviour.

Taken together, these mechanisms show that microbiomes do not merely modulate ecological outcomes; they alter the mapping between plant phenotype and fitness. Selection on floral signals, nectar chemistry, defensive compounds or seed traits can therefore be indirect and contingent on microbial community composition, assembly and dispersal (Ashra and Nair, 2022; Ilyasov et al., 2025; Quevedo-Caraballo et al., 2024; Vannette, 2020). Recognizing these pathways helps explain why ostensibly similar plant-animal interactions frequently exhibit context-dependent evolutionary outcomes and why coevolutionary trajectories may depend as much on microbial ecology as on the genetics of the macroscopic partners (Table 3).

12 Plasticity versus genetic adaptation in plant responses

Plant responses to animals and to changing environments arise from a combination of phenotypic plasticity (environmentally induced, often reversible changes within a genotype) and genetic adaptation (heritable changes in allele frequencies). Plasticity allows rapid adjustment of traits such as nectar production, flowering phenology and induced defenses, often acting on ecological timescales relevant to fluctuating pollinator and herbivore communities, whereas genetic adaptation shapes longer term evolution of interaction syndromes (Fox et al., 2019; Laitinen and Nikoloski, 2018; Li et al., 2025; Napier et al., 2022; Schneider, 2022).

Reproductive traits mediating pollinator interactions show extensive plasticity. Floral organs tend to be developmentally robust yet can exhibit plastic adjustments in size, longevity and physiology under varying temperature and light regimes, reflecting joint control by stability and plasticity promoting genes (Li et al., 2025). Floral longevity itself is widely plastic: a global meta-analysis across 188 angiosperm species found that supplemental pollination shortened floral longevity by ~21%, whereas pollinator exclusion lengthened it by ~35%, with stronger plasticity in species experiencing pollen limitation and in climates with high temperature and drought variability (Xu et al., 2025). This plastic extension of flower life under low pollination can buffer reproduction when pollinators are scarce or unpredictable. Plastic changes in nectar quantity and quality in response to pollination environment, resource status or stress are also common, allowing plants to adjust reward provisioning to local pollinator conditions and abiotic constraints (Briggs and Anderson, 2025; Schneider, 2022). Such plasticity can modulate

TABLE 3 Microbiome-mediated plant-animal interfaces.

Interaction context	Dominant microbiome role in plant–animal interaction	Link to the broader evolutionary framework	Evolutionary/ecological implications for the plant–animal–microbiome system	References
Flowers and pollinators	Nectar yeasts and bacteria alter nectar chemistry and volatile profiles, changing pollinator attraction, recognition, and choice.	Selection on floral traits; reciprocal ecological feedbacks; context-dependent selection.	Indirect selection on floral rewards and scent through pollinator-structured nectar microbiomes; microbial modification of the plant phenotype can alter pollinator-mediated fitness differences among plants.	De Vega et al., 2021; Deng et al., 2024; Ilyasov et al., 2025; Martin et al., 2022; Quevedo-Caraballo et al., 2024; Rering et al., 2018; Vannette, 2020.
Flowers, herbivores and parasitoids	Nectar microbes modify resources and chemical cues affecting herbivores and parasitoids.	Multitrophic selection; indirect effects; diffuse interaction networks.	Microbe-mediated changes in tri-trophic interactions can modify selection on plant defense and reward traits and alter the balance among mutualistic and antagonistic interactions.	Cusumano and Lievens, 2023; Deng et al., 2024; Martin et al., 2022.
Plants, herbivorous insects and their microbiomes	Gut and endophytic microbes shape digestion, defense responses, and tolerance to plant toxins.	Reciprocal selection; plant–herbivore arms races; ecological fitting and counter-adaptation.	Modulation of plant–insect arms races and plasticity in defense and counter-defense; microbial mediation can alter the strength and direction of selection on both plant defenses and herbivore detoxification traits.	Ashra and Nair, 2022; Quevedo-Caraballo and Álvarez-Pérez, 2025; Wang et al., 2023.

pollinator mediated selection on floral traits by altering which phenotypes are expressed under different environments (Briggs and Anderson, 2025; Rering et al., 2018; Schneider, 2022).

Induced defenses exemplify plasticity in plant-herbivore interactions. Herbivory can trigger systemic increases in chemical and structural defenses, with epigenetic changes enabling transmission of defense related plastic phenotypes across generations, thereby helping offspring cope with insect feeding (Wang et al., 2023). Reviews of plant-insect interactions emphasize that phenotypic plasticity in both plants and insects has been central in their long coevolution, allowing rapid adjustment to new enemies, hosts or environmental conditions and providing raw material for the evolution of stable defense and counter defense traits under sustained selection (Ashra and Nair, 2022; Wang et al., 2023). Experimental evolution work shows that chronic herbivory can favor higher constitutive defenses and lower herbivore induced plasticity, whereas pollination regime (bee versus hand pollination) can strongly influence how herbivory shapes the evolution of plasticity in both defensive chemistry and floral traits (Ramos and Schiestl, 2020). These results highlight that plasticity in defense and floral traits evolves in a multidimensional selective landscape where mutualists and antagonists jointly shape costs and benefits of inducibility.

Conceptual syntheses on phenotypic plasticity in plants stress that plasticity is genetically encoded and heritable but constrained by costs, limits and the reliability of environmental cues (Laitinen and Nikoloski, 2018; Napier et al., 2022; Schneider, 2022). Not all genotypes express plasticity for a given trait, and not all plastic responses are adaptive: some are passive consequences of physiological constraints or can even be maladaptive under novel conditions (Fox et al., 2019; Schneider, 2022). Plasticity can facilitate adaptation to rapid environmental change by "buying time": shifting phenotypes toward new fitness peaks before genetic change occurs, or exposing cryptic genetic variation when environments change, thereby enabling genetic accommodation of initially plastic traits (Fox et al., 2019; Laitinen and Nikoloski, 2018; Napier et al., 2022; Vahsen et al., 2023). However, plasticity can also slow adaptation by buffering populations from selection, or create ecological traps when cues no longer reliably predict environments (Fox et al., 2019; Napier et al., 2022). The net effect on evolutionary rates thus depends on trait- and context-specific trade-offs.

Floral traits under global change illustrate these dynamics. Climate driven shifts in temperature and precipitation, combined with pollinator declines, alter both the expression of floral traits via plasticity and the direction of selection imposed by pollinators, herbivores and abiotic stressors (Briggs and Anderson, 2025). For instance, selection by pollinators for larger flowers can conflict with selection by drought for smaller, less costly flowers, and plastic reductions in flower size or nectar under stress may mitigate immediate fitness losses but also reshape the selective landscape for future genetic evolution (Briggs and Anderson, 2025; Schneider, 2022). Gene by environment interaction studies and recent genomic work are beginning to uncover the molecular architecture of plasticity, showing how standing genetic variation in responsiveness to cues underlies differences in adaptive plasticity among genotypes and species (Laitinen and Nikoloski, 2018; Li et al., 2025; Napier et al., 2022).

Overall, plant responses to animals cannot be understood solely as outcomes of slow genetic change. Plasticity in nectar production, flowering time, flower longevity and inducible defenses provides a first, rapid line of response to variable and unstable environments and to changing pollinator and herbivore communities (Briggs and Anderson, 2025; Fox et al., 2019; Quevedo-Caraballo et al., 2024; Schneider, 2022; Xu et al., 2025). Over longer timescales, these plastic responses can be refined, canalized or replaced by genetically fixed adaptations, depending on their costs, reliability and fitness consequences. The central challenge is to disentangle when plasticity primarily buffers plants against environmental and biotic variability and when it serves as a stepping stone toward genetic specialization in plant-animal coevolution (Table 4).

13 Geographic mosaics of coevolution

Coevolutionary dynamics rarely unfold uniformly across a species' entire range; instead, they are structured as geographic mosaics shaped by spatial variation in ecological context and selective regimes. Within this framework, populations experience differing intensities and directions of reciprocal selection, resulting in a patchwork of coevolutionary "hotspots, " where reciprocal adaptation is strong, and "coldspots, " where such interactions are weak, absent, or asymmetric (Gomulkiewicz et al., 2000). This heterogeneity emerges from variation in community composition,

TABLE 4 Plastic traits versus genetic specialization in plant-animal interactions.

Focal trait in plant–animal interactions	Dominant response mode (plastic vs. genetic)	Ecological and evolutionary context for plasticity vs. specialization	References
Floral longevity, nectar provisioning	Strong, widespread plasticity; heritable baselines	Plasticity favored under variable pollination and climate; specialization in stable systems	Briggs and Anderson, 2025; Li et al., 2025; Quevedo-Caraballo et al., 2024; Schneider, 2022; Xu et al., 2025.
Induced chemical and structural defenses	Highly inducible plastic responses; genetic variation in inducibility and baselines	Plasticity advantageous with patchy or episodic herbivory; constitutive defense under chronic attack	Ashra and Nair, 2022; Cusumano and Lievens, 2023; Ramos and Schiestl, 2020; Wang et al., 2023.
Flowering phenology and floral display traits	Substantial plasticity to temperature, drought and pollination; genetic shifts over time	Plastic tracking of climate and pollinators under rapid change; genetic evolution under persistent trends	Briggs and Anderson, 2025; Fox et al., 2019; Li et al., 2025; Napier et al., 2022; Schneider, 2022.

local abiotic conditions, and the presence or absence of key interacting partners.

