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 is widely defined 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?”. This re-framing 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 (Carl-

Correspondence: jeremy.yoder@csun.edu

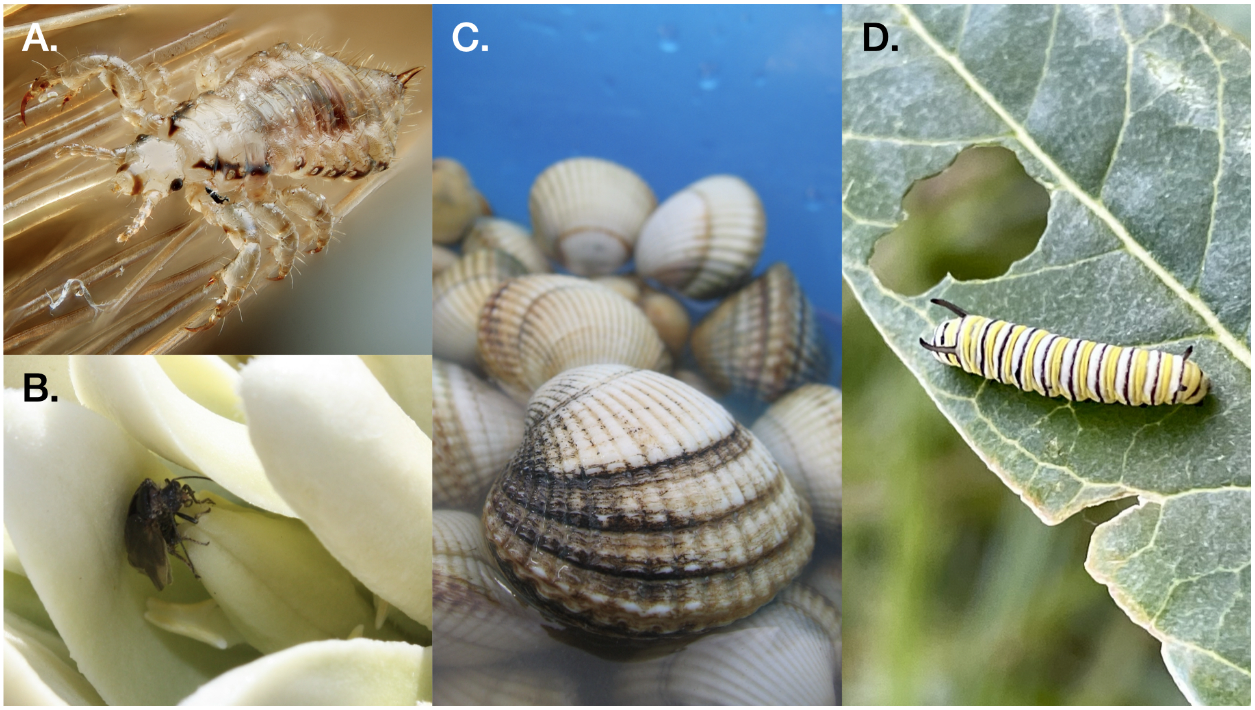

Fig. 1. Strict-sense coevolutionary selection has not been measured in many "textbook" species interactions, including (A) lice (*Pediculus humanus capitis* pictured) and their vertebrate hosts, (B) yuccas and obligate-pollinating yucca moths (*Tegeticula synthetica* on a flower of *Yucca brevifolia*), or (C) shelled mollusks (*Cerastoderma edule*) and their predators. 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, Gilles San Martin via Flickr, CC BY-SA 2.0; B, Christopher I. Smith, by permission; C, Féron Benjamin via Wikimedia Commons, CC BY-SA 2.0; D, the author.)

son 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 linked species interactions to patterns of evolutionary radiation, convergence, and diversification (Agrawal et al., 2024; Haldane, 1949; McKenna et al., 2009; Vamosi and Vamosi, 2010); and we have traced their origins and effects through the fossil record (Azevedo-Schmidt et al., 2022; Bao et al., 2019). 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).

