Fifty years after Ehrlich and Raven, is there support for plant–insect coevolution as a major driver of species diversification?

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Abstract

Since Ehrlich & Raven’s seminal paper 50 years ago, coevolution has been seen as a major driver of species diversification. Here, we review classical and more recent case studies on the coevolution of plants and associated insects, to examine whether the coevolutionary component holds as an explanation of their current diversity. We discuss the main dogmas in coevolution and argue that coevolutionary processes should not be considered as major drivers of diversification in plants and insects. Instead, we suggest that coevolution essentially occurs through relatively short ‘interludes’, making the pattern difficult to detect. We also criticize the use of comparative phylogenetics to investigate coevolutionary processes, as coevolution may not necessarily produce congruent phylogenies among interacting lineages and, in turn, other processes may produce patterns of codivergence. Finally, we propose new lines of investigation for future research.

Introduction

The idea that coevolution promotes biodiversity is both popular and intuitive (Bascompte & Jordano, 2007; Thompson, 2009). Indeed, Darwin and Wallace already recognized the importance of interactions among plants and animals in an evolutionary perspective, and proposed that many selective pressures may be the outcome of interactions between organisms (Darwin, 1859, 1862; Wallace, 1889). Although not using the word coevolution itself, Brues (1924) not only hypothesized that the apparent narrow host preferences of some insect herbivores might be explained by parallel evolution of insect clades and their host plants, but also acknowledged the role of host switches in acquiring more distant plant lineages. He also noted the importance of host races and behavioral preferences of insects towards their host plants. It was Ehrlich & Raven (1964) who eventually brought the term ‘coevolution’ to a broad audience through a comprehensive study of butterflies and their host plants, hypothesizing that the evolution of plant defenses followed by counter-adaptations in insects could lead to bursts of adaptive radiation. Also using concepts of reciprocal selective pressures, Grant & Grant (1965) suggested that pollinator-driven speciation could be an important source of diversity in plants. As we will discuss below, the processes imagined in each of these situations are different, leading to some confusion about the expected outcomes of coevolutionary processes.

In this review, we focus on the perhaps most often cited, and earliest formulated example of coevolutionary diversification—that between the flowering plants and insects. Indeed, the rapid rise of angiosperms in the early Cretaceous led Darwin to speculate that insect–plant interactions could be one of the drivers of this evolution, from which no footprints can be found in the fossil record—his ‘abominable mystery’ (Friedman, 2009; Buerki et al., 2014). The two groups account for most of the planet’s diversity, angiosperms with 352 000 described species being the most widespread land plants (Paton et al.,
2008), and insects being by far the most numerous animals, with estimates of species richness varying from one to several million species (Erwin, 1982; May, 1988; Ødegaard, 2000). They are connected by a large number of trophic interactions. For instance, it is estimated that almost 90% of flowering plants are biotically pollinated (Ollerton et al., 2011). Moreover, evidence of both herbivory (Labandeira, 1994) and animal pollination (Grimaldi, 1999) is found throughout the fossil record from the beginning of angiosperm history, although both processes predated the radiation of angiosperms (Labandeira, 2013). As a result, despite alternative hypotheses, either biotic or abiotic (Bakker, 1978; Midgley & Bond, 1991; Barrett & Willis, 2001; Gorelick, 2001; Berendse & Scheffer, 2009; Crepet & Niklas, 2009; Crisp & Cook, 2011), the widespread and diverse interactions among angiosperms and their herbivores and pollinators are often hypothesized to be the main catalyst for the radiation of flowering plants (Crepet & Friis, 1987; Bronstein et al., 2006; Hu et al., 2008; Table 1). In turn, phytophagy (Mitter et al., 1988) and pollination (Armbruster, 2014) are often used to explain species radiations within many insect groups, and have been generally shown to promote insect diversification (Table 1).

However, despite decades of research, the empirical support for the hypothesis that coevolution promotes diversification is still weak (Althoff et al., 2014). Here, we aim to provide theoretical explanation of processes at work in putative examples of coevolution between plants and insects, as well as clarify some misused terms. In particular, in line with other authors (Janzen, 1980; De Vienne et al., 2013) we argue for careful use of the terms ‘coevolution’ and ‘coevolutionary diversification’. As noted by Futuyma (2000), despite widespread usage of the term ‘coevolution’ in ecological and evolutionary studies, remarkably few actually test reciprocal coadaptation. Finally, we review current support for coevolution as the main process at work in the diversification and radiation of plant and insect lineages on the macroevolutionary scale. Although biotic interactions are, certainly, an important component of species evolution, the weak support for coevolutionary diversification in plant–insect interactions is striking. We propose that the time during which species are affected by coevolutionary processes, although key for driving new adaptations, might in fact represent relatively short periods of a species’ evolutionary history, for which we introduce the concept of ‘coevolutionary interludes’. Coinciding with