Geographic variation in selection is most commonly measured by combining three complementary approaches. First, reciprocal transplant or common-garden experiments quantify local adaptation by comparing relative fitness of plant genotypes in native versus non-native sites that differ in animal partners. Second, phenotypic selection analyses (selection gradients and differentials) are performed across multiple populations to estimate the strength and direction of selection on the same traits under different interaction regimes. Third, spatial comparisons of trait-matching and interaction outcomes (e.g., pollination efficiency, seed dispersal effectiveness, or herbivore damage) are linked to environmental and community covariates to identify the ecological drivers of selection mosaics.

As a consequence, the same pair of species may engage in qualitatively different interactions across their distribution. In some regions, interactions may be strongly mutualistic, with both partners experiencing fitness benefits that reinforce trait matching, while in other areas the same interaction may shift toward antagonism or neutrality (Medeiros et al., 2018). Classic empirical examples illustrate how ecological conditions drive these shifts (Chamberlain and Holland, 2009; Henry et al., 2018). In the plant–ant protective mutualism involving *Acacia* and *Pseudomyrmex*, high ant density and reliable defence produce clear mutualism (Janzen, 1966; Heil et al., 2009); under low ant abundance or high alternative resource availability the interaction becomes neutral or even antagonistic because ants may consume plant tissues without providing protection (Janzen, 1966; Heil et al., 2009; Henry et al., 2018; Clement et al., 2007; Janzen, 1975). Similarly, in seed-dispersal systems involving scatter-hoarding rodents, high seed availability (mast years) or low predator density favour caching and thus mutualism (Zhang et al., 2024; Li and Zhang, 2007; Zhang et al., 2008; Zwolak et al., 2023), whereas food scarcity or high competition among rodents increase immediate consumption and shift the interaction toward antagonism (Zwolak et al., 2023; Bogdziewicz et al., 2019). In plant–pollinator systems, the same floral visitor can act as a mutualist when pollen transfer is efficient and as an antagonist (nectar robber) when morphological mismatch or resource limitation reduces pollination effectiveness (Lichtenberg et al., 2018; Aubert et al., 2025; Solís-Montero and Vallejo-Marín, 2017; Cha et al., 2025; Traveset et al., 1998). Abiotic factors further modulate these outcomes: drought, elevated temperature, or nutrient limitation can reduce plant reward production, thereby decreasing the mutualistic benefit relative to the costs of the interaction and favouring antagonistic outcomes (Descamps et al., 2021, 2018; Cha et al., 2025; Duell et al., 2024; Gorden and Adler, 2013; Keeler et al., 2021).

Importantly, gene flow among populations connects these local dynamics, allowing traits shaped under strong selection in hotspots to spread into regions where selection is weaker or absent. This interplay between local adaptation and gene flow produces complex evolutionary trajectories that cannot be understood without an explicitly spatial perspective. Integrating geographic mosaics into the study of plant–animal interactions therefore provides a unifying framework that links local ecological processes with large-scale evolutionary patterns (Gomulkiewicz et al., 2000).

14 Extinction debt and evolutionary anachronisms

Contemporary plant traits often bear the imprint of past interactions that are no longer present, reflecting a temporal lag between ecological change and evolutionary response. This phenomenon is particularly evident in evolutionary anachronisms, where traits that evolved under now-extinct selective agents persist despite the disappearance of their original functional context. Such traits can be interpreted as "ghosts of interactions past, " revealing historical relationships with extinct megafauna or other lost partners (Gargiulo et al., 2025; Guerrero and Agnolín, 2026; Janis, 2002).

Classic examples include large, fleshy fruits whose size, structure, or nutrient composition suggest adaptation to dispersal by large-bodied animals that no longer exist in modern ecosystems, as well as robust physical defenses such as oversized spines that appear mismatched with current herbivore assemblages. In the absence of their original interactors, these traits may become functionally redundant, suboptimal, or dependent on substitute agents, including humans or domesticated animals, for their continued ecological relevance (Connell, 1980; Janis, 2002).

The persistence of such traits reflects both evolutionary inertia and constraints on rapid adaptation. When the loss of interacting partners occurs faster than populations can evolve new strategies, species may experience an extinction debt, wherein current populations persist temporarily despite reduced functional integration within their ecological networks. Over longer timescales, this mismatch can lead to reduced reproductive success, limited dispersal, or increased vulnerability to environmental change. Alternatively, novel interactions may partially compensate for lost partners, but these substitutions often differ in efficiency or selectivity, thereby reshaping selective pressures in unpredictable ways (Connell, 1980; Janis, 2002).

15 Eco-evolutionary feedbacks and rapid evolution

Ecological and evolutionary processes are increasingly recognized as tightly coupled, operating on overlapping timescales and influencing each other through feedback loops (Oroian et al., 2025; Păpuc and Bora, 2023). In plant-animal interactions, changes in community composition or interaction strength can rapidly alter selective pressures, leading to measurable evolutionary responses within relatively short periods, sometimes on the order of decades. These evolutionary changes, in turn, can modify the structure and function of ecological interactions, generating dynamic feedbacks between ecological and evolutionary processes (Thomann et al., 2013; Van Donk et al., 2025).

For instance, a decline or loss of key animal partners can shift the selective landscape experienced by plant populations (Cheptou, 2021). Reduced availability of effective pollinators may favor traits associated with autonomous self-pollination, leading to rapid genetic changes in mating systems, floral morphology, or phenology. As these traits become more prevalent, they further alter the ecological context by reducing dependence on animal-mediated interactions, potentially weakening or eliminating previously important mutualisms (Whittall and Carlson, 2009).

Such feedbacks can also operate in more complex ways, where evolutionary changes in one species cascade through interaction networks, affecting multiple partners simultaneously. The resulting dynamics are inherently nonlinear, with the potential for rapid shifts in both trait distributions and interaction patterns. Recognizing the role of eco-evolutionary feedbacks highlights the need to consider evolution not as a slow background process, but as an active and ongoing component of ecological systems (Angulo et al., 2022; Petrescu-Mag, 2023a, b).

16 Invasive species and novel interactions

The introduction of species beyond their native ranges creates ecological contexts in which interactions arise without a shared evolutionary history (Oroian et al., 2014; Păpuc et al., 2025). These novel assemblages provide a natural context for examining how plant-animal interactions are initiated, modified, and potentially stabilized in the absence of long-term reciprocal selection. In such systems, interactions may initially be governed by ecological fitting, whereby organisms exploit pre-existing traits that allow them to interact effectively despite the absence of a shared evolutionary history.

Invasive pollinators (Kovács-Hostyánszki et al., 2022), non-native frugivores (Case et al., 2024), and introduced herbivores can establish functional interactions with native plants and thereby alter the direction and intensity of selection. Because these interactions are not the product of prolonged coevolution, the degree of trait matching may differ substantially from that observed in established mutualisms or antagonisms. Morphological, phenological, and behavioral mismatches can consequently affect reproductive success, seed dispersal efficiency, or defense effectiveness (Case et al., 2024; Kovács-Hostyánszki et al., 2022).

The evolutionary consequences of such mismatches depend on whether the novel interaction creates consistent selection and whether the affected plant population contains sufficient variation to respond (Stotz et al., 2016). A novel animal may impose selection on floral traits, fruit characteristics, reproductive timing, or defensive phenotypes simply because previously uncommon plant variants experience different fitness under the new interaction regime (Alonso et al., 2018). In this sense, invasion can rapidly restructure the mapping between plant phenotype and fitness without requiring the evolution of new traits in the first instance (Colautti and Lau, 2015). Pre-existing variation may therefore be sorted by the novel selective environment, while subsequent generations may experience directional selection on the traits that increase fitness under the altered community (Stotz et al., 2016; Beans and Roach, 2015).

At the same time, novel interactions can impose strong and sometimes unprecedented selective pressures, potentially driving rapid evolutionary change (Stotz et al., 2016; Colautti and Lau, 2015). Native species may adapt to new partners, resist or tolerate new antagonists, or shift their reliance toward alternative interactions (Stotz et al., 2016; Colautti and Lau, 2015). These responses may involve both phenotypic plasticity and contemporary evolution (Colautti and Lau, 2015; Marin et al., 2019). Plasticity can provide an immediate adjustment to novel cues, whereas persistent selection may favor genotypes with altered trait means or reaction norms (Marin et al., 2019; O'Dea et al., 2016). Existing evidence that plant-animal interactions can generate heritable variation in plastic responses suggests that the evolutionary trajectory of a population may depend not only on the direction of selection but also on the genetic architecture underlying responsiveness to the novel interaction environment (Colicchio, 2017).

Epigenetic mechanisms may further contribute to this early phase of response (Alonso et al., 2018; Marin et al., 2019). When novel herbivores or other biotic stressors induce defense-related phenotypes, epigenetic modifications can contribute to the persistence of induced responses across generations, potentially allowing populations to respond before substantial genetic differentiation has accumulated (Colicchio, 2017; O'Dea et al., 2016). This mechanism is particularly relevant to invasive contexts because the ecological change can occur within a few generations, creating a temporal mismatch between the rate of environmental change and the rate at which conventional genetic adaptation can proceed (O'Dea et al., 2016; Marin et al., 2019).

