

# TANGLED TREES

Phylogeny, Cospeciation, and Coevolution

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THE ECOLOGICAL BASIS  
OF COEVOLUTIONARY HISTORY

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## THE ECOLOGICAL BASIS OF COEVOLUTIONARY HISTORY

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Macroevolutionary patterns are difficult to interpret because they are the product of a time scale so vast that deterministic and chance events are hard to distinguish. Although the macroevolutionary history of a group can be reconstructed from extant species, determining the ecological context in which that group evolved is a tall order. Ecology involves interactions between organisms and both the living and nonliving components of their environments. These interactions are important because they influence selection, dispersal, drift, and other microevolutionary processes that govern macroevolution. Short of inventing time travel, the best bet for obtaining data on ecological history has traditionally been to focus on groups that have an unusually good fossil record. A more recent approach, however, is to focus on groups having a history of prolonged coevolution that yields congruent phylogenies.

Congruent phylogenies are produced by repeated bouts of parallel speciation in unrelated lineages. If every speciation event in one group is accompanied by a "cospeciation" event in the other group, and if no species are lost from their original associations, then phylogenies will be completely congruent (although branch lengths may differ). In reality, however, phylogenies seldom show absolute congruence. Generally speaking, the degree of congruence is correlated with the ecological intimacy of the groups, whose interactions vary from obligate association to opportunistic encounters. One end of the spectrum is represented by mitochondria, chloroplasts, and other eukaryotic organelles evolved from free-living prokaryotic ancestors. The other end of the spectrum consists of far less intimate interactions, such as those between generalist herbivores and their host plants. Most interactions lie between these two extremes.

Inferences about the ecological history of interacting groups are perhaps easiest when the environment of one species is delineated completely by

the members of another species, as in the case of "permanent" parasites. For such parasites, which carry out their entire life cycle on the body of the host, the branching pattern of the host phylogeny provides a detailed record of vicariance events that may influence the parasites. The host phylogeny also can be used to draw inferences about the habitat parameters of ancestral parasites. For example, estimating the body size of an ancestral host is tantamount to knowing the size of the resource base available to its parasites. Unfortunately, it is not usually possible, even in cases of extensive congruence, to reconstruct specific ecological processes, such as demographic fluctuations, or competitive interactions. On the other hand, processes generating congruence can be illuminated to some extent by extrapolating backwards from data on modern ecological parameters. In this chapter we adopt such a reverse engineering approach, using information about the ecology of extant species to explain differences in the degree of phylogenetic congruence among related host-parasite systems. Although we have chosen to focus on host-parasite interactions, we make an effort to address issues that are applicable to coevolving systems in general.

The ecological basis of coevolutionary history can be explored by comparing interactions that vary in their degree of phylogenetic congruence. Unfortunately, adequate comparative ecological data are not available for many of the systems that have been subjected to cophylogenetic analysis. A fortunate exception is provided by parasitic lice (Insecta: Phthiraptera), which occur on birds and mammals. For a few genera of lice, enough data are now available to begin exploring the relationship between ecology and congruence. Making comparisons among taxa of lice helps ensure against spurious conclusions drawn from comparisons of distantly related taxa that may have evolved in entirely different environmental contexts.

Phylogenetic congruence is governed by several kinds of macroevolutionary events, which we review below. We then consider the impact of various ecological factors on the relative frequency of these macroevolutionary events. We conclude the chapter by comparing the ecology of four genera of lice that have histories ranging from extensive phylogenetic congruence with their hosts, to a complete lack of congruence.

### Macroevolutionary Events governing Phylogenetic Congruence

Phylogenetic congruence is a historical pattern produced by repeated bouts of *cospeciation*. Cospeciation is a process in which speciation in one lineage is accompanied by speciation in an associated, but unrelated lineage (fig. 13.1a). All else being equal, phylogenies containing a high proportion

