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## Interspecific Coevolution

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### Introduction

The term coevolution has been applied to many kinds of interactions among organisms, but it was introduced to describe the evolution of interactions between butterflies and their host plants in particular (Ehrlich and Raven, 1964). Ehrlich and Raven (1964) attributed the feeding habits of butterfly larvae and the diversity of plant defences to a reciprocal evolutionary process in which herbivores have influenced changes in host plant chemistry and plants have selected for herbivore specialization in feeding preferences. They further suggested that this process has contributed to the impressive diversification of flowering plants and their herbivores.

Consider how monarch butterflies have circumvented the chemical defences of their milkweed hosts through physiological adaptations that enable the larvae to sequester toxic alkaloids in their bodies, which in turn provide defence against predators such as birds. Even if this physiological adaptation of monarchs evolved in response to selection pressure by milkweeds, it does not necessarily follow that these butterflies were the agents of selection that produced milkweed defences. Latex, cardiac glycosides, alkaloids and other defences are present throughout the plant order Gentianales, the lineage to which milkweeds belong. It is possible that the defences of milkweeds were inherited from an ancestor that evolved these defences in response to a diverse guild of herbivores quite unrelated to the milkweed specialists of the present day. Janzen (1980) argued against the use of the term coevolution to describe such situations. The example also points the distinction between pairwise and diffuse coevolution (Fox, 1988). Diffuse coevolution refers to multiple interacting lineages that have influenced one another in some reciprocal manner, as would an assemblage of insect herbivores attacking a particular host plant lineage. The more restrictive definition of pairwise coevolution refers to the case in which two interacting populations are agents of selection on each other. The same microevolutionary forces that shape the population-level definition are a source of macroevolutionary patterns of speciation and specialization.

Specialization is a hallmark of pairwise coevolution. Phylogenetic congruence of two lineages can provide evidence that the interacting partners have been associated with one another through evolutionary time. Parallel diversification or cospeciation occurs when speciation in one lineage is accompanied by speciation in the other. However, cospeciation is neither necessary nor sufficient for pairwise coevolution strictly speaking. Consider the example of aphids and their endosymbiotic bacteria that are passed from one generation of aphid to the next through the gut of the host. Suppose an ancestral aphid species splits into two descendant species due to factors such as geographical isolation of aphid populations, or divergence in feeding preferences for two host plants. This will result in the reproductive isolation of two bacteria populations which may, in turn, give rise to two descendant bacteria species. Codivergence of this sort does not imply coevolution as defined reciprocal evolutionary change in aphids and their gut bacteria. Thus, it is helpful to separate aspects of evolving species associations into components of cospeciation and reciprocal adaptation or coadaptation.

Coevolution has occurred when two or more lineages have acted as agents of selection on each other and have responded to one another through changes that increase fitness. Reciprocal adaptation is possible whenever an ecological interaction has fitness consequences for both partners. An introductory example is the interaction between phytophagous *Tetraopes* beetles (Chrysomelidae) and their milkweed hosts. Beetles specializing on these toxic plants have evolved elaborate behavioural and physiological means of escaping host defences. For instance, they may disrupt the flow of defensive latex to leaves by tapping secretory canals at the leaf bases and feeding on the distal portion. *Tetraopes* have recently evolved physiological tolerance to specific compounds in response to cardiac glycosides in their milkweed hosts (Farrell and Mitter, 1998). Secondary chemicals have also changed during the evolution of associations with *Tetraopes* such that defensive compounds of recent lineages are more toxic than those of their closest relatives. The escalation of plant defence and herbivore counterresponse is a fine example of an evolutionary 'arms race' that may have led to the diversification of these lineages (Farrell *et al.*, 1991).