Invasive species may also alter evolutionary trajectories indirectly by changing the demographic and genetic structure of native plant populations (Stotz et al., 2016; Smith et al., 2020). Strong herbivory, reproductive interference, or altered dispersal can reduce population size and increase spatial isolation (Stotz et al., 2016). Such demographic effects may generate genetic bottlenecks and reduce effective population size, potentially limiting the standing variation available for subsequent adaptation (Bock et al., 2015). Conversely, repeated immigration among populations may introduce novel genetic variation and modify the evolutionary response to the invader (Smith et al., 2020). Thus, the evolutionary consequences of invasion depend on the interaction between selection imposed by the novel species and the demographic history of the affected plant population (Smith et al., 2020).

These processes are often asymmetric, with invasive species exerting disproportionate influence because of differences in abundance, competitive ability, or enemy release (Smith et al., 2020). As a result, the establishment of an invader can rapidly shift the balance of interactions within an ecological network rather than simply adding one additional interaction (Gleditsch and Sperry, 2020). The effects may propagate through shared partners, modifying pollination, seed dispersal, herbivory, and competition simultaneously (Alonso et al., 2018). Consequently, selection imposed by an invasive species may be amplified or counteracted by indirect

effects generated elsewhere in the interaction network (Gleditsch and Sperry, 2020).

An important implication is that invasion can create evolutionary trajectories that differ fundamentally from classical coevolutionary pathways (Colautti and Lau, 2015). Rather than reciprocal adaptation developing gradually between long-associated partners, contemporary evolution may begin with ecological fitting, followed by rapid selection on standing variation, plastic responses, and, where sustained, genetic differentiation (Gleditsch and Sperry, 2020; Colautti and Lau, 2015). Over time, repeated interaction may generate new forms of ecological dependence or even initiate processes of coadaptation (Colautti and Lau, 2015). However, the speed and direction of these processes will depend on interaction strength, population size, generation time, genetic variation, and the stability of the novel community (Stotz et al., 2016; Smith et al., 2020).

The Anthropocene is therefore characterized not only by the erosion of historical plant-animal interactions but also by the formation of new and rapidly changing interaction networks. This phenomenon is observed not only in terrestrial ecosystems but also in marine ecosystems (Herlon et al., 2025; Pinasang et al., 2025; Kamlasi et al., 2025; Sujatmiko et al., 2025). Species introductions can simultaneously remove established selective regimes and create novel ones, producing complex combinations of ecological fitting, phenotypic plasticity, contemporary evolution, and demographic constraint (Păpuc and Petrescu-Mag, 2023; Petrescu-Mag and Gavriloaie, 2019; Pricop and Negrea, 2018). Understanding these mechanisms is essential for determining whether native plant populations can accommodate novel animal communities, evolve under the new selective regime, or decline when ecological change exceeds their adaptive capacity.

17 Predictive frameworks and modeling plant evolution under shifting animal interactions

Predicting how plant traits will evolve under rapidly changing animal communities remains one of the central challenges in contemporary evolutionary ecology (Fox et al., 2019; Strauss and Irwin, 2004). While classical coevolutionary theory has been largely retrospective - explaining trait diversification after it has occurred - recent advances increasingly emphasize the development of predictive frameworks that integrate ecological dynamics, trait variability, and interaction networks into forward-looking models (Huitzil and Huepe, 2024; Chaparro-Pedraza and Bank, 2025; Sun et al., 2025).

At the core of this shift is the recognition that plant evolution in response to animals is not governed by isolated pairwise interactions, but by high-dimensional systems in which multiple selective agents act simultaneously and often nonlinearly. Network-based approaches provide a critical foundation for such predictions. By incorporating species interaction matrices, trait matching functions, and the topology of ecological networks (e.g., nestedness and modularity), these models allow researchers to simulate how changes in species composition - such as the loss of key pollinators or the introduction of novel dispersers - propagate through communities and reshape selective landscapes. Importantly, these approaches reveal that indirect effects can generate emergent evolutionary trajectories that are not predictable from direct interactions alone.

Trait-based modeling frameworks further enhance predictive capacity by linking measurable plant traits (e.g., flower size, nectar production, seed mass, defensive chemistry) to fitness outcomes under different interaction scenarios. These models often rely on adaptive landscapes that incorporate multiple fitness peaks corresponding to alternative ecological strategies, such as specialization versus generalization in pollination systems or defense-dominated versus reproduction-dominated allocation strategies under herbivore pressure. When combined with empirical data, such frameworks can be used to estimate the direction and strength of selection under specific ecological perturbations, including defaunation, climate-driven phenological shifts, or biological invasions.

A major challenge for predictive models lies in incorporating phenotypic plasticity and behavioral variability of animal partners. As shown throughout this review, plastic responses in plants and consistent individual differences in animal behavior can significantly alter interaction outcomes (Ashra and Nair, 2022; Fox et al., 2019; Laitinen and Nikoloski, 2018; Li et al., 2025; Napier et al., 2022; Ramos and Schiestl, 2020; Xu et al., 2025). Integrating these sources of variability requires moving beyond static trait values toward probabilistic representations of interactions, where fitness outcomes are defined by distributions rather than fixed means. This perspective aligns with recent developments in eco-evolutionary modeling, where stochasticity and variance are treated as central components of evolutionary dynamics rather than as noise.

Another emerging direction involves coupling genomic data with ecological interaction models (Wagey et al., 2025). Advances in quantitative genetics and genomics now allow the identification of loci associated with key interaction traits, such as floral signals or defensive compounds. Embedding such genetic architectures into eco-evolutionary models opens the possibility of predicting not only phenotypic change but also the underlying genetic trajectories of plant populations under shifting selective regimes. This integration is particularly relevant for understanding the limits of adaptation, including genetic constraints, trade-offs, and the potential for evolutionary rescue in rapidly changing environments.

Despite these advances, predictive accuracy remains constrained by the inherent complexity and context dependency of plant-animal interactions. Environmental variability, spatial heterogeneity, and historical legacies all influence the strength and direction of selection, often in ways that are difficult to parameterize. As a result, current models are best viewed as tools for generating scenarios and identifying general patterns rather than precise forecasts. Nevertheless, they represent a critical step toward a more mechanistic and anticipatory understanding of plant evolution.

In the context of accelerating anthropogenic change, the development of predictive frameworks is not merely an academic exercise but a practical necessity (Fox et al., 2019; Strauss and Irwin, 2004). Anticipating how plant traits and interaction networks

will respond to ongoing disturbances - such as pollinator decline, species invasions, and climate shifts - can inform conservation strategies aimed at preserving both biodiversity and ecosystem function. Ultimately, integrating ecological networks, trait-based approaches, and evolutionary theory into cohesive predictive models will be essential for understanding and managing the future trajectories of plant-animal coevolution (Tables 5, 6; Figure 1).

18 Conclusions

Animal-mediated interactions constitute dynamic components of the selective environments in which plants evolve. Their evolutionary effects cannot be reduced to isolated examples of pollination, herbivory, or seed dispersal because the fitness consequences of these interactions depend on community structure, environmental context, historical contingencies, and feedbacks among interacting species.

A central implication of the synthesis is that plant evolutionary responses to animals operate across multiple timescales. Immediate responses can arise through phenotypic plasticity and changes in trait expression, whereas persistent interaction regimes can generate contemporary evolutionary change and longer-term genetic differentiation. Epigenetic processes may provide an additional mechanism linking environmentally induced responses with transgenerational phenotypic variation. At the population level, however, the capacity for adaptation is constrained by standing genetic variation, demographic history, gene flow, and the maintenance of sufficiently large populations.

The same framework is particularly important under accelerating anthropogenic change. Climate change, habitat fragmentation, species loss, and biological invasions do not simply alter the magnitude of existing selection; they can change the identity of selective agents, disrupt historical interactions, and generate novel

TABLE 5 Cross-scale linkages among major mechanisms through which animals shape plant evolution.

