



# The historical biogeography of co-evolution: emerging infectious diseases are evolutionary accidents waiting to happen

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## ABSTRACT

Ecological fitting refers to interspecific associations characterized by ecologically specialized, yet phylogenetically conservative, resource utilization. During periods of biotic expansion, parasites and hosts may disperse from their areas of origin. In conjunction with ecological fitting, this sets the stage for host switching without evolving novel host utilization capabilities. This is the evolutionary basis of emerging infectious diseases (EIDs). Phylogenetic analysis for comparing trees (PACT) is a method developed to delineate both general and unique historically reticulated and non-reticulated relationships among species and geographical areas, or among parasites and their hosts. PACT is based on 'Assumption 0', which states that all species and all hosts in each input phylogeny must be analysed without modification, and the final analysis must be logically consistent with all input data. Assumption 0 will be violated whenever a host or area has a reticulated history with respect to its parasites or species. PACT includes a Duplication Rule, by which hosts or areas are listed for each co-evolutionary or biogeographical event affecting them, which satisfies Assumption 0 even if there are reticulations. PACT maximizes the search for general patterns by using Ockam's Razor – duplicate only enough to satisfy Assumption 0. PACT applied to the host and geographical distributions of members of two groups of parasitic helminths infecting anthropoid primates indicates a long and continuous association with those hosts. Nonetheless, *c.* 30% of the host associations are due to host switching. Only one of those involves non-primate hosts, suggesting that most were constrained by resource requirements that are phylogenetically conservative among primates (ecological fitting). In addition, most of the host switches were associated with episodes of biotic expansion, also as predicted by the ecological fitting view of EIDs.

## Keywords

Co-evolution, ecological fitting, emerging infectious diseases, evolution, historical biogeography, PACT, phylogeny.

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## INTRODUCTION

The biodiversity crisis is not just a crisis of extinction; it is also a crisis of introduced species and emerging diseases (Grenfell & Gulland, 1995; Daszak *et al.*, 2000; Harvell *et al.*, 2002). Such events produce complex geographical distributions and host-pathogen relationships. How do these anthropogenic phenomena compare with area and host relationships produced on evolutionary time scales? Do they differ in degree or in kind? Answering such questions requires that we assess both the geographical and the host context of pathogen/host co-evolution.

Studies of co-evolution emerged from consideration of host and geography, beginning with von Ihering's (1891, 1902) observations about the similarities between some temnocephalidean (flatworm) parasites inhabiting freshwater crayfish in New Zealand and in the mountains of Argentina. He postulated that the species in the two disjunct areas were derived from ancestral crayfish and flatworms that were themselves associated, and therefore South America and New Zealand must once have been connected by fresh water. A generation later, biogeographical considerations had largely disappeared from discussions of co-evolution. Fahrenholz (1913) postulated that the occurrence of related blood-sucking

lice on different primates demonstrated that the catarrhines were more closely related to hominoids than to any other primates. By the late 1930s, the orthogeneticists had produced an integrated view of co-evolution: parasites are highly host specific, so they coevolve with their hosts, and because they coevolve with their hosts, they become highly host specific. Since host specificity was the 'cause' of co-evolution, rather than a function of the ecological interaction between lineages, any conflicting or inconsistent observations were erroneous or irrelevant because they failed to conform to the orthogenetic view of co-evolution.

For most of the twentieth century, parasitologists continued to study co-evolution within an orthogenetic framework despite calls to integrate with mainstream evolutionary biology (e.g. Mayr, 1957; Manter, 1966; Janzen, 1985a; Brooks & McLennan, 1993, 2002). Vestiges of orthogenetic thinking persist today; this is especially true for the assumption that hosts and parasites 'ought' to have congruent phylogenies, embodied in the maximum co-speciation research programme (Page, 2002; see also Brooks, 2003).

There is a second tradition of thought about the nature of co-evolution. Kellogg (1896, 1913) suggested that while some host-parasite systems might show strong phylogenetic associations, there were substantial cases of what he termed 'straggling', referring in some cases to hosts speciating when the parasites did not and in other cases to parasites switching hosts. Kellogg cast his observations about the relationship between birds and their biting lice in a Darwinian framework, which helped initiate a different approach to co-evolution. Most researchers who adopted this perspective were interested in studying the interactions between plants and phytophagous insects (e.g. Verschaffelt, 1910; Brues, 1920, 1924). Because those associations often showed no clear phylogenetic component with respect to host species (though they often were extremely specific), researchers in this tradition focused on discovering the ecological ties between organisms, particularly the cues insects used to locate their host plants.

