Don’t ask “when is it coevolution?” — ask “how?”

Jeremy B. Yoder[a,b,✉]

[a]Department of Biology, California State University Northridge; Northridge, CA 91330 USA

[b]ORCID 0000-0002-5630-0921

Coevolution has come to be widely understood as specific, simultaneous, reciprocal adaptation by pairs of interacting species. This strict-sense definition arose from a desire for conceptual clarity, but it has never reflected the much wider diversity of ways in which interacting species may shape each other’s evolution. As a result, much of the literature on the evolutionary consequences of species interactions pays homage to the strict-sense definition while addressing some other form of coevolution. This tension suggests we should re-frame the key question in coevolution research, from “when is it coevolution?” to, rather, “how is it coevolution?”. The result is not so much a definition of coevolution as a mission statement: We can describe how species coevolve by documenting the ways that each species shaped the other’s genetic diversity over a shared history of interaction. Making this change shifts our focus from identifying case studies for a single, narrowly defined process to describing the many ways — specific and diffuse, simultaneous and stepwise, adaptive and non-adaptive — in which species evolve together.

Keywords: coevolution, species interactions, escape-and-radiate, ecological opportunity, Geographic Mosaic Theory of Coevolution

Etymologically, “coevolution” simply means “evolving together”. The term can refer to processes at any level of biological organization from genes to clades (Dixit, 2024); but most of us who study the evolution of interacting species have come to define it rather narrowly. We typically say coevolution is the *reciprocal adaptation* of interacting species, and describe a process that is also *specific*, arising from the interaction of two species, and *simultaneous*, with each species adapting to the other continuously. This definition has shaped the literature on the evolution of species interactions ever since Janzen’s (1980) call for linguistic clarity (Clayton et al., 2016; Futuyma and Slatkin, 1983; Janz, 2011; Thompson, 1989).

Correspondence: jeremy.yoder@csun.edu

Our understanding of the ecology and evolution of species interactions has advanced substantially since 1980 — bearing out Janzen’s own belief in the vital importance of coevolution (Janzen, 1966, 1984). We have seen that species interactions shape community structure (Carlson et al., 2019; Jordano, 1987; Yoder et al., 2020) and diversity within and among populations of interacting species (Epstein et al., 2023; Hoang et al., 2024; Yoder et al., 2022). We have come to see that species interactions are a source of resilience, and a point of vulnerability, in biological communities’ responses to global change (Baker et al., 2004; Carlson et al., 2022; Schweiger et al., 2010). We have seen how species interactions shape genetic diversity in interacting populations (Epstein et al., 2023; Gómez and Buckling, 2011; Thrall et al., 2012). We have seen how they contribute to evolutionary radiations, convergence, and diversification (Agrawal et al., 2024; Haldane, 1949; McKenna et al., 2009; Vamosi and Vamosi, 2010). We have even traced their origins and effects through the fossil record (Azevedo-Schmidt et al., 2022; Bao et al., 2019).

Nevertheless, *specific, simultaneous, reciprocal adaptation* of interacting species remains challenging to document in nature, because it requires characterization of phenotype-fitness relationships in two species, as well as attribution of fitness effects to those species’ interaction (Janz, 2011; Week and Nuismer, 2019). Many textbook examples of species interactions — including yuccas and obligate-pollinating yucca moths (Smith and Leebens-Mack, 2024), shelled mollusks and their predators (e.g., Bijleveld et al. 2015), and frugivorous vertebrates and the plants whose seeds they disperse (Tiffney, 2004) — lack documentation of strict-sense reciprocal natural selection (Fig. 1). Even in one of the most charismatic species interactions, that of milkweeds (genus *Asclepias*) and monarch butterflies (*Danaus plexippus*), reciprocal selection was only recently demonstrated in full: selection on monarchs’ capacity to detoxify and sequester milkweeds’ defensive cardenolides was

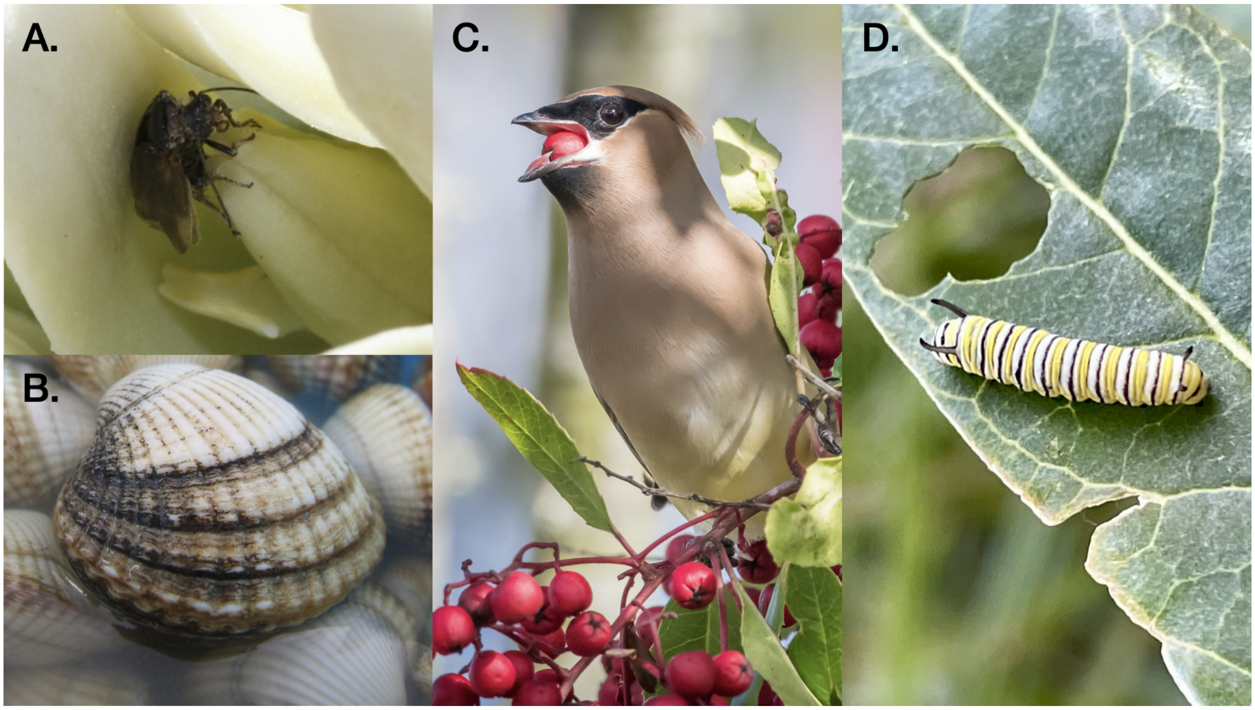

Fig. 1. Strict-sense coevolutionary selection has not been measured in many "textbook" species interactions, including (A) yuccas and obligate-pollinating yucca moths (*Tegeticula synthetica* on a flower of *Yucca brevifolia*), or (B) shelled mollusks (*Cerastoderma edule*) and their predators, or (C) vertebrate frugivores (*Bombycilla cedrorum*) and plants with colorful fruits (*Heteromeles arbutifolia*). In the flagship case of monarch butterflies and milkweeds (D, *Danaus plexippus* on *Asclepias curassavica*), selection on host plant defensive chemistry (Agrawal, 2005) was measured 16 years before selection on monarchs' detoxification and sequestration of those defensive compounds (Agrawal et al., 2021). (Image credits: A, Christopher I. Smith, by permission; B, Féron Benjamin via Wikimedia Commons, CC BY-SA 2.0; C, Becky Matsubara via Flickr, CC BY 2.0; D, the author.)

quantified in 2021, 16 years after quantification of selection on milkweeds' cardenolide production (Agrawal, 2005; Agrawal et al., 2021). Strict-sense coevolution of natural populations is, in fact, one of the rarest empirical results in studies of species interactions (Althoff et al., 2014; Carmona et al., 2015; Clayton et al., 2016; Hembry et al., 2014; Nuismer et al., 2022; Week and Nuismer, 2019).