The conditions necessary for coevolution are the same whether the interaction involves plants and insects, hosts and parasites, hosts and parasitoids, hosts and brood parasites, or predators and prey. There must be phenotypic variation in traits that influence the costs and benefits of the interaction for each player, whether parasitic, mutualistic or otherwise. Then there must be genetic components of this variation that can be selected by either lineage such that dynamic changes in fitness occur through time on both sides of the interaction. Fitness consequences for the players are also likely to vary across the geographic range of the interaction because the phenotypes and genetic architecture of the interacting populations usually vary from one location to another. When the intensity of selection varies across the range, we may observe hotspots where reciprocal selection is very strong and cold spots where it is weak. These processes at the population level are translated into a geographic mosaic of coevolution at the species level (Thompson, 1994). Subsequent sections develop these aspects of coevolution with examples from different types of biotic interactions.

## Plant–Insect Coevolution

The spectacular radiation of flowering plants and their insect herbivores, particularly beetles, butterflies and moths, is one of the most striking examples of the impact of coevolutionary processes on macroevolutionary pattern. The history of plant–insect interactions from the Cretaceous to the present (~135 million years) provides countless illustrations of how specialized associations evolve in general. Consider the phylogenetic relationships of beetles feeding on milkweeds, for example. If the beetles are specialized to the extent that offspring feed on the same host species as their parents, and beetles have cospeciated with their hosts, then we expect the phylogenies of the interacting lineages to be congruent (Figure 1a). In contrast to cospeciation, evolutionary events that result in phylogenetic incongruence include speciation in the beetle but not in the host (duplication), loss of a beetle lineage associated with a particular host lineage (extinction), and host speciation in the absence of beetle speciation ('missing the boat'). These patterns of association by descent are different from those of association by colonization, where beetles may have switched from one host lineage to another at some point in the past (host switching). If colonization by host shifts is common, incongruence between the phylogenies of beetles and their plants is expected. It is possible, however, that congruent phylogenies could result from recent, stepwise colonization of an already diverged host lineage. Congruent speciation times and branch lengths of phylogenies in hosts and associates, however, can rule out this less likely possibility. Phylogenetic patterns of speciation and specialization can help to identify potential causes of coadaptation.

The population genetics of reciprocal selection predicts covariation in the trait values of ecologically associated lineages through time. In evolutionary arms races, we see how the escalation of defence in a host plant lineage can select for herbivore counteradaptations. The costs of defence and counterattack can also drive traits in the opposite direction under the right ecological conditions. Time lag between the responses of plants and their herbivores to selection and geographic variation in fitness outcomes further add to the complexity of trait microevolution. However, correlated changes in interacting traits are expected to emerge at macroevolutionary scales, which can be inferred from phylogenies (Figure 1b). Ancestral reconstructions for a pair of interacting traits, each with two states, show coincident changes even though the phylogenies are not in perfect agreement. Mere correlations inevitably fall short of proving that two traits are reciprocally selected, but the overwhelming variety of apparent counteradaptations in plant–insect interactions is compelling evidence for coevolution.

The previous discussion has focused on antagonistic interactions where the insects benefit while having negative impact on their host plants. For example, *Setora* caterpillars (Limacodidae, Lepidoptera) defoliate fig trees and sequester latex in their brilliantly coloured bodies to warn and deter predators (Figure 2b). However, a remarkable feature of plant–insect interactions is the common occurrence of mutualism, ecological associations from which each party derives a fitness advantage. The same theoretical framework of costs and benefits that has been developed for antagonistic coevolution also applies to mutualism.

Associations between figs (*Ficus* species) and fig wasps (Agaonidae, Hymenoptera) are ideal comparative examples of plant–insect coevolution because they run the

gamut from mutualism to antagonism. Figs are characterized by a unique inflorescence, an enclosed receptacle containing many unisexual flowers (Figure 2a). The interior of the receptacle is accessible by a tight pore at one end, to which female fig wasps are attracted by chemical cues. The interior of the fig is the location of a remarkable mutualism wherein female wasps transport pollen from one fig to another while laying their eggs in some but not all of the flowers. Pollinating fig wasps are also seed predators because they feed on a fraction of the developing seeds as larvae. Male fig wasps are rather like cave dwellers; their activities being restricted to the fig interior, they have lost eyes, wings and other body parts (Figure 2c). Mated females emerge into the fig cavity, where they collect pollen from staminate flowers and escape their natal fig in search of a receptive fig in which to complete their life cycle. Striking correlations among various morphologies and behaviours are suggestive of coevolution. For example, variation in the shape of heads and mandibular appendages of different pollinator species is tightly correlated with the shape of the fig opening.

