

# TANGLED TREES

Phylogeny, Cospeciation, and Coevolution

EDITED BY Roderic D. M. Page

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THE ECOLOGICAL BASIS  
OF COEVOLUTIONARY HISTORY

*Dale H. Clayton, Sarah Al-Tamimi,  
and Kevin P. Johnson*

THE UNIVERSITY OF CHICAGO PRESS  
Chicago and London

2003

## THE ECOLOGICAL BASIS OF COEVOLUTIONARY HISTORY

*Dale H. Clayton, Sarah Al-Tamimi,  
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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

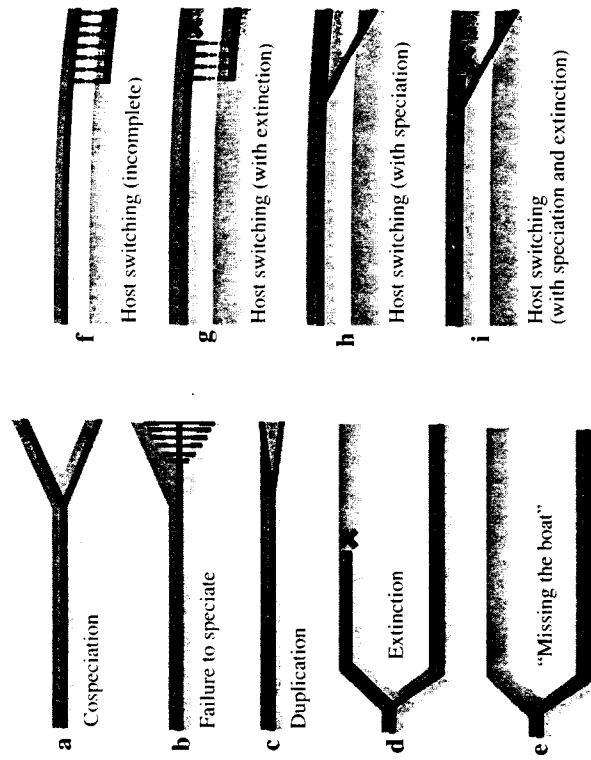


FIGURE 13.1. Macroevolutionary events that influence phylogenetic congruence. Gray lines represent hosts; black lines represent parasites. Black stippling represents gene flow between parasite populations. See text for discussion.

of cospeciated nodes will show more congruence than those containing a low proportion. However, the amount of cospeciation cannot be inferred directly from the amount of congruence between two phylogenies because it is possible for “false” congruence to be generated by processes other than cospeciation, such as extinction. Moreover, incongruence between phylogenies does not necessarily mean that there has been no cospeciation. As outlined below, other macroevolutionary events can reduce congruence between lineages that have undergone a considerable amount of cospeciation.

Aside from cospeciation (fig. 13.1a), all the events depicted in figure 13.1b–i effectively reduce congruence. For example, if a reproductive barrier affects a host lineage, but not its parasite, the parasite will *fail to speciate*, thereby reducing congruence (fig. 13.1b). Conversely, reproductive barriers that affect only the parasite lineage promote parasite *duplication* (fig. 13.1c), which also reduces congruence. Congruence is further reduced when parasites are lost from a host lineage, either through parasite *extinction* (fig. 13.1d), or by “*missing the boat*,” which occurs when parasites fail to disperse onto one of two new host clades (fig. 13.1e).

The final macroevolutionary event governing congruence is *host switching*, in which parasites colonize a “foreign” host species on which they did not previously occur. Host switching involves an initial expansion of the parasite’s host range (fig. 13.1f). This expansion is not a host switch, in and of itself, because the parasite persists on the original host. The host switch is completed by extinction of the parasite on the original host (fig. 13.1g), or by concurrent speciation and speciation (fig. 13.1i). It is not possible, using phylogenies reconstructed from extant species, to distinguish switching with extinction (fig. 13.1g) from switching with speciation and extinction (fig. 13.1i). However, information on the ecology of the descendant species can suggest the relative likelihood of the two types of host switches. A parasite with poor dispersal ability is more likely to speciate after colonizing a new host, since there will be little or no parasite gene flow between the original and new host species. In such cases, the host switch is completed by the speciation event, which may later be followed by extinction (fig. 13.1i). In contrast, when parasite dispersal is common, incomplete host switching may be a frequent event (fig. 13.1f).