So we have something of a paradox. Species interactions have unquestionably shaped the history of life on Earth, even — perhaps especially — interactions that have not been shown to meet the strict-sense definition of coevolution. This tension between adherence to a clear-cut but narrow definition of "coevolution" and our interest in describing how interacting species actually evolve together has been a theme in the literature on species interactions nearly from its origins (Brooks, 1979; Clayton et al., 2016; Futuyma and Slatkin, 1983; Janz, 2011). I propose that a solution lies in rethinking the key question in studies of species evolving together: not so much "when is it coevolution?" as Janzen (1980) asked, but "*how* is it coevolution?" That is, our task should not be to determine which species interactions have evolved under a single restrictively defined process, but to describe the many ways — adaptive and non-adaptive, pairwise and diffuse, simultaneous and stepwise — in which interacting species shape each other's history (Fig. 2; Clayton et al. 2016; Janz 2011). Reframing the study of species interactions and their evolutionary consequences to ask "how is it coevolution?" is a more fruitful choice, and it is a better description of the state of our field. Biologists have in fact learned a great deal about how living things evolve together since Janzen proposed his definition (1980), without adhering to the standard that emerged after that proposal.

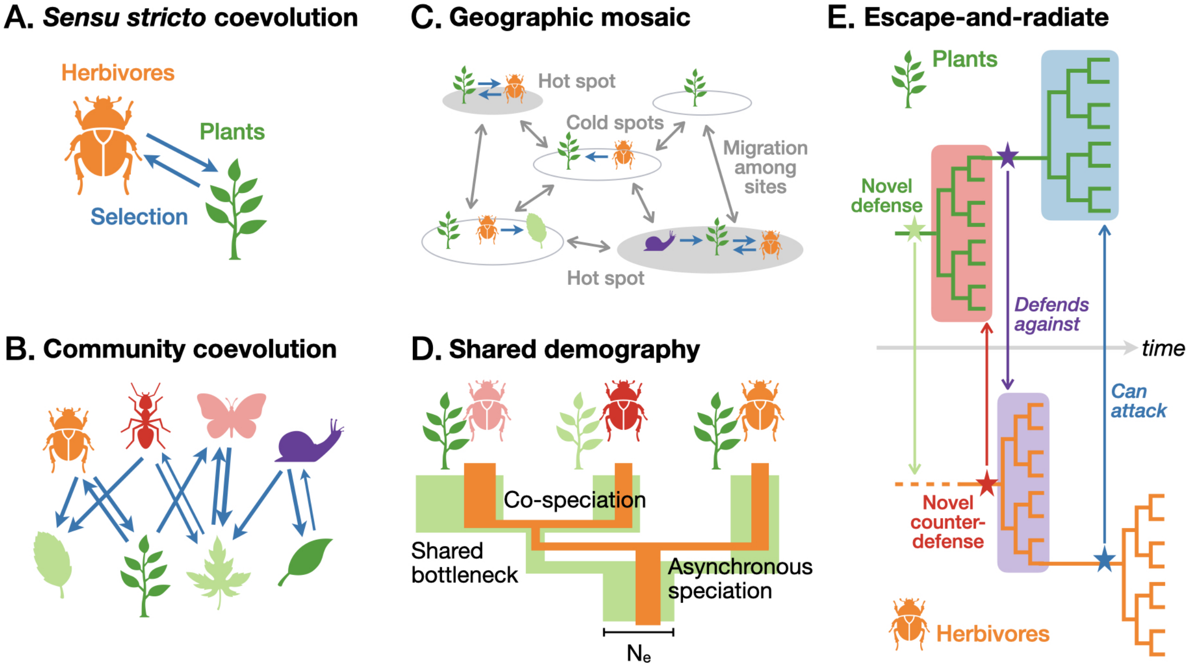

Fig. 2. Well-described ways in which organisms may evolve together, illustrated via plant-herbivore interactions, with arrows indicating natural selection exerted by one species on another: (A) *Sensu stricto* specific, simultaneous, reciprocal adaptation; (B) community, or "diffuse" coevolution; (C) coevolution on a geographic mosaic of spatially varying populations; (D) effects of shared demography and vicariance for intimately associated lineages; (E) escape-and-radiate patterns over macroevolutionary time.

On the origins and uses of a definition

The first published usage of "coevolution" is likely Mode's 1958 paper presenting a model of frequency-dependent selection created by the interactions of plants and fungal pathogens (Thompson, 1989). Mode does not define the term, perhaps because it is clear from context: the host and pathogen evolve specifically in response to each other; that evolution is driven by adaptation to resist infection, or to overcome that resistance; and change in the frequency of resistance or infectivity alleles in one species immediately feeds back to alter selection acting on infectivity or resistance alleles in the other (Mode, 1958).

The term and the process were not inextricably linked from the start, however. Three years after Mode (1958), Pimentel (1961) published a model of a "genetic feedback mechanism" between the population dynamics of a victim species and its antagonist. Pimentel (1961) describes a process of specific, simultaneous, reciprocal adaptation by interacting species, but never uses the term "coevolution", with or without the hyphen. He does not cite Mode (1958), which may explain the omission of the term.

Three years further on, Ehrlich and Raven (1964) explicitly applied "coevolution" to a macroevolutionary process that we now call "escape-and-radiate" (Thompson, 1989). In their model, a plant lineage evolves a new defense trait to "escape" herbivory and "radiates" into a clade of daughter species carrying the new defense; until an herbivore species evolves a counter-defense and, in its turn, radiates into a clade of species feeding on the recently diversified plant resource (Fig. 2E). Adaptation occurs at all stages of escape-and-radiate, but it otherwise differs substantially from what Mode (1958) or Pimentel (1961) described. Plants can escape whether or not they exert selection on attacking herbivores, because herbivory in general creates selection favoring a novel defense. Similarly, the later radiation of herbivores need not exert specific selection on individual host plants — they may simply adapt to the diversity of hosts they can attack with their new counter-defense.

Reading these works with an eye to the early usage of "coevolution" is clarifying. Pimentel (1961) shows that we can think coherently about specific, simultaneous, reciprocal adaptation without giving it a special name. Ehrlich and Raven (1964), on the other hand, demonstrate that species interactions can shape biodiversity in ways well beyond specific, simultaneous, reciprocal adaptation.

What Janzen (1980) did, and did not, ask

Janzen (1980) effectively ended this period of flexible terminology. However, criteria we now often associate with this article are not necessarily found within it. It opens with a proposed definition:

> 'Coevolution' may be usefully defined as an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first.

This establishes the criteria of *specificity*, that coevolution is the result of population-level interactions between two species, and *reciprocity*, that change in one species causes change in the other. Janzen also mentions "selective pressure" in defining "diffuse coevolution", indicating an interest in *adaptation*. However, he does not require *simultaneity*. He objects to Ehrlich and Raven's (1964) application of "coevolution" to describe the very non-simultaneous process of escape-and-radiate — but primarily because the interactions driving escape-and-radiate are diffuse, lacking specificity. The rest of the piece describes usages of "coevolution" Janzen considers inappropriate, which preview a concern he would later explain in greater detail: that interactions observed in the present day may often be the result of "ecological fitting", in which species that do not share extended histories of interaction end up interacting in the course of community assembly, simply because their traits are already compatible when they first encounter each other (Janzen, *pers. comm*; Janzen 1985). That is, Janzen was most concerned with whether or not putatively coevolved species had evolved together *over an extended history of interaction*.

