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

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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?”. 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

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Etymologically, “coevolution” simply means “evolving together”, but most of us who study the evolution of interactions among species have come to use a narrower definition. 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).

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 *and* 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*), quantifying coevolutionary selection was only recently accomplished: selection monarchs’ capacity to detoxify and sequester milkweeds’ defensive cardenolides 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;

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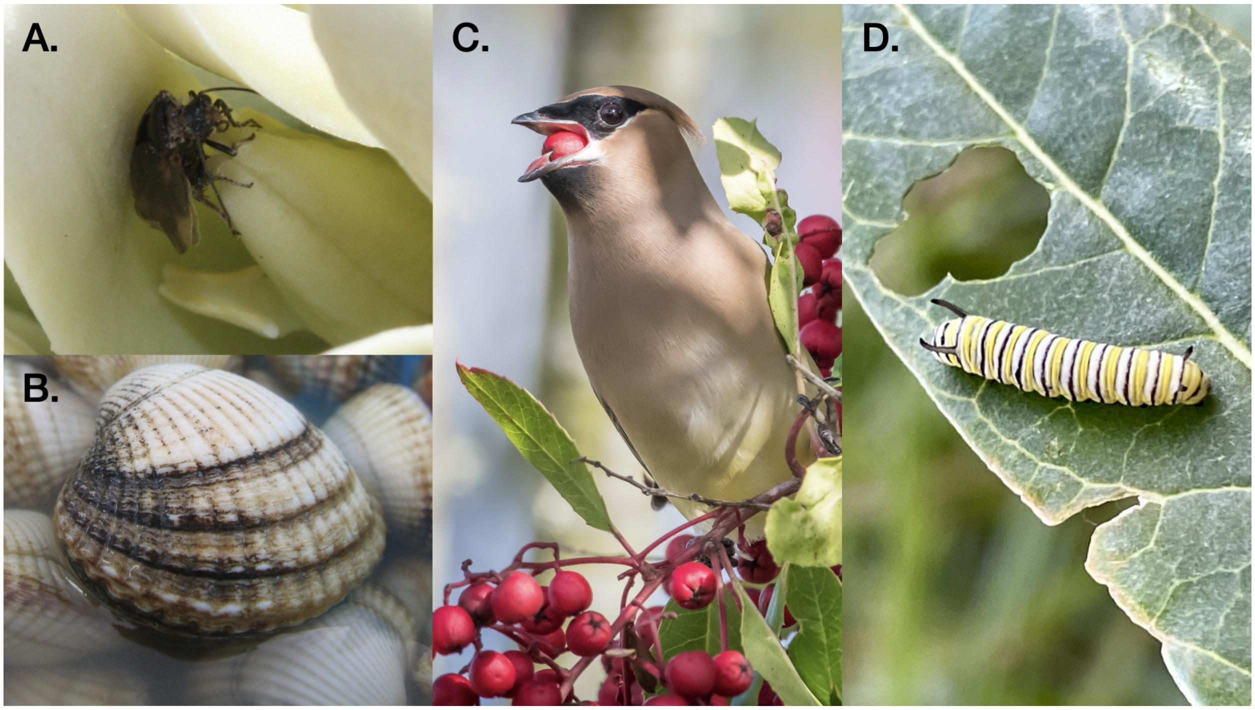

Fig. 1. Strict-sense coevolutionary selection has not been measured in many "textbook" species interactions, including (A) yuccas and obligate-pollinating yucca moths (*Tegeticula synthetica* on a flower of *Yucca brevifolia*), or (B) shelled mollusks (*Cerastoderma edule*) and their predators, or (C) 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.)

Nuismer et al., 2022; Week and Nuismer, 2019).

So we have 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 suggests the key question in studies of species evolving together is no longer "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). The tension between adherence to a clear-cut 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), but we have not yet resolved it. Re-framing the study of species interactions and their evolutionary consequences to ask "how is it coevolution?" is a more fruitful choice, and a more honest one. 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.