Major topic	Primary selective agents/ processes	Key plant traits affected	Dominant evolutionary scale(s)	Cross-scale linkages with other topics	Typical outcome under anthropogenic change
Pollination	Animal pollinators (insects, birds, bats, etc.)	Floral morphology, colour, scent, nectar chemistry, phenology, mating system	Microevolutionary (selection on floral traits) → macroevolutionary (diversification of angiosperms)	Linked to herbivory (trade-offs between attraction and defence); to microbiomes (nectar microbes alter rewards); to plasticity (floral longevity and nectar plasticity)	Pollinator decline → increased selfing, reduced floral investment, phenological mismatches.
Herbivory	Insect and vertebrate herbivores	Chemical defences, structural defences (spines, toughness, silica), reproductive allocation	Microevolutionary (defence–reproduction trade-offs) → historical (evolutionary anachronisms)	Linked to reproduction (resource allocation trade-offs); to seed dispersal (defence of fruits); to plasticity (induced defences and epigenetic transmission)	Loss of large herbivores → relaxation of selection on costly defences; novel invasive herbivores → rapid induction or constitutive defence evolution.
Seed dispersal	Frugivores, scatter-hoarders, granivores	Fruit size, colour, pulp traits, seed size, hardness, nutrient content	Microevolutionary (dispersal syndromes) → macroevolutionary (angiosperm diversification)	Linked to herbivory (coupled defence–dispersal traits); to synzoochory (mutualism–antagonism continuum); to geographic mosaics (spatial variation in disperser assemblages)	Defaunation → reduced long-distance dispersal, shifts toward smaller-bodied or abiotic dispersal modes.
Microbiome mediation	Nectar yeasts/ bacteria, endophytes, gut microbes of herbivores	Nectar chemistry and volatiles, induced defences, reward quality	Ecological (short-term fitness effects) → microevolutionary (indirect selection on plant traits)	Mediates both mutualistic (pollination) and antagonistic (herbivory) interactions; interacts with plasticity (microbe-induced phenotypic variation)	Climate change and habitat alteration restructure microbial communities → altered selective filters on floral and defence traits.
Phenotypic plasticity	Fluctuating animal abundance, abiotic stress	Floral longevity, nectar production, induced defences, flowering time	Ecological (within-generation responses) → evolutionary (genetic accommodation of plastic traits)	Buffers immediate effects of pollinator/ herbivore fluctuations; can facilitate or constrain genetic adaptation under anthropogenic change	Rapid plastic tracking of novel conditions; potential evolutionary rescue or ecological traps if cues become unreliable.
Geographic mosaics of coevolution	Spatial variation in partner abundance and community composition	Trait matching, interaction outcome (mutualism ↔ antagonism)	Spatial microevolution → regional patterns of adaptation	Integrates all pairwise interactions across space; gene flow connects hotspots and coldspots	Habitat fragmentation intensifies mosaic structure; local coevolutionary hotspots may become isolated.
Anthropogenic change	Climate change, fragmentation, invasions, defaunation	Multiple traits simultaneously	Contemporary microevolution + rapid eco-evolutionary feedbacks	Alters the selective context of all previous topics; creates novel interaction networks	Novel selective regimes (loss of historical partners + arrival of new ones); divergent evolutionary trajectories among lineages.

TABLE 6 Comparison of major classes of theoretical models used to predict plant evolutionary responses under changing animal interaction networks.

Model class	What can actually be predicted	Data requirements	Major assumptions that constrain inference	Typical application to plant–animal systems
Adaptive-dynamics models	Long-term evolutionary endpoints (evolutionary singular strategies, branching points, evolutionary stability); conditions for evolutionary branching or continuous trait evolution	Fitness functions linking plant traits to demographic rates; functional forms of frequency- or density-dependent selection; invasion fitness of rare mutants	Continuous trait space; rare mutants; separation of ecological and evolutionary timescales; often assumes asexual reproduction or simple genetics; neglects demographic stochasticity	Evolution of floral traits under frequency-dependent pollinator preference; evolution of defence levels under herbivore density dependence.
Trait-based network models	Changes in interaction structure and emergent selective pressures resulting from species loss, addition or abundance shifts; indirect effects transmitted through shared partners; predicted direction of selection on plant traits under restructured networks	Quantitative interaction matrices (or proxies based on trait matching); species abundances; functional traits of plants and animals; network topological metrics (nestedness, modularity)	Interactions determined primarily by trait matching; static or slowly changing network topology relative to evolutionary timescales; often assumes pairwise interaction strengths are independent of higher-order effects	Predicting shifts in selection on fruit or flower traits after loss of key frugivores or pollinators; identifying plant lineages most vulnerable to network simplification.
Eco-evolutionary dynamical models	Short- to intermediate-term joint trajectories of ecological variables (abundances, interaction frequencies) and evolving traits; feedbacks between ecological change and evolutionary response; potential for evolutionary rescue or maladaptation	Time-series of abundances and trait distributions; estimates of heritability or genetic variance; functional relationships between traits, fitness and interaction rates; demographic parameters	Overlapping ecological and evolutionary timescales; heritable variation is maintained; often requires simplifying assumptions about genetic architecture (e.g., quantitative genetics or single-locus models); computational intensity limits system size	Rapid evolution of selfing rates under pollinator decline; joint dynamics of plant defence and herbivore abundance; evolutionary responses to invasive mutualists or antagonists.

combinations of partners. Consequently, future plant evolution may increasingly involve simultaneous loss of coevolved interactions and selection imposed by novel animal communities. Whether populations persist through plasticity, contemporary evolution, interaction switching, or evolutionary rescue will depend on the balance between the rate of environmental change and the capacity of populations to respond.

Across these cases, several general principles emerge that determine whether an animal-mediated interaction produces transient ecological effects, plastic responses, contemporary evolution, or longer-term diversification. First, the evolutionary outcome depends on the strength, direction, and persistence of selection imposed by the animal community. Second, selection can translate into evolutionary change only when sufficient heritable variation, demographic capacity,

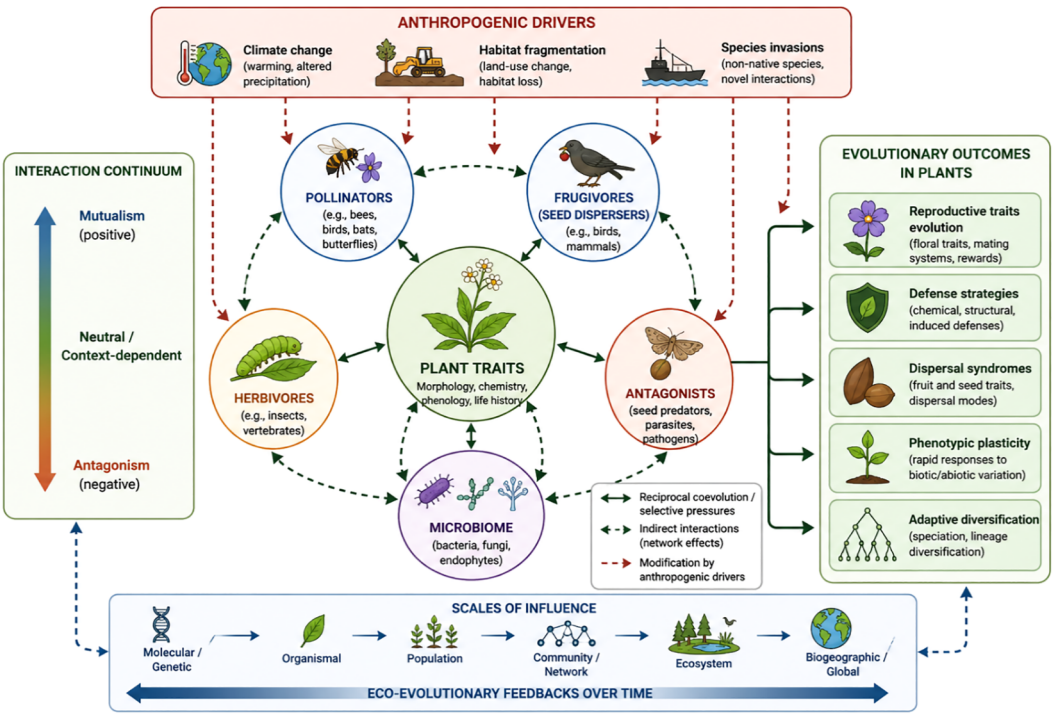


FIGURE 1
Conceptual framework illustrating how animals shape plant evolution across ecological and evolutionary scales (original plate, designed by I. V. Petrescu-Mag, edited using OpenAI).

and genetic connectivity are available. Third, the outcome is shaped by the degree of reciprocity and by whether selection is imposed by a single partner, a functional guild, or a multispecies interaction network. Fourth, ecological context, spatial heterogeneity, temporal variability, and historical contingency can alter both the fitness consequences of a trait and the identity of the effective selective agents. Finally, microbiomes, phenotypic plasticity, and behavioral variation can modify the phenotype-fitness relationship itself, thereby changing the direction or magnitude of selection. These factors explain why similar plant-animal interactions can produce divergent evolutionary outcomes across populations, species, and environments.

The review also indicates that prediction should move beyond static descriptions of plant traits toward mechanistic, network-based approaches that integrate ecological interactions with phenotypic variability, demographic structure, and evolutionary processes. Extended SDE frameworks, interaction networks, trait-based models, and genomic approaches provide complementary tools for identifying populations and lineages that are most vulnerable to interaction loss or most capable of responding to novel selective environments.

Future research should therefore prioritize studies that explicitly connect changes in animal communities with measurable changes in plant fitness, heritable variation, reaction norms, and allele-frequency dynamics. Such integration would help distinguish transient ecological responses from genuine evolutionary change and clarify when plasticity facilitates adaptation, when it constrains selection, and when demographic deterioration prevents evolutionary responses from occurring.

Ultimately, the evolutionary future of plants will be determined not only by the persistence of individual species interactions, but by the capacity of entire interaction networks to reorganize under environmental and anthropogenic change. Understanding this reorganization will be essential for predicting evolutionary trajectories and for conserving both plant diversity and the ecological functions maintained by plant-animal interactions.