The lack of a requirement for simultaneous change is also evident in Janzen's larger body of work. Most notably, he described the ant-aphid defense mutualism as coevolved both before and after the 1980 essay (c.f., Janzen 1966, 1984). Janzen's major work in this system pre-dates modern approaches for quantifying natural selection in the wild (Lande, 1977; Lande and Arnold, 1983), so much of his inference that ants and acacias have coevolved relies not on a population perspective, but a phylogenetic one. Janzen (1966) observed that traits supporting the mutualism, such as host plants' food-producing structures and domatia, or ants' behaviors that facilitate host defense, are derived, and likely appeared after the origin of the interaction. Ants' and acacias' traits could have been acquired in a series of innovations as a single lineage of ants and a single lineage of acacias became better and better adapted to their mutualism — but the mutualism-supporting traits could also have been acquired as ants and acacias swapped their associations between better and better partner species. Janzen (1966) hints at that scenario, hypothesizing that once one ant-acacia pair starts down the road to mutualism, other co-occurring acacia species would benefit from adapting to host ants themselves.

A *sensu* too *stricto* for the real world?

Coevolution fully defined as specific, simultaneous, reciprocal adaptation may not emerge from Janzen (1980), but it does appear in the literature soon after. When it does, it is frequently accompanied by veiled (or overt) complaints about the restrictiveness of that definition, and a pivot to discussing the evolution of species interactions that do not fit its constraints. A prominent example is in the introductory chapter to the 1983 book *Coevolution* (Futuyma and Slatkin, 1983): the editors cite Janzen (1980) as giving a "restrictive" definition, but also note that simultaneity would be "still more restrictive". They then explain that the book will contain multiple considerations of evolutionary processes in species interactions that do not meet those restrictive criteria. As a result the chapter, and the book that follows, have something of a double consciousness. Futuyma and Slatkin assert that we must narrowly circumscribe what we consider as coevolution to focus the field — writing that "Coevolution, too broadly defined, becomes equivalent to evolution" — but almost in the same sentence they note the broad ecological and evolutionary importance of species interactions and the need to consider perspectives beyond the strict-sense definition.

This two-step is repeated to this day, with authors first citing Janzen (1980) for a *sensu stricto* definition of coevolution, then admitting they do not have evidence meeting its criteria for the species interaction they study — but nevertheless presenting data or observations to describe how those interacting species have evolved as a result of their interaction. Examples turn up in studies of interactions from those between primates and the plants whose fruit they disperse (Regan et al., 2001) to mammals and the bacteria inhabiting their guts (Groussin et al., 2020), among others (Clayton et al., 2016; Janz, 2011; Smith and Leebens-Mack, 2024). This is due in no small part to the challenge of tracking or quantifying natural selection in multiple species, especially outside the laboratory (Week and Nuismer, 2019). Decades after Janzen (1980), evolutionary biologists have certainly documented specific, simultaneous, reciprocal selection and adaptation (Benkman et al., 2003; Clayton et al., 1999; Gómez and Buckling, 2011), but among studies of wild populations these remain more the exception than the rule (Carmona et al., 2015).

Experimental demonstrations of *sensu stricto* coevolution have been more successful (Brockhurst and Koskella, 2013; Chevallereau et al., 2022). Specific, simultaneous, reciprocal adaptation has been directly observed in a diverse array of tractable systems, including bacteria and phage (reviewed by Koskella and Brockhurst 2014), ciliates and bacterial prey (Cairns et al., 2020), yeast lines engineered into resource-exchange mutualisms (Vidal et al., 2025), and even invertebrates (Kerstes et al., 2012; King et al., 2016; Koskella and Lively, 2007; Schulte et al., 2010). Experimental studies have revealed coevolutionary dynamics in different kinds of interaction (Blazanin et al., 2024; Vidal et al., 2025), how coevolution contributes to the maintenance of sex and recombination (Kerstes et al., 2012; Morran et al., 2011), how coevolution can drive divergence among populations (Forde et al., 2008; Marston et al., 2012), and how pairwise coevolutionary dynamics depend on co-occurring species (Blazanin and Turner, 2021). However, this success is something of an exception that proves the rule. Many of the difficulties of quantifying reciprocal selection in wild populations of macrofauna also apply to work in wild populations of species that are amenable to experimental evolution in the laboratory (Chevallereau et al. 2022; Koskella and Brockhurst 2014; but see, e.g., Gómez and Buckling 2011).

Indirect evidence for *sensu stricto* coevolution

We can also draw on less direct approaches than measurements of selection to infer that specific, simultaneous, reciprocal adaptation is occurring in natural populations. These approaches are not complete solutions, however. First, many studies have tested for a predicted outcome of *sensu stricto* coevolution, local adaptation of interacting species to each other (e.g., Ballabeni and Ward 1993; Douda et al. 2017; Gross et al. 2023; Hanks and Denno 1994; Piel et al. 2022; reviewed by Biere and Verhoeven 2008; Briscoe Runquist et al. 2020; Hoeksema and Forde 2008; Kaltz and Shykoff 1998). The link between strict-sense coevolution and local adaptation is modified by gene flow, selection strength, and ecological context (Gandon, 2002; Gandon and Michalakis, 2002; Gomulkiewicz et al., 2007; Kaltz and Shykoff, 1998). This means local adaptation can occur in the absence of strict-sense coevolution, and strict-sense coevolution need not lead to detectable local adaptation (Gandon and Michalakis, 2002; Gomulkiewicz et al., 2007; Nuismer, 2017; Nuismer and Gandon, 2008). Thus, local adaptation can provide evidence that two species have coevolved, but it is not conclusive. Time-shifting experimental designs can give more definitive answers by (for instance) assaying hosts' fitness in interaction with parasite isolates from the contemporary population and from previous generations. However this effectively ends up tracking host and parasite adaptation directly, and is so is not necessarily less challenging (Gaba and Ebert, 2009; Thrall et al., 2012).

The second indirect option lies in the genetic variation of interacting species, which allows either testing for changes in the frequency of alleles at loci that mediate the interaction (Thrall et al., 2012), or testing for population genetic and genomic patterns indicating recent adaptive evolution at those loci (Amandine et al., 2022; Ebert and Fields, 2020; Yoder, 2016). Population genomic approaches have characterized strict-sense coevolutionary selection in host-pathogen interactions (Duxbury et al., 2019; Piel et al., 2022), plant-pollinator (Zhang et al., 2020) and resource-exchange (Epstein et al., 2023; Wilson and Duncan, 2015) mutualisms. However, genomic approaches can be limited by the need for prior knowledge of loci that mediate the interaction of two species. Methods exist to identify those coevolving loci from genomic data, but these arguably require some prior sense that the species under consideration experience coevolutionary selection (Amandine et al., 2022; Ebert and Fields, 2020; MacPherson et al., 2018). Genomic approaches also face the same basic logistic challenge presented to studies measuring reciprocal selection — collecting data for not one but two species. Many studies of adaptation at loci mediating species interactions focus on one side of an interaction, (e.g., Obbard et al. 2009; Treindl et al. 2024), treating the other as a diffuse source of selection pressure — for instance, the vertebrate major histocompatibility complex loci coevolving with pathogens in general (Radwan et al., 2020).