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 re-

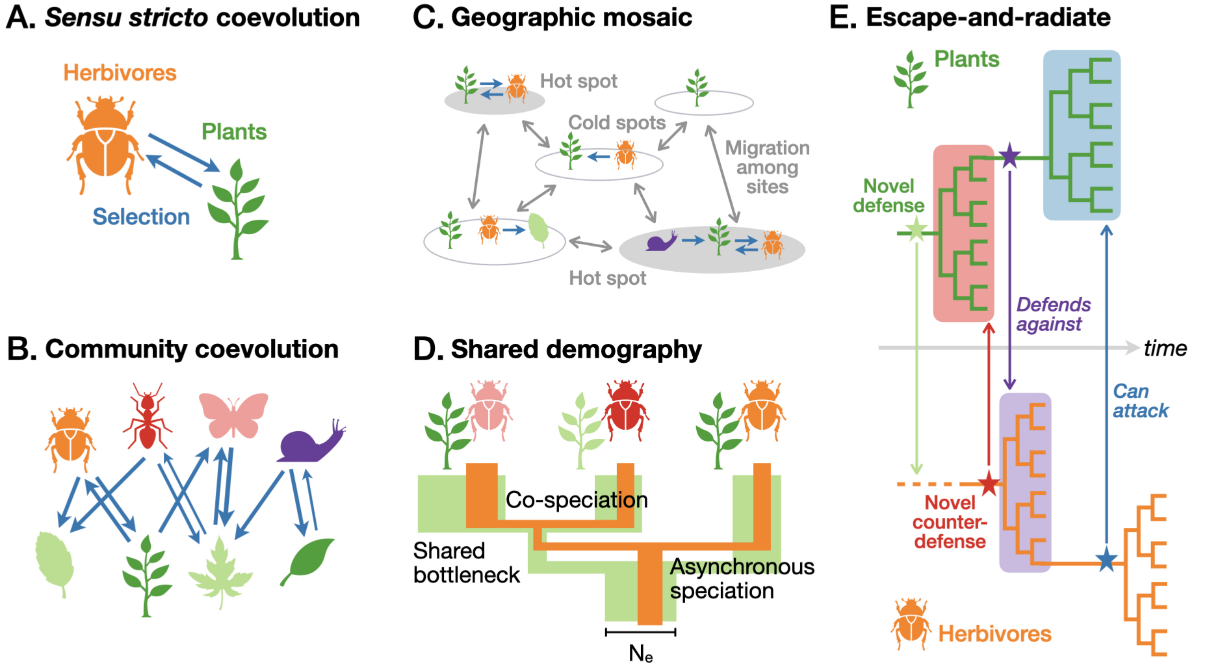

Fig. 2. Well-described ways in which organisms may evolve together, illustrated via plant-herbivore interactions, with arrows indicating natural selection exerted by one species on another: (A) *Sensu stricto* specific, simultaneous, reciprocal adaptation; (B) community, or "diffuse" coevolution; (C) 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.

sist infection, or to overcome that resistance; and change in the frequency of resistance or infectivity alleles in one species immediately feeds back to alter the 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 difficulties of quantifying coevolutionary selection in wild populations of macrofauna also apply to quantifying specific, simultaneous, reciprocal selection in wild populations of species that can be easily propagated in a 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 — assaying (for instance) hosts' fitness in interaction with parasite isolates from the contemporary population and from previous generations — give more definitive answers, but at the cost of logistics that effectively end up tracking host and parasite adaptation directly (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, in its description of “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 of research 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 a point at which species may be said to evolve *without* 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 (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). The challenges of rigorously characterizing selection acting on two species, or better yet track-

Table 1. Previously described and possible new modes of coevolution, in terms of whether they are specific or diffuse, simultaneous or stepwise, and adaptive or nonadaptive

Mode of coevolution	Specificity	Simultaneity	Adaptivity	Published example
Sensu stricto	Specific	Simultaneous	Adaptive	Benkman et al. (2003)
Community coevolution	Diffuse	Simultaneous	Adaptive	Dal Grande et al. (2018)
Stepwise coadaptation	Specific	Stepwise	Adaptive	Janzen (1966)
Escape-and-radiate	Mostly diffuse	Stepwise	Adaptive	McKenna et al. (2009)
Geographic mosaics	Mostly specific	Mostly simultaneous	Adaptive *and* nonadaptive	Toju et al. (2011)
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)

ing 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). Determining how often specific, simultaneous, reciprocal adaptation plays a role in species' evolution together remains an interesting question.

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).

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.

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 correlated across trophic levels, and processes of horizontal transmission often create bottlenecks at the point where symbionts establish infections in new hosts. Often these processes are treated as obscuring 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 non-photosynthetic 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).

Demonstrating a hypothesized reciprocal evolutionary effect could mean quantifying natural selection exerted on one species by another, or finding population genetic evidence of that selection (Amandine et al., 2022; Ebert and Fields, 2020). However, because the range of possible evolutionary processes includes more than natural selection, demonstrating coevolution *sensu lato* could also mean documenting one species' role in dispersing the gametes or propagules of another species (Starr et al., 2013); or in limiting or facilitating its population growth (Azevedo-Schmidt et al., 2022). Reciprocal evolutionary change requires a shared history, so phylogenetic congruence, either in the structure or timing of diversification events, is also evidence of broad-sense coevolution (Hayward et al., 2021; McKenna et al., 2009).

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.

In fact, it is possible to envision a more commodious definition of "coevolution" in the context of species interactions that more or less recapitulates Janzen (1980): "Coevolution" may be practically defined as an evolutionary change — adaptive or nonadaptive — in a trait of the individuals in one population that results from interactions — direct or indirect — with individuals in a second population, followed — immediately or eventually — by a reciprocal evolutionary change in the second population.

The interjected clarifications are more awkward than the original, but they reflect the true diversity of processes that we have found in studies of species interactions. Trading an understanding that *coevolution* is limited to specific, simultaneous, reciprocal adaptation for one in which we admit that species may influence each other's evolution in a multitude of ways lets us focus on describing that multitude 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".

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