Author contributions

PP: Conceptualization, Writing – original draft. AT: Writing – review & editing. F-DB: Writing – review & editing. IP-M: Methodology, Conceptualization, Supervision, Writing – original draft.

Funding

The author(s) declared that financial support was not received for this work and/or its publication.

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author PP declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Generative AI statement

The author(s) declared that generative AI was used in the creation of this manuscript. OpenAI ChatGPT-5.3 - https://openai.com - was used to assist with figure formatting and visual layout editing. The authors assume full responsibility for the content and the materials selected and processed for publication.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

References

Agrawal, A., and Zhang, X. (2021). The evolution of coevolution in the study of species interactions. *Evolution* 75, 1594–1606. doi: 10.1111/evo.14293

Aguirrebengoa, M., Müller, C., Hambäck, P., and González-Megías, A. (2023). Density-dependent effects of simultaneous root and floral herbivory on plant fitness and defense. *Plants* 12, 283. doi: 10.3390/plants12020283

Aguirrebengoa, M., Müller, C., Hambäck, P., and González-Megías, A. (2025). Detritivore-driven seed viability gains offset seed loss from florivores in a semiarid herb. *Plant Soil* 524, 229–243. doi: 10.1007/s11104-025-07939-w

Ali, J., Tonğa, A., Islam, T., Mir, S., Mukarram, M., Konôpková, A., et al. (2024). Defense strategies and associated phytohormonal regulation in *Brassica* plants in response to chewing and sap-sucking insects. *Front. Plant Sci.* 15, 1376917. doi: 10.3389/fpls.2024.1376917

Alonso, C., Ramos-Cruz, D., and Becker, C. (2018). The role of plant epigenetics in biotic interactions. *New Phytol.* 221, 731–737. doi: 10.1111/nph.15408

Angulo, V., Beriot, N., Garcia-Hernandez, E., Li, E., Masteling, R., and Lau, J. A. (2022). Plant–microbe eco-evolutionary dynamics in a changing world. *New Phytol.* 234, 1919–1928. doi: 10.1111/nph.18015

Ashra, H., and Nair, S. (2022). Review: Trait plasticity during plant-insect interactions: From molecular mechanisms to impact on community dynamics. *Plant Sci.* 317, 111188. doi: 10.1016/j.plantsci.2022.111188

Aubert, S., Duchenne, F., Tinoco, B., Santander, T., Guevara, E. A., and Graham, C. H. (2025). Trait matching affects the probability of nectar robbing in plant–pollinator networks. *Oikos* 2026, e11552. doi: 10.1002/oik.11552

Azis, N., Kasim, M., Lawelle, S. A., Mansyur, A., Siang, R. D., and Piliana, W. O. (2025). The stock assessment of *Siganus* spp. in the seagrass ecosystem. *Aquacult. Aquarium Conserv. Legis.* 18, 2653–2664.

Beans, C. M., and Roach, D. (2015). An invasive plant alters phenotypic selection on the vegetative growth of a native congener. *Am. J. Bot.* 102, 217–224. doi: 10.3732/ajb.1400355

Bock, D. G., Caseys, C., Cousens, R., Hahn, M., Heredia, S. M., Hübner, S., et al. (2015). What we still don't know about invasion genetics. *Mol. Ecol.* 24, 2277–2297. doi: 10.1111/mec.13032

Bogdziewicz, M., Crone, E., and Zwolak, R. (2019). Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. *J. Ecol.* 108, 1009–1018. doi: 10.1111/1365-2745.13307

Bora, F. D., Rusu, T., Popescu, M., Petrescu-Mag, I. V., Păsărin, B., Dăescu, A. M., et al. (2025). Shade-tolerant plants and their adaptation to low-light environments. *Extreme Life. Biospeol. Astrobiol.* 17, 22–27.

Bordea, D., and Popescu, M. (2023). The impact of climate change on plant physiology and adaptation mechanisms. *Adv. Agric. Bot.* 15, 135–139.

Brehm, A., and Mortelliti, A. (2022). Small mammal personalities generate context dependence in the seed dispersal mutualism. *Proc. Natl. Acad. Sci. U.S.A.* 119, e2113870119. doi: 10.1073/pnas.2113870119

Briggs, S., and Anderson, J. (2025). The effect of global change on the expression and evolution of floral traits. *Ann. Bot.* 135, 9–24. doi: 10.1093/aob/mcae057

Byers, K. J. R. P., and Bradshaw, H. D. Jr. (2021). Rational design of a novel hawkmoth pollinator interaction in *Mimulus* section Erythranthe. *Front. Ecol. Evol.* 9, 658710. doi: 10.3389/fevo.2021.658710

CaraDonna, P., Burkle, L., Schwarz, B., Resasco, J., Knight, T., Benadi, G., et al. (2020). Seeing through the static: the temporal dimension of plant-animal mutualistic interactions. *Ecol. Lett.* 24, 149–161. doi: 10.1111/ele.13623

Case, S. B., Kawelo, K., Hoh, J., O'hearn, D., Sperry, J. H., Foster, J. T., et al. (2024). Effects of fruit novelty on feeding preference in four globally invasive frugivorous birds. *Biol. Invasions* 26, 4179–4198. doi: 10.1007/s10530-024-03436-w

Cha, Y.-P., Irwin, R. E., Wu, Y., Sha, S., and Zhang, Z. (2025). Soil moisture influences nectar robbing and plant fitness in a primrose species. *J. Ecol.* 113, 1807–1819. doi: 10.1111/1365-2745.70067

Chamberlain, S., and Holland, A. (2009). Quantitative synthesis of context dependency in ant-plant protection mutualisms. *Ecology* 90, 2384–2392. doi: 10.1890/08-1490.1

Chaparro-Pedraza, P. C., and Bank, C. (2025). Evolving life-history traits promote biodiversity via eco-evolutionary feedback mechanisms. *PloS Biol.* 23, e3003492. doi: 10.1371/journal.pbio.3003492

Charles, F., Reside, A., and Smith, A. (2025). The influence of changing fire regimes on specialized plant–animal interactions. *Philos. Trans. R. Soc. B. Biol. Sci.* 380, 20230448. doi: 10.1098/rstb.2023.0448

Cheptou, P. O. (2021). Pollination strategies in the face of pollinator decline. *Bot. Lett.* 168, 316–323. doi: 10.1080/23818107.2021.1884900

Clement, L., Köppen, S. C. W., Brand, W., and Heil, M. (2007). Strategies of a parasite of the ant–*Acacia* mutualism. *Behav. Ecol. Sociobiol.* 62, 953–962. doi: 10.1007/s00265-007-0520-1

Colautti, R., and Lau, J. A. (2015). Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. *Mol. Ecol.* 24, 1999–2017. doi: 10.1111/mec.13162

Colicchio, J. M. (2017). Transgenerational effects alter plant defense and resistance in nature. *J. Evol. Biol.* 30, 664–680. doi: 10.1111/jeb.13042

Connell, J. H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35, 131–138. doi: 10.2307/3544421

Coverdale, T. C. (2019). Defence emergence during early ontogeny reveals important differences between spines, thorns and prickles. *Ann. Bot.* 124, iii–iiv. doi: 10.1093/aob/mcz189

Cusumano, A., and Lievens, B. (2023). Microbe-mediated alterations in floral nectar: consequences for insect parasitoids. *Curr. Opin. Insect Sci.* 60, 101116. doi: 10.1016/j.cois.2023.101116

Daouda, B. B. B., Kouagou, M., Assédé, É., and Gaoue, O. (2025). Biotic pressure outweighs the influence of resource availability on physical defence investment in a tropical tree. *AoB Plants* 17, plaf027. doi: 10.1093/aobpla/plaf027

Del-Claro, K., and Torezan-Silingardi, H. M. (2021). "An evolutionary perspective on plant-animal interactions," in *Plant-Animal Interactions*. Eds. K. Del-Claro and H. M. Torezan-Silingardi (Springer, Cham). doi: 10.1007/978-3-030-66877-8_1

Deng, G., Dai, C., Song, Q., Zhang, Y., Zhang, X., Wang, X., et al. (2024). Disruption of pollination by herbivores is rescued by nectar yeasts. *J. Ecol.* 112, 1719–1730. doi: 10.1111/1365-2745.14358

Descamps, C., Quinet, M., Baijot, A., and Jacquemart, A. (2018). Temperature and water stress affect plant–pollinator interactions in *Borago officinalis* (Boraginaceae). *Ecol. Evol.* 8, 3443–3456. doi: 10.1002/ece3.3914

Descamps, C., Quinet, M., and Jacquemart, A. (2021). The effects of drought on plant–pollinator interactions: What to expect? *Environ. Exp. Bot.* 182, 104297. doi: 10.1016/j.envexpbot.2020.104297

De Vega, C., Álvarez-Pérez, S., Albaladejo, R., Steenhuisen, S., Lachance, M., Johnson, S., et al. (2021). The role of plant–pollinator interactions in structuring nectar microbial communities. *J. Ecol.* 109, 3379–3395. doi: 10.1111/1365-2745.13726

Duell, E., Baum, K. A., and Wilson, G. (2024). Drought reduces productivity and anti-herbivore defences, but not mycorrhizal associations, of perennial prairie forbs. *Plant Biol. J.* 26, 204–213. doi: 10.1111/plb.13604

Endara, M., Forrister, D. L., and Coley, P. D. (2023). The evolutionary ecology of plant chemical defenses: from molecules to communities. *Annu. Rev. Ecol. Evol. Syst.* 54, 107–127. doi: 10.1146/annurev-ecolsys-102221-045254

Eriksson, O. (2016). Evolution of angiosperm seed disperser mutualisms: the timing of origins and their consequences for coevolutionary interactions between angiosperms and frugivores. *Biol. Rev.* 91, 168–186. doi: 10.1111/brv.12164

Farooq, J., Cîmpean, A., and Petrescu-Mag, I. V. (2026). Plant–microbiome relations as a holobiont: critical perspectives from botany. *Adv. Environ. Sci.* 18, 83–92.