The geographic mosaic theory of coevolution advanced by Thompson (2005) is in some respects a different kind of attempt to rescue the field from the need to quantify specific, simultaneous, reciprocal adaptation before species can be said to be coevolving (Janz, 2011). Across the spatially structured landscape of a geographic mosaic, two interacting species may experience *sensu stricto* coevolution in only some locations, as a result of varying environmental or community context (Fig. 2C; Thompson 2005). Thompson taxonomized "concepts of coevolution" on multiple occasions (Thompson, 1989, 2005), identifying Janzen's (1980) definition as the strictest option in a larger diversity of processes. At the same time, the geographic mosaic theory still gives pride of place to specific, simultaneous, reciprocal adaptation, describing "selection mosaics" created by geographically dispersed "hot spots" with measurable reciprocal adaptation and "cold spots" without it (Thompson, 2005). Non-adaptive processes of genetic drift and migration feature in the geography of selection mosaics, but they are supporting players to the dynamics of reciprocal adaptation. Then, too, the logistic challenges of describing a selection mosaic are often more, not less, than those of measuring selection acting on two species in a single location (Gomulkiewicz et al., 2007; Week and Nuismer, 2019).

Considering coevolution *sensu lato*

Even apart from the difficulties of finding *sensu stricto* coevolution in the wild, many research questions about the role of species interactions in evolutionary history can be addressed without first meeting the *sensu stricto* definition. These range from descriptions of patterns in ecological associations shaped by species' traits (Carlson et al., 2019; Jordano, 1987; Yoder et al., 2020) to Ehrlich and Raven themselves (1964) and descendant studies of diversification in interacting lineages and clades (Clayton et al., 2016; Hayward et al., 2021; McKenna et al., 2009), to studies of local adaptation to interacting species (Briscoe Runquist et al., 2020; Hargreaves et al., 2020) and population genomic patterns arising from important interactions (Obbard et al., 2009). The extent of work along these lines suggests evolutionary biologists have already been studying coevolution *sensu lato*, without perhaps explicitly declaring it. This thought may make it less daunting to envision coevolution mediated by the full range of evolutionary processes. Indeed it is already possible to identify several categories of processes that may link the evolution of different species — and even without holding to the strictest sense of "coevolution", it remains possible to identify cases in which we can say species are *not* evolving together.

The strict-sense definition provides a useful starting point for a broader vision of coevolution. If we want to delineate the range of processes by which interacting species could influence each other's evolution, we can start by considering what we find when we relax the constraints of specific, simultaneous, reciprocal adaptation, individually or in concert (Table 1). Doing so rapidly identifies concepts of coevolution enumerated over the decades (Brooks, 1979; Clayton et al., 2016; Janz, 2011; Thompson, 1989, 2005) — and it helps to organize the relationships among these different ways species may evolve together. Diffuse coevolution and escape-and-radiate processes suggest what we might find beyond specificity and simultaneity, and considering nonadaptive processes is not much more challenging (Bubrig and Gibson, 2025; Papkou et al., 2016). In contrast to some of these prior considerations (e.g., Janz 2011), however, I would argue that reciprocity is the one element of the strict-sense definition that ties together all possible coherent senses of "coevolution". If there is no feedback at all, adaptive or otherwise, between one lineage's evolution and that of another, how can the two lineages be said to be evolving together? Holding on to reciprocity also aligns with Janzen's (1980; 1985) thinking, that the essence of coevolution is a shared history of interaction.

Evolving together through specific, simultaneous, reciprocal adaptation. Species interactions may, and do, create the specific, simultaneous, reciprocal adaptation envisioned since Janzen (1980), and determining how often specific, simultaneous, reciprocal adaptation plays a role in species' evolution together remains an interesting question. The challenges of rigorously characterizing selection acting on two species, or tracking reciprocal adaptive change, mean that studies presenting such results will undoubtedly continue to be highly interesting to evolutionary biologists. Moreover, strict-sense coevolution may contribute to more complex processes: within broader communities (Fig. 2B; Crutsinger 2016), on geographic mosaics (Fig. 2C; Gomulkiewicz et al. 2000; Thompson 2005), and as one cause of escape-and-radiate and co-speciation processes (Fig. 2D, E; Althoff et al. 2014; Ehrlich and Raven 1964; Hembry et al. 2014). Methods for demonstrating that two species experience reciprocal natural selection have been a longstanding focus of coevolution studies (e.g., Brodie and Ridenhour 2003), with new approaches continuing to emerge (Week and Nuismer, 2019).

Evolving together in communities and across geographic mosaics. Species interactions occur in larger biological communities (Fig. 2B), and they may vary across geographically diverse landscapes, influencing partner species' evolution without creating consistent reciprocal selection (Fig. 2C; Gomulkiewicz et al. 2000; Thompson 2005). The great insight of the geographic mosaic theory of coevolution is that interacting species rarely, if ever, occupy fully identical geographic ranges, or experience environmental variation in perfect parallel. This variation in interacting species' ecological experience creates variation in the selection arising from their interaction, and thereby selection mosaics. Local adaptation to that variation can tip populations onto differing evolutionary trajectories, and towards speciation (Thompson, 2013; Yoder et al., 2022). That variation can also dampen the longer-term effects of specific, reciprocal adaptation, if gene flow from "cold spots" swamps selection generated in "hot spots", or if additional interacting species exert conflicting selection (Benkman et al., 2003; Gross et al., 2023). Because of the multiple evolutionary processes involved, documenting selection mosaics is complex (Gomulkiewicz et al., 2007), but it may be increasingly facilitated by the accessibility of population genomic methods to document patterns of gene flow, isolation, and adaptive differentiation within interacting species.

Evolving together by shaping ecological opportunity. Interacting species may create or constrain ecological opportunity for each other without experiencing specific, simultaneous adaptation (Fig. 2E; Ehrlich and Raven 1964; Yoder et al. 2010). Antagonists in general can create selection favoring broadly effective defenses (Agrawal, 2007; Agrawal et al., 2009), such that the origin of new defenses opens enemy-free space for their victims; and the origin of new counter-defenses opens up new victims for the antagonists (McKenna et al., 2009). Mutualists can similarly provide resources or services that make otherwise unsuitable habitats accessible (Sprent, 2007; Sprent et al., 2017). If these effects are reciprocal across clades of interacting species, it seems reasonable to follow Ehrlich and Raven (1964) in saying that members of those clades are evolving together. Coevolution in this mode has likely been one of the grand engines driving the diversification of life — biodiversity on one side of a trophic or mutualistic interaction begetting biodiversity on the other side. Evidence for coevolution in this sense comes from phylogenetic and fossil studies, as much as from data on the evolutionary effects of extant species, to establish the relative timing of origin for lineages and clades of interacting species that may or may not exert specific reciprocal selection on each other (Geier et al., 2025; McKenna et al., 2009; Ramírez et al., 2011).