| Key trait               | Focal taxon            | Direction of change in diversification rate | Reference                                                                 |
|------------------------|------------------------|---------------------------------------------|---------------------------------------------------------------------------|
| Pollination of plants  | Insects                | +                                           | Dodd et al. (1999)                                                        |
| Herbivory              | Insects                | +                                           | Mitter et al. (1988)                                                      |
| Herbivory              | Beetles                | +                                           | Farrell (1998)                                                            |
| Herbivory              | Beetles                | 0                                           | Hunt et al. (2007)                                                        |
| Leaf-mining            | Insects                | 0                                           | Connor & Taverner (1997)                                                  |
| Biotic pollination     | Angiosperms            | +                                           | Dodd et al. (1999); Kay et al. (2006)                                     |
| Biotic pollination     | Angiosperms            | 0                                           | Bolmgren et al. (2003)                                                    |
| Floral nectar spurs    | Angiosperms            | +                                           | Hodges & Arnold (1995); Hodges (1997)                                    |
| Floral nectar spurs    | Aquilegia spp.         | +                                           | Ree (2005)                                                                |
| Floral nectar spurs    | Euphorbia spp.         | 0                                           | Cacho et al. (2010)                                                       |
| Bilateral symmetry     | Angiosperms            | +                                           | Sargent (2004); Vamosi & Vamosi (2010, 2011)                               |
| Bilateral symmetry     | Angiosperms            | 0                                           | Kay et al. (2006)                                                         |
| Self-incompatibility   | Angiosperms            | +                                           | Igic et al. (2008); Ferrer & Good (2012)                                  |
| Apomixy                | Oenothera spp.         | +                                           | Johnson et al. (2011)                                                     |
| Heterostyly            | Primulaceae            | +                                           | de Vos et al. (2014)                                                      |
| Dioecy                 | Angiosperms            | -                                           | Helmbuth (2000); Kay et al. (2006)                                        |
| Latex and resin canals | Gymno- and angiosperms | +                                           | Farrell et al. (1991)                                                     |
| Chemical defenses      | Apioideae              | +                                           | Berenbaum (1983)                                                          |

1 No formal statistical test.
2 Corrected for geographic ranges.
Thompson’s (2005) theory on the geographic mosaic of coevolution, we also argue that ‘coevolutionary interludes’ may occur only in a restricted portion of a species’ distribution area. Last but not least, as we will see, a pattern of codivergence could be disconnected from coevolutionary diversification itself, as it may be caused by a wide array of alternative processes.

What is coevolution?

Coevolution has been given many different meanings, from a narrow to a broad perspective, and used as a catch-all term to explain numerous different processes, from radiations of major groups of organisms to population-level changes, and from mutualistic to antagonistic interactions (Thompson, 1994). In its strict sense, coevolution is defined as ‘an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals in a second population, followed by an evolutionary response by the second population to the change in the first’ (Janzen, 1980). As such, sequential reciprocal dynamic is essential to the definition of coevolution, and the process should be distinguished from simple cases of interactions involving two or more species, or adaptation of one species to another without an evolutionary response of the latter.

Controlled, experimental approaches support the hypothesis that organisms connected by trophic webs can exert selective pressures on each other, and that their interactions indeed promote genetic polymorphisms (Duffy & Forde, 2009; Brown & Tellier, 2011), leading to measurable changes in gene frequency or quantitative traits (Brockhurst & Koskella, 2013), and reciprocal adaptations over time in interacting populations (Gaba & Ebert, 2009). The reciprocal evolution of tolerance and virulence in hosts and parasites provides a good example (Little et al., 2010). More generally, we know from both laboratory experiments (Buckling & Rainey, 2002; Benmayor et al., 2008) and empirical data (Laine, 2009), that coevolutionary interactions can generate diversity by producing divergent selection trajectories in interacting organisms. Thus, there is no doubt that coevolution occurs on an ecological scale, and that it drives processes associated with genetic diversity.

However, in natural populations, a species is usually embedded in a multi-level interaction network with an array of other species, resulting in outcomes that can range from mutualism to antagonism, and that can vary in time and space (Thompson, 1994), and be context dependent (Chamberlain et al., 2014). The chances of strict one-to-one interactions are thus low, which led Janz (2011) to conclude that the requirements of Janzen’s narrow definition were so restrictive that virtually no study could prove coevolution. Instead he argued for a broader, more inclusive treatment, ‘in which we want to refer to interacting species that are coevolving as in ‘evolving together.’ We believe that even under this broader definition, coevolution should not be just synonymous with every case of evolution when two or more species interact. We argue that it is not simply semantics and, as with all scientific hypotheses, we need alternative hypotheses—unidirectional selection in the context of biotic interactions being a reasonable one. In particular, studying evolutionary change in only one interacting partner is insufficient to claim coevolution.

