



Current opinion

Multi-host parasite species in cophylogenetic studies

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Abstract

Cophylogenetic studies examine the relationship between host and parasite evolution. One aspect of cophylogenetic studies that has had little modern discussion is parasites with multiple definitive hosts. Parasite species with multiple host species are anomalous as, under a codivergence paradigm, speciation by the hosts should cause speciation of their parasites. We discuss situations such as cryptic parasite species, recent host switching or failure to speciate that may generate multi-host parasites. We suggest methods to identify which of the mechanisms have led to multi-host parasitism. Applying the suggested methods may allow multi-host parasites to be integrated more fully into cophylogenetic studies.

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Cophylogenetic studies of relationships between parasites and their hosts have been revitalised recently. Studies have been conducted on diverse host–parasite assemblages such as chewing lice and pocket gophers (Hafner et al., 1994) and parasitic copepods and teleost fish (Paterson and Poulin, 1999). The principles underpinning host–parasite cophylogenetic studies have also been applied to other systems such as herbivore–plant interactions (Futuyma and McCafferty, 1990). Most, if not all, of these studies investigate the origins of current associations, asking whether they arose by descent or by colonisation. Association by descent proposes that current host–parasite associations have arisen because each host species has inherited the association from its ancestral species. Association by colonisation proposes that host switching, a parasite switching to a host species from a lineage other than the host's ancestor, is the predominant explanation for the parasites' distributions (Brooks and McLennan, 1991).

Cophylogenetic studies have traditionally assessed the extent of codivergence, i.e. parallel speciation in

the unrelated host and parasite lineages (Clayton et al., 2003), by examining the degree of congruence between host and parasite phylogenies. Incongruent host and parasite phylogenies suggests host switching in the parasite lineage (Brooks and McLennan, 1991). However, incongruence does not necessarily imply host switching as congruence can be hidden by other cophylogenetic events, such as sorting (e.g. extinction) and duplication (intra-host speciation) events (Paterson and Banks, 2001; Clayton et al., 2003). Likewise, congruent host and parasite phylogenies do not necessarily indicate a history of cospeciation as processes other than cospeciation may generate 'false' congruence (Clayton et al., 2003). False congruence can arise, for example, if a parasite species has undergone a series of sequential host switches, successively colonising the host's closest relatives and then speciating (Brooks and McLennan, 1991).

While most of the events potentially affecting the distribution of parasite species on their hosts have been discussed, especially by Clay (1949), one aspect of cophylogenetic studies that has had little modern discussion is the distribution of a single parasite species on multiple definitive host species (the host on which a parasite reproduces sexually) and the influence such parasites have on coevolutionary history. Studies of host–parasite interactions have often concentrated on the chewing lice, with

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gophers and their lice being a textbook example of host–parasite cospeciation. As lice are able to coexist with their hosts for evolutionary long periods, and have few opportunities to transfer between host species, they should be host specific and show a high degree of codivergence with their hosts (Page and Hafner, 1996). Lice with multi-host distributions at first appear to be somewhat anomalous within a codivergence paradigm. However, louse species infesting multiple host species are relatively common. For example, eight of the 15 species of obligate ectoparasitic chewing lice, Phthiraptera, parasitising penguins, Spheniscidae; two of the seven species of lice parasitising kiwi, Apterygidae; and 13 of the 14 louse species parasitising albatrosses, Diomedidae, in the New Zealand region, have multiple hosts (Price et al., 2003). Some louse species have a very wide distribution indeed, for example, the louse *Menacanthus eurysternus* (Burmeister, 1838) parasitises 176 bird species in 100 genera and 34 families and there are only three small bird orders on which all species of lice are host specific (Price et al., 2003).

In this paper, we comment on the different processes that may produce multi-host parasitism and how these processes may mask instances of cospeciation or host switching by parasites. We examine factors that enable populations of multi-host parasites to remain in genetic contact despite parasitising different host species and suggest that population genetic techniques may be required to fully explain host–parasite associations.