Evolving together without adaptation. Species interactions also influence the evolutionary process through other means than natural selection. Symbionts can experience the speciation of their hosts as a vicariance event (Blasco-Costa et al., 2021; Brooks, 1979; Hayward et al., 2021), and speciation by pollinators can create prezygotic reproductive isolation in the flowering plants they serve (Smith and Leebens-Mack, 2024). Interacting species may shape each other's demography even if they do not exert selection, especially pairwise selection, on each other (Fig. 2D; Papkou et al. 2016). Population densities, and therefore opportunities for mutation and adaptive evolution, should often be cor-

Table 1. Possible modes of coevolution, in terms of whether they are specific or diffuse, simultaneous or stepwise, and adaptive or nonadaptive, and published empirical examples or theoretical descriptions

Mode of coevolution	Specificity	Simultaneity	Adaptivity	Published example(s) or description(s)
Sensu stricto	Specific	Simultaneous	Adaptive	Zangerl and Berenbaum (1993, 2004); Benkman et al. (2003); Lyon and Eadie (2004)
Community coevolution	Diffuse	Simultaneous	Adaptive	Dal Grande et al. (2018)
Stepwise coadaptation	Specific	Stepwise	Adaptive	Janzen (1966); Pellmyr and Leebens-Mack (1999)
Escape-and-radiate	Mostly diffuse	Stepwise	Adaptive	Ehrlich and Raven (1964); McKenna et al. (2009)
Geographic mosaics	Mostly specific	Mostly simultaneous	Adaptive *and* nonadaptive	Hanifin et al. (2008); Toju et al. (2011); Gross et al. (2023)
Co-vicariance	Specific	Simultaneous	Nonadaptive	Light and Hafner (2008)
Co-cladogenesis	Mostly diffuse	Simultaneous *or* stepwise	Nonadaptive	Groussin et al. (2020)
Demographic feedbacks	Mostly specific	Simultaneous	Nonadaptive	Papkou et al. (2016) Bubrig and Gibson (2025)

related across trophic levels (Bubrig and Gibson, 2025), and processes of horizontal transmission can create bottlenecks at the point where symbionts establish infections in new hosts. Demonstrating coevolution *sensu lato* could therefore mean showing that one species has shaped the genetic diversity of another species via dispersing propagules of that species (Starr et al., 2013), or by limiting or facilitating its population growth (Azevedo-Schmidt et al., 2022). Often these processes are treated as subordinate to population genetic or phylogenetic signals of adaptive coevolution — for instance, the treatment of "phylogenetic hitchhiking" or "resource tracking" as a sort of null expectation from which to distinguish co-diversification driven by reciprocal adaptation (Althoff et al., 2014; Brooks, 1979; Hembry et al., 2014; Janz, 2011). However, if the interaction of two taxa creates natural selection on one and opportunities for vicariance in the other — as in symbionts or parasites and their hosts (Clayton et al., 2016; Groussin et al., 2020; Yoder et al., 2022) — it seems strange to say that they are not evolving together.

At the broadest level, incumbent taxa limit the resource base, and thereby diversification, of emerging competitors — for instance, as seen in Muroid rodents colonizing new continents, which diversified more slowly if another Muroid clade was already present (Schenk et al., 2013). The diversification of one clade could also facilitate the diversification of another, in a process we might call "co-cladogenesis". This would be distinct from escape-and-radiate inasmuch as it is the result of facilitation rather than a trophic relationship (Table 1). An example might be the oxygenation of Earth's atmosphere by photosynthetic cyanobacteria, which enabled the proliferation of aerobic nonphotosynthetic lineages (Lyons et al., 2021; Sessions et al., 2009). These may be rare events, and they certainly constitute the weakest coherent sense in which species may evolve together. At these scales of time and diversity, the reciprocity of evolutionary effects becomes truly tenuous.

Evolving, but not together. Have we now discussed such a wide array of processes linking the evolution of two species that it is no longer possible to identify when two lineages have *not* coevolved in some sense, as Futuyma and Slatkin (1983) feared? I think we have not. As noted above, there is one element of the *sensu stricto* definition that I do not propose to relax: reciprocity. Evolving together must by definition mean that evolution of one taxon or lineage influences the evolution of another taxon or lineage, and vice versa. The means of evolution may vary, as may the specificity of the feedback — between species, or between ecological guilds, or between clades. But if we cannot identify causal arrows that point in both directions, over a shared history of interaction, it seems straightforward to say we have not found coevolution, in any sense (Janzen, 1985).

For example, showing that a particular species of bee effectively transfers pollen of a particular species of clover in one time and place would not be sufficient to say the bee and the clover are coevolving, or have coevolved. The question would be, has pollination by this species of bee contributed to changes in the clover's genetic diversity over a generation or more? Reciprocal evolutionary change requires a shared history over which reciprocal changes can play out. The kinds of data described above for different senses of coevolution — measurement of phenotypic natural selection, estimates of selection inferred from population genomics, phylogenetic reconstruction of ancestral traits and historical associations — are necessary to define the form and temporal scope of coevolution, beyond the immediately observable "ecological fitting" that worried Janzen (1985).

Clear examples of non-coevolving species interactions under the *sensu lato* perspective include many cases identified as non-coevolving under *sensu stricto*, like commensalisms. Disease vector organisms such as mosquitoes or sap-feeding Hemiptera certainly provide an ecological opportunity for the parasites they transmit, but how their role as "flying syringes" impacts their own evolution is often unclear (Backus et al., 2015; Tabachnick, 1998). Similarly, domestic cats have undeniably adapted to close association with humans (Nilson et al., 2022), but it seems unlikely their presence — however welcome — has changed the evolutionary history of human populations.

Asking "how", rather than "when"

Janzen's (1980) letter well deserves its reputation for bringing precision and clarity to the emerging sub-field of coevolution studies. Arguably it helped to define that sub-field at a moment when it could, perhaps, have remained subsumed in evolutionary ecology, as one of a number of phenomena that shape variation and population dynamics over single-generation timescales. However, the strict-sense definition that has come to be associated with Janzen (1980) has never reflected the diversity of processes that evolutionary biologists find in our studies of species interactions, and does not reflect Janzen's own thinking.

A more commodious vision of coevolution, in the spirit of Janzen (1980), would focus on the question of *how* rather than *when*: *We can describe how species coevolve by documenting the ways that each species shaped the other's genetic diversity over a shared history of interaction*. The ways of coevolution may be specific or diffuse, simultaneous or stepwise, adaptive or non-adaptive, and documenting these different processes presents evolutionary biologists with widely varying challenges. Trading an understanding that *coevolution* is limited to specific, simultaneous, reciprocal adaptation for one in which we admit that species influence each other's evolution in a multitude of ways lets us focus on describing that broad array of possible coevolutionary processes. By asking "how is it coevolution?" we can turn to contemplate the full diversity of life's history at play in Darwin's "entangled bank".

Data availability

No original data were generated for this article.

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J.B.Y. conceived and wrote the article.

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References

Agrawal, A. A. 2005. Natural selection on common milkweed (*Asclepias syriaca*) by a community of specialized insect herbivores. Evolutionary Ecology Research 7:651–667.

———. 2007. Macroevolution of plant defense strategies. Trends in Ecology & Evolution 22:103–109.

Agrawal, A. A., K. Böröczky, M. Haribal, A. P. Hastings, R. A. White, R.-W. Jiang, and C. Duplais. 2021. Cardenolides, toxicity, and the costs of sequestration in the coevolutionary interaction between monarchs and milkweeds. Proceedings of the National Academy of Sciences 118:e2024463118.

Agrawal, A. A., A. P. Hastings, P. A. Lenhart, M. Blecher, C. Duplais, G. Petschenka, D. Hawlena, V. Wagschal, and S. Dobler. 2024. Convergence and divergence among herbivorous insects specialized on toxic plants: revealing syndromes among the cardenolide-feeders across the insect tree of life. The American Naturalist page 731277.

Agrawal, A. A., J.-P. Salminen, and M. Fishbein. 2009. Phylogenetic trends in phenolic metabolism of milkweeds (*Asclepias*): Evidence for escalation. Evolution 63:663–673.