The pollinators of figs are highly specific to their host species and hundreds of pairwise associations are known. There are also parasitic fig wasps that do not provide any beneficial pollination services to the host. In contrast to a similar interaction between pollinating moths and yucca plants, it appears that fig pollination evolved once and that multiple independent lineages of parasitic wasps have colonized figs subsequently. The occurrence of pollinating and nonpollinating on the same host plants provides an intriguing comparison of how mutualistic and parasitic associations evolve through time. Molecular phylogenies for *Sycomorus* fig species and their specific *Ceratosolen* pollinators show evidence of cospeciation (Figure 2a). On the other hand, *Apocryptophagus* parasites attacking the same figs show fewer instances of cospeciation, and several parasite lineages have duplicated, missed the boat, or switched hosts (Figure 2b). Reconciliation analysis indicates that the agreement between pollinator and fig phylogenies is greater than expected by chance while congruence of fig–parasite phylogenies is not (Weiblen and Bush, 2002). A likely explanation for this difference is the fact that pollinator fitness is tightly coupled with the fertilization of fig flowers, while *Apocryptophagus* induce the abnormal development of unpollinated fig flowers. Mutualists that transport host gametes from cradle to grave, such as fig pollinators, are likely to exhibit the most extreme levels of parallel diversification with their hosts. These observations illustrate the kinds of evolutionary insights that can be gained from inspection of tangled phylogenetic trees and different life histories.

## Host–Parasite Coevolution

Organisms that do not suffer from some form of parasitism are exceedingly rare. Parasites generally reduce the fitness of their hosts by feeding in or on the host, resulting in death or reduced fecundity. Virulence is the extent to which parasites have negative impacts on their hosts, while resistance refers to the capacity of a host to avoid or tolerate these negative impacts. Simple models of virulence and resistance have assumed one-to-one interactions between attack and defence genes in parasites and hosts. An additional consideration is the mode of transmission, or how parasites infect their hosts and spread throughout populations. There has been great interest in understanding the conditions that favour the evolutionary stability or instability of parasitism, and less attention has been paid to the coevolution of virulence,

transmission and resistance in the narrow sense. [Gandon \*et al.\* \(2002\)](#) developed a model in which correlations between host and parasite traits are predicted in the presence of spatial variation in the fecundity and survival of the host. These predictions follow the general theory of a geographical mosaic of coevolution ([Thompson, 1994](#)).

### Host–Parasitoid Coevolution

Parasitoids are insects, usually Hymenoptera, that feed as larvae internally on a host, such as another insect, eventually killing the host and becoming free-living as adults. Host–parasitoid associations are a special case in which levels of specialization are as extreme as in the example of figs and fig wasps. As with host–parasite interactions, evolutionary studies have focused primarily on the question of stability. If extreme specialization limits opportunities for colonizing new hosts, how are parasitoids prevented from extinguishing their resource base? Although models have often focused on single homogeneous populations of interacting species, patchiness or spatial aggregations of parasitoids appears to be a major factor in stabilizing these interactions ([Godfray and Pacala, 1992](#)).

### Host–Brood Parasite Coevolution

One of the most remarkable examples of coevolutionary arms races is avian brood parasitism. Brood parasitism among nesting birds that depend on parental care has evolved repeatedly, in [cuckoos](#) and [cowbirds](#) for instance ([Payne, 1997](#)). When a foster parent rears others offspring, parasite fitness is increased by avoiding the cost of parental care at the expense of the host. Cowbirds may remove eggs from the host nest when laying their own. Cuckoo nestlings, on the other hand, negatively impact host reproductive success soon after they hatch by removing eggs and young from the nest. The impact of cuckoos is particularly extreme because they eliminate all offspring from the nest. Such strategies increase the investment of resources by the foster parent in the parasite. A wide range of defensive adaptations are also found in hosts, such as hiding or defending the nest, piercing or ejecting parasite eggs, or abandoning the nest when attacked. Behaviours such as abandoning the nest carry the cost of time and resources lost to nesting, not to mention the offspring left behind. Ejecting eggs from the nest also bears the risk of mistaking offspring for parasites. Rather than risk a costly defence, some hosts just accept parasitism.