The putative examples of coevolution should be interpreted with caution. As noted by Janzen (1985), even seemingly coadapted species do not have to be coevolved. For instance, the fact that two species are involved in mutualistic interaction does not prove that they are a product of coevolution. They may simply possess the traits that allow them to persist and interact within a particular community, in the form of preadaptations—a phenomenon called ‘ecological fitting’ (Janzen, 1985; Agosta, 2006). For instance, invasive plants are often well integrated into native plant–pollinator networks (Vilà et al., 2009), or even take a central role (Bartomeus et al., 2008), despite they did not coevolve with the native pollinators. Thus, although species interactions are key for ecosystem stability (Bascompte & Jordano, 2007), traits related to such interactions are not necessarily a result of coevolution. This does not, however, exclude subsequent coevolutionary change in the partners (Leger & Espeland, 2010).

This view of coevolution suggests that the time during which it occurs and during which interactions drive the evolution of novel species traits may be relatively brief, followed by the spread and use of these traits in novel environments. One could use the metaphor that species only share a brief coevolutionary waltz during the evolutionary ball or, as proposed by Strong et al. (1984), of coevolutionary vortices in an evolutionary stream. The rarity of such ‘coevolutionary interludes’ through time and space is likely to be the reason for the dearth of contemporaneous biological examples in which coevolution has been detected (Appendix 1).

What is coevolutionary diversification?

Coevolutionary diversification as defined by Althoff et al. (2014) is ‘a process by which coevolution between two or more taxa increases net diversification (speciation rate minus extinction rate) in at least one of the interacting taxa’. It is thus important to note that, similar to the fact
that not all interspecific interactions are coevolved, not all processes generating diversification in a context of biotic interactions can be called coevolutionary diversification. As reviewed below, if the selective pressures between populations are highly asymmetric, one population may just track the speciation events of the other (Althoff et al., 2014). Alternatively, one clade can diversify utilizing resources of an already existing clade (Jermy, 1976). In a broader context, many biotic features have been shown to be correlated with macroevolutionary patterns of diversification (Table 1), but whether they account for meaningful amounts of variation in diversification rates (Davies et al., 2004), and whether coevolution has participated in generating this diversity, remain as open questions.

Furthermore, patterns of codivergence should be distinguished from coevolutionary processes. Brooks (1979) was one of the first to observe that these are two different phenomena, and that one can occur without the other. For instance, early on it was proposed that the systematics of hosts should correspond with that of their parasites—a phenomenon called Fahrenholz’s rule (Eichler, 1948; Nieberding & Olivieri, 2007). However, as argued by Althoff et al. (2014), such a pattern can be produced without coevolutionary processes being involved. If its degree of specialization is sufficiently high, the only way for a parasite to survive is to phylogenetically ‘track’ its host (Althoff et al., 2014). Moreover, parasites usually evolve in such a way that their virulence is not high (Little et al., 2010), and thus it is unlikely they represent a source of divergence for the hosts (although this does not exclude the possibility of coevolutionary host–parasite dynamics). As such, a pattern of codivergence could be generated without coevolution being the main trigger for speciation. Similarly, an insect clade can start using a plant clade, and eventually undergo adaptive radiation to use other members of that clade, thus producing a pattern of speciation parallel to that of the plant (Jermy, 1984). A similar situation may occur when biogeographic boundaries are shared among (not necessarily) interacting organisms (Alvarez et al., 2009, 2010; Althoff et al., 2014). The weakness of the link between coevolutionary processes and phylogenetic patterns will be discussed more thoroughly below.

Is coevolution really driving species diversification? Revisiting the dogmas

Many hypotheses explaining the link between coevolution (or lack thereof) and observed macroevolutionary patterns have been proposed during the last 50 years. Here, we summarize the most frequently cited ones along two main axes: (1) the asymmetric vs. symmetric nature of the selective strength between the interacting organisms, formalized along the gradient between parallel coevolutionary dynamics and purely one-way selective pressure, and (2) the convergent vs. divergent—or concordant vs. discordant—selection pressures experienced in the interaction, formalized along the continuum between mutualistic and antagonistic types of interaction (Figure 1).