The modern version of this second perspective emerged in the early 1960s. Following a mathematical model proposed by Mode (1958), Ehrlich & Raven (1964) hypothesized that the evolutionary diversification of plants and insects had been fuelled by complex co-evolutionary interactions involving mutual modification. Such co-evolutionary dynamics might have a general phylogenetic context, but the fine details need not parallel the evolutionary history of the specific taxa involved. The distribution of insects among plants followed the evolution of host resources and the evolution of insects' abilities to utilize those resources, rather than the evolution of host species themselves. Janzen (1968, 1973a,b, 1980, 1981, 1983, 1985a,b) reintroduced an explicit biogeographical element to this discussion. He argued that the appearance of tight co-evolutionary associations at any single locality could be misleading. No matter where a given species evolved in the first place, its inherited functional abilities may allow it to survive in a variety of places under a variety of conditions through arbitrary amounts of time. In other words, species and

their phylogenetically conservative traits may disperse readily through time and space. He termed this interaction between the past history of the species and their present day associations 'ecological fitting'. One particularly critical manifestation of ecological fitting is that any given species may be a resource specialist but may also share that specialist trait with one or more close relatives. That is, specialization on a particular resource can be plesiomorphic. In a complementary manner, the resources themselves may be very specific and yet still be taxonomically and geographically widespread, if they are persistent plesiomorphic traits of the hosts.

The phylogenetic revolution has given rise to modern versions of these two traditional schools of thought. The maximum co-speciation, or co-phylogeny, school has been based on the belief that host-parasite associations are so ecologically specialized that parasites have few opportunities to switch hosts. Various models or assumptions are invoked to 'reconcile' portions of parasite phylogenies that are incongruent with host phylogeny to the host phylogeny. This can be accomplished for every case of incongruence by postulating that each one actually represents at least two past episodes, one of sympatric speciation by the parasite (which the maximum co-speciation school calls 'lineage duplication') coupled with one or more episodes of particular extinctions (which the maximum co-speciation school calls 'lineage sorting'). This methodology, sometimes called 'tree reconciliation', can make every putative case of host switching disappear (Van Veller & Brooks, 2001). It is then up to the discretion of the investigator to decide if any cases of host switching will be permitted. Although generally unacknowledged by its advocates, the theoretical basis for this approach can be found in orthogenetic theory (for a historical discussion, see Brooks & McLennan, 1993, 2002), in which parasites are evolutionarily tied to their host species.

The alternative approach is based on the assumption that the extent to which host-parasite associations are specialized is decoupled from the extent to which there might be host switching. Brooks (1979) made this point in distinguishing between co-speciation and co-accommodation (more recently co-adaptation), arguing that one could not extrapolate from one to the other. This sentiment has also been formalized as diffuse co-evolution (Futuyma & Slatkin, 1983), and, as noted above, ecological fitting (Janzen, 1985b). Brooks & McLennan (2002) suggested that ecological fitting be used as the general term, as it best embodies the envisioned process. Basically, no matter how ecologically specialized an association between species at any particular place and time, the traits (resources) characterizing the association may be phylogenetically conservative. Therefore, if geographical and/or ecological circumstances change, a parasite might easily switch to new host species simply because they are sources of the same specialized resources that were previously available only from another host. Furthermore, if these highly specialized resources are plesiomorphic, the host switches need not be restricted to hosts belonging to a single clade, although we might expect them not to be very distantly related (for a recent example, see Radtke

*et al.*, 2002). As a consequence, Brooks (1979) suggested that one could not simply extrapolate from the degree of host specificity, or the perceived degree of specialization of any host–parasite association to an expectation of the probability of co-speciation or host switching. Furthermore, co-speciation patterns might simply be a by-product of allopatric speciation events experienced by both hosts and parasites (frozen accidents of history) rather than evidence of strong and exclusive co-evolutionary interactions (Brooks, 1981; for a review with numerous references, see Brooks & McLennan, 2002).