### Relationship of Ecological Factors to Macroevolutionary Events

Ecological factors can have a fundamental impact on the probability of host switching and other macroevolutionary events governing the congruence of interacting clades (fig. 13.1). Ecological factors, which, by definition, affect the *distribution* and *abundance* of organisms (Begon et al., 1990), influence congruence through their impact on the host, the parasite, or both. For example, any factor that causes a parasite to be patchily distributed over the range of its host may increase the probability of parasite duplication (fig. 13.1c). Ecological factors that affect the abundance of the host and/or its parasite can also have an important influence. For example, stochastic extinction is far more likely in the case of a parasite that is typically found only in small numbers on host individuals.

Generally speaking, the distributions of host taxa have been reasonably well documented (e.g., Sibley and Monroe, 1990; Nelson, 1994; Nowak, 1999). In contrast, the distributions of most parasite taxa remain poorly known (Brooks and McLennan, 1993; Clayton and Moore, 1997). Parasites with indirect life cycles are especially problematic in this regard, since they involve one or more intermediate host species, in addition to free living stages and the final host. Distributions of parasites with direct life cycles are much simpler to characterize, being tied largely to the distribution of a single host species. Permanent parasites, which complete their entire life

cycle on the body of the host, have distributions that are particularly easy to characterize.

Given their close association with the host, the abundance of permanent parasites also can be measured accurately. This is particularly true for permanent ectoparasites, such as lice, which can even be observed and counted on live hosts (Clayton and Drown, 2001). These advantages make it possible to track the distribution and abundance of such parasites over the course of longitudinal studies. It is also possible to add or remove the parasites in controlled experiments designed to test the relative importance of the ecological factors thought to influence phylogenetic congruence (see below).

It is difficult to overemphasize the need for rigorous data on parasite abundance. Sampling errors can create the false impression of parasite-free host individuals, populations, or species, leading to erroneous conclusions about extinction or missing the boat (Paterson and Gray, 1997). Parasite ecologists normally measure two main components of parasite abundance: *prevalence* and *intensity* (Bush et al., 1997). Prevalence is the percent of individuals in a host population that actually have parasites. Intensity is the number of parasites on a parasitized individual; mean intensity is the average number of parasites across all parasitized individuals. Accurate measures of parasite prevalence and intensity require sampling methods that have demonstrated efficacy. Such methods have been tested thoroughly for lice (Clayton and Drown, 2001).

Ecological factors relevant to phylogenetic congruence vary in both time and space. Data from long-term studies are often required to document how ecological factors vary over time. In contrast, spatial variation can be relatively easy to document. However, is important to recognize that spatial variation exists on a variety of scales, ranging from variation among the microhabitats on a single host individual, to variation among host individuals, populations, and species (fig. 13.2). In the next section we consider the relevance of each of these four scales to the macroevolutionary events that govern phylogenetic congruence.

#### Variation among Microhabitats within a Host Individual

Different species of parasites appear to partition microhabitats on individual hosts (Poulin, 1998). For example, species of helminth worms tend to be concentrated in different regions of the host intestinal tract (Stock and Holmes, 1988). This pattern is consistent with competitive displacement owing to interspecific competition for limited resources, such as food. If competitive displacement is pervasive, it could influence the composition of parasite communities, leading to an absence of congeneric species on

