18

Coevolution

◀ Bees visit a water lily at Mole National Park, Ghana.

All over the planet, lichens grow on rocks and trees. Everything about lichens—the way they look, the way they reproduce, the way they respond to environmental change—would make the casual observer think that they are well-integrated multicellular organisms. And they are, but not in the usual sense: Every lichen is made up of two different species (Brodo et al. 2001).

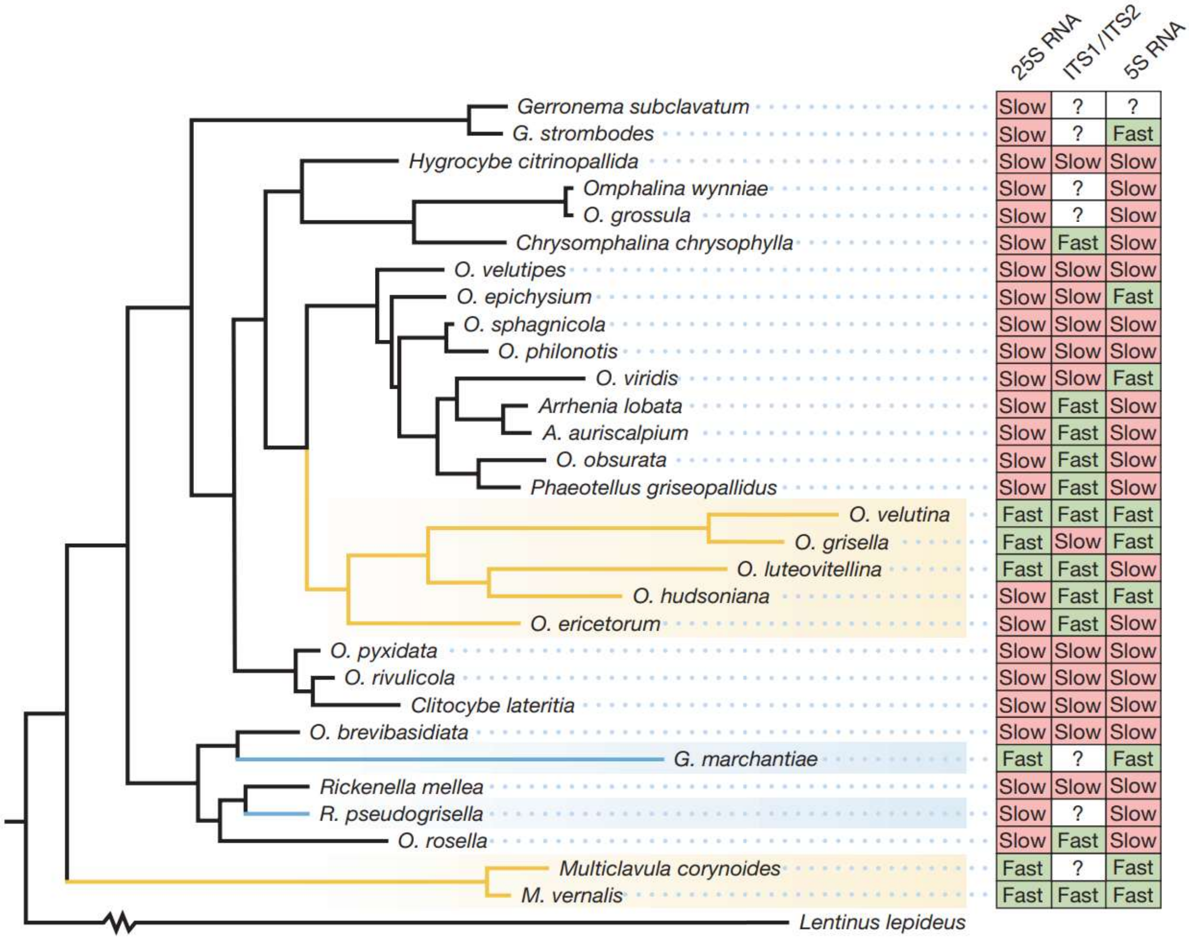
There are thousands of different kinds of lichens, each of which is composed of one fungal species and one species of either photosynthetic algae or cyanobacteria. In the case of fungal–algal lichens, fungal cells typically surround the algal cells to form the body, or thallus, of a lichen. Each species in a lichen derives benefits from the other. The fungi use sugars produced by photosynthesis in the algae. The algae benefit from the fungi's ability to retain water, and they also use some of the resources that fungal cells extract from soil. The algae and fungi in a lichen live in a mutualistic relationship—each benefits the other. The codependency between algae and fungi is so complete that, for most lichens, neither the fungal nor the algal species can survive in the absence of its partner. As a result, the fungi and algae have evolved to disperse together. One remarkable form of reproduction in lichens occurs through the spread of *diaspores*, which contain both algal and fungal cells.

When species interact in a deep and integrated fashion, as fungi and algae do in lichen, natural selection acting on one species may cause selection to operate in new ways on the other species. Evolutionary biologists say that coevolution occurs when changes to heritable traits in species 1 drive changes to heritable traits in species 2, which in turn feed back to affect heritable traits in species 1, and so on, back and forth. When the interaction of the two species increases the fitness of both species, this is called a mutualism.

In the case of fungi and algae, we can examine how the two species can coevolve in lichen. Above and beyond their remarkable natural history, lichens are an excellent model system for formulating and testing hypotheses about coevolution, particularly molecular genetic and phylogenetic questions regarding coevolution. This is because: (1) biologists have the tools to make molecular genetic comparisons among many species involved in lichen formation, and (2) many species of fungi that are part of a lichen have sister species that are not in a lichen association, which allows us to use the comparative method to address coevolutionary questions. For example, evolutionary biologists have hypothesized that the transition to, and the maintenance of, a mutualistic relationship like that seen in lichens must be complex and require many changes to the genomes of both species involved. We can then ask: Is there evidence for such changes to the genomes of algae and fungi that associate to form lichens?

To answer that question, François Lutzoni and Marc Pagel used the comparative method and examined the rate of nucleotide substitution in free-living versus mutualistic fungi (Lutzoni and Pagel 1997). They compared 1550 ribosomal nucleotide sites in 16 species of mutualistic fungi (primarily in lichens, but some in liverworts) and 13 species of free-living fungi that are closely related to the mutualistic lichens species. Lutzoni and Pagel found that there was a faster rate of molecular evolution in the mutualistic fungi. Specifically, the rates of nucleotide substitution were much higher in fungal species involved in mutualistic relationships with algae and liverworts than the rates in the closely related, free-living fungal species. Moreover, the researchers found evidence consistent with the hypothesis that the transition to mutualism was responsible for accelerating the rate of molecular evolution. They discovered that the increased rate of nucleotide substitution occurred only during and after the transition to the mutualistic relationship, not before. Finally, they also found that the increased rate of nucleotide substitution in mutualistic species was not constrained to one specific area of the genome, but rather it was widespread across many sections of the genome (**Figure 18.1**). Not only are the fungal and algal species that are in a lichen association coevolving, but also the process of coevolution has quickened the pace of evolutionary change throughout the genome of at least one of the partners in this mutualistic relationship. Subsequent work suggests that rates of substitution may be especially high when lichens move to new niches with new moisture requirements—where new selective conditions are at play (Lumbsch et al. 2008).

At a very general level, the long-term evolutionary dynamics of coevolution can lead to (1) mutualistic interactions, where each species benefits the other species (Boucher 1985; Bronstein 1994; Connor 1995; Thompson



	25S RNA	ITS1/ITS2	5S RNA
Gerronema subclavatum	Slow	?	?
G. strombodes	Slow	?	Fast
Hygrocybe citrinopallida	Slow	Slow	Slow
Omphalina wynniae	Slow	?	Slow
O. grossula	Slow	?	Slow
Chrysomphalina chrysophylla	Slow	Fast	Slow
O. velutipes	Slow	Slow	Slow
O. epichysium	Slow	Slow	Fast
O. sphagnicola	Slow	Slow	Slow
O. philonotis	Slow	Slow	Slow
O. viridis	Slow	Slow	Fast
Arrhenia lobata	Slow	Fast	Slow
A. auriscalpium	Slow	Fast	Slow
O. obsurata	Slow	Fast	Slow
Phaeotellus griseopallidus	Slow	Fast	Slow
O. velutina	Fast	Fast	Fast
O. grisella	Fast	Slow	Fast
O. luteovitellina	Fast	Fast	Slow
O. hudsoniana	Slow	Fast	Fast
O. ericetorum	Slow	Fast	Slow
O. pyxidata	Slow	Slow	Slow
O. rivulicola	Slow	Slow	Slow
Clitocybe lateritia	Slow	Slow	Slow
O. brevibasidiata	Slow	Slow	Slow
G. marchantiae	Fast	?	Fast
Rickenella mellea	Slow	Slow	Slow
R. pseudogrisella	Slow	?	Slow
O. rosella	Slow	Fast	Slow
Multiclavula corynoides	Fast	?	Fast
M. vernalis	Fast	Fast	Fast

FIGURE 18.1 Rates of evolutionary change in mutualistic and free-living fungal species. A phylogenetic tree of the fungal genus *Omphalina* and related species reveals a more rapid pace of molecular evolution in the species involved in mutualistic associations. On the phylogenetic tree, clades associated with lichen-forming algae are indicated in yellow; species involved in mutualistic associations with liverworts are shown in blue. In the columns on the right, the rate of molecular evolution for each species is assessed in three different ribosomal RNA regions: the 25S RNA region, the regions around the spacers ITS1/ITS2, and the 5S RNA region. The columns on the right indicate slow (in red) and fast (in green) rates of nucleotide substitution in the fungi. An unknown rate of molecular evolution is indicated by a question mark. Fast evolutionary change tends to be associated with a mutualistic lifestyle. Adapted from Lutzoni and Pagel (1997).

2005), and (2) **antagonistic coevolution**, in which each species decreases the fitness of the other species. While we will often consider these separately throughout the chapter, keep in mind that a species may be involved in antagonistic coevolution with one partner and mutualistic coevolution with another partner. For example, *Photorhabdus luminescens*, a bacteria that is pathogenic to many insects (an antagonistic relationship), forms a mutualistic relationship with certain nematode species (Somvanshi et al. 2012).

A classic example of antagonistic coevolution is the relationship between predators and their prey, where selection for antipredator traits in prey—faster escape time, camouflage ability, and so on—favors traits in predators that produce better success at catching these prey, which selects for new antipredator behavior in the prey, and on and on. Antagonistic coevolution produces an "evolutionary arms race" between predator and prey that may go on indefinitely, producing a wide array of both mechanisms by which prey can protect themselves against predators and systems by which predators can find and capture prey. We will discuss such evolutionary arms races in depth later in this chapter.

So far, we have been presenting a particular coevolutionary relationship as involving only two species; that is, what is often called pairwise coevolution. Pairwise coevolution is so common that sometimes the word *coevolution* is used as a synonym for it. In many instances, though, coevolution will involve more than two species. When this is the case, changes in any of the species involved may cause changes in some or all of the other species, which then set in motion the feedback loop we described in pairwise evolution. The more species involved, the more difficult it is to tie a specific change in one species to specific changes in one or more of the other species. This is referred to as **diffuse coevolution**. For example, imagine a simple case of diffuse coevolution in which a species of hawk preys upon a species of rabbit and a species of mouse. Changes in habitat preferences of the mouse species may impose new selection pressures on the hawk population, leading to new traits being favored in the hawk species. Resultant changes in the physiology of the hawks may set in motion further selection not only on the mouse population, as in pairwise coevolution, but also on the rabbit population. Moreover, the new strength of selection may not be the same on the rabbits as it is on the mice.

Diffuse coevolution is not limited to antagonistic interactions. It also plays an important role in mutualistic coevolution. For example, panic grass, *Dichanthelium lanuginosum*, can live in the geothermally heated soils of Yellowstone National Park, where soil temperature often exceeds 130°F. To survive in this scorching environment, the plant requires the presence of a fungus, *Curvularia protuberata*. For the fungus to survive in the soil, it in turn requires that a virus, called the *Curvularia* thermal tolerance virus (CThTV), be present in the environment (Marquez et al. 2007). Changes in any of these species feed back and affect selection on the others (**Figure 18.2**).