Empirically, advocates of the maximum co-speciation school assert that maximum co-speciation should be the preferred explanation even when there is incongruence between host and parasite phylogenies because it is a simpler *a priori* theory, and worry that ecological fitting permits too many *a priori* possibilities. Advocates of ecological fitting argue that host switching should be preferred for such cases, because one host switch is simpler than one sympatric speciation event and one or more extinction events, and argue that maximum co-speciation prohibits too many possibilities *a priori*. Thus, the two approaches invoke parsimony differently, ontologically and epistemologically respectively. This parallels the case of cladistic and phylogenetic approaches to historical biogeography, previously presented in this journal (Van Veller & Brooks, 2001; see also Brooks, 2003; Brooks *et al.*, 2004).

Happily, there are signs of a synthesis. Brooks & McLennan (2002) suggested that the evolutionary basis for such fitting is simple and its manifestations are ubiquitous. If specific environmental cues/resources are widespread or if traits can have multiple functions (or both), then the stage is set for the appearance of ecological specialization and close (co)evolutionary tracking, without losing the ability to establish novel associations. In this context, it is important to remember that resource availability is not the same as resource distribution. Trophic segregation and allopatry are two powerful ‘indirect effects’ that may limit actual (vs. potential) host utilization (the observed host range) at any given time. These effects actually lower the long-term evolutionary cost of specialization (i.e. increased risk of extinction over time) for a given pathogen by increasing the chances that it will come into contact with additional susceptible hosts if there is a change in the environment, leading to altered trophic interactions or to geographical dispersal.

Less than 2 years later, *Systematic Biology* published the proceedings of a symposium by the maximum co-speciation school that marked a singular change in their perspective. Parasitologists and zoo veterinarians have long known that parasites switch hosts under conditions of close confinement (and stress). Noting this, Johnson & Clayton (2004) and Clayton *et al.* (2004) suggested that host switches are not limited by inherent inability to establish on new hosts but by lack of opportunity, and called for more study of the ecology of host–parasite associations, not just to understand systems that appear to show high degrees of co-speciation but also to gain more insight into those that show substantial amounts of host

switching, such as those reported in the symposium (Degnan *et al.*, 2004; Percy *et al.*, 2004; Ricklefs *et al.*, 2004; Sorenson *et al.*, 2004; Weiblen, 2004). Interestingly, Johnson & Clayton (2004) and Clayton *et al.* (2004) suggested that avian lice, the model system used by Kellogg (1896, 1913) to study straggling, would be an excellent system to study ... straggling!

Notable among those contributions was the one by Weckstein (2004), who concluded that historical biogeographical phenomena might play a role in mediating both co-speciation and host switching, an idea first proposed by Brooks (1979, 1980, 1981), consistent with the results of many published studies ranging from particular parasite groups, such as malaria (Escalante & Ayala, 1994; Escalante *et al.*, 1995) and some human tapeworms (*Taenia* spp.) (Hoberg *et al.*, 2000), to entire biotas, such as the host–parasite assemblage of the Arctic (Hoberg, 1986, 1989, 1992, 1995, 1996, 1997a,b, 2002, 2005; Hoberg & Adams, 1992, 2000; Hoberg *et al.*, 1995, 1999a,b, 2000, 2001, 2002, 2003, 2004; Hoberg & Klassen, 2002), and summarized for vertebrate parasites in book form by Brooks & McLennan (1993). This list is only representative, not exhaustive, as virtually all phylogenetic studies of insect–plant systems also show extensive host-switching, as first suggested by Mitter & Brooks (1983).