Fontaine, C., Guimarães, P., Kéfi, S., Loeuille, N., Memmott, J., Van Der Putten, W., et al. (2011). The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* 14, 1170–1181. doi: 10.1111/j.1461-0248.2011.01688.x

Fox, R., Donelson, J., Schunter, C., Ravasi, T., and Gaitán-Espitia, J. (2019). Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. *Philos. Trans. R. Soc Lond. B. Biol. Sci.* 374, 20180174. doi: 10.1098/rstb.2018.0174

Fuzessy, L., Silveira, F., Culot, L., Jordano, P., and Verdú, M. (2021). Phylogenetic congruence between Neotropical primates and plants is driven by frugivory. *Ecol. Lett.* 25, 320–329. doi: 10.22541/au.162203886.61175566/v1

Fuzessy, L., Verdú, M., and Pizo, M. (2025). Ecological function over evolutionary legacy: The limited role of shared evolutionary history in shaping modern frugivory interactions. *Funct. Ecol.* 39, 3688–3703. doi: 10.1111/1365-2435.70173

Gargiulo, R., Budde, K. B., and Heuertz, M. (2025). Mind the lag: understanding genetic extinction debt for conservation. *Trends Ecol. Evol.* 40, 228–237. doi: 10.1016/j.tree.2024.10.008

Gelmi-Candusso, T. A., and Hämäläinen, A. M. (2019). Seeds and the city: The interdependence of zoochory and ecosystem dynamics in urban environments. *Front. Ecol. Evol.* 7, 41. doi: 10.3389/fevo.2019.00041

Gleditsch, J. M., and Sperry, J. (2020). Ecomorphological relationships and invasion history of non-native terrestrial bird species on Oahu, Hawaii, suggest ecological fitting during novel community assembly. *Ecol. Evol.* 10, 12157–12169. doi: 10.1002/ece3.6843

Gómez, J., Schupp, E., and Jordano, P. (2018). Synzoochory: the ecological and evolutionary relevance of a dual interaction. *Biol. Rev.* 94, 874–902.

Gomulkiewicz, R., Thompson, J. N., Holt, R. D., Nuismer, S. L., and Hochberg, M. E. (2000). Hot spots, cold spots, and the geographic mosaic theory of coevolution. *Am. Nat.* 156, 156–174. doi: 10.2307/3079216

Gorden, N. S. L., and Adler, L. S. (2013). Abiotic conditions affect floral antagonists and mutualists of Impatiens capensis (Balsaminaceae). *Am. J. Bot.* 100, 679–689. doi: 10.3732/ajb.1200460

Graham, N., Krehenwinkel, H., Lim, J., Staniczenko, P., Callaghan, J., Andersen, J., et al. (2023). Ecological network structure in response to community assembly processes over evolutionary time. *Mol. Ecol.* 32, 6489–6506. doi: 10.1111/mec.16873

Green, A., Baltzinger, C., and Lovas-Kiss, Á. (2022). Plant dispersal syndromes are unreliable, especially for predicting zoochory and long-distance dispersal. *Oikos* 131, 1–11. doi: 10.1111/oik.08327

Guerrero, E. L., and Agnolín, F. L. (2026). *Phytolacca tetramera*, an ecological anachronism from the Pleistocene surviving in the Pampean Grasslands. *Diversity* 18, 303. doi: 10.3390/d18050303

Guimarães, P., Pires, M., Jordano, P., Bascompte, J., and Thompson, J. (2017). Indirect effects drive coevolution in mutualistic networks. *Nature* 550, 511–514. doi: 10.1038/nature24273

Heil, M., González-Teuber, M., Clement, L., Kautz, S., Verhaagh, M., and Bueno, J. (2009). Divergent investment strategies of *Acacia* myrmecophytes and the coexistence of mutualists and exploiters. *Proc. Natl. Acad. Sci.* 106, 18091–18096. doi: 10.1073/pnas.0904304106

Henry, L. P., Tokita, C. K., Misra, M., Forrow, A. B., and Rubenstein, D. (2018). Mutualistic acacia ants exhibit reduced aggression and more frequent off-tree movements near termite mounds. *Biotropica* 50, 559–562. doi: 10.1111/btp.12572

Herlon, M., Ridho, Z., Mustaqim, M., Andrina, H., Metananda, A. A., Masruri, N. W., et al. (2025). Analysis of factors influencing coastal community behavior in mangrove forest management in Riau Province, Indonesia. *Aquacult. Aquarium Conserv. Legis.* 18, 1719–1730.

Hoeksema, J. (2010). Ongoing coevolution in mycorrhizal interactions. *New Phytol.* 187, 286–300. doi: 10.1111/j.1469-8137.2010.03305.x

Hu, Y., Wang, X., Xu, Y., Yang, H., Tong, Z., Tian, R., et al. (2023). Molecular mechanisms of adaptive evolution in wild animals and plants. *Sci. China Life Sci.* 66, 453–495. doi: 10.1007/s11427-022-2233-x

Huitzil, S., and Huepe, C. (2024). Life's building blocks: the modular path to multiscale complexity. *Front. Syst. Biol.* 4, 1417800. doi: 10.3389/fsysb.2024.1417800

Ilyasov, R., Ilyasova, A., Danilenko, V., Kekeçoğlu, M., Slađan, R., Thaı, P., et al. (2025). Strategies and mechanisms of plant-microbiome-pollinator coadaptation. *Uludağ Arıcılık Dergisi* 25, 171–196. doi: 10.31467/uluaricilik.1675598

Janis, C. (2002). The ghosts of evolution: nonsensical fruit, missing partners, and other ecological anachronisms. *Q. Rev. Biol.* 77, 52–124. doi: 10.1086/343594

Janzen, D. (1966). Coevolution of mutualism between ants and acacias in Central America. *Evolution* 20, 249–275. doi: 10.1111/j.1558-5646.1966.tb03364.x

Janzen, D. (1975). *Pseudomyrmex nigropilosa*: a parasite of a mutualism. *Science* 188, 936–937. doi: 10.1126/science.188.4191.936

Johnson, M., Campbell, S., and Barrett, S. (2015). Evolutionary interactions between plant reproduction and defense against herbivores. *Annu. Rev. Ecol. Evol. Syst.* 46, 191–213. doi: 10.1146/annurev-ecolsys-112414-054215

Johnson, S., Waterman, J., Hartley, S. E., Cooke, J., Ryalls, J. M. W., Lagisz, M., et al. (2024). Plant silicon defences suppress herbivore performance, but mode of feeding is key. *Ecol. Lett.* 27, e14519. doi: 10.1111/ele.14519

Kamlasi, Y., Rejeki, S., Prayitno, S. B., Purwanti, F., Wijayanto, D., and Elfitasari, T. (2025). Socio-economic characteristics of seaweed farms on Semau Island, Kupang Regency, East Nusa Tenggara, Indonesia. *Aquacult. Aquarium Conserv. Legis.* 18, 2449–2457.

Katz, O. (2020). Silicon and plant–animal interactions: Towards an evolutionary framework. *Plants* 9, 430. doi: 10.3390/plants9040430

Keeler, A. M., Rose-Person, A., and Rafferty, N. E. (2021). From the ground up: Building predictions for how climate change will affect belowground mutualisms, floral traits, and bee behavior. *Clim. Change Ecol.* 1, 100013. doi: 10.1016/j.ecochg.2021.100013

Kooi, C., Vallejo-Marín, M., and Leonhardt, S. (2020). Mutualisms and (a)symmetry in plant–pollinator interactions. *Curr. Biol.* 31, R91–R99. doi: 10.1016/j.cub.2020.11.020

Kovács-Hostyánszki, A., Szigeti, V., Miholcsa, Z., Sándor, D., Soltész, Z., Török, E., et al. (2022). Threats and benefits of invasive alien plant species on pollinators. *Basic Appl. Ecol.* 64, 89–102. doi: 10.1016/j.baae.2022.07.003

Laitinen, R., and Nikoloski, Z. (2018). Genetic basis of plasticity in plants. *J. Exp. Bot.* 70, 739–745. doi: 10.1093/jxb/ery404

Li, P., An, Z., Xu, N., Li, J., Li, Q., and He, C. (2025). Phenotypic plasticity and stability in plants: Genetic mechanisms, environmental adaptation, evolutionary implications, and future directions. *Plant.* 48, 5847–5860. doi: 10.1111/pce.15566

Li, Z., Wei, J., Zhou, X., Tian, Q., He, W., and Cao, X. (2024). Dynamic restoration mechanism of plant community in the burned area of northeastern margin of Qinghai-Tibet Plateau. *Front. Plant Sci.* 15, 1368814. doi: 10.3389/fpls.2024.1368814

Li, H.-J., and Zhang, Z. (2007). Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus Armeniaca* (Rosaceae). *For. Ecol. Manage.* 242, 511–517. doi: 10.1016/j.foreco.2007.01.063

Lichtenberg, E. M., Irwin, R. E., and Bronstein, J. (2018). Costs and benefits of alternative food handling tactics help explain facultative exploitation of pollination mutualisms. *Ecology* 99, 1815–1824. doi: 10.1002/ecy.2395

Lomáscolo, S., Giannini, N., Chacoff, N., Castro-Urgal, R., and Vázquez, D. (2019). Inferring coevolution in a plant-pollinator network. *Oikos* 128, 775–789.