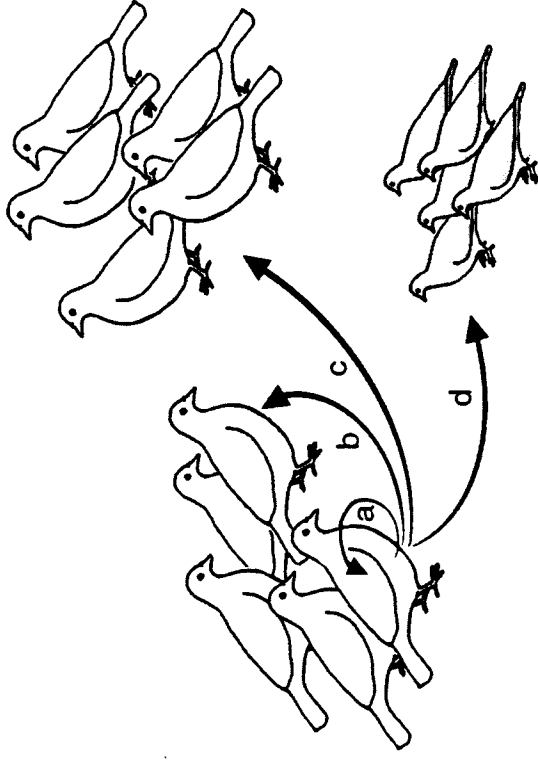


FIGURE 13.2. Ecological factors that influence host-parasite congruence vary among (a) microhabitats within a host individual (e.g., body versus wing); (b) host individuals; (c) host populations; and (d) host species.

a single species of host (e.g., Barker and Close, 1990; see also chap. 8). Competitive displacement may also operate between higher taxa. For example, since dispersing to dogs from its original host (a wallaby), the louse *Heterodoxus spiniger* appears to have displaced the louse *Trichodectes canis* from much of its former range (Barker, 1994).

Although intriguing, such patterns do not constitute robust evidence for competition (Simberloff, 1990; Page et al., 1996). Rigorous tests of competition require an experimental approach in which the population response of one or more species to the removal of a potential competitor(s) is carefully monitored (Poulin, 1998). Figure 13.3 summarizes the results of such a test that we recently conducted with wing lice (*Columbicola columbae*) and body lice (*Campanulotes bidentatus compar*) on Feral Pigeons (*Columba livia*). Wing lice spend most of their time on the host's wing and tail feathers, whereas body lice reside primarily on the abdominal feathers (see chap. 11). Despite these microhabitat differences, both species depend on abdominal contour feathers for food (Nelson and Murray, 1971). Figure 13.3 shows that body lice have a negative impact on the population growth of wing lice. Although the reason for this negative impact is unknown, it may have to do with better foraging ability on the part of body lice, assuming abdominal feathers are a limiting resource.

If interspecific competition influences the structure of parasite communities in general, then it is reasonable to predict that it could influence host switching in particular (Barker, 1994). For example, successful host switches should be more likely in the case of parasites dispersing to hosts that have depauperate parasite communities, because such hosts will represent greater ecological opportunity, that is, more untapped resources. This prediction could be tested by comparing the survival and reproductive success of parasites experimentally transferred to foreign hosts with and without other species of parasites already present. If interspecific competition reduces the fitness of parasites transferred to foreign hosts, then it clearly has the potential to influence host switching.

The direction of interspecific competition could also influence host switching. Asymmetric competitive effects have been documented in a number of parasite communities (Poulin, 1998). Figure 13.3 provides an example of asymmetric competition in which wing lice do worse in the presence of body lice, while body lice are unaffected by wing lice. These results predict that it would be easier for body lice to switch to foreign hosts already parasitized by wing lice, than for wing lice to switch to hosts with body lice. Body lice are significantly more host specific than wing lice (Johnson et al., 2002), further suggesting that host specific parasites may have a competitive edge over generalists. Data on the underlying causes of asymmetric competition are needed to begin exploring this intriguing possibility.