Althoff, D. M., K. A. Segraves, and M. T. Johnson. 2014. Testing for coevolutionary diversification: linking pattern with process. Trends in Ecology & Evolution 29:82–89.

Amandine, C., D. Ebert, E. Stukenbrock, R. C. Rodríguez De La Vega, P. Tiffin, D. Croll, and A. Tellier. 2022. Unraveling coevolutionary dynamics using ecological genomics. Trends in Genetics 38:1003–1012.

Azevedo-Schmidt, L., E. K. Meineke, and E. D. Currano. 2022. Insect herbivory within modern forests is greater than fossil localities. Proceedings of the National Academy of Sciences 119:e2202852119.

Backus, E. A., H. J. Shugart, E. E. Rogers, J. K. Morgan, and R. Shatters. 2015. Direct Evidence of Egestion and Salivation of *Xylella fastidiosa* Suggests Sharpshooters Can Be “Flying Syringes”. Phytopathology® 105:608–620.

Baker, A. C., C. J. Starger, T. R. McClanahan, and P. W. Glynn. 2004. Corals' adaptive response to climate change. Nature 430:741–741.

Ballabeni, P., and P. I. Ward. 1993. Local Adaptation of the tremadote Diplostomum phoxini to the European minnow Phoxinus phoxinus, its second intermediate host. Functional Ecology 7:84.

Bao, T., B. Wang, J. Li, and D. Dilcher. 2019. Pollination of Cretaceous flowers. Proceedings of the National Academy of Sciences 116:24707–24711.

Benkman, C., T. Parchman, A. Favis, and A. Siepielski. 2003. Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. The American Naturalist 162:182–194.

Biere, A., and K. J. F. Verhoeven. 2008. Local adaptation and the consequences of being dislocated from coevolved enemies. New Phytologist 180:265–268.

Bijleveld, A. I., S. Twietmeyer, J. Piechocki, J. A. Van Gils, and T. Piersma. 2015. Natural selection by pulsed predation: survival of the thickest. Ecology 96:1943–1956.

Blasco-Costa, I., A. Hayward, R. Poulin, and J. A. Balbuena. 2021. Next-generation cophylogeny: unravelling eco-evolutionary processes. Trends in Ecology & Evolution 36:907–918.

Blazanin, M., J. Moore, S. Olsen, and M. Travisano. 2024. Fight not flight: Parasites drive the bacterial evolution of resistance, not escape. The American Naturalist pages 000–000.

Blazanin, M., and P. E. Turner. 2021. Community context matters for bacteria-phage ecology and evolution. The ISME Journal 15:3119–3128.

Briscoe Runquist, R. D., A. J. Gorton, J. B. Yoder, N. J. Deacon, J. J. Grossman, S. Kothari, M. P. Lyons, S. N. Sheth, P. Tiffin, and D. A. Moeller. 2020. Context dependence of local adaptation to abiotic and biotic environments: A quantitative and qualitative synthesis. The American Naturalist 195:412–431.

Brockhurst, M. A., and B. Koskella. 2013. Experimental coevolution of species interactions. Trends in Ecology & Evolution 28:367–375.

Brodie, E. D., and B. J. Ridenhour. 2003. Reciprocal Selection at the Phenotypic Interface of Coevolution. Integrative and Comparative Biology 43:408–418.

Brooks, D. R. 1979. Testing the context and extent of post-parasite coevolution. Systematic Zoology 28:299–307.

Bubrig, L. T., and A. K. Gibson. 2025. Boom-Bust Cycles Constrain Host-Parasite Dynamics, Suppress Parasite Spread, and Drive Parasites Extinct. The American Naturalist 206:261–271.

Cairns, J., F. Moerman, E. A. Fronhofer, F. Altermatt, and T. Hiltunen. 2020. Evolution in interacting species alters predator life-history traits, behaviour and morphology in experimental microbial communities. Proceedings of the Royal Society B: Biological Sciences 287:20200652.

Carlson, C. J., G. F. Albery, C. Merow, C. H. Trisos, C. M. Zipfel, E. A. Eskew, K. J. Olival, N. Ross, and S. Bansal. 2022. Climate change increases cross-species viral transmission risk. Nature 607:555–562.

Carlson, C. J., C. M. Zipfel, R. Garnier, and S. Bansal. 2019. Global estimates of mammalian viral diversity accounting for host sharing. Nature Ecology & Evolution 3:1070–1075.

Carmona, D., C. R. Fitzpatrick, and M. T. J. Johnson. 2015. Fifty years of co-evolution and beyond: integrating co-evolution from molecules to species. Molecular Ecology 24:5315–5329.

Chevallereau, A., B. J. Pons, S. Van Houte, and E. R. Westra. 2022. Interactions between bacterial and phage communities in natural environments. Nature Reviews Microbiology 20:49–62.

Clayton, D. H., S. E. Bush, and K. P. Johnson. 2016. Coevolution of Life on Hosts: Integrating Ecology and History. University of Chicago Press, Chicago.

Clayton, D. H., P. L. M. Lee, D. M. Tompkins, and E. D. Brodie Iii. 1999. Reciprocal Natural Selection on Host-Parasite Phenotypes. The American Naturalist 154:261–270.

Crutsinger, G. M. 2016. A community genetics perspective: opportunities for the coming decade. New Phytologist 210:65–70.

Dal Grande, F., G. Rolshausen, P. K. Divakar, A. Crespo, J. Otte, M. Schleuning, and I. Schmitt. 2018. Environment and host identity structure communities of green algal symbionts in lichens. New Phytologist 217:277–289.

Dixit, T. 2024. A synthesis of coevolution across levels of biological organization. Evolution 78:211–220.

Douda, K., H. Liu, D. Yu, R. Rouchet, F. Liu, Q. Tang, C. Methling, C. Smith, and M. Reichard. 2017. The role of local adaptation in shaping fish-mussel coevolution. Freshwater Biology 62:1858–1868.

Duxbury, E. M., J. P. Day, D. Maria Vespasiani, Y. Thüringer, I. Tolosana, S. C. Smith, L. Tagliaferri, A. Kamacioglu, I. Lindsley, L. Love, R. L. Unckless, F. M. Jiggins, and B. Longdon. 2019. Host-pathogen coevolution increases genetic variation in susceptibility to infection. eLife 8:e46440.

Ebert, D., and P. D. Fields. 2020. Host–parasite co-evolution and its genomic signature. Nature Reviews Genetics 21:754–768.

Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution pages 586–608.

Epstein, B., L. T. Burghardt, K. D. Heath, M. A. Grillo, A. Kostanecki, T. Hämälä, N. D. Young, and P. Tiffin. 2023. Combining GWAS and population genomic analyses to characterize coevolution in a legume-rhizobia symbiosis. Molecular Ecology 32:3798–3811.

Forde, S. E., J. N. Thompson, R. D. Holt, and B. J. M. Bohannan. 2008. Coevolution drives temporal changes in fitness and diversity across environments in a bacteria-bacteriophage interaction. Evolution pages ???–???

Futuyma, D. J., and M. Slatkin, eds. 1983. Coevolution. Sinauer Associates.

Gaba, S., and D. Ebert. 2009. Time-shift experiments as a tool to study antagonistic coevolution. Trends in Ecology & Evolution 24:226–232.

Gandon, S. 2002. Local adaptation and the geometry of host–parasite coevolution. Ecology Letters 5:246–256.

Gandon, S., and Y. Michalakis. 2002. Local adaptation, evolutionary potential and host–parasite coevolution: interactions between migration, mutation, population size and generation time. Journal of Evolutionary Biology 15:451–462.