Losapio, G., Montesinos-Navarro, A., and Saiz, H. (2019). Perspectives for ecological networks in plant ecology. *Plant Ecol. Divers.* 12, 102–187. doi: 10.1080/17550874.2019.1626509

Marin, P., Genitoni, J., Barloy, D., Maury, S., Gibert, P., Ghalambor, C., et al. (2019). Biological invasion: The influence of the hidden side of the (epi)genome. *Funct. Ecol.* 34, 385–400. doi: 10.1111/1365-2435.13317

Martin, V., Schaeffer, R., and Fukami, T. (2022). Potential effects of nectar microbes on pollinator health. *Philos. Trans. R. Soc B.* 377, 20210155. doi: 10.1098/rstb.2021.0155

McCall, A., and Irwin, R. E. (2006). Florivory: the intersection of pollination and herbivory. *Ecol. Lett.* 9, 1351–1365. doi: 10.1111/j.1461-0248.2006.00975.x

Medeiros, L. P., Garcia, G., Thompson, J. N., and Guimaraes, J. P. Jr. (2018). The geographic mosaic of coevolution in mutualistic networks. *Proc. Natl. Acad. Sci. U.S.A.* 115, 12017–12022. doi: 10.1073/pnas.1809088115

Mertens, D., De Bobadilla, M. F., Rusman, Q., Bloem, J., Douma, J., and Poelman, E. (2021). Plant defence to sequential attack is adapted to prevalent herbivores. *Nat. Plants* 7, 1347–1353. doi: 10.1038/s41477-021-00999-7

Mezzomo, P., Weinhold, A., Aurová, K., Jorge, L., Kozel, P., Michálek, J., et al. (2023). Leaf volatile and nonvolatile metabolites show different levels of specificity in response to herbivory. *Ecol. Evol.* 13, e10123. doi: 10.1002/ece3.10123

Molina, J. R. H., Bersaldo, M. J. I., and Roquero, D. D. (2026). Influence of human pressure and environment variables to seagrass community in Sarangani, Davao Oriental, Philippines. *Aquacult. Aquarium Conserv. Legis.* 19, 87–99.

Napier, J., Heckman, R., and Juenger, T. (2022). Gene-by-environment interactions in plants: molecular mechanisms, environmental drivers, and adaptive plasticity. *Plant Cell* 35, 109–124. doi: 10.1093/plcell/koac322

Nascimento, L., Guimarães, P., Onstein, R., Kissling, W., and Pires, M. (2020). Associated evolution of fruit size, fruit colour and spines in Neotropical palms. *J. Evol. Biol.* 33, 858–868. doi: 10.1111/jeb.13619

O'Dea, R., Noble, D., Johnson, S. L., Hesselson, D., and Nakagawa, S. (2016). The role of non-genetic inheritance in evolutionary rescue: epigenetic buffering, heritable bet hedging and epigenetic traps. *Environ. Epigenet.* 2, dvv014. doi: 10.1093/eep/dvv014

Oroian, C., Balint, C., Popescu, M., Bora, F. D., Petrescu-Mag, I. V., Rusu, T., et al. (2025). Evolutionary compatibility in lichen symbiosis. *Extreme Life. Biospeol. Astrobiol.* 17, 41–47.

Oroian, I. G., Petrescu-Mag, I. V., and Gavriloaie, C. (2014). Some brief considerations regarding the invasive potential of the wild populations of *Sus scrofa ferus* and *Sus scrofa domesticus* outside their native range. *Porc. Res.* 4, 23–29.

Pandey, P., Petrescu-Mag, I. V., and Farooq, J. (2026). Phenotypic plasticity vs. genetic adaptation in plants under rapid climate change. *Adv. Environ. Sci.* 18, 49–57.

Păpuc, T., and Bora, F. D. (2023). The role of mycorrhizal associations in plant health and soil ecology. *Adv. Agric. Bot.* 15, 140–143.

Păpuc, T., and Petrescu-Mag, R. M. (2023). Ten of the most notorious invasive plant species around the world. *Adv. Agric. Bot.* 15, 55–64.

Păpuc, T., Popescu, M., and Coroian, C.-O. (2025). Parallel evolution of behavioral, life-history, and sexual traits in guppies, *Poecilia reticulata* Peters 1859, under variable predation regimes. *Poec. Res.* 15, 4–7.

Păsărin, B., Oroian, I., Rusu, T., Braşovean, I., Bora, F. D., Păpuc, T., et al. (2025). Coevolution of mushroom toxicity and animal consumer behavior. *Adv. Agric. Bot.* 17, 16–23.

Petrescu-Mag, I. V. (2023a). Beyond beauty: The evolutionary perspective on aesthetics. *Anim. Biol. Anim. Husb.* 15, 84–85.

Petrescu-Mag, I. V. (2023b). *Trebouxia* - a key player in the formation of many different lichen species. *Adv. Environ. Sci.* 15, 47–49.

Petrescu-Mag, I. V. (2025). Sexual selection in animals: pigment-based signaling and eco evolutionary trade-offs. *Stud. Univ. Vasile Goldis Arad Ser. Stiint. Vietii* 35, 106–116.

Petrescu-Mag, I. V., Bora, F. D., Popescu, M., Bordea, D., Papuc, T., Oroian, C., et al. (2024). Mechanisms and milestones in the evolution of flowering plants. *Adv. Agric. Bot.* 16, 74–83.

Petrescu-Mag, I. V., and Gavriloaie, C. (2019). The invasion mediated by aquarium hobbyists in the case of water lettuce, *Pistia stratiotes*. *Adv. Agric. Bot.* 11, 144–147.

Petrescu-Mag, I. V., Lozinsky, L. R., Csep, L., and Petrescu-Mag, R. M. (2008). Vegetation and predators mediate color pattern frequencies in *Poecilia sphenops* Valenciennes. *Aquacult. Aquarium Conserv. Legis.* 1, 51–61.

Pinasang, D. R. Y., Mantiri, D. M. H., Lumingas, L. J. L., Rumengan, A. P., Kalesaran, O. J., Pangemanan, J. F., et al. (2025). Mangrove community structure in Blongko, Kapitu and Sondaken Villages, South Minahasa Regency, Indonesia. *Aquacult. Aquarium Conserv. Legis.* 18, 2002–2013.

Popescu, M., and Tripathi, S. N. (2026). Evolution of plant water-use strategies from isohydry to anisohydry: an eco-physiological and evolutionary perspective. *Adv. Environ. Sci.* 18, 58–66.

Pricop, E., and Negrea, B.-M. (2018). Considerations concerning the distribution and impact of the most infamous invasive plant species from Bistrita River Basin (Neamt and Suceava Counties, Romania). *Adv. Agric. Bot.* 10, 40–56.

Proorocu, M., and Kovacs, E. (2023). The evolutionary explanation of the tendency of plants to enclose the seed in the fruit. *Adv. Agric. Bot.* 15, 37–39.

Quevedo-Caraballo, S., and Álvarez-Pérez, S. (2025). The role of phenotypic plasticity and within-environment trait variability in the assembly of the nectar microbiome and plant–microbe–animal interactions. *Ecol. Evol.* 15, e71059. doi: 10.1002/ece3.71059

Quevedo-Caraballo, S., De Vega, C., Lievens, B., Fukami, T., and Álvarez-Pérez, S. (2024). Tiny but mighty? Overview of a decade of research on nectar bacteria. *New Phytol.* 245, 1897–1910. doi: 10.1111/nph.20369

Ramos, S., and Schiestl, F. (2020). Herbivory and pollination impact on the evolution of herbivore-induced plasticity in defense and floral traits. *Evol. Lett.* 4, 556–569. doi: 10.1002/evl3.200

Rehling, F., Jaroszewicz, B., Braasch, L. V., Albrecht, J., Jordano, P., Schlautmann, J., et al. (2021). Within-species trait variation can lead to size limitations in seed dispersal of small-fruited plants. *Front. Ecol. Evol.* 9, 698885. doi: 10.3389/fevo.2021.698885

Rering, C., Beck, J., Hall, G., McCartney, M., and Vannette, R. (2018). Nectar-inhabiting microorganisms influence nectar volatile composition and attractiveness to a generalist pollinator. *New Phytol.* 220, 750–759. doi: 10.1111/nph.14809

Rumengan, A. P., Angmalisang, P. A., Angkouw, E., Mandiangan, E. S., Lasabuda, R., and Paruntu, C. P. (2025). Ecological suitability and tourism carrying capacity of mangrove ecosystems for sustainable ecotourism development: a case study in Budo village, North Sulawesi. *Aquacult. Aquarium Conserv. Legis.* 18, 3002–3013.