We suggest the following explanations for the presence of multi-host parasites:

- (i) cryptic parasite species,
- (ii) misclassified (over-split) hosts,
- (iii) recent host switches,
- (iv) failure to speciate by parasite populations despite their host taxa diverging,
- (v) incomplete host switching (sensu Clayton et al., 2003).

Note that for (i)–(iii), although the parasite populations infesting divergent host taxa appear to be the same species, the parasite populations are actually genetically isolated from each other.

Parasite morpho-species may appear to have multiple host species if parasite populations are isolated on their hosts and have diverged genetically but the parasite species are morphologically conservative, i.e. cryptic species. Cryptic species can be identified relatively easily using genetic data. The lack of morphological differences in the parasites may be due to factors such as similar selection pressures on the parasite species causing conservation of morphology (Fig. 1A).

Cryptic species may also be present if morphological convergence has occurred between parasite species that are not closely related (Fig. 1B), for example, if the parasite species face similar selection pressure. Once divergent parasite taxa are identified from genetic data, they should be

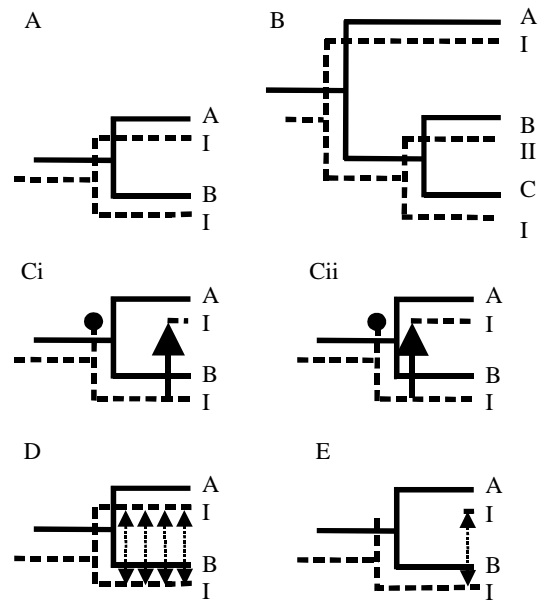


Fig. 1. Stacked hypothetical phylogenies for host (solid lines) and parasite (broken lines) morpho-species representing the processes that can produce a pattern of multi-host parasitism in cophylogenetic studies. Branch lengths are proportional to time. The parasite phylogeny is displaced to the left and is below the host phylogeny. Apparent multi-host parasites due to: (A) Cryptic species. Parasite I is in reality two species but classified as a single species due to failure to detect differences between the two populations. (B) Morphological convergence. Parasite I is two species but classified as a single species due to convergence. (C_i) Host switching, recent. Parasite I is in reality two species but classified as a single species as insufficient time has elapsed for differences to accumulate. (C_{ii}) Host switching, ancient. Parasite I is in reality two species but classified as a single species as no differences have been identified, perhaps due to morphological similarity. True multi-host parasites due to (D) failure to speciate. Parasite I is a single species due to gene flow between parasite populations. The double-headed broken arrows designate ongoing gene flow between the parasite populations. (E) Host switching, incomplete. Parasite I has colonised a new host species but the parasite populations on the two host species are not genetically isolated from each other.

treated as separate taxa in cophylogenetic analyses and may support either association by descent (Fig. 1A) or colonisation (Fig. 1C), depending on their position in the phylogeny.

Cryptic louse species parasitising doves have been identified using genetic data. For example, the chewing louse, *Columbicola passerinae* (Wilson, 1941) parasitising the blue ground dove, *Claravis pretiosa* (Ferrari-Pérez, 1886), differs from *C. passerinae* parasitising the common ground dove, *Columbina passerina* (L., 1758) by 11.3% for a portion of the mitochondrial cytochrome oxidase *c* subunit I (COI) gene suggesting the two louse populations could be reclassified as two species (Johnson et al., 2002). The chewing louse genus *Physoconelloides* also contains multi-host louse taxa implying considerably more host specificity than apparent from a consideration of morpho-species alone (Johnson et al., 2002).

Parasites may appear to have several hosts if host ‘species’ are over-split. If two host species are actually a single species then a parasite species will appear to

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