Geier, C., M. S. Engel, J. M. Bouchal, S. Ulrich, J. Schönenberger, D. Uhl, T. Wappler, S. Wedmann, L. Boudet, and F. Grímsson. 2025. 24 million years of pollination interaction between European linden flowers and bumble bees. New Phytologist page nph.70531.

Gomulkiewicz, R., D. M. Drown, M. F. Dybdahl, W. Godsoe, S. L. Nuismer, K. M. Pepin, B. J. Ridenhour, C. I. Smith, and J. B. Yoder. 2007. Dos and don'ts of testing the geographic mosaic theory of coevolution. Heredity 98:249–258.

Gomulkiewicz, R., J. N. Thompson, R. D. Holt, S. L. Nuismer, and M. E. Hochberg. 2000. Hot spots, cold spots, and the geographic mosaic theory of coevolution. The American Naturalist 156:156–174.

Gross, K., M. Undin, J. N. Thompson, and M. Friberg. 2023. Components of local adaptation and divergence in pollination efficacy in a coevolving species interaction. Ecology 104:e4043.

Groussin, M., F. Mazel, and E. J. Alm. 2020. Co-evolution and co-speciation of host-gut bacteria systems. Cell Host & Microbe 28:12–22.

Gómez, P., and A. Buckling. 2011. Bacteria-Phage Antagonistic Coevolution in Soil. Science 332:106–109.

Haldane, J. B. S. 1949. Disease and evolution. Supplement to La Ricerca Scientifica 19:68–76.

Hanifin, C. T., E. D. Brodie, and E. D. Brodie. 2008. Phenotypic mismatches reveal escape from arms-race coevolution. PLoS Biology 6:e60.

Hanks, L. M., and R. F. Denno. 1994. Local adaptation in the armored scale insect Pseudaulacaspis pentagona (Homoptera: Diaspididae). Ecology 75:2301–2310.

Hargreaves, A. L., R. M. Germain, M. Bontrager, J. Persi, and A. L. Angert. 2020. Local adaptation to biotic interactions: A meta-analysis across latitudes. The American Naturalist 195:395–411.

Hayward, A., R. Poulin, and S. Nakagawa. 2021. A broadscale analysis of host-symbiont cophylogeny reveals the drivers of phylogenetic congruence. Ecology Letters 24:1681–1696.

Hembry, D. H., J. B. Yoder, and K. R. Goodman. 2014. Coevolution and the diversification of life. The American Naturalist 184:425–438.

Hoang, K., T. D. Read, and K. C. King. 2024. Defense heterogeneity in host populations gives rise to pathogen diversity. The American Naturalist page 731996.

Hoeksema, J. D., and S. E. Forde. 2008. A meta-analysis of factors affecting local adaptation between interacting species. The American Naturalist 171:275–290.

Janz, N. 2011. Ehrlich and Raven revisited: Mechanisms underlying codiversification of plants and enemies. Annual Review of Ecology, Evolution, and Systematics 42:71–89.

Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. Evolution 20:249–275.

———. 1980. When is it coevolution? Evolution 34:611–612.

———. 1984. The most coevolutionary animal of them all. Crafoord Lectures .

———. 1985. On ecological fitting. Oikos 45:308.

Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. The American Naturalist 129:657–677.

Kaltz, O., and J. A. Shykoff. 1998. Local adaptation in host – parasite systems 81:361–370.

Kerstes, N. A., C. Bérénos, P. Schmid-Hempel, and K. M. Wegner. 2012. Antagonistic experimental coevolution with a parasite increases host recombination frequency. BMC Evolutionary Biology 12:18.

King, K. C., M. A. Brockhurst, O. Vasieva, S. Paterson, A. Betts, S. A. Ford, C. L. Frost, M. J. Horsburgh, S. Haldenby, and G. D. D. Hurst. 2016. Rapid evolution of microbe-mediated protection against pathogens in a worm host. The ISME Journal 10:1915–1924.

Koskella, B., and M. A. Brockhurst. 2014. Bacteria–phage coevolution as a driver of ecological and evolutionary processes in microbial communities. FEMS Microbiology Reviews 38:916–931.

Koskella, B., and C. M. Lively. 2007. Advice of the rose: Experimental coevolution of a trematode parasite and its snail host. Evolution 61:152–159.

Lande, R. 1977. Statistical tests for natural selection on quantitative characters. Evolution 31:442–444.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution pages 1210–1226.

Light, J. E., and M. S. Hafner. 2008. Codivergence in heteromyid rodents (Rodentia: heteromyidae) and their sucking lice of the genus Fahrenholzia (Phthiraptera: anoplura). Systematic biology 57:449–65.

Lyon, B. E., and J. M. Eadie. 2004. An obligate brood parasite trapped in the intraspecific arms race of its hosts. Nature 432:390–393.

Lyons, T. W., C. W. Diamond, N. J. Planavsky, C. T. Reinhard, and C. Li. 2021. Oxygenation, life, and the planetary system during Earth's middle history: An overview. Astrobiology 21:906–923.

MacPherson, A., S. P. Otto, and S. L. Nuismer. 2018. Keeping pace with the Red Queen: identifying the genetic basis of susceptibility to infectious disease. Genetics 208:779–789.

Marston, M. F., F. J. Pierciey, A. Shepard, G. Gearin, J. Qi, C. Yandava, S. C. Schuster, M. R. Henn, and J. B. H. Martiny. 2012. Rapid diversification of coevolving marine *Synechococcus* and a virus. Proceedings of the National Academy of Sciences 109:4544–4549.

McKenna, D. D., A. S. Sequeira, A. E. Marvaldi, and B. D. Farrell. 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. Proceedings of the National Academy of Sciences 106:7083–7088.

Mode, C. J. 1958. A mathematical model for the co-evolution of obligate parasites and their hosts. Evolution 12:158–165.

Morran, L. T., O. G. Schmidt, I. A. Gelarden, R. C. Parrish, and C. M. Lively. 2011. Running with the Red Queen: Host-Parasite Coevolution Selects for Biparental Sex. Science 333:216–218.

Nilson, S. M., B. Gandolfi, R. A. Grahn, J. D. Kurushima, M. J. Lipinski, E. Randi, N. E. Waly, C. Driscoll, H. Murua Escobar, R. K. Schuster, S. Maruyama, N. Labarthe, B. B. Chomel, S. K. Ghosh, H. Ozpinar, H.-C. Rah, J. Millán, F. Mendes-de Almeida, J. K. Levy, E. Heitz, M. A. Scherk, P. C. Alves, J. E. Decker, and L. A. Lyons. 2022. Genetics of randomly bred cats support the cradle of cat domestication being in the Near East. Heredity 129:346–355.

Nuismer, S. L. 2017. Rethinking conventional wisdom: Are locally adapted parasites ahead in the coevolutionary race? The American Naturalist 190:584–593.

Nuismer, S. L., and S. Gandon. 2008. Moving beyond common-garden and transplant designs: insight into the causes of local adaptation in species interactions. The American Naturalist 171:658–668.

Nuismer, S. L., B. Week, and L. J. Harmon. 2022. Uncovering cryptic coevolution. The American Naturalist 199:869–880.

Obbard, D. J., J. J. Welch, K.-W. Kim, and F. M. Jiggins. 2009. Quantifying Adaptive Evolution in the Drosophila Immune System. PLoS Genetics 5:e1000698.