Escape-and-radiate

Perhaps the most influential hypothesis for how coevolutionary processes can lead to macroevolutionary patterns was proposed by Ehrlich & Raven (1964), later named ‘escape-and-radiate’ by Thompson (1994). Ehrlich and Raven were the first to use a coevolutionary framework to interpret the fact that herbivores usually have narrow host preferences and that closely related insects use closely related plants. They proposed a scenario for the evolution of such assemblages, in which a plant evolves a novel trait allowing it to escape from its predators and colonize an ‘enemy free space’. This novel lineage can then radiate, but it represents an attractive niche for herbivores, and eventually some of them will evolve a counter-adaptation allowing them to exploit this resource, and later radiating to exploit other species of the plant clade. In Table 2, we review the main examples of plant defenses and counter-defenses in insects.
An implicit assumption of Ehrlich and Raven’s hypothesis is that a trait beneficial for the individual, allowing it to occupy a new enemy-free niche, can promote diversification. So far, however, the mechanisms linking these two aspects are unclear (Futuyma, 2000). For the plants it was proposed that enemy release—i.e., the absence of herbivores—could promote diversification, by increasing population persistence and thus favor opportunities for local drift and local adaptation, one of the evolutionary steps required for allopatric speciation (Allmon, 1992). However, there is to our knowledge, no empirical support for this hypothesis. For the insects, once a counter-adaptation has evolved, radiation may follow that of the plant, by means of increased number of opportunities for adaptation to the plant diversity produced, which creates an array of new ecological niches for herbivores. Winkler et al. (2009) provide—to our knowledge—the unique statistically supported example of consistently elevated net diversification of insects accompanying shifts to new plant clades. In contrast, most observations show that enemy release does not necessarily cause increased speciation rates (Nyman et al., 2007), and diversification itself can be linked with non-coevolutionary processes. Irrespective of diversification rates, recurrent cycles of escape-and-radiate might theoretically lead to an arms race between plants and insects, resulting in novel defenses in plants and counter-adaptations in insects (Table 2), or to qualitative and quantitative escalation in defense mechanisms (Table 3).

Another important point is that in Ehrlich and Raven’s model, the evolution of plants and insects is decoupled (Futuyma, 2000), with a temporal lag between the two. Also, the taxa exerting the main selective pressure for the evolution of a novel plant defense can be completely different from those that overcome the defense, thus obscuring the pattern. Although some authors use the congruence or incongruence of phylogenies as an argument for or against coevolution (see below), it is important to note that the ‘escape-and-radiate’ scenario never predicted congruence in phylogenies or the timing of radiation.

The concept of ‘ecological fitting’, mentioned above, suggests that the time during which coevolution occurs and during which species evolve novel traits, might represent only a short period of evolutionary history, followed by the spread and use of these traits in novel environments. As observed by Althoff et al. (2014), this can be applied to the ‘escape-and-radiate’ model, where ‘coevolution happens at key moments to drive the evolution of plant defenses and insect counter-defenses, and then other speciation processes (e.g., allopatric speciation) come into play as plants and insects increase their geographic ranges or further subdivide resources.’

### Diversifying coevolution

As opposed to the escape-and-radiate hypothesis, Thompson (1994) proposed a scenario in which speciation is a direct outcome of the coevolutionary process in the situation where one partner has control over the movement of the gametes of the other. According to this hypothesis, this may take place, for instance, in the interactions between flowering plants and their pollinators (van der Niet & Johnson, 2012). Thompson proposed that such coevolving

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**Table 2** Examples of plant defenses and putative counter-defenses in insects; modified from Rausher (2001) and updated

| Plant taxon              | Defense trait  | Insect taxon            | Counter-defense trait          | References                                      |
|--------------------------|----------------|-------------------------|--------------------------------|-------------------------------------------------|
| Asclepiadaceae           | Fouranocoumarins | Butterfly Papilio polyxenes | Cytochrome P450             | Berenbaum (1983); Cohen et al. (1992); Berenbaum et al. (1996) |
| Asclepiadaceae, Moraceae | Latex          | Various insects         | Leaf vein cutting            | Compton (1987); Dussourd & Eisner (1987)         |
| Conifers                 | Resin          | Scolytidae              | Mass attack                  | Trapp & Croteau (2001); Rosenthal et al. (1976) |
| Dioclea megacarpa        | Toxic L-kanavanine amino acid | Bruchid Caryodes brasiliensis | Modified arginyl-tRNA synthetase |                                            |
| Solanum                  | Trichomes      | Butterfly Mechanitis isthmia | Silk scaffolding over the trichomes | Rathcke & Poole (1975)                         |
| Acacia                   | Mutualism with ants | Polyhymno moth         | Shelter by silking plant leaves together | Eubanks et al. (1997)                           |
| Lophocereus schottii     | Sterols        | Drosophila pachea       | Cytochrome P450              | Frank & Fogleman (1992)                          |
| Brassicales              | Glucosinolate–myrosinase defense system | Pieridae              | Nitrile-specifier protein | Wittstock et al. (2004); Fischer et al. (2008) |
| Various plant species    | Toxic glycosides, alkaloids, steroids | Diverse Lepidoptera | Sequestration                | Malcolm (1994); Abe et al. (2001); Nishida (2002); Zagrobelny & Møller (2011) |
pairs of populations would eventually lose the ability to mate successfully with conspecific lineages, thereby causing speciation. As noted by Althoff et al. (2014), although we still lack a complete framework to link such coevolutionary processes with phylogenetic patterns, the mechanism could rely on ecological speciation. This requires three elements: divergent selection, reproductive isolation, and a genetic mechanism linking the two (Nosil, 2012).