It is believed that counteradaptations to host defence are as diverse in brood parasites as the adaptations of their hosts. A fitness advantage is predicted for any trait that limits parasite egg rejection or helps parasitic young outcompete host offspring for parental resources. Potentially coevolved parasite traits include thickened eggshells, egg size and colour patterns, incubation time, and nestling behaviour. Thicker eggshells in parasitic cuckoos relative to nestling cuckoos could provide protection against puncture. Cuckoo eggshells often mimic those of their foster parents in colour and pattern, a likely consequence of selection by egg-rejecting hosts. Shorter incubation periods in parasites relative to hosts advance the competitive ability of parasite offspring. Cuckoo nestlings even have flat backs with which to lift and eject eggs from the nest. These adaptations are likely the result of dynamic and ongoing

coevolutionary processes that enable a multitude of species interactions to vary between extremes of stability and instability.

## Predator–Prey Coevolution

Dynamic models of the interactions between predators and prey have provided testable predictions about the role of coevolution with regard to the stability or instability of ecological interactions in general (Abrams, 2000). Predators, defined as individuals of one species that consume individuals or biomass of prey species, may include parasites and parasitoids but not disease organisms or herbivores. Such an inclusive definition is useful for modelling predator–prey interactions mathematically (Abrams, 2000). Most models predict that coevolution can produce cycles in population densities and trait values, and that cycling may be evolutionarily stable under some conditions. Capture rate is a key parameter in these models, a function of predator and prey population densities and traits related to prey detection, predator avoidance, and defence.

If a predator reduces the size of its prey population and the predator is not satiated, the risk of capture increases for the prey. This increases the intensity of selection for predator avoidance and defence traits, eventually reducing the size of the predator population to the point where selection favours for the reduction of costly resistance traits. Coevolutionary cycles can result if there is a sufficient time lag between predator population dynamics and changes in prey vulnerability traits.

Evolution of capture-related traits in the predator appears to confer stability while prey evolution may increase the instability of the interaction. Instability can result in cycling of population and trait values, or in species extinction. Cycling is most likely to result when evolutionary change in prey vulnerability is possible in both directions, such that prey lower their risk by modifying traits relative to a most-vulnerable form that is, in turn, dependent on the predator's phenotype. Some of the additional conditions for coevolutionary cycling of predators and prey include faster evolutionary rates in prey than in predators, stabilizing selection imposed by trait costs, and less than optimal efficiency in conversion of prey resources into the next generation of predators.

An excellent example of coevolutionary dynamics in predators and prey is the interaction between garter snakes (*Thamnophis*) and their poisonous prey, *Taricha* newts (Brodie *et al.*, 2002). These newts produce levels of tetrodotoxin that are lethal to predators except for garter snakes that have evolved tetrodotoxin resistance. As predicted by the geographic mosaic theory of coevolution (Thompson, 1994), there is variation in tetrodotoxin resistance across the predator's range that is strongly correlated with local levels of newt toxicity. Phylogeny suggests that there are at least two hotspots where tetrodotoxin resistance has evolved independently across the geographic range of the predator. Where reciprocal selection has intensified the arms race between predator and prey in hotspots of coevolution, snakes may assess toxicity relative to resistance and reject prey that are too toxic. This provides a dramatic demonstration of the role that geographic variation plays in the coevolutionary process.