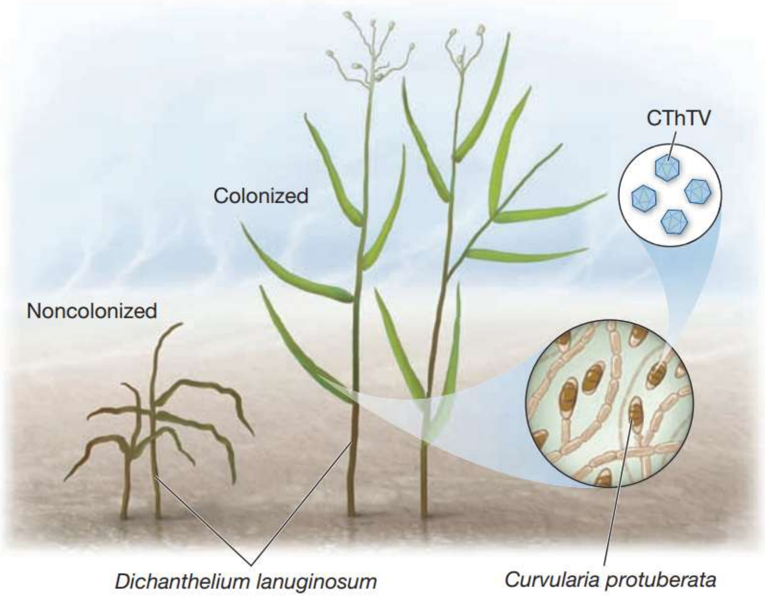


FIGURE 18.2 A diffuse three-way mutualism. *Dichanthelium lanuginosum* lives in the hot soils of Yellowstone National Park. To survive, the plant needs the fungus *Curvularia protuberata*. For the fungus to survive, the *Curvularia* thermal tolerance virus (CThTV) must be present. The plant on the left has not been colonized by *Curvularia protuberata* or CThTV, while the plant on the right has been colonized by *Curvularia protuberata* and CThTV. Adapted from Roossinck (2011).

Diffuse coevolution may also involve a combination of antagonistic and mutualistic interactions (Vannette et al. 2013). For example, a mutualistic relationship exists between hummingbirds and the hummingbird-pollinated shrub *Mimulus aurantiacus*. Prior work on plant–pollinator mutualisms had found that microbes that live in floral nectaries may affect the strength of such plant–pollinator mutualisms. To examine the effect of such "third parties" on the mutualism between hummingbirds and *Mimulus*, Racheal Vannette and her team experimentally manipulated the presence of two microbes—a bacterium and a fungus—known to inhabit the floral nectary of *Mimulus aurantiacus*. They found the bacterium *Gluconobacter* had detrimental effects on the seed set of the plant, the amount of nectar consumed by pollinators, and the pollination success in *M. aurantiacus*. None of these detrimental effects were found when the microbe in the floral nectary was the fungus. The bacterium and the fungus, though both inhabitants of floral nectaries, had dramatically different effects on the costs and benefits of the hummingbird–shrub mutualism.

In this chapter, we will examine the following questions:

- How can mutualistic interactions between members of different species increase the fitness of individuals in each species and result in coevolution?
- In what situations does antagonistic coevolution occur between interacting species, and what are the evolutionary consequences of antagonistic coevolution?
- How can natural selection result in mosaic coevolution, in which there are mutualistic interactions between members of two species in some communities but antagonistic interactions between members of the same two species in other communities?
- What is gene–culture coevolution?

Before we move on to these questions, it is important to recognize the general power of coevolution. In a sense, coevolution may be the most important process driving evolutionary change. What we mean here is this: Evolutionary biologists are interested in understanding the history and diversity of life. Natural selection is a primary driver of biological diversity, and the sources of selection on a population at any point in time will be both abiotic (temperature, humidity, acidity, and so on) and biotic (the results of other living creatures). Traits that are favored in response to some abiotic factor in the environment, however, do not necessarily feed back on the environment, causing the environment to change and create further selection. If thicker fur is favored in Arctic environments, that has no effect on the temperature there. But, as we have argued earlier, traits that are favored in response to biotic factors—that is, other species, be they symbionts, competitors, predators, prey, or parasites—feed back on these other species.

Coevolution, and the changes it produces, can have dramatic effects on diversity in ways that abiotic factors cannot. This change in diversity can be studied in real time in certain systems. For example, antagonistic coevolution between the blue-green algae *Synechococcus* and the RIM8 virus was studied for 6 months in a series of laboratory microcosms. In each microcosm, in just 6 months, researchers documented 4–13 new viral phenotypes and 4–11 newly evolved *Synechococcus* phenotypes that differed in viral resistance (Marston et al. 2012). Similar sorts of rapid change and diversification have been found in other experimental microcosms in which the process of coevolution can be monitored and measured in real time (Kashiwagi and Yomo 2011; Brockhurst and Koskella 2013).

Coevolution can lead to changes in diversity in other ways as well. When novel traits are favored in a species as a result of coevolution, such novel traits may open up completely new, potentially very large, niches to that species in a process called *escape-and-radiate coevolution* (Ehrlich and Raven 1964; Fordyce 2010). An extreme example of escape-and-radiate coevolution is evident in the evolutionary history of interactions between beetles and angiosperms (flowering plants). A molecular phylogeny, combined with evidence from the fossil record, has found that beetle diversity increased dramatically, via a series of adaptive radiations, as this clade evolved new ways of feeding on angiosperms. The increase in beetle diversity as a result of this escape-and-radiate coevolution is estimated at an astonishing 100,000 species (Farrell 1998).

18.1 Coevolution and Mutualism

In Chapter 17, we examined the evolution of intraspecific (that is, within-species) cooperation. The mutualisms that we discuss in this chapter are examples of interspecific cooperation. But why make a distinction between intraspecific and interspecific cooperation? Part of the answer is historical. Different sets of researchers, with different research questions, have studied intraspecific versus interspecific interactions, and many of them have developed their own set of terms. But there is also a conceptual reason to make such a distinction. When interactions are intraspecific, the interactants share the same gene pool, and natural selection operates on alternative alleles in that gene pool. In contrast, as we will see throughout the course of this chapter, when interactions are interspecific, and interactants do not share the same gene pool, evolutionary interactions are different from those in the intraspecific case. To see why, we will begin with a discussion of how mutualistic relationships originate.

The Origin of Mutualisms

When we study a specific mutualism, we are looking at a snapshot of one point in evolutionary time. But we can also ask how mutualisms evolved. The answer is that there is no one set path by which a mutualism originates and evolves. In some cases, mutualisms have evolved from initially neutral interactions between species, in which neither party initially affected the other's fitness. Some mutualisms have evolved from interactions in which one species benefited and the other species was initially unaffected. Yet other mutualisms have evolved from an initially parasitic relationship when the costs and benefits of that parasitic relationship changed and favored mutualism. And in yet other instances, the relationship between species has been mutualistic from the very start of their interaction.

In **Table 18.1**, we present a few of the numerous systems in which the evolution of mutualism has been studied. While this gives us a sense of the wide array of mutualisms that exist in nature, to understand fully the exquisite adaptations that result from the evolutionary dynamics of mutualisms and to comprehend better the complex, often indirect interactions between the parties in such mutualisms,

TABLE 18.1

Examples of Mutualisms

Example	Partner 1	Partner 2	Context
		SURVIVAL AND GROWTH	
Mitochondria	Eukaryotes	Bacteria	Cellular energy
Chloroplasts	Eukaryotes	Cyanobacteria	Photosynthesis
Marine reefs	Corals	Dinoflagellates	Photosynthesis
Lichens	Fungi	Green algae/cyanobacteria	Nutrition
Mycorrhizae	Plants	Fungi	Plant nutrition
Rhizobia	Plants	Bacteria	Nitrogen fixation in soil
Gut symbionts	Animals	Bacteria	Digestion in animals
Gut symbionts	Termites	Protozoa, bacteria	Ability to digest cellulose
Fungus gardens	Ants	Fungi	Agriculture by ants
Chemosymbiosis	Bacteria	Invertebrates	Colonization of deep sea vents
		REPRODUCTION	
Pollination	Plants	Animals	Sexual reproduction in plants
Seed dispersal	Plants	Animals	Sexual reproduction in plants

Adapted from Thompson (2010).

we need to delve more deeply into some well-studied systems. We will begin with a mutualism between ants and fungus.

Ant–Fungus Mutualisms

Approximately 50 million years ago, ants began cultivating their own food by entering into mutualisms with certain species of fungi and tending "fungal gardens" (**Figure 18.3**) (Mueller and Rabeling 2008). These mutualisms continue to this day, and ants are one of the few taxa on the planet that grow their own food. The ants promote the growth of the fungi, while eating some of the vegetative mycelium—threadlike hyphae that absorb nutrients from the soil and break down plant material—produced by their fungal partners.

Cameron Currie and his colleagues have found a fascinating adaptation in attine ants such as the leaf-cutter ant *Acromyrmex octospinosus* and other fungal gardening ant species such as *Cyphomyrmex costatus* and *Apterostigma pilosum*. Remarkably, these ants not only provide a safe haven for fungi to grow but also protect the fungi from disease (Currie et al. 1999a,b; Cafaro and Currie 2005; Mangone and Currie 2007;

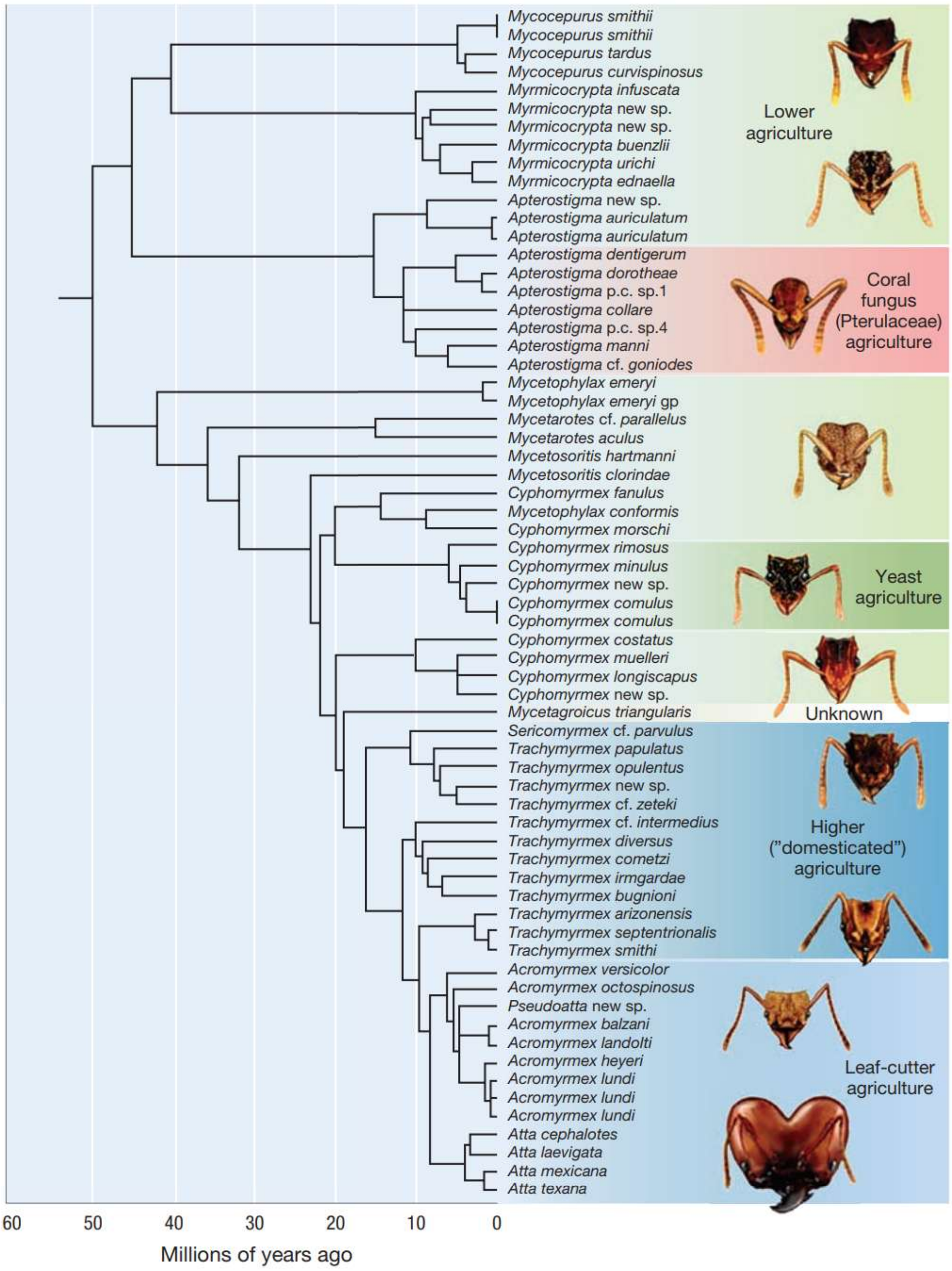


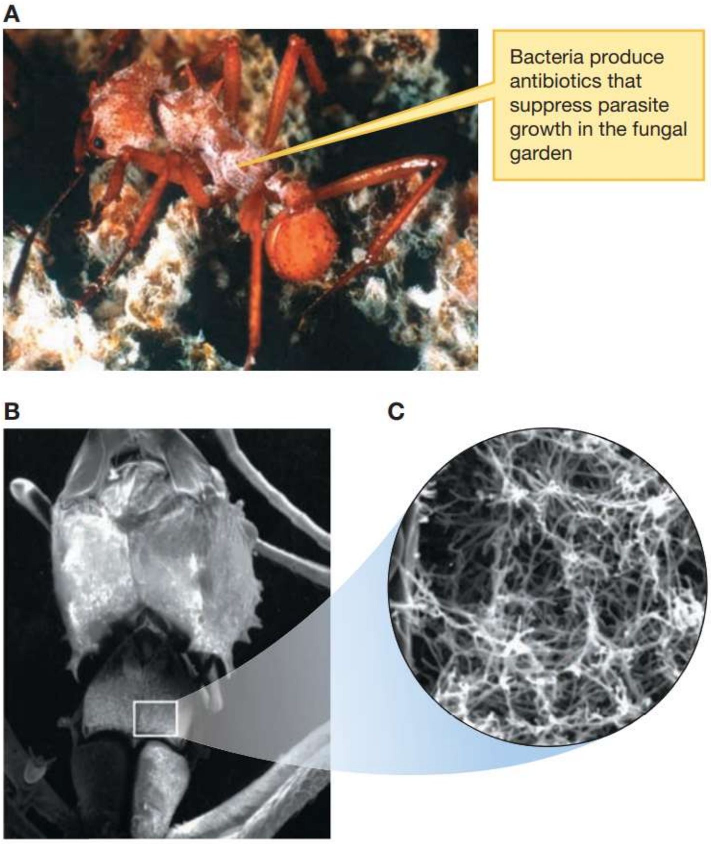
FIGURE 18.3 A phylogeny of attine, fungus-growing ants. The phylogenetic history of the five known ant agricultural systems: lower agriculture, coral fungus agriculture, yeast agriculture, higher agriculture, and leaf-cutter agriculture. Adapted from Schultz and Brady (2008).