Hypotheses about the sources of divergent selection were already proposed by Grant & Grant (1965) and Stebbins (1970). Grant & Grant (1965) proposed that diversification in flower morphology can be the simple outcome of relative abundance of different pollinators in spatially isolated plant populations. Such contrasting pollination environments, in a pattern of geographic mosaic in pollinator availability (Thompson, 2005), could promote divergence in flower traits, whereby plants adapt to locally abundant pollinators, with speciation occurring as a consequence of specialization to different classes of pollinators. Indeed, it has been shown that pollinators can cause divergent selective trajectories on the flowers in a geographical context, as for instance in the variation in spur length through space (Boberg et al., 2014).

The above model was subsequently expanded by Stebbins (1970), emphasizing the role of the most frequent pollinator in shaping floral characteristics, proposing that evolutionary shifts in pollinators proceed through an intermediate stage during which two pollinators co-occur, but also underlying limitations to such changes imposed by the existing flower morphology. In Table 4, we review some examples of the selective pressures imposed on floral traits by insects and plant diversification caused by pollinator shifts. However, these mechanisms are not linked to insect evolution. Although pollinating insects can cause divergence and reproductive isolation in plants (Table 4), the opposite is not true except in very special cases (see Appendix 2) pointing to the limit to which such processes can be considered within a coevolutionary framework. In addition to the asymmetric nature of plant–pollinator interactions, not all floral traits are selected for by pollinators, but also by other floral functions or adaptations (Schiestl et al., 2010; Sakai et al., 2013).

Non-coevolutionary mechanisms that can generate codivergence

Two alternative mechanisms, ‘phylogenetic tracking’ and ‘sequential evolution’, can produce matching phylogenetic patterns, not relying on a reciprocal coevolutionary process. Phylogenetic tracking (Althoff et al., 2014)—largely inspired by the Fahrenholz’s rule—implies that a specialized species would speciate ‘in tandem’ with its host (Thompson, 1994).

A similar scenario was proposed by Jermy (1976), who observed that the interactions between phytophagous

Table 3 Examples of escalation in plant defense

| Plant taxon     | Escalating chemical defense | Outcome                                                                 | References               |
|-----------------|-----------------------------|-------------------------------------------------------------------------|--------------------------|
| Apiaceae        | Coumarins                   | No phylogenetic structure in the evolution of the various coumarin molecules | Berenbaum (1983)         |
| Asclepias       | Cardenolides in latex       | Phylogenetic progression in the potency and location of milkweed cardenolides | Farrell & Mitter (1998)  |
| Asclepias       | Latex exudation             | Conflicting results—overall negative correlation between amount of evolutionary change and amount of latex exudation; however, ancestral state reconstructions indicated that most speciation events were associated with increases in latex | Agrawal et al. (2008)    |
| Asclepias       | Latex exudation             | Species-rich lineages underwent a larger decline in latex and cardenolides than species-poor lineages in early stages of adaptive radiation; reduced investment in defensive traits accelerated diversification | Agrawal et al. (2009)    |
| Anacardiaceae   | Alkylcatechols              | The basal clade does not produce defenses, whereas alkylcatechols and alkylresorcinols are produced by many derived genera (Hemiptera do not feed on taxa producing alkylcatechols) | Aguilar-Ortigoza & Sosa (2004) |
insects and plants are largely asymmetric—that is, phytophagous insects usually occur at too low densities to exert important selective pressures on their hosts. Instead, Jermy proposed that plants evolve in response to other factors, and their diversification is followed by diversification in insect clades, a process he referred to as sequential evolution. In such a scenario, the insect overcomes plant defense and radiates in the available ecological space: it is plant resource heterogeneity itself that causes insect diversification and speciation. We would be cautious, however, in interpreting speciation patterns purely in this way, i.e., that the selective pressures generated by insects on plants are too weak to promote plant evolution. Indeed, there is much evidence of selective pressures exerted on plants by insect herbivores (e.g., Becerra, 1997), and even seemingly low levels of damage at a key developmental time (e.g., seed predation) can cause significant selective pressure (Thompson, 1994). In addition, there are many examples in which herbivore or predator load may be low precisely because of host defenses, which often work in a density-dependent manner (Underwood, 2000; Agrawal, 2004; Duquette et al., 2005; Chen, 2008). Indeed, although plant defenses can have many alternative roles, including protection against UV radiation or extreme climates (e.g., Jwa et al., 2006), the ubiquity and diversity of plant secondary compounds suggest that phytophagous insects impose selection on plants.