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;

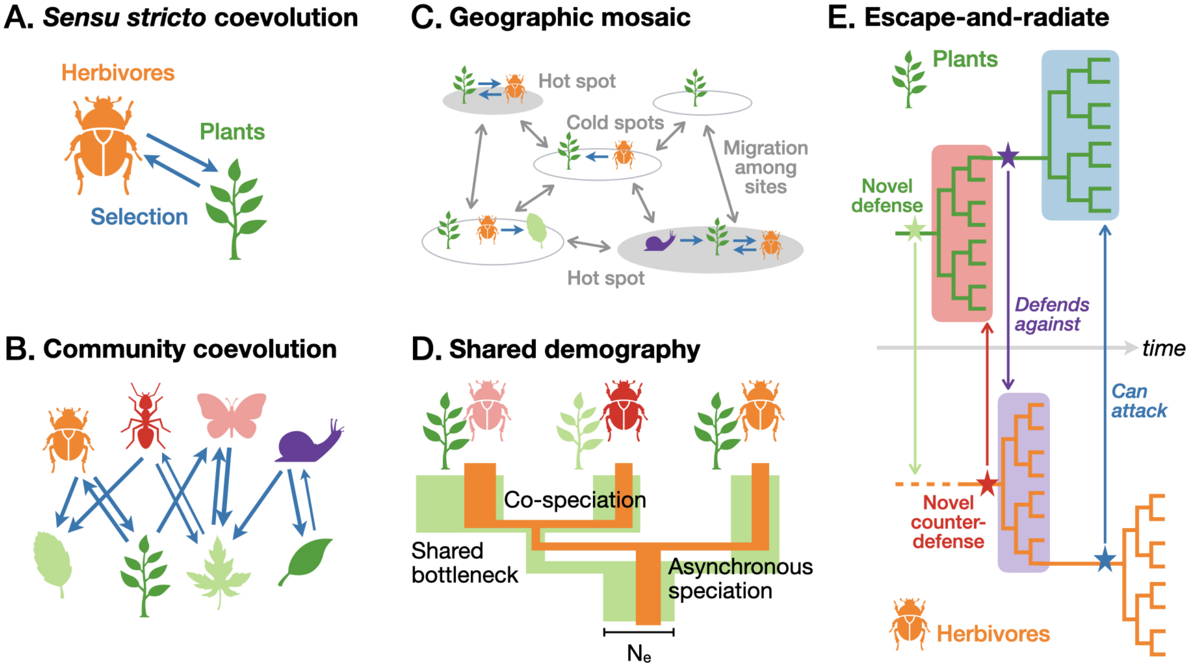

Fig. 2. Well-described ways in which organisms may evolve together, illustrated via plant-herbivore interactions: (A) *Sensu stricto* specific, simultaneous, reciprocal adaptation; (B) community, or "diffuse" coevolution; (C) coevolution on a geographic mosaic of spatially varying populations; (D) effects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

Week and Nuismer, 2019). Many textbook examples of species interactions — including lice and their vertebrate hosts (Clayton et al., 2016), yuccas and obligate-pollinating yucca moths (Smith and Leebens-Mack, 2024), even shelled mollusks and their predators (e.g., Bijleveld et al. 2015) — lack documentation of strict-sense reciprocal natural selection (Fig. 1). In even one of the most charismatic plant-herbivore interactions, that of milkweeds (genus *Asclepias*) and monarch butterflies (*Danaus plexippus*), selection on variation in monarchs' capacity to detoxify and sequester milkweeds' defensive cardenolides was not quantified until 16 years after quantification of selection on milkweeds' cardenolide production (Agrawal, 2005; Agrawal et al., 2021). Strict-sense coevolution is, in fact, one of the rarest empirical results in evolutionary studies of species interactions (Althoff et al., 2014; Clayton et al., 2016; Hembry et al., 2014).

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 honest choice — and a fruitful one.