Clardy et al. 2009; Cafaro et al. 2011). Researchers who study ants that tend fungal food gardens have long known of a whitish-gray crust found on and around many species of these ants (but not in species who do not tend gardens) (**Figure 18.4**). Currie and his team discovered that this whitish material is a mass of bacteria—primarily *Pseudonocardia* and *Streptomyces* bacteria.

Pseudonocardia and *Streptomyces* bacteria produce numerous antibiotic substances. Knowing this, Currie and his colleagues hypothesized that ants use the antibiotics produced by these bacteria to kill parasites that grow in their fungal gardens, thereby protecting their fungal food supply. A number of lines of evidence support this hypothesis: (1) all 20 species of the fungus-growing ants that

Currie and his team examined had *Streptomyces* bacteria associated with them; (2) these bacteria prevent the growth of certain parasitic fungi on the ants' fungal crop; (3) the antibiotics produced by these bacteria inhibit only *certain* parasitic diseases that directly threaten the fungal crop; (4) ants transmit the bacteria across generations, with parents—primarily mothers—passing the bacteria on to offspring; and (5) some species of fungus-growing ants—but no other ant species—have specialized indentations known as fovea all over their bodies. The bacteria live in these fovea, and the fovea appear to be supplied with nutrients of some type by exocrine glands (Currie et al. 2006).

One thing that makes the use of antibiotics by the ants in this mutualism so remarkable is that the antibiotics are specifically targeted toward pathogens that are dangerous to the fungal food crop growing in the ants' garden. When Currie and his colleagues tested the antibiotics produced by the bacteria that made up the white crust on the ant, they found that these antibiotics were potent only against the parasitic *Escovopsis* fungus—a serious threat to the ants' fungal garden. Other parasitic fungal species (those not a danger to fungus-growing ants) were unaffected by the antibiotics produced by *Streptomyces*, suggesting that selection has favored the use of the *Streptomyces* bacteria by the ants. These kinds of protective mutualisms are not found among ants alone. Recent work suggests that termite species that grow fungus also use antibiotics to protect their fungal gardens (Visser et al. 2012).



Bacteria produce antibiotics that suppress parasite growth in the fungal garden

FIGURE 18.4 Leaf-cutter ants protect their fungal garden. **(A)** A worker of the leaf-cutter ant (*Acromyrmex octospinosus*) tending a fungal garden. The thick whitish-gray coating on the worker is composed of bacteria that produce the antibiotics that suppress the growth of parasites in the fungal garden. **(B)** Scanning electron micrograph of a worker, showing the location of the bacteria. **(C)** Detail of the micrograph in panel B.

Other work by Currie and his team has uncovered even more subtle components to the ant–fungus mutualism. In addition to directly using the antibiotics produced by *Streptomyces* to protect their fungal gardens, the ants meticulously groom these gardens and physically remove fungus from their garden that has been infected with *Escovopsis* (Mangone and Currie 2007). Ants pick up parasitic fungal *Escovopsis* spores and hyphae and place them in areas of their body called infrabuccal pockets. Inside these pockets, the spores and hyphae are killed by the antibiotics that are also present in the infrabuccal pockets. The ants then take the dead spores and hyphae and deposit them in a separate pile away from the fungal garden (Little et al. 2003, 2006).

Because many leaf-cutter ants grow their own food via fungal gardens, and because the fungal gardens break down lots of plant material that then becomes available to the ants, Currie and his team predicted that compared to species that do not grow their own food, leaf-cutter genomes would show evidence for the loss of genes associated with nutrient acquisition and normal digestion. When a team of researchers sequenced the entire genome of one leaf-cutter species (*Atta cephalotes*) that relies on fungal gardens, they discovered a number of lines of evidence supporting this prediction. For example, they found extensive reduction in the production of enzymes (serine proteases) typically used during digestion. Currie and his team also found evidence for the loss of genes involved in producing the amino acid arginine, leading to a new, but as of yet untested, hypothesis that leaf-cutter ants obtain this amino acid directly from the fungi in their garden (Suen et al. 2011).

As complex as this multiorganism symbiosis seems, recent studies have also revealed another player, a black yeast that grows upon the ants' cuticle where the *Pseudonocardia* and *Streptomyces* bacteria are found (Little and Currie 2007). These yeast appear to feed on the bacteria themselves, rather than on the ants or the fungal garden. The consequences propagate on to the garden, though: Black yeast inhibits bacterial growth, which reduces antibiotic production, which in turn allows the *Escovopsis* parasite to grow, with a negative effect on the productivity of the fungal garden (Little and Currie 2008) (**Figure 18.5**).

The relationship between ants and their fungal gardens demonstrates that mutualistic relationships involve not only pairs of species, but also whole ecological communities joined together by complex and subtle interactions that generate a network of positive and negative relationships.

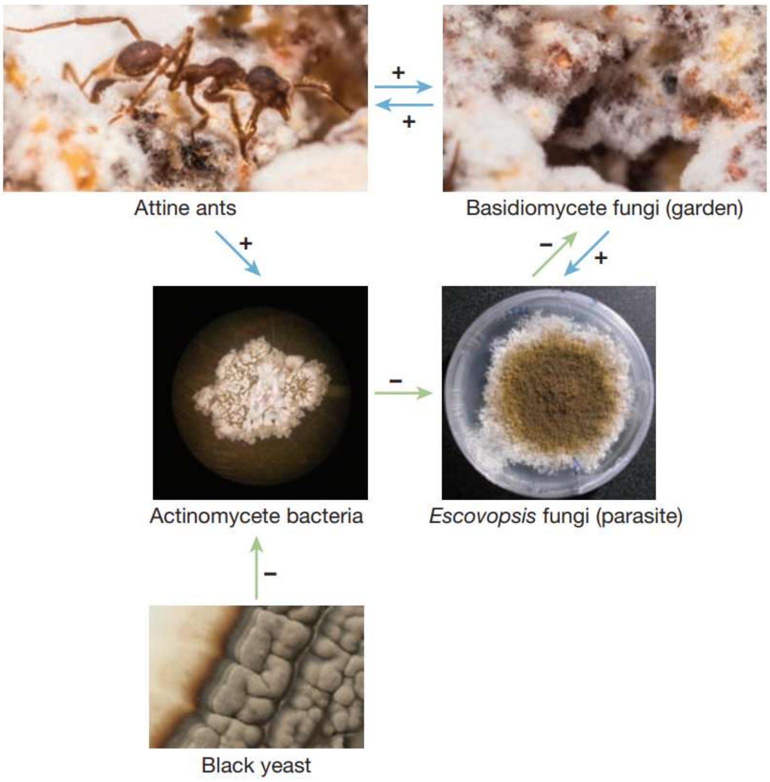


FIGURE 18.5 Five species are linked in a web of mutualistic interactions. Arrows indicate positive (+) or negative (–) direct effects of one species on another. There is an even more extensive web of indirect effects, such as the harmful effect that black yeast have on ants by feeding on the actinomycete bacteria (*Pseudonocardia* and *Streptomyces*) that help the ants exclude the *Escovopsis* parasite from their basidiomycete fungal gardens. Adapted from Little and Currie (2008).

Ants and Butterflies: Mutualism with Communication

Natural selection should favor communication between individuals from different species that are involved in a mutualistic relationship if such communication increases the fitness of the individuals in each species. To examine the role of communication in mutualistic relationships, Naomi Pierce and her colleagues studied a mutualistic relationship between the imperial blue butterfly (*Jalmenus evagoras*) and the ant *Iridomyrmex anceps* (Pierce et al. 2002) (**Figure 18.6**). Both parties benefit substantially from this mutualism. The butterfly larvae and pupae secrete a sugary nectar composed of sucrose and fructose that nourishes the ants; the ants protect the larvae and pupae from predators such as wasps. Pierce and her colleagues have found that butterfly larvae have reduced survival rates when ants are experimentally removed. While ants can survive in the absence of the nectar that they consume from larvae and pupae, under normal conditions they obtain a significant portion of their nutrients from their butterfly larvae partners (Pierce et al. 1987; Fiedler and Maschwitz 1988).

Though the net effect of the mutualism is positive for both species, this ant–butterfly mutualism involves costly investment by both parties. Butterfly larvae that are not tended by ants develop into much larger pupae than butterfly larvae that are tended (Pierce et al. 1987). Why? Larvae that are not tended by ants reduce the amount of nectar they secrete and use the nutrients normally provided

FIGURE 18.6 Butterfly–ant mutualism. Butterflies and ants in a mutualistic relationship. In the mutualism between the butterfly *Jalmenus evagoras* shown here and the ant *Iridomyrmex anceps*, butterfly larvae are less likely to survive in the absence of ants, and ants receive some of their food from the nectar produced by the butterfly larvae.

to ants for their own development. Because size in both male and female butterflies is related to reproductive success, pupating early leads to lower reproductive success for the butterflies, and hence it represents a significant investment in the mutualistic relationship (Elgar and Pierce 1988; Hill and Pierce 1989; Hughes et al. 2000) (**Figure 18.7**). There is probably also a cost to ants for protecting butterfly larvae. Ants involved in a mutualistic relationship with butterflies probably have an increased risk of detection by their own predators and parasitoids and bear metabolic costs that are associated with defense of the butterfly larvae (Pierce et al. 1987).

Given that ants and butterflies are tied together in a mutualism that is costly to maintain, researchers hypothesized that communication between the two species would be favored by natural selection. They decided to test whether such communication was indeed taking place. Because ants are almost deaf when it comes to airborne sounds but are quite sensitive to vibrational signals traveling through solid substrates, Travasso and Pierce (2000) focused on vibrational communications. They noticed that when ants were in the vicinity, the buttefly larvae more vigorously produced vibrational signals by rubbing their stridulatory organs together. This observation *suggests* that the larvae use these signals as a way to communicate with their ant guardians.

In a follow-up experiment, Travasso and Pierce, "muted" one of a pair of butterfly pupae by applying nail polish to its stridulatory organs and allowing the other member of the pair to stridulate normally. Then, using a preference testing device that included two bridges on which the ants could move about, Travasso and Pierce tested which butterfly pupae the ants were more attracted to (**Figure 18.8**). They found that ants demonstrated a clear preference for associating with the pupae that could and did produce vibrations, providing evidence that vibrational communication plays a role in this ant–butterfly mutualistic relationship.

Although Travasso and Pierce did not directly measure whether the butterfly pupae stridulate more when their ant partners are present, it appears that the fitness benefits accrued by both parties in the ant–butterfly mutualism are valuable enough that natural selection has favored a form of vibrational communication between these mutualistic partners.