Can phylogenetic patterns be used to infer coevolutionary processes?

When comparing the phylogenies of herbivorous insects with their hosts, the lack of congruence and concurrent divergence is striking (Nyman, 2010; De Vienne et al., 2013), with the exception of a few examples mostly based on morphology or on inconclusive phylogenies (Farrell & Mitter, 1990, 1998; a review of congruent phylogenies and concordant codivergence is presented in Table 5).

Instead, another pattern emerges, in which most herbivores display a narrow host range and phylogenetic conservatism in host use, so that phylogenetically close species tend to use chemically similar and thus often phylogenetically close hosts, with host switches to more distantly related taxa occurring at relatively low frequency (Spencer, 1990; Thompson, 1994; Kergoat et al., 2005; Alvarez et al., 2006). Winkler & Mitter (2008) and Nyman et al. (2010) estimated that between 20 and 50% of speciation events involved a shift to a different host–plant species and, hence, were candidates for ecological speciation. Although molecular studies only allowed such insight into herbivore phylogenies for the last three decades, this general pattern had already been proposed by Brues (1924). Such a pattern

| Taxon Represented by Authors | Mechanism | References |
|-----------------------------|-----------|------------|
| Polemonium viscosum (Polemoniaceae) | Selection for large corollas by Bombus | Galen (1989) |
| Ten flowering plant species in Spain, Denmark, and Sweden | Selection for zygomorphy | Moller & Eriksson (1995) |
| Delphinium nelsonii (Ranunculaceae) | Stabilizing selection on flower color | Waser & Price (1981) |
| Dactylorhiza sambucina (Orchidaceae) | Negative frequency-dependent selection maintaining flower color polymorphism | Gigord et al. (2001) |
| Helianthus annuus (Asteraceae) | Natural selection on flower phenology by herbivore attack | Pilson (2000) |

Table 4 Processes at work in pollinator-based diversification

Reproductive isolation by floral traits and pollinator preference

| Taxon Represented by Authors | Mechanism | References |
|-----------------------------|-----------|------------|
| Salvia spp. | Pollen deposition on various body parts of visiting insects | Clasenbockhoff (2004) |
| Three species of Pedicularis (Orobanchaceae) | No support for mechanical reproductive isolation | Armbruster et al. (2014) |
| Ophrys, sexually deceptive orchid | High floral isolation due to pollinator specificity | Xu et al. (2011) |
| Chiloglottis, sexually deceptive orchid | Scent-mediated wasp pollinator specificity | Peakall et al. (2010) |
may also be retrieved in plant–pollinator interactions in which diversifying coevolution was hypothesized to take place (Thompson, 1994), but where pollinator shifts might play an important role in floral evolution (see Table 4).

Despite such evidence, the assumption that coevolution should produce congruent phylogenies has become widespread and persistent. Further confusion has been added by authors synonymizing coevolution with any instance of parallel cladogenesis (Miller, 1987). For example, Nyman (2010) stated, that ‘the weight of evidence has begun to converge on the ‘Jermyist’ scenario: although evidence for cospeciation […] or roughly coincident radiations of plants and herbivores […] has been found, it is becoming increasingly clear that present insect–plant associations mainly are a result of continuous host-shifting among pre-existing host taxa.’ This statement seems premature,