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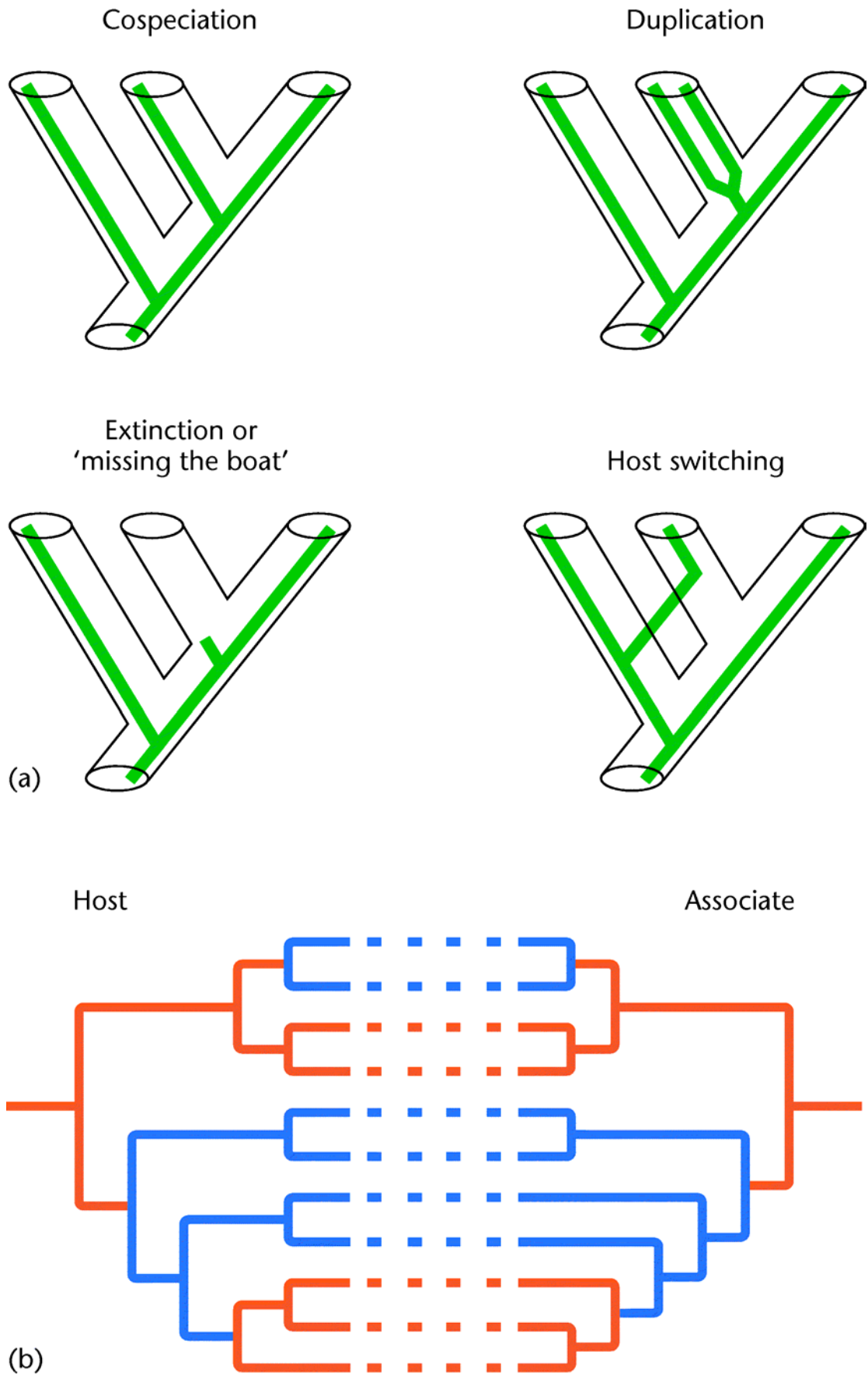