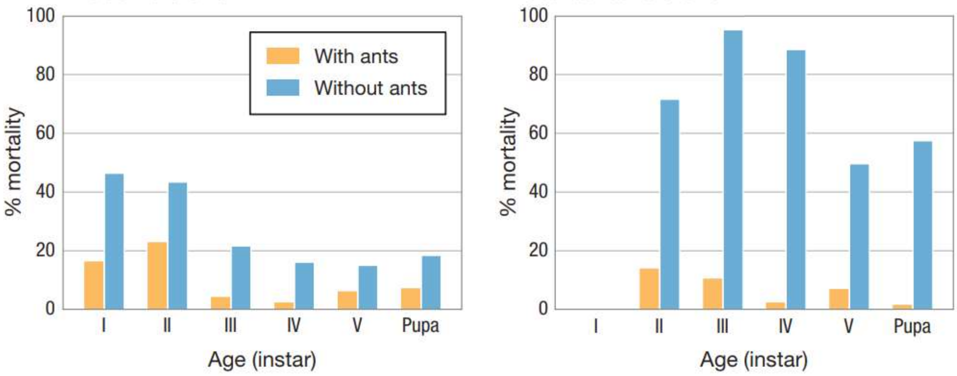


FIGURE 18.7 Butterflies benefit from their ant partners. The probability of mortality of *Jalmenus evagoras* larvae and pupae when faced by predation was much lower (and thus survival was much higher) when ants were present than when they were experimentally excluded at two Australian field sites: **(A)** Mt. Nebo site and **(B)** Canberra site. Adapted from Pierce et al. (1987).

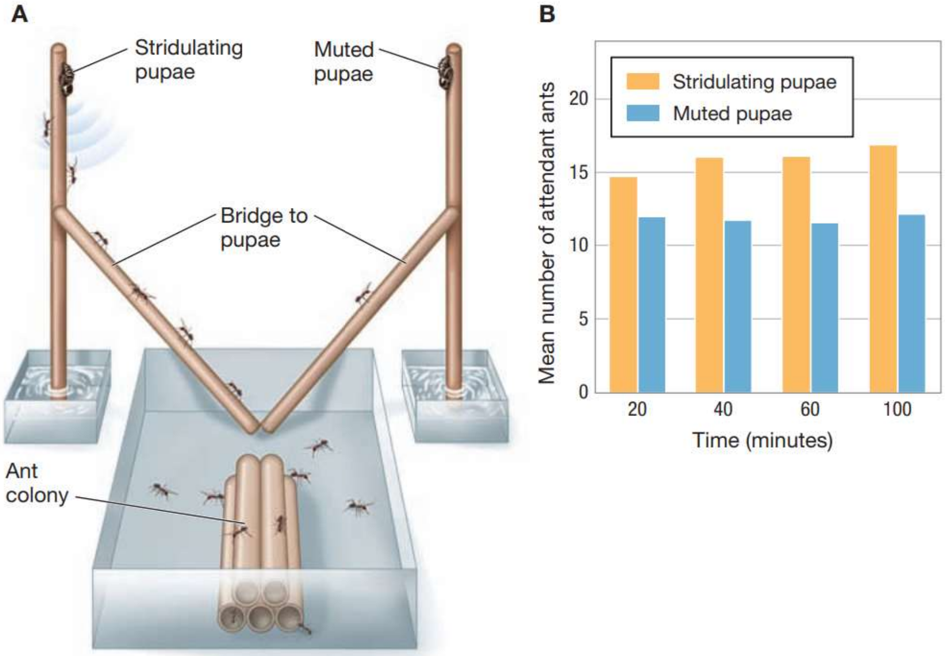


FIGURE 18.8 Communication between mutualists. **(A)** The apparatus used in preference tests. Ants from a colony could choose to move along either bridge. One of the pupae at the top was "muted." **(B)** Stridulating attracts ants. Stridulating *J. evagoras* pupae attracted more ants than *J. evagoras* pupae that had been experimentally muted. Differences between treatments were significant at all time intervals (20, 40, 60, and 100 minutes). Adapted from Travasso and Pierce (2000).

KEYCONCEPT QUESTION

18.1 Many species of ants and acacia trees have evolved a mutualistic relationship, in which the ants protect the acacia from mammalian and insect predators, and the acacia trees provide food for the ants. The acacias provide a carbohydrate-rich liquid (via extrafloral nectary glands) that the ants eat. Acacias also have Beltian bodies that produce proteins which the ants consume. How might you design an experiment to test the hypothesis that if the protection that the ants provide becomes less necessary, natural selection will favor acacia trees that produce fewer resources for ants?

FIGURE 18.9 Soybean–rhizobial bacterium mutualism. Soybean legumes (*Glycine max*) are involved in a mutualistic relationship with rhizobial bacteria (*Bradyrhizobium japonicum*). Pictured here is a soybean with nodules containing *B. japonicum*.

Mutualism and the Response to Cheaters

As we discussed in Chapter 17, where there is cooperation, there are often corresponding incentives for one or more of the parties involved to cheat, as cheaters can reap the benefits of cooperation without having to pay the associated costs. How do interspecific mutualists handle this "cheater problem"? Does cheating occur, and equally important, does one partner in a mutualism respond when the other cheats? To address this question, Toby Kiers and her colleagues examined the mutualism between a soybean legume, *Glycine max*, and a rhizobial bacterium, *Bradyrhizobium japonicum*, a soil bacterium that forms nodules on the roots of the soybean plant (Kiers et al. 2003) (**Figure 18.9**). In a process known as nitrogen fixation, *B. japonicum* converts inorganic N_2 in the root nodules of the plant into an organic form of nitrogen, providing a critical resource that the plant uses for growth and synthesis. On the flip side of this mutualism, the soybean plant provides carbohydrates and other energetic resources to B. *japonicum*, which the bacteria use for their growth and maintenance.

What would happen if one party in this mutualism cheated? For example, nitrogen fixation is costly for B. *japonicum*, as the resources used to fix nitrogen could instead be used by the rhizobial bacterium for its own growth and reproduction. What if B. *japonicum* cheated in such a manner? Could soybean plants respond to reduced nitrogen fixation by B. *japonicum* in a way that would reduce such cheating (Denison 2000; West et al. 2002a,b; Kiers et al. 2006; Kiers and Denison 2008)?

To address this question, Kiers and her team experimentally forced B. *japonicum* to "cheat"—that is, to not fix nitrogen in the root nodules of their hosts—by creating a nitrogen-free atmosphere in one treatment condition of their study. The nitrogen-free atmosphere per se did not reduce the growth rate of B. *japonicum*, which can survive without fixing nitrogen, but such an atmosphere created an indirect cost for the plant—the absence of accessible nitrogen produced by B. *japonicum* (Layzell et al. 1979). Did soybean plants in the nitrogen-free treatment respond and "punish" B. *japonicum* for failing to fix nitrogen?

Even though the nitrogen-free atmosphere does not itself affect growth rates in B. *japonicum*, Kiers and her team found that B. *japonicum* populations grew to much larger numbers in plant nodules in an experimental treatment in which nitrogen was present compared with B. *japonicum* population numbers in a treatment in which the atmosphere was nitrogen-free. This was the case even in a "split root" treatment in which, by a clever experimental protocol involving precise control of atmospheric conditions in growth chambers, a single plant had some nodules subjected to a normal nitrogen atmosphere and some nodules subjected to a nitrogen-free atmosphere.

One interpretation of these results is that the soybean plant punished cheating by the bacteria, leading to decreased B. *japonicum* growth in the nitrogen-free treatment. How did the soybean plant do so? The mechanism appears to be curtailing the O_2 available to B. *japonicum* by changing the permeability of the nodule membrane, which in turn reduces B. *japonicum's* growth rate. The split-nodule control treatment condition also demonstrated it isn't just that plants with B. *japonicum* that fail to fix nitrogen have lower levels of O_2 themselves, and hence have less to put into nodules. Rather, the results indicated that plants differentially allocated O_2 to nodules with nitrogen-fixing B. *japonicum* over nodules containing experimentally created B. *japonicum* cheaters. These results suggest that when one party of a mutualism cheats, the other party responds in kind. This ability to punish cheating has the effect of stabilizing the mutualism by reducing cheating. Subsequent work in plant–fungal mutualisms suggests that other mechanisms also exist for stabilizing these mutualisms: Plants provide more carbohydrates to those fungal species that provide them with the best resources, while fungal partners increase the amount of nutrients they provide to plants whose roots provide them the most carbohydrates (Kiers et al. 2011).

Mutualism and Cospeciation

When the benefits of mutualism to both species are high and the mutualistic relationship has been in place over long periods of evolutionary time, the link between mutualists may result in **cospeciation**, in which speciation in one partner in a coevolutionary relationship leads to speciation in the other (de Vienne et al.

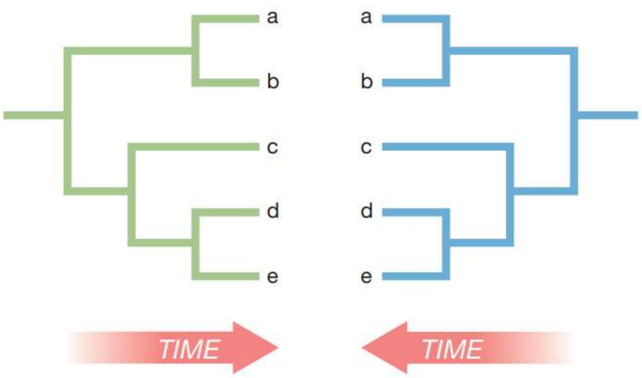


FIGURE 18.10 Cospeciation. Cospeciation in two clades (shown in green and blue). In this case of perfect cospeciation, the left and right phylogenies are mirror images of one another. Adapted from de Vienne et al. (2013).

2013) (**Figure 18.10**). But how might a simultaneous breakdown of gene flow *within each* of two mutualistic species occur and allow for cospeciation? Geographic separation provides one possible mechanism (Chapter 14). If some physical barrier separates communities that contain both mutualistic species, then a pair of species involved in a mutualistic relationship in community 1 could evolve independently of a pair in community 2, leading to cospeciation in allopatry.

As an example of cospeciation, we will examine the mutualism that exists between *Glochidion* trees and the *Epicephala* moths that pollinate them (Kawakita et al. 2004; Hembry et al. 2013). The *Glochidion* trees and *Epicephala* moth study system (which we label as the G–E system) is an **obligate mutualism**, in which each partner can only survive and reproduce successfully in the presence of the other (Thompson 1994, 2005).

In the G–E system, a female moth transports pollen between *Glochidion* tree flowers on a tubelike mouthpart called a proboscis. A comparison of the proboscis of male and female moths shows that female moths possess specialized hairlike projections called sensilla that play a role in pollination. Females lay their eggs in the flower's style, and their larvae feed on developing seeds, destroying a small portion of the seeds in the process (**Figure 18.11**). The larvae rely on these seeds as their food source, and the trees rely on the moths for pollination (Kawakita et al. 2004; Kawakita and Kato 2006).

The G–E system is made up of 300 species of *Glochidion* distributed across Asia, Australia, and Polynesia. The exact number of *Epicephala* moth species associated with these trees is unknown, but evidence suggests that the number is likely large, with some *Epicephala* species specializing in pollinating a single *Glochidion* species (Kato et al. 2003). To examine cospeciation in the G–E system, Kawakita and colleagues used molecular phylogenetic analysis of nuclear ribosomal DNA to investigate relationships among 18 species of *Glochidion* and their respective *Epicephala* pollinators. They then compared patterns of speciation across these mutualistic species (Kawakita et al. 2004).

After reconstructing the phylogenetic history for each partner in the G–E mutualism, the researchers used two different statistical approaches to see whether speciation in *Glochidion* trees was associated with speciation in their moth pollinators (Ronquist 1995). Their results indicate that although speciation patterns in trees and their moths were not identical, they were very similar, with somewhere between 6 and 10 cospeciation events (**Figure 18.12**). The reciprocal reliance in the G–E system, wherein each species cannot survive in the absence of the other, has led to significant cospeciation, and hence an increase in diversity in both *Glochidion* trees and *Epicephala* moths.

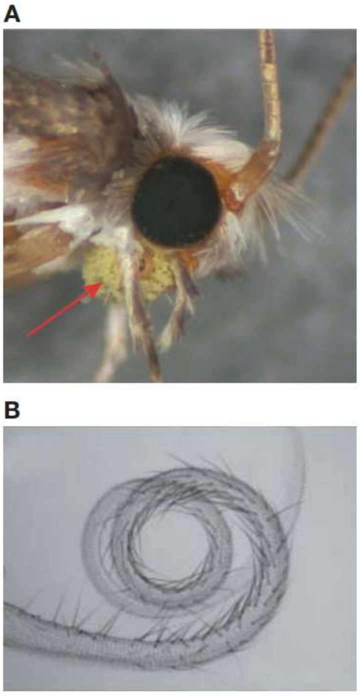


FIGURE 18.11 Pollination of *Glochidion* tree flowers by *Epicephala* moths. **(A)** Pollen on the proboscis of a female moth is shown at the tip of the red arrow. **(B)** One section of the proboscis of a female *Epicephala* moth. The hairlike projections (sensilla) in the females of pollinating *Epicephala* have likely evolved as a specialized trait associated with pollination. Panel B from Kawakita and Kato (2006).