| Insect taxon | Plant taxon | Support | References |
|--------------|-------------|---------|------------|
| Tests for congruence | | | |
| Urophora (Diptera: Tephritidae) | Centaureinae, Carduinae (Asteraceae) | No evidence for congruent phylogenetic patterns of herbivores and hosts | Brändle et al. (2005) |
| Phyllonorycter (Lepidoptera: Gracillariidae) | 44 plant genera | Level of cospeciation between moth and host plants not greater than expected by chance, but closely related moths feed on closely related plants | Lopez-Vaamonde et al. (2003) |
| Hemiptera: Aphididae: Lachninae | Cupressaceae and Pinaceae | Switching hosts has played a key role in the speciation of the subfamily; feeding site fidelity plays a more important role in speciation than does host fidelity | Favret & Voegtlin (2004) |
| Hymenoptera: Tenthredinidae: Heterarthrinae | Several angiosperm genera | Extant host plant associations result from a combination of host conservatism and occasional shifts among plant taxa | Leppanen et al. (2012) |
| Uroleucon (Hemiptera: Aphididae) | Asteraceae | No documented cospeciation events between aphids and plants, but frequent host shifts accompanying divergence events | Pecquod et al. (2010) |
| Tests for concurrent divergence | | | |
| Urophora (Diptera: Tephritidae) | Centaureinae, Carduinae (Asteraceae) | Lag in the divergence time of herbivores and hosts | Brändle et al. (2005) |
| Asteromyia (Diptera: Cecidomyiidae) | Asteraceae | Herbivores radiated after their host plants, despite strong host clade conservatism | Stireman et al. (2010) |
| Hymenoptera: Tenthredinidae: Heterarthrinae | Several angiosperm genera | Herbivores diversified long after host taxa | Leppanen et al. (2012) |
| Coleoptera: Chrysomelidae | Angiosperms | Herbivores radiated long after their hosts | Gómez-Zurita et al. (2007) |
| Coleoptera: Curculionoidea | Gymno- and angiosperms | Herbivores diversified on gymnosperms in the Jurassic, subsequently diversified onto angiosperms, but that did not lead to immediate and major diversification | McKenna et al. (2009) |
| Hemiptera: Sternorrhyncha | Genisteae from the Canary Islands | Despite congruent phylogenies, the timing does not match | Percy et al. (2004) |
as the lack of congruence or lag in divergence time in phytophagous insects and their hosts do not tell anything about the processes at work, and do not allow us to identify a scenario for the radiations of interacting lineages, which are—as we have seen—largely decoupled.

As discussed above, coevolution per se is not expected to produce patterns of codivergence. Instead, other phenomena, namely host shifting and lineage duplication, usually cause highly incongruent patterns (De Vienne et al., 2013). Host shifting may blur the footprint of ‘interludes’ of coevolution in phylogenies, whereas lineage duplication within one lineage followed by partial extinction may produce incongruent phylogenies despite long-term diversifying coevolution among the associated lineages. Similarly, it is not correct to use the timing of putative parallel radiations as an argument for or against coevolutionary diversification. For instance, when evolutionary trajectories mimic what would be commonly but incorrectly assumed from a coevolutionary framework. This underlies the need for a ‘holistic’ treatment of case studies, including investigation of the biogeographical history of the associated species and testing for alternative hypotheses, as well as the use of simulation studies to predict the expected patterns.

On the other hand, some non-coevolutionary processes, either biogeographic, such as vicariance, or biotic, such as host tracking, can produce congruent patterns (Althoff et al., 2014). Host tracking is particularly challenging in such a context, as it predicts not only codivergence patterns but also parallel timing of divergence events, thus mimicking what would be commonly but incorrectly assumed from a coevolutionary framework. This underlies the need for a ‘holistic’ treatment of case studies, including investigation of the biogeographical history of the associated species and testing for alternative hypotheses, as well as the use of simulation studies to predict the expected patterns.

Concluding remarks and future research directions

We have shown that the link between coevolution and diversification of plant and insect lineages is neither obvious theoretically nor clearly supported empirically. Beyond the semantic issues and the often neglected need for reciprocity when investigating coevolutionary processes (if coevolution is driving species diversification, can herbivores cause speciation in plants and can plants cause speciation in pollinators?), diversification in both groups is a result of multi-dimensional processes. Their diversity—both at the within- and the among-species levels—is shaped by a combination of coevolutionary processes, asymmetric biotic interactions (Davies et al., 2004), stochastic changes in community assemblages (Cavender-Bares et al., 2009), spatiotemporal variation along the continuum from mutualism to antagonism in species trophic networks (Thompson, 1994), as well as a dynamic environmental background (Ezard et al., 2011). In addition, both insects and plants possess unique adaptations, which have led them to become the most successful groups of higher land organisms. As suggested by Crepet & Niklas (2009), the remarkable diversity and ubiquity of plant–insect interactions could be an effect of the intrinsic adaptability of plants and insects, rather than a primary cause of their success.

Even when coevolution plays a role in molding biodiversity, coevolutionary processes will generally occur during narrow reciprocal ‘coevolutionary interludes’ in both space and time (see Appendix 1). Therefore, when investigating the link between coevolution and biodiversity, ecological and evolutionary scales also matter (Hembry et al., 2014). This also calls for a rethinking of the equilibrium assumptions usually taken as granted by evolutionary ecologists (Agosta, 2006), for instance by incorporating dynamic ‘ecological fitting’ into the analysis of interacting networks.