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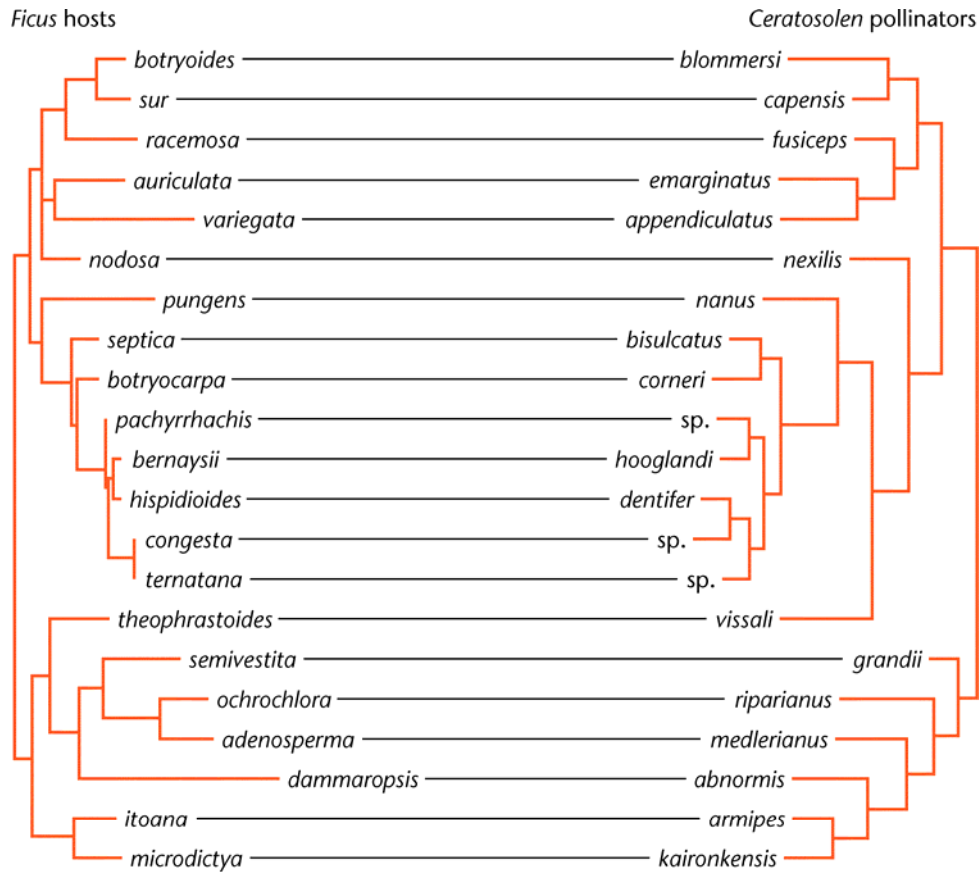