18.2 Antagonistic Coevolution

Antagonistic coevolution occurs when each of two species has a negative effect on the other. Here, we will examine the two most common forms of this type of coevolution: (1) between predator and prey, and (2) between parasite and host.

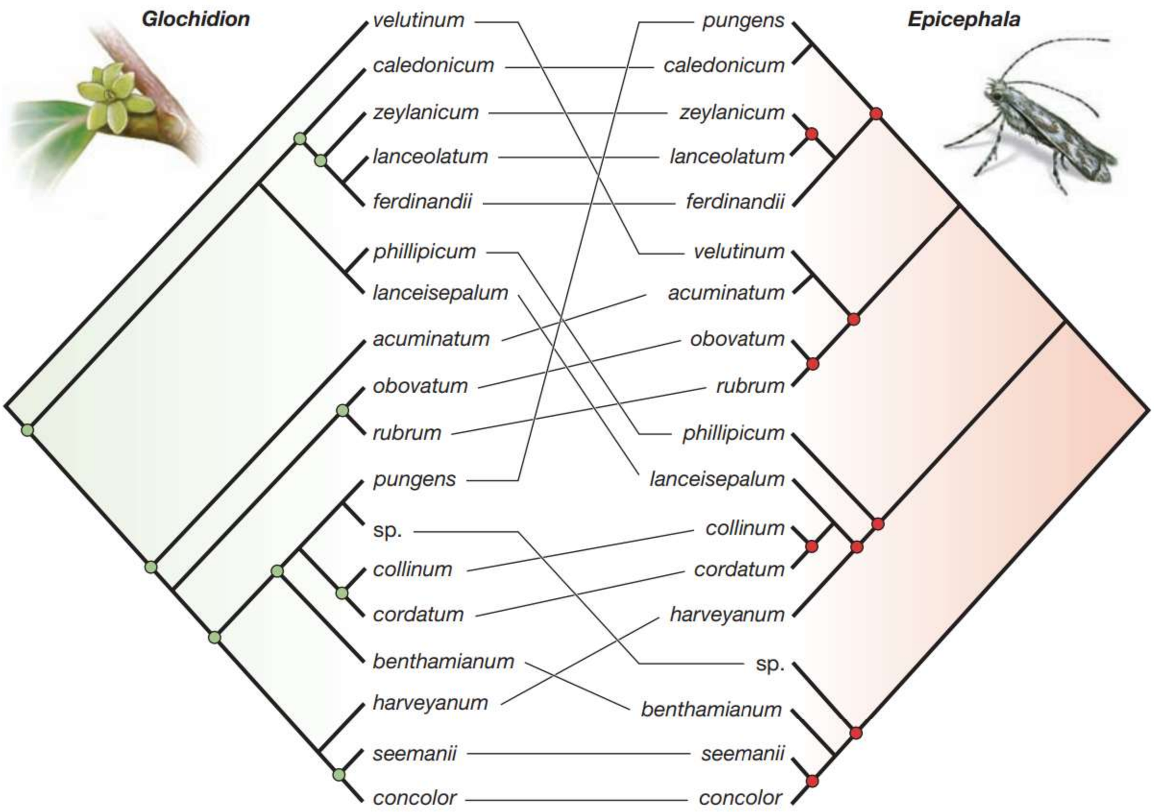


FIGURE 18.12 Cospeciation in *Glochidion* and *Epicephala*. Phylogenetic trees for *Glochidion* (left) and *Epicephala* (right) showing tree–moth associations. Species of *Glochidion* are also designated by their species names ("sp." indicates an unnamed species). The *Epicephala* moths in this study were all undescribed species, so each is indicated here by the species name of its host tree. Lines connect moth species and tree species that are associated with them. Nodes associated with cospeciation are indicated with colored circles. Adapted from Kawakita et al. (2004).

Predator–Prey Coevolution

Consider a simple predator–prey system in which a predator feeds on only one species of prey, and this species of prey is preyed on by only this one predator. All else equal, selection will favor any trait in the prey that increases its chances of escaping predation. If such a trait evolves in prey, this immediately intensifies selection on predators for traits that increase their probability of capturing and consuming their now better-adapted-to-escape prey. Such a trait in predators will then favor any trait in prey that allows them to escape their now better-adapted-to-kill predators, and so on (Vermeij 1993). This coevolutionary dynamic is known as an evolutionary arms race.

To understand such evolutionary arms races better, let's examine predator–prey interactions between the predatory whelk *Sinistrofulgur* and its bivalve prey *Mercenaria* (Dietl 2003a,b). In this system, the fossil record is detailed enough that it is possible to record both successful and unsuccessful attempts at predation over very long periods of evolutionary time. During an attack, a whelk "mounts" its prey, and it uses its shell lip to chip away at the bivalve shell. When it is successful, it kills the prey, but even when it is unsuccessful, the telltale chips and cracks from a failed predation attempt are preserved in the fossil record. The cost of predation can also be documented in the fossil record, as the whelk occasionally breaks its own shell while trying to open its prey, and such damage and subsequent repair can be seen when examining whelk shells (**Figure 18.13**).

Evidence for an evolutionary arms race can be seen in the fossil record of the *Sinistrofulgur–Mercenaria* system. Over evolutionary time, selection has favored an increased shell size and shell thickness in *Mercenaria* prey, which would reduce its probability of being eaten by *Sinistrofulgur*. As *Mercenaria* evolved a thicker shell, selection then favored any trait in *Sinistrofulgur* that allowed it to kill its thicker-shelled *Mercenaria* prey. The fossil record shows that over the same time period that *Mercenaria* were evolving a thicker shell, *Sinistrofulgur* predators were also increasing in size. Larger *Sinistrofulgur* predators would have been able to penetrate the shells of their *Mercenaria* prey more easily (and would have been safer from their own predators). This would also produce selection for increased size in *Mercenaria* prey, and back and forth in an evolutionary arms race with *Sinistrofulgur* with respect to size.

Is it possible that, rather than a predator–prey arms race, natural selection acted on size, outside the context of predator–prey interaction, and independently in each species? Could this explain the increase in size in both *Sinistrofulgur* and *Mercenaria*? In principle this is possible, but the fossil record also shows that over evolutionary time, *Sinistrofulgur* predators changed the typical position they assumed during an attack in such a way as to increase the probability of successfully killing their *Mercenaria* prey. The positional change recorded in the predator is consistent with the hypothesis that the adaptive change was in response to adaptations in its prey rather than selection acting independently on predator and prey.

Evolutionary arms races may even leave their marks long after one of the species involved is extinct. Take the case of the pronghorn antelope, a modern-day species in which individuals can run at speeds approaching 60 miles an hour—much faster than any of the predators they face today. Why can pronghorns run that fast? John Byers has hypothesized that the pronghorn's speed today is a result of a predator–prey arms race that ended more than 10,000 years ago (Byers 1997). For millions of years, pronghorns shared their environment with speedy predators such as the

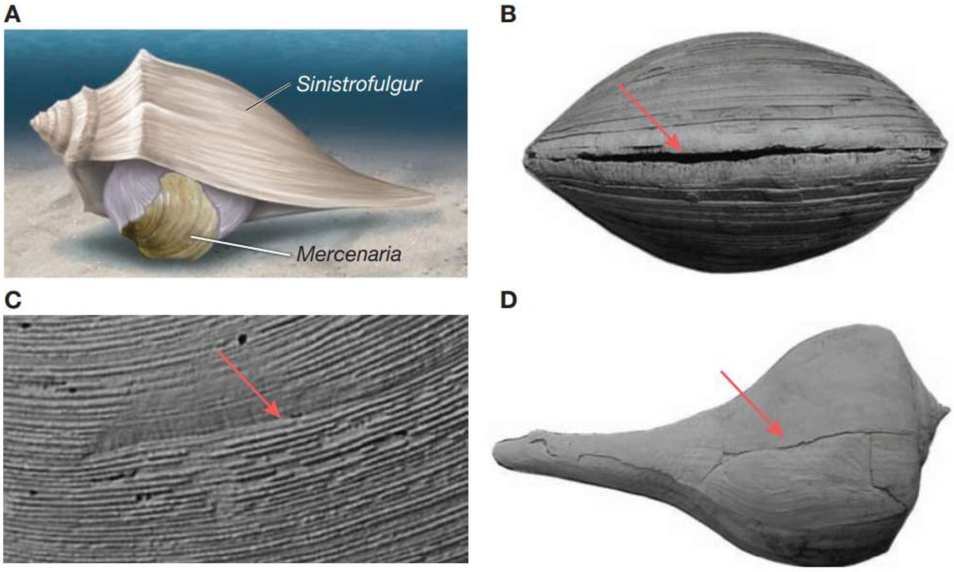


FIGURE 18.13 Predator–prey interactions and coevolution. **(A)** A predatory whelk *Sinistrofulgur* mounts its bivalve prey *Mercenaria* and chips away at its shell. Panel A adapted from Dietl (2003a). **(B)** Evidence of a successful attack on *Mercenaria* (red arrow). **(C)** Evidence of an unsuccessful attack on *Mercenaria*. The *Mercenaria* shell is worn down (red arrow) but not cracked by *Sinistrofulgur* shell chipping. **(D)** A whelk occasionally breaks its own shell while trying to open its prey. Damage is indicated by the red arrow. Panels B–D from Dietl (2003b).

North American cheetah (*Miracinonyx*) and the North American lion (*Panthera leo atrox*), both of which went extinct about 10,000 years ago. While this hypothesis remains to be tested, it suggests that evolutionary arms races can have lasting consequences even after one of the participating species is gone.

Host–Parasite Coevolution and Cospeciation

Earlier in this chapter, we discussed how mutualistic interactions can result in cospeciation and a resulting increase in species diversity. Parasites and hosts may also cospeciate, as initially suggested more than 100 years ago by Kellogg and later by Fahrenholz, both of whom hypothesized that phylogenies of parasites and hosts often change in parallel (Kellogg 1896; Fahrenholz 1909; Klassen 1992).

When populations of a host species become geographically isolated from one another, this will often produce geographic isolation among the parasite populations. As the host populations diverge, selection acts in new ways, not only on individuals in the host populations but also on the parasite populations they carry. If divergence in the host species is great enough, and host speciation occurs, this could lead to speciation in the parasite as well (Moran and Baumann 1994; Wade 2007).

Dale Clayton and his colleagues examined the role of parasite–host coevolution and cospeciation in ectoparasitic feather lice (*Columbicola*) that complete their life cycle on their pigeon and dove hosts, feeding on the bird's abdominal feathers (Clayton and Johnson 2003; Clayton et al. 2004; Johnson et al. 2009, 2011). Using nuclear and mitochondrial DNA sequences, these researchers constructed phylogenies of both lice and their hosts, and then they compared these phylogenies to test whether cospeciation had occurred. Their analysis uncovered eight cospeciation events (**Figure 18.14**).

What drove cospeciation in this system? One clue came when Clayton and his team found that the lice species that had larger individuals tended to live on larger species of pigeons and doves. The researchers hypothesized that there were benefits to lice if they stayed on size-matched species: small lice with small host species and large lice with large host species. If this was correct, then when speciation occurred in birds, their lice were constrained to remain on their hosts because of the benefits of size matching. The result was a tight linkage between host and parasite, leading to cospeciation events. But what exactly were the benefits that lice received for size matching with their hosts?