Russell, K., and McFrederick, Q. (2022). Floral nectar microbial communities exhibit seasonal shifts associated with extreme heat: Potential implications for climate change and plant-pollinator interactions. *Front. Microbiol.* 13, 931291. doi: 10.3389/fmicb.2022.931291

Schneider, H. (2022). Characterization, costs, cues and future perspectives of phenotypic plasticity. *Ann. Bot.* 130, 131–148. doi: 10.1093/aob/mcac087

Segar, S., Fayle, T., Srivastava, D., Lewinsohn, T., Lewis, O., Novotný, V., et al. (2020). The role of evolution in shaping ecological networks. *Trends Ecol. Evol.* 35, 454–466. doi: 10.1016/j.tree.2020.01.004

Smith, A. L., Hodkinson, T., Villellas, J., Catford, J., Csergő, A., Blomberg, S., et al. (2020). Global gene flow releases invasive plants from environmental constraints on genetic diversity. *Proc. Natl. Acad. Sci. U.S.A.* 117, 4218–4227. doi: 10.1073/pnas.1915848117

Solís-Montero, L., and Vallejo-Marín, M. (2017). Does the morphological fit between flowers and pollinators affect pollen deposition? An experimental test in a buzz-pollinated species with anther dimorphism. *Ecol. Evol.* 7, 2706–2715. doi: 10.1002/ece3.2897

Stotz, G., Gianoli, E., and Cahill, J. (2016). Spatial pattern of invasion and the evolutionary responses of native plant species. *Evol. Appl.* 9, 939–951. doi: 10.1111/eva.12398

Strauss, S. Y., and Irwin, R. E. (2004). Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annu. Rev. Ecol. Evol. Syst.* 35, 435–466. doi: 10.1146/annurev.ecolsys.35.112202.130215

Sujatmiko, W., Karnaningroem, N., Santoso, I. B., and Aliah, R. S. (2025). An application of partial least squares-structural equation modeling (PLS-SEM) to analyze the factors contributing to the decline in *Kappaphycus alvarezii* (Doty) Doty ex P.C. Silva 1996 seaweed production in the Kepulauan Seribu, Indonesia. *Aquacult. Aquarium Conserv. Legis.* 18, 406–424.

Sun, Y., Silvestro, D., Mathes, G. H., van Der Heijden, M. G., and Müller-Schärer, H. (2025). Eco-evolutionary dynamics of plant–soil feedbacks explain the spread potential of a plant invader under climate warming and biocontrol herbivory. *Glob. Change Biol.* 31, e70110. doi: 10.1111/gcb.70110

Teixido, A., Fuzessy, L., Souza, C., Gomes, I., Kaminski, L., Oliveira, P., et al. (2022). Anthropogenic impacts on plant-animal mutualisms: A global synthesis for pollination and seed dispersal. *Biol. Conserv.* 266, 109461. doi: 10.1016/j.biocon.2022.109461

Thomann, M., Imbert, E., Devaux, C., and Cheptou, P. O. (2013). Flowering plants under global pollinator decline. *Trends Plant Sci.* 18, 353–359. doi: 10.1016/j.tplants.2013.04.002

Thompson, G., and Goggin, F. (2006). Transcriptomics and functional genomics of plant defence induction by phloem-feeding insects. *J. Exp. Bot.* 57, 755–766. doi: 10.1093/jxb/erj135

Traveset, A., Willson, M., and Sabag, C. (1998). Effect of nectar-robbing birds on fruit set of Fuchsia magellanica in Tierra Del Fuego: a disrupted mutualism. *Funct. Ecol.* 12, 459–464. doi: 10.1046/j.1365-2435.1998.00212.x

Tripathi, A., Traore, K., and Bănăţean-Dunea, I. (2026). Convergent evolution in plant adaptations to extreme environments. *Adv. Environ. Sci.* 18, 67–76.

Twayana, M., Girija, A. M., Mohan, V., and Shah, J. (2022). Phloem: At the center of action in plant defense against aphids. *J. Plant Physiol.* 273, 153695. doi: 10.1016/j.jplph.2022.153695

Vahsen, M. L., Kleiner, H. S., Kodak, H., Summers, J. L., Vahsen, W. L., Blum, M. J., et al. (2023). Complex eco-evolutionary responses of a foundational coastal marsh plant to global change. *New Phytol.* 240, 2121–2136. doi: 10.1111/nph.19117

Van Donk, N., Raynal, A., and Asin-Garcia, E. (2025). A *Pseudomonas fluorescens* AND-gate biosensor for protein expression at plant root proximity. *Front. Syst. Biol.* 5, 1620608. doi: 10.3389/fsysb.2025.1620608

Van Leeuwen, C. H. A., Villar, N., Mendoza Sagrera, I., Green, A. J., Bakker, E. S., Soons, M. B., et al. (2022). A seed dispersal effectiveness framework across the mutualism–antagonism continuum. *Oikos*, e09254. doi: 10.1111/oik.09254

Vannette, R. (2020). The floral microbiome: plant, pollinator, and microbial perspectives. *Annu. Rev. Ecol. Evol. Syst.* 51, 363–386. doi: 10.1146/annurev-ecolsys-011720-013401

Vázquez-González, C., Barbour, K. M., Lago-Núñez, B., Rodriguez-Garrido, B., Dean, L. S., Vicente-Díez, I., et al. (2025). Leaf-chewing but not sap-feeding herbivores create soil legacies that shape plant resistance through trait-mediated, guild-specific effects in Baccharis salicifolia. *Funct. Ecol.* 40, 486–500. doi: 10.1111/1365-2435.70208

Wagey, B. T., Paruntu, C. P., Tilaar, F. F., and Kepel, R. C. (2025). Study of the morphology and genetics of the seagrass *Halophila ovalis* in the Wallace Line coastal waters on the Minahasa Peninsula, Indonesia. *Aquacult. Aquarium Conserv. Legis.* 18, 2475–2487.

Wang, X., Kang, J., Wang, H., Wang, S., Tang, B., and Lu, J. (2023). Phenotypic plasticity plays an essential role in the confrontation between plants and herbivorous insects. *CABI Agric. Biosci.* 4, 58. doi: 10.1186/s43170-023-00201-2

War, A., Paulraj, M. G., Buhroo, A., Hussain, B., Ignacimuthu, S., and Sharma, H. (2012). Mechanisms of plant defense against insect herbivores. *Plant Signal. Behav.* 7, 1306–1320. doi: 10.4161/psb.21663

Whittall, J., and Carlson, M. (2009). Plant defense: a pre-adaptation for pollinator shifts. *New Phytol.* 182, 5–8. doi: 10.1111/j.1469-8137.2009.02796.x

Wickman, J., Koffel, T., and Klausmeier, C. (2023). A theoretical framework for trait-based eco-evolutionary dynamics: population structure, intraspecific variation, and community assembly. *Am. Nat.* 201, 501–522. doi: 10.1086/723406

Xu, Y., Qian, L., Sun, L., Sun, H., Arroyo, M., and Song, B. (2025). A global meta-analysis of floral longevity reveals widespread plasticity and ecological correlates. *New Phytol.* 248, 1542–1556. doi: 10.1111/nph.70501

Youngsteadt, E., and Keighron, M. C. (2023). Urban pollination ecology. *Annu. Rev. Ecol. Evol. Syst.* 54, 21–42. doi: 10.1146/annurev-ecolsys-102221-044616

Zhang, H., Cheng, J., Xiao, Z., and Zhang, Z. (2008). Effects of seed abundance on seed scatter-hoarding of Edward's rat (*Leopoldamys edwardsi* Muridae) at the individual level. *Oecologia* 158, 57–63. doi: 10.1007/s00442-008-1114-y

Zhang, H., Niu, H., Steele, M., Peng, L., He, H., Li, A., et al. (2024). Masting promotes transformation from predation to mutualism in an oak-weevil-rodent system. *Sci. China Life Sci.* 67, 1514–1524. doi: 10.1007/s11427-023-2517-1

Zhang, J., Wang, H., Xia, J., Sha, K., He, S., Dai, H., et al. (2022). Coevolutionary insights between promoters and transcription factors in the plant and animal kingdoms. *Zool. Res.* 43, 805–812. doi: 10.24272/j.issn.2095-8137.2022.111

Zhao, T., Wan, S., Li, S., and Feng, Z. (2024). Leaf mining induced chemical defense of a Late Triassic ginkgophyte plant. *New Phytol.* 245, 27–32. doi: 10.1111/nph.20154

Zwolak, R., Clement, D., Sih, A., and Schreiber, S. J. (2023). Granivore abundance shapes mutualism quality in plant-scatterhoarder interactions. *New Phytol.* 241, 1840–1850. doi: 10.1111/nph.19443