In the context of emerging infectious disease, the traditional distinction between these two schools of thought is striking. For traditional advocates of maximum co-speciation, the co-evolutionary process itself provides a safeguard against emerging diseases, which should be rare, if not ruled out altogether. For advocates of ecological fitting, and the emerging modification of the maximum co-speciation school, however, the world is a mosaic of specialized but evolutionarily conservative ecologies, into which large numbers of pathogens could fit, given the right circumstances. And those circumstances involve geographical and/or climatological alteration of ecosystems, such that hosts and pathogens are able to move out of their areas of origin, coming into contact with novel hosts and pathogens as a result of dispersal with or without modifications of trophic structure. If observed incongruence between host and parasite phylogenies were due to lineage duplication plus extinction, there would be no particular biogeographical signature of the event (duplications being due to sympatric speciation). Emerging diseases imply that there has been host switching coupled with geographical movement. Either new hosts have moved into the area of origin of a given pathogen, which has incorporated them into its host range, or the pathogen has moved out of its area of origin into an area where susceptible hosts live, and has added them to its host range. Thus, we would expect to find a preponderance of cases of host switching associated with episodes of geographical dispersal.

## METHODOLOGY

The ecological fitting perspective is based on the notion that evolution has been complex and historically contingent; however, that history includes both general (law-like) and unique (contingent) phenomena. Extending this to

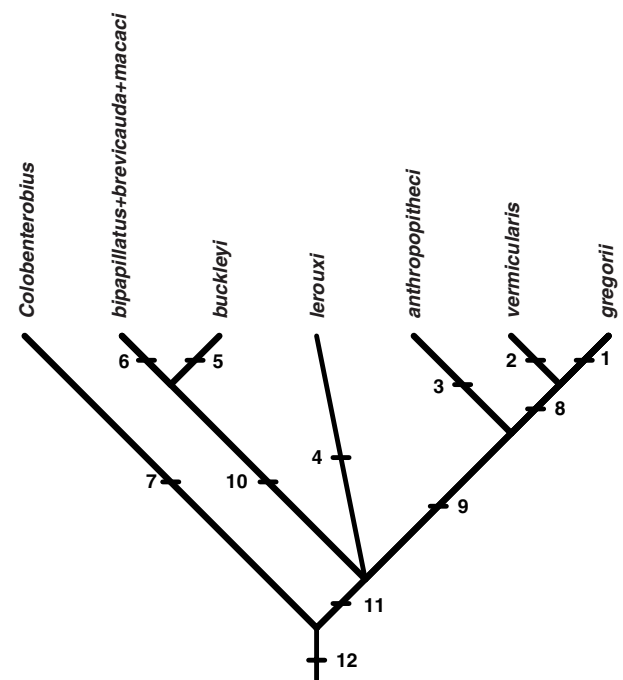
co-evolutionary studies leads us to predict that phylogenetic comparisons of parasite–host cladograms (i.e. parasite phylogenies in which the parasite species names have been replaced by the names of their hosts) should be historically unique combinations of phenomena that are congruent with host phylogeny (co-speciation, extinction, sympatric speciation and extinction) as well as episodes of host switching. Furthermore, we would predict that our ability to document those patterns would be obscured most by the use of models and methods that over-simplify the process by invoking *a priori* assumptions or prohibitions. This leads us to recognize several essential elements of the analytical method required to study host–parasite evolution, which together form the basis for the new algorithm PACT (phylogenetic analysis for comparing trees; Wojcicki & Brooks, 2004, 2005).

First, it is not permissible to remove or modify data. Wiley (1986a,b,c, 1988a,b) and Zandee & Roos (1987) already formalized this as ‘Assumption 0’, which states that you must analyse all species and all hosts in each input phylogeny without modification, and your final analysis must be logically consistent with all input data. Recognition of the fundamental importance of Assumption 0 was obscured by Page (1990), who used ‘Assumption 0’ to refer to the protocol of coding ‘absence’ as ‘0’ in preparing a matrix of data for analysis. Brooks (1981) proposed that protocol because computer programs at that time did not accept missing data. It was eliminated when Wiley (1986a) proposed using missing data coding for absences for analyses using Brooks’ method, which Wiley dubbed Brooks Parsimony Analysis (BPA). Assumption 0 does not imply that the input phylogenies are true or complete. It does imply, however, that the method of analysis for biogeographical or co-evolutionary studies cannot be used to assess the accuracy of the phylogenies, as that would introduce an unacceptable degree of subjectivity, or even circularity, into the process. Therefore, if one is dissatisfied with the results of a co-evolutionary analysis, and suspects that this is due to a poor phylogenetic hypothesis or un-sampled species, the solution is to get more data, improve the input phylogeny, and re-do the co-evolutionary analysis.