Clayton and his team experimentally examined whether body size matching allowed lice to remain attached to their hosts more efficiently. Lice were placed on feathers from either a host species or a nonhost species, and these feathers were attached to a fan to test the ability of the lice to remain on their hosts. Results indicate that size matching did not improve the ability of lice to attach to the feathers. Other work also found that body size matching did not affect the feeding ability of lice. Body size matching did, however, have a significant effect on the ability of lice to escape the defensive preening behavior of their host species. Compared to the case of lice on their natural hosts, when lice were experimentally placed on nonhost species that differed in size from their host species, they were unable to evade preening (self-cleaning) and they were eaten by

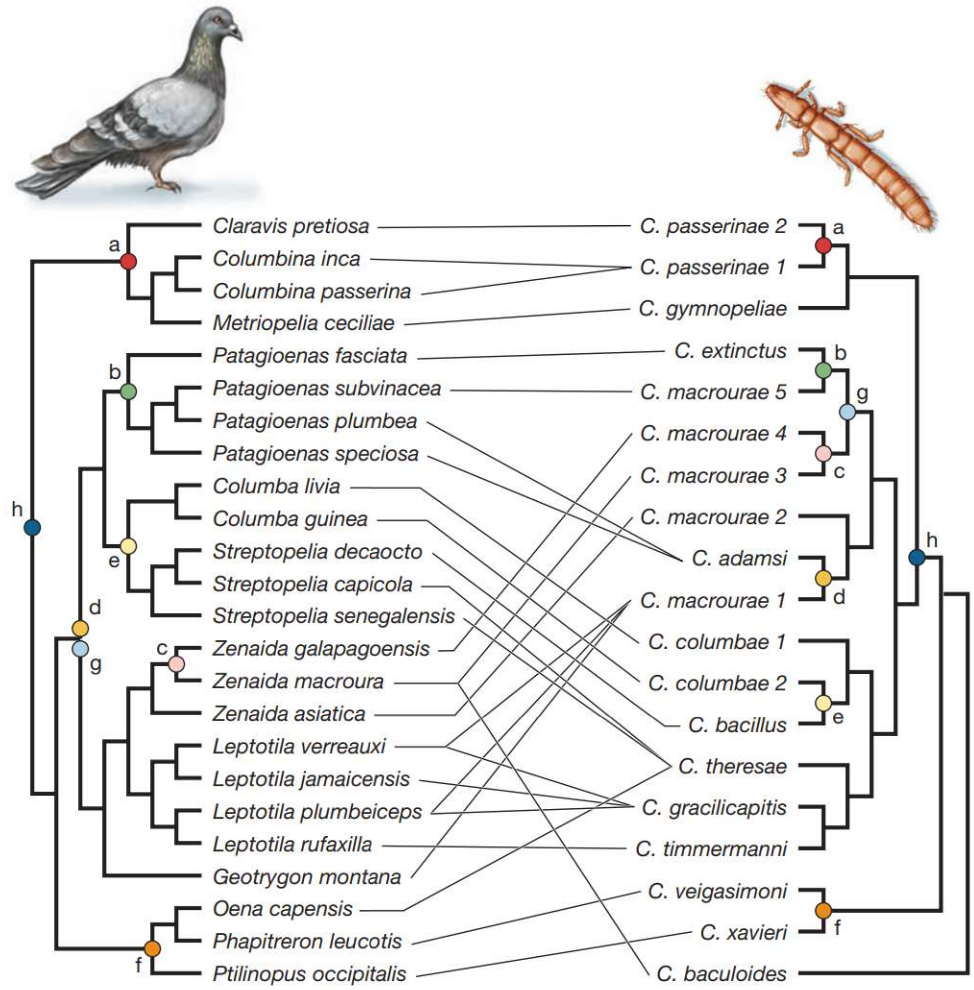


FIGURE 18.14 Parasite–host cospeciation. Phylogenies of pigeons and doves and their lice (genus *Columbicola*). Lines connect host–parasite associations. Cospeciation events are color coded: Matching colors and letters on each side indicate cospeciation events. Adapted from Clayton et al. (2003).

birds at high rates; as such, lice could not establish populations on hosts that differed in size from their normal host (**Figure 18.15**).

The process of cospeciation between birds and their parasitic lice in this example appears to unfold as follows: After a speciation event occurs in a bird group, lice are constrained to remain on their host species because they often fare poorly when switching hosts. Such switches might involve living on a new host that is a different size than their original host, which could potentially make the lice susceptible to significant predation by the new host. The lice are constrained to remain on their original bird host, and when natural selection acts on the bird host, its lice also experience selection operating in new ways. This can lead to new adaptations by the parasites as well, and cospeciation leading to an increase in species diversity in both parasite and host may occur.

Mimicry and Coevolution

In this subsection, we look at another way that coevolution may occur and result in increased species diversity. Recall the *Ensatina* salamanders we discussed as a classic example of a ring species in Chapter 14. Here, we return to these salamanders, but we will focus on one particular subspecies, *Ensatina eschscholtzii xanthoptica,* also known as the yellow-eyed salamander. This subspecies displays striking colors—an orange ventral region and yellow eyes, neither of which are found in other *Ensatina* salamanders. Why have these dramatic colors evolved in *Ensatina eschscholtzii xanthoptica*? One hypothesis is that they are warning signals to predators that *E. e. xanthoptica* is unpalatable. Such **aposematic** (warning) **coloration** is common in salamanders and other animals—but *E. e. xanthoptica* is *not* unpalatable to predators. Instead, orange body color and yellow eyes in *E. e. xanthoptica* appear to be the result of coevolution. In the case of the yellow-eyed salamander, the second species in this story of coevolution is the California newt, *Taricha torosa*, which lives sympatrically with *E. e. xanthoptica* populations (**Figure 18.16**).

The California newt, in addition to possessing orange body coloration and yellow eyes, also produces a neurotoxin called tetrodotoxin in its skin. While this toxin is potent, predators whose attacks fail but who ingest a small dose of tetrodotoxin often survive and learn to avoid this potential prey type.

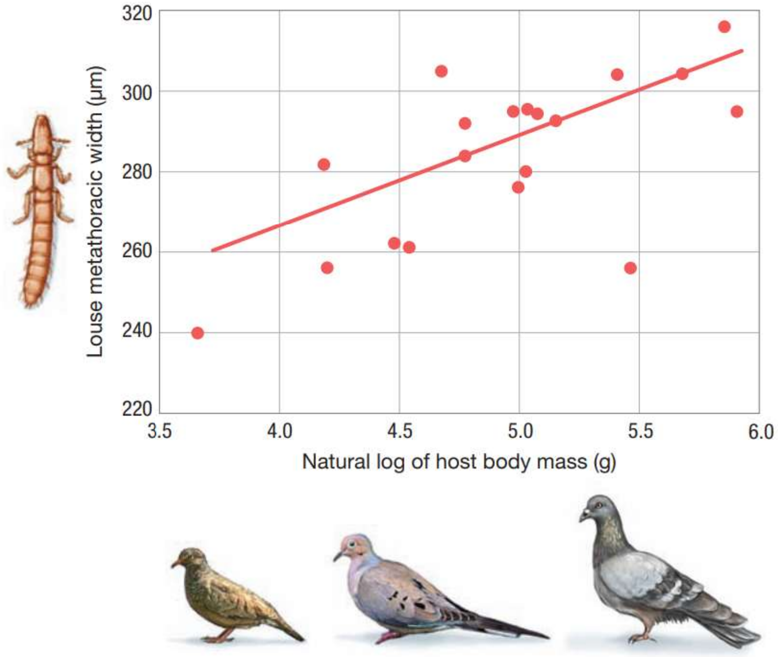


FIGURE 18.15 Body size in parasite and host. Parasite body size in relation to host body size across the associations shown in Figure 18.14. Adapted from Clayton et al. (2003).

More than 60 years ago, George Ledyard Stebbins (1906–2000) hypothesized that the orange body color and yellow eyes of the yellow-eyed salamander had been selected because these traits mimic the coloration of the California newt. Such mimicry would protect yellow-eyed salamanders from predators who might confuse it with the toxic California newt (Stebbins 1949). This sort of mimicry, in which one species is palatable and the other is not, is called **Batesian mimicry** (Bates 1862), and it is different from **Müllerian mimicry** (Müller 1879), in which multiple *unpalatable* species evolve similar phenotypes which reinforces warning signals that predators can pick up.

A *Ensatina eschscholtzii xanthoptica*

B *Taricha torosa*

C *E. e. xanthoptica* and *T. torosa*

D *E. e. oregonensis*

FIGURE 18.16 Mimicry and coevolution. **(A)** The nontoxic mimic, *Ensatina eschscholtzii xanthoptica*, **(B)** the toxic model, *Taricha torosa*, **(C)** the mimic (*E. e. xanthoptica*, on the left) and the toxic model (*T. torosa*, on the right) together, and **(D)** *E. e. oregonensis*, a non-toxic salamander species used as an experimental control because it lacks orange and yellow coloration.

KEYCONCEPT QUESTION

18.2 What sort of differences would you expect in coevolutionary dynamics between Batesian mimicry and Müllerian mimicry? For example, what differences might you expect with respect to antagonistic coevolution and mutualistic coevolution?

But how can we test whether the yellow-eyed salamander's brilliant colors are a result of coevolution via Batesian mimicry? Shawn Kuchta first attempted to answer this question by setting up an experiment in which he placed in the field clay salamander models that either looked like *E. e. xanthoptica* or were otherwise identical models that lacked the orange body color and yellow eyes of *E. e. xanthoptica*. His results showed that predators attacked the yellow-eyed salamander models significantly less often than models without the yellow-eyed salamander coloration (Kuchta 2005).

In a follow-up experiment, Kuchta and his colleagues examined rates of predation on yellow-eyed salamanders in a controlled laboratory setting in which a predator was provided with the opportunity to feed on live salamanders (Kuchta et al. 2008). Western scrub jays taken from the field were used as predators because they had experience with toxic California newts. But the Western scrub jays also had no experience with yellow-eyed salamanders, which are not usually found in the Western scrub jay habitat. The researchers presented a scrub jay with a California newt, and then they presented the jay with either a yellow-eyed salamander or an individual from the closely related subspecies *Ensatina eschscholtzii oregonensis*, which is morphologically similar to the yellow-eyed salamander but lacks orange and yellow coloration. Kuchta and his team found that after experience with the California newts—some of which the jays attacked—the jays took more time to approach yellow-eyed salamander than to approach *E. e. oregonensis* individuals.

From their encounters with the California newts, the scrub jays had learned to avoid creatures that had orange body color and yellow eyes and a newt-like body. As a result, jays were very hesitant to approach yellow-eyed salamanders, even though that species does not possess the neurotoxin found in the newts. In an encounter in the wild, such extra time could make the difference between survival or being eaten by a jay (**Figure 18.17**).

In this case, we have seen how traits in one species (the toxic California newt) influence the operation of selection on another (the nontoxic yellow-eyed salamander), but, unlike many of the other examples we have discussed, we do not know yet whether the yellow-eyed salamander has a reciprocal influence on the toxic California newt. There is, however, a testable prediction here: Because predators will occasionally eat yellow-eyed salamanders, they also will occasionally eat a *Taricha torosa* newt, and in so doing they select upon newts to signal their toxicity in a slightly different way. Future research could look for hints of such a change and continue to explore whether coevolution, in this case via mimicry, leads to increased diversity of antipredator traits.

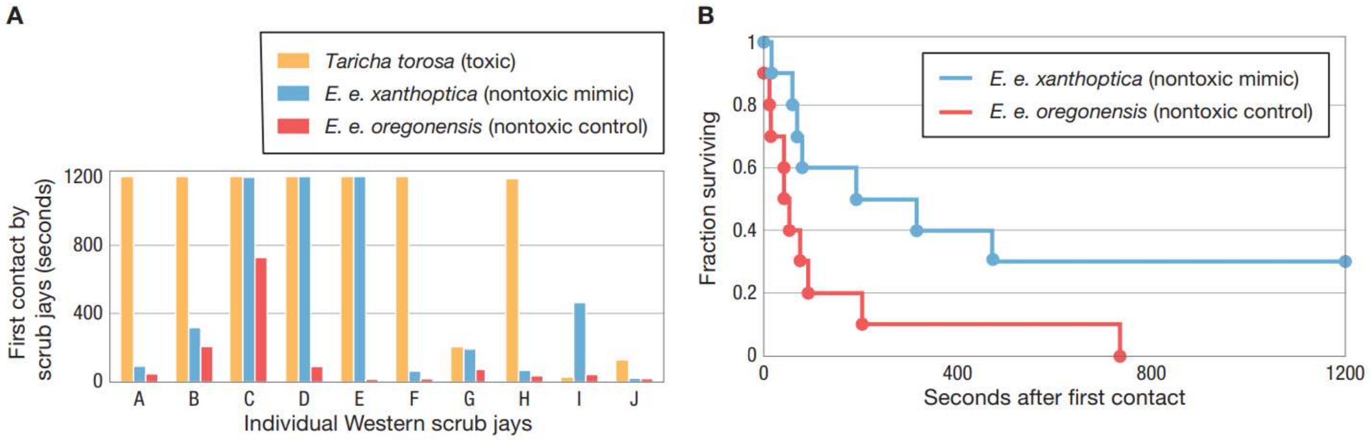


FIGURE 18.17 Survival from predation based on mimicry of toxic species. **(A)** Most Western scrub jays take longer to first contact a toxic salamander species and its non-toxic mimic than the non-toxic control. **(B)** The non-toxic mimic *E. e. xanthoptica* survives in the presence of a jay predator for longer than non-toxic control *E. e. oregonensis*. Adapted from Kuchta et al. (2008).

18.3 Mosaic Coevolution

Up to this point we have examined the dynamics of coevolution leading to mutualism or antagonistic coevolution between species. But it is important to understand that depending on the ecology and behavioral interactions, natural selection can result in mutualism between a pair of species in some communities, but antagonistic interactions between the *same* pair of species in other communities. This idea, which shows another way in which coevolution can lead to diversity, centers on geographic *variation* in coevolutionary outcomes and has been dubbed the theory of **mosaic coevolution** (Thompson 1982, 1994, 1999, 2009).