In our opinion, comparative phylogenetic methods have proved insufficient to resolve questions related to coevolutionary processes. We argue that phylogenetic patterns alone can only identify whether partner fidelity or host switches are correlated with speciation and diversification, but cannot greatly advance the field. This fits in with Ollerton’s (1996) idea, that phylogenies are, in essence, of limited use to infer ecological processes sensu lato. Instead, it would be more pertinent to investigate postulated mechanisms of diversification—that is, novel defenses and counter-adaptations, and in particular, their escalation (Tables 2 and 3)—in each of the interacting clades.

More mechanistic understanding of defense and counter-defense dynamics can be achieved in a genomic perspective, by studying the underlying adaptations at the molecular level. A notable study of a detoxifying enzyme (nitrile-specifier protein) in the lepidopteran family Pieridae is a good example (Wittstock et al., 2004; Fischer et al., 2008). The identified mechanism was characterized at the genetic level, with its origin estimated to have occurred shortly after the evolution of the host plants. Acquisition of this novel defense is also temporally correlated with elevated diversification rates of the herbivore group, thus underlying the role of key traits in adaptive radiations (Wheat et al., 2007). Moreover, molecular characterization of the mechanisms allows a test of hypotheses about the genetic processes involved, such as gene duplication, including investigation of the driving forces for adaptation (Fischer et al., 2008), and tracking the dynamics at the population level (Heidel-Fischer et al., 2010). Tackling such adaptive dynamics in both plant and
insect groups at the molecular level would certainly be a valuable research direction.

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Appendix 1: Reciprocal coevolutionary dynamics

A striking example of how reciprocity in the coevolutionary process can occur, is the interaction between the passion flower Passiflora spp. and butterflies of the genus Heliconius. Passion fruit plants produce toxic cyanogenic compounds that protect the plant from most herbivores. Heliconius butterflies have evolved unique mechanisms of detoxification and sequestration of these toxic substances (Engler et al., 2000; Zagrobelny et al., 2004), a counter-defense that allowed this genus to specialize and diversify on Passiflora species (Benson et al., 1975). As insects managed to overcome the chemical defense, many passion fruit species evolved to produce egg-like...
structures on the leaves or other parts of the plant, which make female butterflies reluctant to oviposit on shoots that are apparently already occupied (Williams & Gilbert, 1981). In addition, *Passiflora adenopoda* DC. produces hook-like trichomes, guaranteeing full protection against *Heliconius* larvae (Gilbert, 1971).

This interaction differs from the examples of plant defenses and counter-adaptations in insects presented in Table 2, as it is, to our knowledge, the only example that could match Janzen’s definition of coevolution, assuming that the detoxification and sequestration mechanisms of *Heliconius* indeed evolved in response to the defenses of *Passiflora*.

Appendix 2: Breaking the one-to-one coevolution paradigm

Specific plant–insect interactions have long captured the attention of naturalists and ecologists (Bascompte & Jordano, 2013). Besides appearing to be elegant cases of perfectly matching—presumably coevolutionary—interactions, they also formed simple systems in which ecological and evolutionary questions could be addressed. Despite this, cases of coevolutionary diversification are extremely rare (De Vienne et al., 2013).

Figs and their pollinator wasps are undoubtedly the tightest pollination mutualism known (Cook & Rasplus, 2003). It has long been considered as an extreme case of specific one-to-one interactions, in which each fig species is pollinated by one unique species of wasp (Janzen, 1979; Wiebes, 1979; Weiblen, 2002). As figs are only pollinated by fig wasps, and wasp larvae can only develop on *Ficus* spp., the partners are completely dependent on each other for reproduction. Their interdependence is so high, that several Agaonidae lineages evolved to actively pollinate *Ficus* flowers and so ensure their own reproduction (Cruaud et al., 2012).

The complete reliance of each partner on the other for reproduction, combined with the apparent one-to-one specialization, was thus hypothesized to have led to very high levels of codivergence between the two groups.

However, we have recently begun to realize that the ‘one fig species—one pollinating wasp’ rule does not always hold, with multiple wasp species pollinating one fig species in sympatry (Cook & Rasplus, 2003). Similarly, the phylogenetic congruence hypothesis turns out to be only partially true, with host shifts between fig clades occurring among fig wasps, leading to incongruent patterns in phylogenies (Machado et al., 2005). Although recent comparative phylogenetic analyses revealed significant patterns of congruence among the two groups, it is now clear that the strict codivergence paradigm does not hold, with host shifts and duplications altering phylogenetic patterns (Jousselin et al., 2008; Cruaud et al., 2012). Although one cannot rule out that the system has mainly evolved through coevolutionary diversification processes (Cruaud et al., 2012; De Vienne et al., 2013), some level of phylogenetic tracking might also be at work.