**Figure 1** Phylogenetic aspects of coevolution. (a) Evolutionary events influencing the extent of phylogenetic congruence between host lineages and their ecological

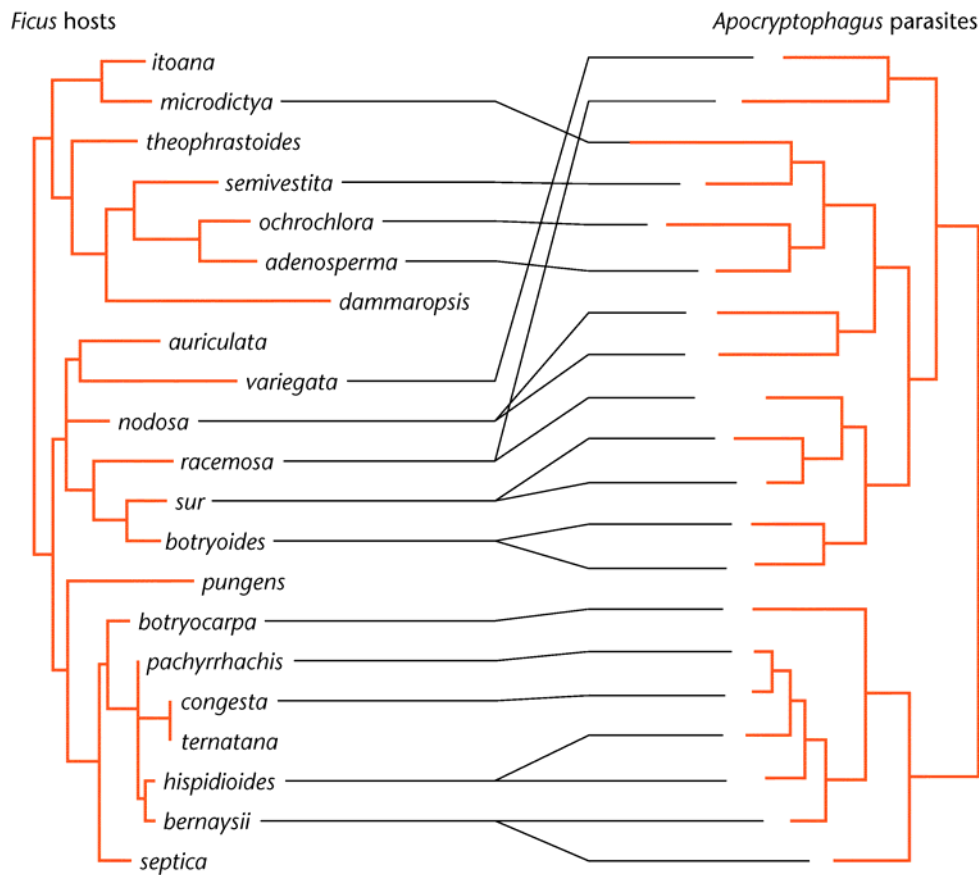
associates. Host lineages are represented by branching tubes and associates by branching lines to illustrate cospeciation, duplication, extinction, ‘missing the boat’, and host switching. (b) Phylogenetic evidence can also support hypotheses of coadaptation, as illustrated by phylogenies for a host and its associate with dotted lines showing current ecological associations. Ancestral reconstructions for a pair of interacting traits, each with two states, grey and black, show coincident changes even though the phylogenies are not perfectly congruent. Reciprocal selection can produce such correlated trait changes in coevolutionary arms races.



**Figure 2** Examples of plant–insect coevolution. (a) The edible fig, *Ficus carica*, showing the unique inflorescence which is home to the pollination mutualism with fig wasps. Scale 10 mm. Reproduced from Ehret GD (1750) *Plantae Selectae*. (b) *Setora* caterpillars (Limacodidae, Lepidoptera) feeding on latex-bearing leaves of *Ficus nodosa* in Papua New Guinea. Scale 10 mm. (c) Scanning electron micrograph of a male fig wasp, *Kradibia ohuensis*, the obligate pollinator of *Ficus trachypison* in Papua New Guinea. Scale 0.1 mm. (d) The female head and mandibular appendage of *Wiebesia brusi* are apparently coadapted with the inflorescence bracts of *Ficus baeuerlenii* from Papua New Guinea. Scale 0.1 mm. Photographs from GD Weiblen.



(a)



(b)

**Figure 3**#The evolution of associations between selected fig species, their pollinating mutualists, and their parasites. (a) Molecular phylogenies for *Sycomorus* figs and their species-specific *Ceratosolen* pollinators suggest a history of cospeciation (Weiblen and Bush, 2002). (b) Phylogeny of *Apocryptophagus* parasites attacking the same figs suggests that fewer cospeciation events have occurred than for pollinators, and several parasite lineages may have switched hosts. Unpublished data from S Silveus and GD Weiblen.

### Glossary

*Brood parasite*#A bird that lays its eggs in the nest of other bird species, leading the parental host to rear its offspring, which may eject the offspring of the host from the nest.

*Coadaptation*#Reciprocal evolutionary change in the traits of two interacting lineages that stems from each lineage acting as the agent of selection on the other lineage.

*Cospeciation*#Simultaneous splitting of ancestral species into two or more descendant species in two ecologically associated lineages.

*Parasitoid*#An insect, usually Hymenoptera, which feeds as a larva internally on the body of a host, such as another insect, eventually killing the host and becoming free-living as an adult.