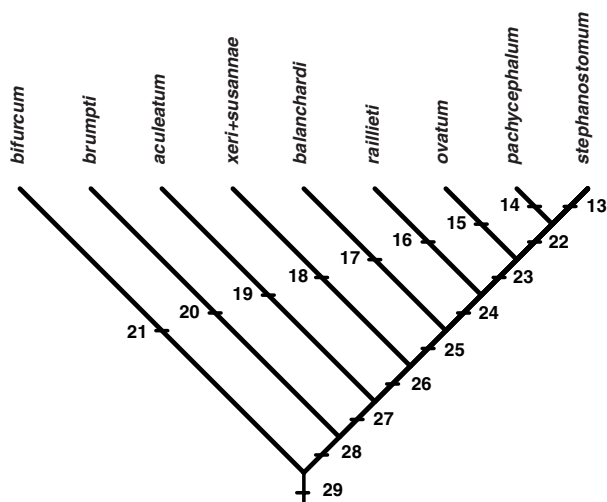
Second, host cladograms based on many parasites inhabiting the same hosts must include reticulated host relationships. If each host species on this planet had a singular history with respect to all the species living in association with it, either there would be one parasite species per host species or one parasite clade per host species. Nowhere on earth does this occur, so we must assume that reticulated host relationships have been common. If we use a method of analysis that produces simple host cladograms (i.e. ones in which parasite data are reconciled to the host phylogeny), Assumption 0 will be violated whenever a host has a reticulated history with respect to any of its parasites. Assumption 0 can be satisfied in such cases by duplicating hosts with reticulated histories. Therefore, a method of analysis for handling complexity requires a Duplication Rule, a mechanism by which hosts are listed for each co-evolutionary event affecting them (see also Brooks & McLennan, 2002).

Finally, if no possibilities, including host reticulations, are prohibited *a priori*, and if co-evolutionary patterns are combinations of unique and general phenomena, how are general patterns found? PACT employs Ockam’s Razor as an epistemological corollary of the Duplication Rule – duplicate only enough to satisfy Assumption 0. Simplicity is used only to determine if there are general patterns, so the ecological fitting perspective is not a ‘maximum host-switching’ analogue of the maximum co-speciation school. PACT searches for the maximum allowable general patterns as well as unique events and reticulated relationships. In this regard, it is most similar to secondary BPA (Brooks, 1990; Brooks & McLennan, 2002), but has been shown to be an improvement on that method (Wojcicki & Brooks, 2004, 2005). PACT produces a simple result when the data warrant it, but is capable of producing complex results when the data demand.

We illustrate the ecological fitting perspective on understanding EIDS using the most recent phylogenetic hypotheses for pinworms (*Enterobius* spp.; Hugot, 1999) (Fig. 1) and hookworms [*Oesophagostomum* (*Conoweberia*) spp.; Glen & Brooks, 1985] (Fig. 2) inhabiting the Great Apes. For details of the phylogenetic analyses of the parasite clades and their sources, see Brooks & McLennan (2003) and references therein. We used PACT to generate (1) a host cladogram, a branching diagram listing hosts as terminal taxa, providing a visual summary of the host context of speciation events implied by the parasite phylogenies; and (2) an area cladogram, a branching diagram listing areas as terminal taxa, providing a visual summary of the geographical context of speciation events implied by the parasite phylogenies. For details of PACT, see Wojcicki & Brooks (2004, 2005).



**Figure 1** Phylogenetic tree of species of *Enterobius*. All branches are numbered for ease of interpreting the host cladogram (Fig. 3).



**Figure 2** Phylogenetic tree of species of *Oesophagostomum* (*Conoweberia*). All branches are numbered for ease of interpreting the host cladogram (Fig. 3).