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 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 also fails to cite Mode (1958), which may explain this omission.

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 a 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 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. He also mentions "selective pressure" in defining "diffuse coevolution", indicating an interest in *adaptation*. However, Janzen 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" that 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).

The lack of a requirement for simultaneity 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.

The *sensu stricto* two-step

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 almost always 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 meet that definition. 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, in paper after paper 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 many 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), studies have certainly documented specific, simultaneous, reciprocal selection and adaptation (Benkman et al., 2003; Carmona et al., 2015; Koskella and Brockhurst, 2014), but these remain more the exception than the rule. More importantly, there are any number of research questions about the role of species interactions in evolutionary history that can be addressed without first proving *sensu stricto* coevolution — 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).

The geographic mosaic theory of coevolution advanced by Thompson (2005) is in some respects an attempt to rescue the field from the need to demonstrate 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.

Considering coevolution *sensu lato*

Truly envisioning coevolution mediated by the full range of evolutionary processes is perhaps daunting, because it opens up so many possibilities. Finding new answers to the question of how species may coevolve is, itself, a potentially fruitful line of research in a new study of broad-sense coevolution. However, it is already possible to identify several categories of processes that may link the evolution of different species — and it remains possible to identify a point at which species may be said to evolve *without* evolving together.

Here, the strict-sense definition provides a useful starting point. 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 (Fig. 3). 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 processes beyond adaptation is not much more challenging. 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

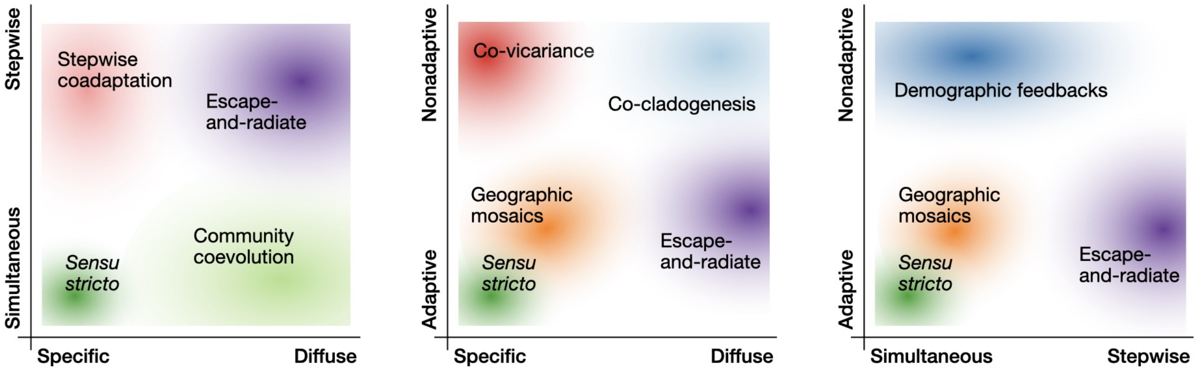

Fig. 3. Mapping existing and prospective new modes of coevolution to the parameter space created by three axes of specific or diffuse, simultaneous or stepwise, and adaptive or nonadaptive.

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, of course, create the specific, simultaneous, reciprocal adaptation envisioned since Janzen (1980). The challenges of rigorously characterizing selection acting on two species, or better yet 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). 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). 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; 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 (Schenk et al., 2013; Schueth et al., 2015); or the diversification of one clade could facilitate the diversification of another, in a process we might call "co-cladogenesis" (Fig. 3). An example of the latter might be the oxygenation of Earth's atmosphere by photosynthetic algae, which enabled the proliferation of aerobic non-photosynthetic lineages (Lyons et al., 2021). These may be rare events, and they certainly constitute the weakest coherent sense in which species may evolve together — because 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). 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 is less clear how 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. Trading our understanding that *coevolution* is circumscribed by 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 diversity of coevolutionary processes. Asking "how is it coevolution?" opens the mind to contemplate the full diversity of life's history at play in Darwin's "entangled bank".

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