Microhabitat diversity and resource availability may also influence parasite duplication. A possible example involves the human body louse (*Pediculus humanus*), which is the sister species of the human head louse (*Pediculus capitis*) (Amevige et al., 2000). The two species are so similar that they are often classified as subspecies rather than full species (e.g., Durden and Musser, 1994). [Crab lice, which are confined to pubic hair, are members of another genus (*Phthirus pubis*).] Body lice attach their eggs to clothing, while head lice attach their eggs to hair. Body lice probably diverged from head lice concurrent with the loss of hair and adoption of clothing by hominids (Busvine, 1978). Clothing may therefore have provided a novel microhabitat that facilitated a duplication event, in which the

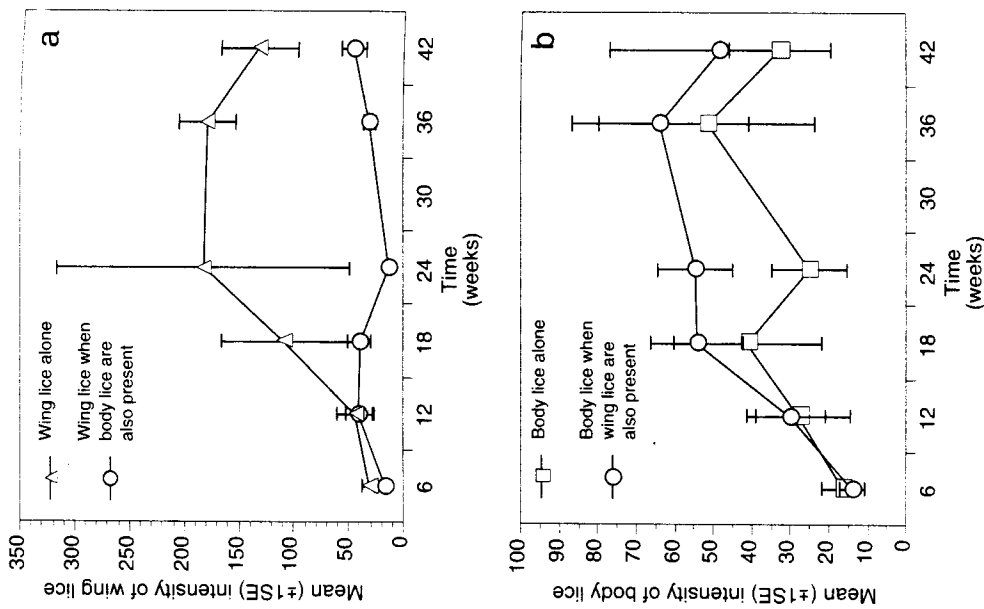


FIGURE 13.3. Competitive interaction between wing lice and body lice on Feral Pigeons. Population growth of wing lice (a) was slower on birds also parasitized by body lice, than on birds only parasitized by wing lice (repeated-measures ANOVA,  $p = .02$ ). In contrast, population growth of body lice (b) was similar with and without wing lice present ( $p = .38$ ). At the start of the experiment birds were "seeded" with identical numbers of lice, as follows: 16 pigeons were captured in Salt Lake City, Utah, then housed at low relative humidity (<30%) for 10 weeks, to exterminate their natural populations of lice and eggs (Moyer et al., 2002). The birds were then isolated in 16 cages and assigned randomly to three "seeding" treatments: 100 wing lice, 100 body lice, or 50 wing and 50 body lice. The data for mixed species of lice (circles in panels a and b) are thus from the same individual birds ( $n = 6$ ). The preening behavior of all birds was impaired with harmless plastic bits to facilitate increases in their lice (Clayton et al., 1999). Louse populations were monitored for approximately 10 months

FIGURE 13.3 (continued) by periodically counting all lice on the underside of one wing, the tail, and lice observed during timed intervals on three additional body regions: back and keel (30 seconds each), and rump (60 seconds). The sum of lice on these five regions significantly predicts the total number of *C. columbae* ( $R^2 = .66$ ) and *C. b. compar* ( $R^2 = .79$ ) on feral pigeons ( $p < .0001$  for both species; Clayton and Drown, 2001).

common ancestor of head and body lice diverged through speciation of a single species of host. Alternatively, head and body lice may have speciated allopatrically and subsequently come into secondary contact (Busvine, 1978). Under either scenario of parasite speciation, the probability of duplication may increase with the diversity of microhabitats available on a given host. This hypothesis could be tested by comparing the number of potential microhabitats among different hosts to the number of congeneric parasites they support.