Papkou, A., C. S. Gokhale, A. Traulsen, and H. Schulenburg. 2016. Host–parasite coevolution: why changing population size matters. Zoology 119:330–338.

Pellmyr, O., and J. Leebens-Mack. 1999. Forty million years of mutualism: Evidence for Eocene origin of the yucca-yucca moth association. Proceedings of the National Academy of Sciences 96:9178–9183.

Piel, D., M. Bruto, Y. Labreuche, F. Blanquart, D. Goudenège, R. Barcia-Cruz, S. Chenivesse, S. Le Panse, A. James, J. Dubert, B. Petton, E. Lieberman, K. M. Wegner, F. A. Hussain, K. M. Kauffman, M. F. Polz, D. Bikard, S. Gandon, E. P. C. Rocha, and F. Le Roux. 2022. Phage–host coevolution in natural populations. Nature Microbiology 7:1075–1086.

Pimentel, D. 1961. Animal population regulation by the genetic feed-back mechanism. The American Naturalist 95:65–79.

Radwan, J., W. Babik, J. Kaufman, T. L. Lenz, and J. Winternitz. 2020. Advances in the Evolutionary Understanding of MHC Polymorphism. Trends in Genetics 36:298–311.

Ramírez, S. R., T. Eltz, M. K. Fujiwara, G. Gerlach, B. Goldman-Huertas, N. D. Tsutsui, and N. E. Pierce. 2011. Asynchronous Diversification in a Specialized Plant-Pollinator Mutualism. Science 333:1742–1746.

Regan, B. C., C. Julliot, B. Simmen, F. Viénot, P. Charles–Dominique, and J. D. Mollon. 2001. Fruits, foliage and the evolution of primate colour vision. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 356:229–283.

Schenk, J. J., K. C. Rowe, and S. J. Steppan. 2013. Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. Systematic Biology 62:837–864.

Schulte, R. D., C. Makus, B. Hasert, N. K. Michiels, and H. Schulenburg. 2010. Multiple reciprocal adaptations and rapid genetic change upon experimental coevolution of an animal host and its microbial parasite. Proceedings of the National Academy of Sciences 107:7359–7364.

Schweiger, O., J. C. Biesmeijer, R. Bommarco, T. Hickler, P. E. Hulme, S. Klotz, I. Kühn, M. Moora, A. Nielsen, R. Ohlemüller, T. Petanidou, S. G. Potts, P. Pyšek, J. C. Stout, M. T. Sykes, T. Tscheulin, M. Vilà, G. Walther, C. Westphal, M. Winter, M. Zobel, and J. Settele. 2010. Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. Biological Reviews 85:777–795.

Sessions, A. L., D. M. Doughty, P. V. Welander, R. E. Summons, and D. K. Newman. 2009. The Continuing Puzzle of the Great Oxidation Event. Current Biology 19:R567–R574.

Smith, C. I., and J. H. Leebens-Mack. 2024. 150 years of coevolution research: Evolution and ecology of yucca moths (Prodoxidae) and their hosts. Annual Review of Entomology 69:375–391.

Sprent, J. I. 2007. Evolving ideas of legume evolution and diversity: a taxonomic perspective on the occurrence of nodulation. New Phytologist 174:11–25.

Sprent, J. I., J. Ardley, and E. K. James. 2017. Biogeography of nodulated legumes and their nitrogen-fixing symbionts. New Phytologist 215:40–56.

Starr, T. N., K. E. Gadek, J. B. Yoder, R. Flatz, and C. I. Smith. 2013. Asymmetric hybridization and gene flow between Joshua trees (Agavaceae: Yucca) reflect differences in pollinator host specificity. Molecular Ecology 22:437–449.

Tabachnick, W. J. 1998. 14 Arthropod-Borne Pathogens: Issues For Understanding Emerging Infectious Diseases. Pages 411–429 *in* Biomedical Research Reports, vol. 1. Elsevier.

Thompson, J. N. 1989. Concepts of coevolution. Trends in Ecology & Evolution 4:179–183.

———. 2005. The geographic mosaic of coevolution. *In* The geographic mosaic of coevolution. University of Chicago Press.

———. 2013. Relentless Evolution. University of Chicago Press.

Thrall, P. H., A. Laine, M. Ravensdale, A. Nemri, P. N. Dodds, L. G. Barrett, and J. J. Burdon. 2012. Rapid genetic change underpins antagonistic coevolution in a natural host-pathogen metapopulation. Ecology Letters 15:425–435.

Tiffney, B. H. 2004. Vertebrate Dispersal of Seed Plants Through Time. Annual Review of Ecology, Evolution, and Systematics 35:1–29.

Toju, H., S. Ueno, F. Taniguchi, and T. Sota. 2011. Metapopulation structure of a seed-predator weevil and its host plant in arms race coevolution. Evolution 65:1707–1722.

Treindl, A. D., J. Stapley, D. Croll, and A. Leuchtmann. 2024. Two-speed genomes of *Epichloe* fungal pathogens show contrasting signatures of selection between species and across populations. Molecular Ecology 33:e17242.

Vamosi, J. C., and S. M. Vamosi. 2010. Key innovations within a geographical context in flowering plants: towards resolving Darwin's abominable mystery. Ecology Letters 13:1270–1279.

Vidal, M. C., C. Liu, S. Wang, and K. A. Segraves. 2025. Partner dependency alters patterns of coevolutionary selection in mutualisms. Proceedings of the National Academy of Sciences 122:e2424983122.

Week, B., and S. L. Nuismer. 2019. The measurement of coevolution in the wild. Ecology Letters 22:717–725.

Wilson, A. C. C., and R. P. Duncan. 2015. Signatures of host/symbiont genome coevolution in insect nutritional endosymbioses. Proceedings of the National Academy of Sciences 112:10255–10261.

Yoder, J. B. 2016. Understanding the coevolutionary dynamics of mutualism with population genomics. American Journal of Botany 103:1742–1752.

Yoder, J. B., E. Clancey, S. Des Roches, J. M. Eastman, L. Gentry, W. Godsoe, T. J. Hagey, D. Jochimsen, B. P. Oswald, J. Robertson, B. A. J. Sarver, J. J. Schenk, S. F. Spear, and L. J. Harmon. 2010. Ecological opportunity and the origin of adaptive radiations. Journal of Evolutionary Biology 23:1581–1596.

Yoder, J. B., A. Dang, C. MacGregor, and M. Plaza. 2022. Plant-associate interactions and diversification across trophic levels. Evolution Letters 6:375–389.

Yoder, J. B., G. Gomez, and C. J. Carlson. 2020. Zygomorphic flowers have fewer potential pollinator species. Biology Letters 16:20200307.

Zangerl, A. R., and M. R. Berenbaum. 1993. Plant Chemistry, Insect Adaptations to Plant Chemistry, and Host Plant Utilization Patterns. Ecology 74:47–54.

———. 2004. Genetic Variation in Primary Metabolites of Pastinaca sativa; Can Herbivores Act as Selective Agents? Journal of Chemical Ecology 30:1985–2002.

Zhang, X., G. Wang, S. Zhang, S. Chen, Y. Wang, P. Wen, X. Ma, Y. Shi, R. Qi, Y. Yang, Z. Liao, J. Lin, J. Lin, X. Xu, X. Chen, X. Xu, F. Deng, L. Zhao, Y.-l. Lee, R. Wang, X.-Y. Chen, Y.-r. Lin, J. Zhang, H. Tang, J. Chen, and R. Ming. 2020. Genomes of the Banyan Tree and Pollinator Wasp Provide Insights into Fig-Wasp Coevolution. Cell 183:875–889.e17.