John Thompson and Bradley Cunningham studied mosaic coevolution in interactions between the herbaceous plant *Lithophragma parviflorum* (also known as the woodland star) and the moth *Greya politella* (Thompson and Cunningham 2002; Thompson and Fernandez 2006; Thompson et al. 2013). The moth lays its eggs into developing flowers of the woodland star by inserting its ovipositor down into the floral ovaries. But while inserting its eggs into numerous plants, the moth also pollinates the woodland star. Woodland star plants pay a cost for this pollination, because when moth larvae mature, they eat some of the woodland star's seeds. *Greya politella* is completely reliant on the woodland star as its sole host. But the woodland star plant is not always reliant on the moth as its sole pollinator. In some populations, the moth is indeed the *sole* pollinator of the woodland star. But in other populations, it is one of many species that act as pollinators for this plant, and many of these other pollinators do not produce larvae that eat the plant's seeds, and so they are less costly to the woodland star. This means that there is geographic variation in the costs and benefits of the plant–moth interactions. Thompson and Cunningham tested whether this geographic variation in costs and benefits was correlated with geographic variation in mutualism versus antagonistic coevolution (**Figure 18.18**). They hypothesized that the more reliant the plant was on this moth species as a pollinator, the more mutualistic the coevolutionary dynamics would be.

In four populations in which *G. politella* acted as the *sole* pollinator and the woodland star was the *sole* host for *G. politella*, Thompson and Cunningham found a mutualistic relationship between plants and moths. In these populations, the woodland star rarely aborted flower capsules that contained moth eggs (doing so

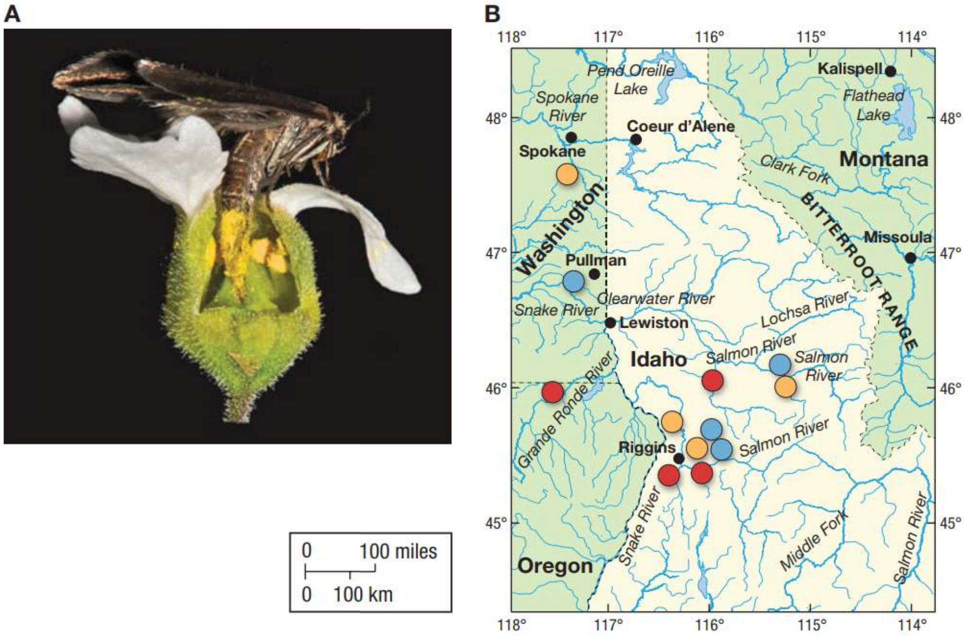


FIGURE 18.18 Mosaic coevolution in plants and moths. **(A)** A female *Greya politella* moth pollinates a woodland star (*Lithophragma* sp.). Researchers cut a small window in the flower to document pollination during oviposition. The moth's ovipositor here is covered in yellow pollen. From Thompson et al. (2013). **(B)** Mosaic coevolution must be studied across many sites. In their work on the interaction between the woodland star and its moth pollinator, Thompson and Cunningham sampled 12 sites. Note the geographic variation in what sort of evolution was occurring. Orange circle = mutualism, red circle = antagonistic coevolution, blue circle = commensal relationship (no effect of *Greya* on *Lithophragma*). Adapted from Thompson and Cunningham (2002).

would also kill the moth larvae) preferentially over capsules that had no moth eggs. But, depending on the costs and benefits to the plants and moths, mutualism need not be the outcome of coevolution in this system. In four other populations, in which the woodland star had numerous pollinators besides *G. politella*, the researchers found evidence of an antagonistic relationship between plants and *G. politella*. The plants selectively aborted flower capsules that contained moth eggs. In these populations, where alternative pollinators were present, the costs of having the moth pollinator outweighed the benefits, and selection favored an antagonistic, rather than a mutualistic, response from the plant. Coevolution was occurring in all cases, but the costs and benefits to the involved parties determined whether selection favored a mutualistic or antagonistic coevolutionary relationship. Just as important, with a solid understanding of the natural history of the species involved, evolutionary biologists can derive hypotheses about which populations will head down one coevolutionary path and which will head down the other.

KEYCONCEPT QUESTION

18.3 In the *G. politella*/woodland star example of mosaic coevolution, there are two species involved. How might yet other species in a community—their absence, presence, or behavior—affect mosaic coevolution of the two primary species a researcher may be studying?

18.4 Gene–Culture Coevolution

In addition to studying coevolution between species, over the past 30 years evolutionary biologists and anthropologists have begun examining **gene–culture coevolution**; that is, the coevolutionary dynamics between genetic and cultural traits, both within and between species. Throughout this book, we have examined how allele frequencies change over time. In that sense, we have already delved deeply into the "gene" part of gene–culture coevolution. Let's briefly examine how cultural evolution operates, and then we will move on to discuss gene–culture coevolution.

In Chapter 3, we noted that for natural selection to act on a trait, a mechanism for transmitting that trait across generations is required. Once Mendel's work on genetics was rediscovered in the early 1900s, it became clear that genes are one means of transmitting traits across generations. Culture provides another means, and recently evolutionary biologists have become interested in this phenomenon as well.

Cultural transmission is typically defined as the transfer of information from individual to individual through social learning. A slightly different way of saying this is that cultural transmission is a system of information transfer that affects an individual's phenotype via social learning (Bonner 1980; Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985).

Although cultural and genetic transmission each provide a means of passing traits down from one generation to another, there are a number of unique aspects of cultural transmission. When individuals learn from others—that is, when social learning occurs—information can be spread through a population very quickly. As a consequence, the behavior of a single individual can dramatically shift the behavior patterns of an entire group. For example, consider the case of Imo, a Japanese macaque monkey who lived on Koshima Island in the 1950s. After Imo learned the trick of washing the potatoes that researchers were providing, others in her group copied her, and potato-washing behavior spread quickly through Imo's group (Kawamura 1959; Kawai 1965). Cultural transmission can change the frequency of behavioral traits not only across generations, when younger individuals learn from older individuals, but also within a single generation, when individuals from the same cohort learn from one another (Boyd and Richerson 1985, 2004). When cultural transmission leads to changes in the frequency of traits within or between generations, we call this **cultural evolution**.

There are different types of cultural transmission. Vertical cultural transmission refers to the case in which information is transmitted between generations from parent(s) to offspring. Horizontal cultural transmission involves the transfer of information between individuals who are in the same age cohort. Oblique cultural transmission involves the transfer of information across generations when young receive information from adults that are not their parents.

For an interesting case study illustrating the importance of cultural evolution and social learning in animals, let's examine foraging behavior in rats. As scavengers, rats sample many new foods. Yet, scavenging can present a dilemma. A new food source may be an unexpected bounty for a rat. But new foods can also be dangerous. They may contain elements such as poisons that are inherently bad for rats. Or, because a rat doesn't know how a new food should smell, it is difficult to tell if a novel food is fresh and will serve as nourishment or spoiled and may make the rat sick.

FIGURE 18.19 Scavenging and cultural transmission. **(A)** A scavenging rat often encounters new food items while foraging. **(B)** Smelling another rat provides olfactory cues about what it has eaten. If this affects a rat's behavior, transfer of information from one rat to another about safe foods is a form of cultural transmission.

Jeff Galef and his colleagues have studied the role of cultural transmission in the scavenging behavior of Norway rats (*Rattus norvegicus*) (Galef and Wigmore 1983; Galef and Laland 2005; Galef and Whiskin 2006). To test whether cultural transmission via social learning plays a role in rat foraging, the researchers examined whether observers could learn about a new food source simply by interacting with a demonstrator that had experienced such a new addition to its diet (**Figure 18.19**).

After two rats had been caged together for days, one rat was removed and taken to another experimental room, where it was given one of two novel diets: either rat chow flavored with cocoa or rat chow mixed with ground cinnamon. This "demonstrator" was then brought back to its home cage and allowed to interact with the other rat, known as the observer rat, for 15 minutes. The demonstrator rat was removed from the cage. For the next 2 days, the observer rat was given two food bowls, one with rat chow and cocoa, the other with rat chow and cinnamon. Although the observer rat had no direct experience with either of the novel food mixes and it had not *seen* the demonstrator rat eating these new food items, it was more likely to eat the food that the demonstrator rat ate, both when the demonstrator had eaten rat chow with cocoa and when it had eaten rat chow with cinnamon, strongly suggesting that Norway rat foraging behavior was affected by cultural transmission via olfactory cues (**Figure 18.20**).

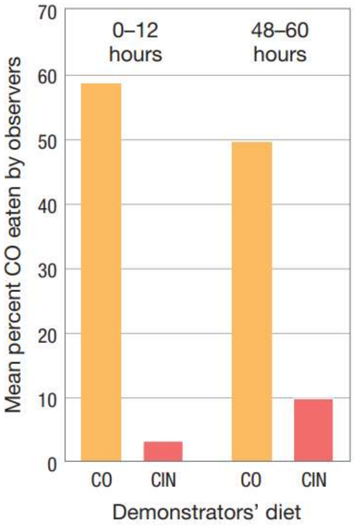


FIGURE 18.20 Cultural transmission across generations. Social learning and foraging in the Norway rat. Observer rats had a "tutor" (demonstrator) who was trained to eat rat chow containing either cocoa (CO) or cinnamon (CIN) flavoring. Rats with "cinnamon tutors" preferred cinnamon-flavored food (not shown here), and rats with "cocoa tutors" preferred cocoa-flavored food (shown here). Adapted from Galef and Wigmore (1983).

With the growing realization that cultural transmission affects many different types of behavior, evolutionary biologists have become interested in the ways in which genetic and cultural transmission can interact. Do genetic changes affect cultural evolution? Do changes in cultural evolution affect genetic evolution? Do they both affect each other? Researchers are actively looking into these questions, and the answers have promise for helping us to understand the coevolution of genetic and cultural transmission.

Gene–Culture Coevolution in Darwin's Finches

We begin with a discussion of gene–culture coevolution in Darwin's finches. The medium ground finch (*Geospiza fortis*) and the cactus finch (*G. scandens*) live on the Galápagos island of Daphne Major. These species are capable of interbreeding. Hybrid offspring produced from *G. fortis* by *G. scandens* matings do not appear to suffer a decrease in fitness compared to offspring from *G. fortis* parents or *G. scandens* parents (**Figure 18.21**). Nevertheless, interbreeding between *G. fortis* and *G. scandens* remains a rare event. Why is it that the two species seldom interbreed? Here, we will examine work that suggests a role for

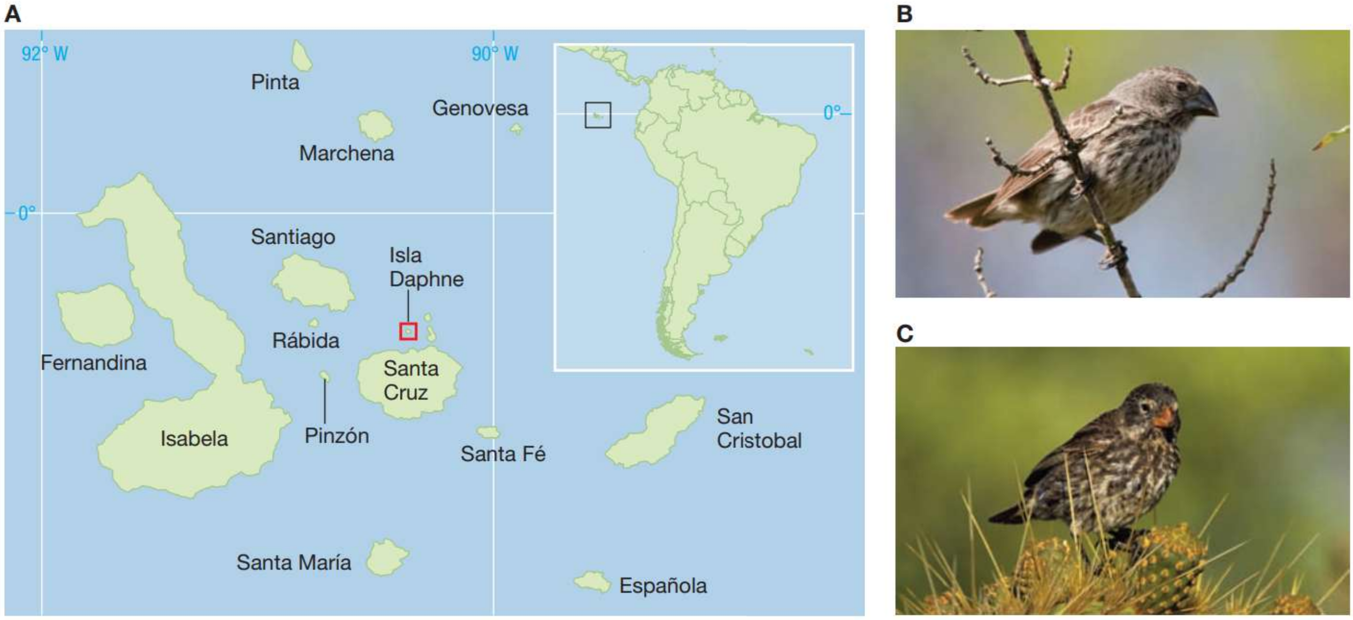


FIGURE 18.21 Cultural evolution in birdsong. **(A)** The Galápagos Islands, including Daphne Major Island (in red). **(B)** *Geospiza fortis*. **(C)** *Geospiza scandens*.

cultural transmission in inhibiting such matings (Nelson et al. 2001; Slabbekoorn and Smith 2002; Freeberg 2004; Lachlan and Servedio 2004).