Microhabitat specialization could conceivably also increase the probability of parasite extinction, assuming the abundance of microhabitat specialists is lower than that of microhabitat generalists. For example, chimpanzees (*Pan troglodytes*) have a single species of louse (*Pediculus schaeffi*) (Durden and Musser, 1994) that presumably roams all of the host's body, given its continuous distribution of hair. If so, then one can predict that the mean abundance of this louse will be greater than that of human lice, all three species of which are more restricted in their microhabitat distributions (see above). The chimp louse may therefore be less prone to extinction if it really is more abundant. Of course, this ignores differences in host body size, population size, and other factors that are already known to influence parasite abundance (Poulin, 1998). The impact of microhabitat specialization on risk of extinction could be explored with comparative analyses that control for these and other factors.

#### Variation among Individuals within a Host Population

Parasite abundance varies within host populations, ranging from heavily parasitized individuals to individuals having no parasites. Low parasite prevalence increases the probability that a parasite will miss the boat, since a dispersing founder population of hosts is more likely to be comprised solely of individuals having no parasites (Paterson et al., 1999). Variation in parasite intensity—the number of parasite individuals on a host (see above)—may also influence the probability that parasites will miss the boat or go extinct (Rózsa, 1993). At the very least, parasites that are rare are more likely to miss the boat or go extinct than those that are abundant. In contrast, parasites that are abundant might increase the probability of host switching, assuming that dispersal is density dependent, that is, attempts at host switching will presumably be higher when parasites are dispersing at a higher rate.

Parasite abundance is usually quite variable even in populations that have a high mean parasite intensity. This is particularly the case for “macroparasites,” such as helminths and arthropods (Anderson and May,

1979). Macroparasites tend to concentrate on a minority of heavily infested individuals, forming an aggregated distribution with the property that the variance in parasite intensity exceeds the mean. Proximal reasons for aggregation are unclear, although variation in host susceptibility and the contagious nature of parasite transmission are probably important factors (Hudson and Dobson, 1995).

Aggregation should increase the probability of parasites missing the boat. A founder population dispersing from a parent population containing aggregated parasites is more likely to be parasite free than one dispersing from a parent population containing an even distribution of parasites. Aggregation could also increase the probability of parasite extinction if heavily parasitized individuals die before their parasites are transmitted to new hosts. This is probably not an overly likely scenario, since parasite virulence is generally correlated with the ease of transmission (Ewald, 1994). Parasites that are transmitted vertically from parent to offspring, such as feather lice, are usually fairly benign, since their reproductive fitness is linked closely with that of the host (Clayton and Tompkins, 1994). More virulent parasites tend to be transmitted horizontally, which prevents them from being marooned on a dead or dying host (Herre, 1993).

#### Variation among Host Populations

Parasites can be rare or absent from some host populations, while abundant on others. For example, feather lice have a patchy distribution in which they are abundant on doves in many areas of the world, yet virtually absent from the same species of doves in arid regions (Moyer et al., 2002). Patchiness can also be generated when host population size falls below the minimum threshold required to support parasites (Rózsa, 1993). Thus, an area of low host density can be a dispersal barrier for parasites, or a sink that limits gene flow between parasite populations in different parts of the host's geographic range.

Patchiness has the potential to influence macroevolutionary events. Nested within their host limits, parasites often show geographic limits to their distribution (see Clay, 1964, 1972). These geographic limits increase the likelihood of parasites missing the boat, since parasites may be absent from hosts involved in founder events (Brown and Wilson, 1975). For example, 18 bird species were historically introduced to New Zealand by humans. The species richness of lice on these birds in New Zealand is significantly lower than that on the same birds in their native environments (Paterson et al., 1999). The founding populations of most of these introduced birds were small—a few individuals to as many as 100 individuals. Although