**RESULTS**

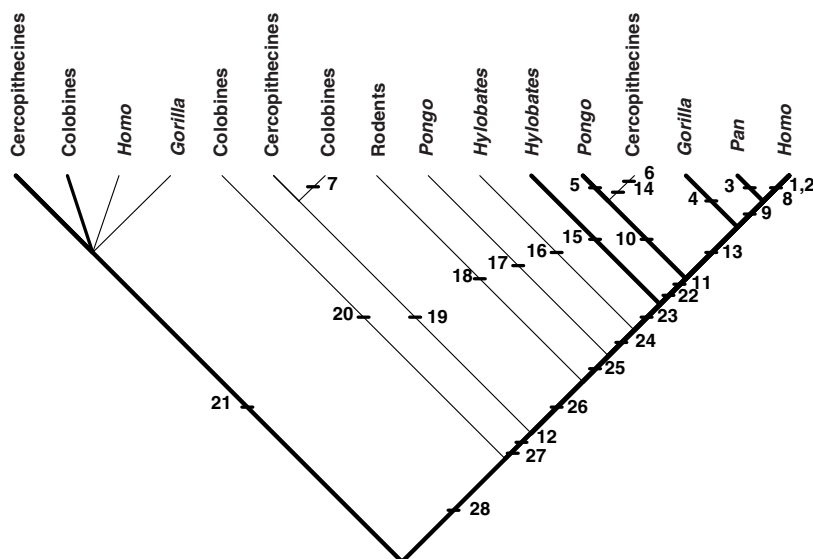
The heavy branches on the PACT host cladogram (Fig. 3) indicate instances of congruence between host and parasite phylogeny (co-speciation; Brooks, 1981). This includes one case (the common ancestor [8] of *Enterobius gregorii* [1] + *E. vermicularis* [2]) in which a parasite clade speciated but the host did not, and another (*Oesophagostomum stephanostomum* [18]) in which the host clade speciated but the parasite did not. These findings suggest that the association between pinworms and hookworms and the Great Apes and their relatives has been a long and continuous one. Despite the substantial amount of co-speciation, the PACT analysis suggests that, among the 28 lineages of *Enterobius* and *Oesophagostomum* included, there have been eight events (29%) that are not congruent with host phylogeny. Only one of those host

switches, that giving rise to the common ancestor of *O. xeri* + *O. susannae* (18 in Fig. 3), represents a switch to a non-primate host (in this case rodents), suggesting phylogenetic conservatism in host specificity among these parasites in accordance with the expectations of ecological fitting. The remaining switches include the acquisition of parasites that are more or less the same age (*Oesophagostomum brumpti* (20 in Fig. 3), *O. aculeatum* (19 in Fig. 3), and the common ancestor of *Enterobius bipapillatus* + *E. brevicaudatum* + *E. macaci* (six in Fig. 3)), that are younger (*O. pachycephalum* (14 in Fig. 3)), and that are older (*O. bifurcum* (21 in Fig. 3), *O. raillieti* (16 in Fig. 3), and *O. blanchardi* (17 in Fig. 3)) than their hosts, again suggesting ecological fitting.

The biogeographical analysis of *Enterobius* and *Oesophagostomum* (*Conoweberia*) (Fig. 4) suggests a history of speciation involving alternating episodes of isolation in, and then movements between, Africa and Asia. This supports a taxon pulse dynamic rather than a simple vicariance scenario (Erwin, 1979; for recent studies of taxon pulses, see Spironello & Brooks, 2003; Bouchard *et al.*, 2004; Halas *et al.*, 2005). Furthermore, five of the eight (63%) host switches discovered in Fig. 3 occurred during periods of biotic expansion discovered in Fig. 4, the exceptions being the switch from primates to rodents in the common ancestor of *O. xeri* + *O. susannae*, which took place in Africa, and *O. blanchardi* in *Pongo* and *O. raillieti* in *Hylobates* (perhaps representing an actual case of sympatric speciation), which took place in Asia. These data clearly support ecological fitting more than maximum co-speciation.

**DISCUSSION**

We began by pointing out that the phenomenon of emerging infectious diseases is the result of species being moved from their areas of origin into novel places, leading to host switches, and we asked if this was a difference in degree or kind from the evolution of host–parasite relationships in the past. Nearly



**Figure 3** Host cladogram produced by PACT, indicating host context of speciation events implied by phylogenies for *Enterobius* and *Oesophagostomum* (*Conoweberia*) (Figs 1 & 2). Thick lines indicate associations congruent with host phylogeny; thin lines indicate host-switching events. Numbers on branches refer to particular branches on the parasite phylogenetic trees.



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