When Peter and Rosemary Grant examined the songs of *G. fortis* and *G. scandens* during the birds' mating season, they found evidence of cultural transmission across generations (Grant and Grant 1996): Sons sing songs similar to their fathers' songs. To understand what was happening, the Grants compared the songs of sons, fathers, and grandfathers. One hypothesis for why father and son finches have very similar songs is that the song is a genetic trait passed from father to son; another hypothesis is that cultural transmission of the song from father to son takes place when the son hears and learns the song sung by his father. To test the two hypotheses, they compared the songs of sons to those of their paternal and maternal grandfathers. If song types are genetically controlled, we normally would expect the songs of the sons to be similar to the songs of both their paternal and maternal grandfathers, as the son inherits genes from both grandfathers. But if cultural transmission from father to son is the mechanism, then the songs of the sons should resemble those of their paternal grandfathers, not those of their maternal grandfathers, as it is the paternal grandfather who would have transmitted the song to the father, who in turn would have transmitted the song to the son (**Figure 18.22**). Comparison of the son's song to those of the maternal and paternal grandfathers shows that the son's song resembles the song of the paternal grandfather, not the song of the maternal grandfather—suggesting that birdsong is culturally transmitted.

KEYCONCEPT QUESTION

18.4 What other type of inheritance would have a male resemble his paternal grandfather but not his maternal grandfather?

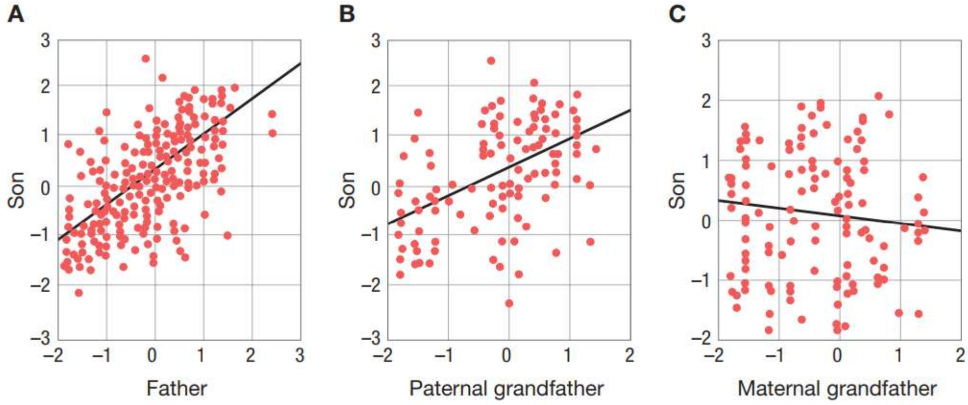


FIGURE 18.22 Finch songs across generations. Male finches' songs are positively correlated with those of their fathers **(A)** and those of their paternal grandfathers **(B)**, but not with those of their maternal grandfathers **(C)**. The significant positive correlation between the songs of sons and paternal grandfathers coupled with the absence of a positive correlation between the songs of sons and maternal grandfathers suggests that songs are culturally transmitted. The horizontal axis and vertical axis are in units that summarize many components of the songs. Adapted from Grant and Grant (1996).

In studying the birdsong of the two finch species, the Grants found that the songs varied significantly from one another: The birdsong of *G. scandens* has shorter components that are repeated more often than the components of the birdsong of *G. fortis* (Grant and Grant 1994, 1997). These differences in their songs—a culturally transmitted trait—have a dramatic impact on gene flow between ground finches and cactus finches. The researchers sampled 482 females and found that more than 95% of them mated only with males who sang the song typically produced by males of their own species. This suggests that cultural transmission plays a large role in why ground and cactus finches rarely mate, even though hybrid offspring suffer no fitness costs. The song sung by males—a culturally transmitted trait—provides females with a means to recognize individuals of their own species, which in turn leads to few between-species matings (the "gene" part of gene–culture coevolution). Further support for this interpretation comes from the fact that the Grants uncovered 11 cases in which the male of one species sang the song of another species; most of these males mated with females from the other species. In such cases of cross-species breeding, viable hybrid offspring were produced. Remove the normal pattern of cultural transmission, and the barrier to breeding across species disappears.

KEYCONCEPT QUESTION

18.5 How might the speed at which cultural evolution operates affect the rate of genetic evolution?

Gene–Culture Coevolution and Lactose Tolerance in Humans

While cultural transmission of information has been studied in many nonhuman species, there is little question that culture is more complex and more prominent in humans than in any other species. Virtually no human behavior is unaffected by what we see, hear, and read about others doing. Within psychology there is a whole subdiscipline—social psychology—devoted to this subject.

Many evolutionary anthropologists argue that gene–culture evolution is a powerful force driving human evolution. "Genes and culture resemble a symbiosis," note leaders in this field; they are "two inheritance systems occupying the same physical body" (Richerson et al. 2010, p. 8986). One of the most well-studied examples of gene–culture coevolution in our species is that of lactose tolerance in certain human populations. The story of lactose tolerance and gene–culture evolution begins at the end of the last glacial age about 11,500 years ago. Once the environment became warmer and wetter, many human populations developed simple agriculture systems. Not long after that, humans began to domesticate animals (though wolves were likely domesticated long before this) as well as plants. In particular, cattle domestication is thought to have emerged on two separate occasions, once about 10,500 years ago, and again about 8500 years ago (Zhang et al. 2013). The many changes in domesticated animals and plants that have occurred over time are the result of artificial selection, but the process of domestication itself is an example of cultural evolution by humans.

When cattle domestication first began, humans could not tolerate drinking milk as adults. This is because the ability to digest lactose, the main carbohydrate present in milk, was present in young children but lost soon after the age of weaning: After weaning, production of lactase-phlorizin hydrolase (also simply called lactase or LPH)—the enzyme that breaks down lactose and makes milk digestible—tails off dramatically. But concurrently with the domestication of cattle, another cultural breakthrough occurred when people learned to ferment milk into cheese and yogurt. This fermentation dramatically reduced the amount of lactose, and thus created dairy products that could be digested. Anthropologists and archaeologists who have reconstructed human migration patterns after the last ice age believe that the added nutrients provided by dairy products like cheese and yogurt helped humans from the Middle East to move through and settle in southern Europe.

So far, our story is one of cultural change. But it turns to one of gene–culture coevolution about 7500 years ago near what is modern-day Hungary. At that time, a point mutation in a stretch of DNA that codes for the transcription of the *LCT* gene occurred. The *LCT* gene is associated with the production of the lactase enzyme that breaks down lactose, and this point mutation resulted in the ability of adult humans to digest milk by prolonging into adulthood the period over which the lactase enzyme breaks down lactose. Now, because of this genetic change, the cultural system of domestication already in place provided even larger benefits. Individuals with the *LCT* gene no longer had to ferment their dairy products, but instead could drink them fresh and obtain increased amounts of carbohydrates, fats, proteins, and calcium (Bersaglieri et al. 2004). Populations of humans with the *LCT* mutation spread north through Europe (**Figure 18.23**). Indeed, evidence from the sequencing of 8000-year-old human bone fragments from central and eastern Europe indicates that the frequency of the *LCT* mutation was very low at this time, perhaps as low as zero. This frequency rose to 25% about 3000 years ago and today is of the order 80% in these regions (Burger et al. 2007).

FIGURE 18.23 Lactose tolerance in humans. A schematic of the development of agriculture and the evolution of lactose tolerance in humans. Adapted from Curry (2013).

7500 YEARS AGO
Lactase persistence, the ability to drink milk in adulthood, emerges in central Europe

6500 YEARS AGO
Well-developed dairy economy established in central Europe

8000 YEARS AGO
Neolithic culture reaches the Balkans

8400 YEARS AGO
Neolithic culture spreads to Greece

11,000–10,000 YEARS AGO
Neolithic culture develops in the Middle East. This is the start of agriculture and possibly the domestication of dairy animals.

Further evidence for gene–culture evolution in the evolution of lactose tolerance can be found in (1) the strong historical and contemporary relationship that exists today between the frequency of dairy farming in an area and the frequency of the *LCT* mutation (Simoons 1969; Kretchmer 1971; Scrimshaw and Murray 1988) and (2) the evidence of strong artificial selection on the genes associated with milk production in cattle in areas where the frequency of the *LCT* mutation is high (Beja-Pereira et al. 2003).

In this chapter, we have seen the many ways that coevolution has shaped the diversity of life around us and the complex interactions that often define between-species relationships, be they mutualistic, parasitic, predator–prey, or gene–culture interactions. In the next chapter of this book, we turn to an in-depth examination of our own (human) evolutionary history.

SUMMARY

1. Coevolution occurs when evolutionary changes to traits in one species cause natural selection to act in new ways on traits in another species, which in turn feed back to alter the nature of selection on traits in the first species, and so forth.
2. Mutualisms may evolve from initially neutral interactions between species or from interactions in which one species initially benefits and the other is initially unaffected in any way. A mutualism can even evolve from an initially parasitic relationship when the costs and benefits of that parasitic relationship change over time to favor the mutualism.
3. Under certain conditions, natural selection may favor communication between individuals of different species involved in a mutualistic relationship.
4. If the benefits of mutualism to both species are high and the mutualistic relationship has been in place over a long period of evolutionary time, the link between mutualists may lead to cospeciation, in which speciation in one species is associated with speciation in the other.
5. The two most common forms of antagonistic coevolution are that between predator and prey and that between parasite and host.
6. The dynamics of antagonistic coevolution can take the form of an evolutionary arms race.
7. Cospeciation may occur in parasite–host systems. Speciation in hosts can drive speciation in their parasites.
8. Natural selection can result in mutualism between a pair of species in some communities but antagonistic interactions between the same species in other communities. This leads to geographic variation in coevolutionary outcomes, known as mosaic coevolution.
9. Evolutionary biologists and anthropologists have begun examining gene–culture coevolution and its consequences, both within and between species. One of the most well-studied examples of gene–culture coevolution in our species is that of lactose tolerance in certain human populations.

KEY TERMS

antagonistic coevolution (p. 649)
aposematic coloration (p. 665)
Batesian mimicry (p. 665)
cospeciation (p. 659)
cultural evolution (p. 669)
cultural transmission (p. 669)
diffuse coevolution (p. 650)
gene–culture coevolution (p. 669)
mosaic coevolution (p. 667)
Müllerian mimicry (p. 665)
obligate mutualism (p. 660)

REVIEW QUESTIONS

1. What did studying the rate of nucleotide substitution in free-living versus mutualistic fungi allow Lutzoni and Pagel to test about the evolution of mutualism in lichens?
2. What is the difference between mutualistic and antagonistic coevolution?
3. What is diffuse coevolution?
4. In ant species that grow fungal gardens, what benefits do the ants receive? What benefits do the fungi receive?
5. With respect to mutualisms, what is "the cheater problem"?
6. What is cospeciation?
7. What are Batesian mimicry and Müllerian mimicry?
8. What is aposematic coloration?
9. What is mosaic coevolution?
10. What is gene–culture coevolution?

KEY CONCEPT APPLICATION QUESTIONS

11. Make the following argument: Compared to environments with abundant resources and little competition, mutualism is especially likely to evolve in environments that are especially harsh, with little food and much competition.
12. Why might microbes found in the guts of a series of host species and the host species themselves be an especially likely system in which to find cospeciation?
13. Why is an understanding of the natural history of the species being studied so critical to using the mosaic theory of coevolution to make specific, testable predictions?
14. Why do you suppose that communication between mutualistic species might speed up the pace of coevolutionary change?

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