

Using phylogenies to reveal rare events

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Evolutionary biology is sometimes described slightly pejoratively as being an historical science, dealing in past events whose uniqueness hinders the derivation of the explanatory generalities that characterise first-class science. I want to argue here that rare – even unique – historical events can be studied with full scientific rigour, in such a way that we learn something quite general about evolutionary processes. I discuss two examples from my own work on marine snails from the family Trochidae, although others could easily have been chosen. Crucially, my examples rely on the use of phylogenetic methods, championed so effectively by David Penny.

Host–parasite co-evolution in snails and trematodes

My first example concerns host–parasite co-evolution and is described in more detail in Donald *et al.* (2004). In recent years, a significant body of work on seabirds and their parasitic feather lice has shown a remarkable degree of congruence between the evolutionary trees of these hosts and parasites: feather-lice parasites generally co-speciate with their seabird hosts and are often confined to a single host species. But seabirds often live in monospecific colonies and lice do not survive well in isolation, dying within a few hours of removal from a bird. The opportunities for lice to switch host species are therefore limited and the co-phylogeny may be more a consequence of this lack of opportunity than something general about host–parasite co-evolution. One way to test this idea is to look at a host–parasite system that exhibits ample opportunity for host switching.

Intertidal gastropods in the genera *Diloma* in New Zealand and *Austrocochlea* in Australia are first-intermediate hosts to a group of closely related trematode parasites. Although the life cycle of this group of parasites is not fully known, trematode eggs are shed in the faeces of the definitive host (probably a fish) and hatch to form free-swimming miracidia that, on contact with a snail, penetrate the first-intermediate host's body. In spite of

small habitat preferences, the different snail species are commonly found very close to each other; I have found six *Diloma* species within a 20 m radius near Dunedin, for example. Thus different potential hosts are exposed to the whole range of possible parasite species, providing a chance every generation for the trematode parasites to switch and share snail hosts.

Before our study, we did not know if host-sharing was common or absent in this system; indeed, we did not know if more than one trematode species was present. The prevailing parasitological paradigm held that trematodes are choosy about their first-intermediate hosts, and so host-sharing should be rare. Ecologists, however, pointed to the opportunities for such a finely tuned correspondence to be subverted, and argued that host-sharing should prevail.

Our fieldwork hinted at intrigue. For example, there was often a great disparity between infection levels of different host species living side by side. At Company Bay on the Otago Peninsula, for instance, about 17.5% of *Diloma subrostrata* individuals were infected, but not a single *D. aethiops* out of 300 was. Two of the six New Zealand snail species we examined were never found to act as hosts; just two of the four Australian species were ever infected.

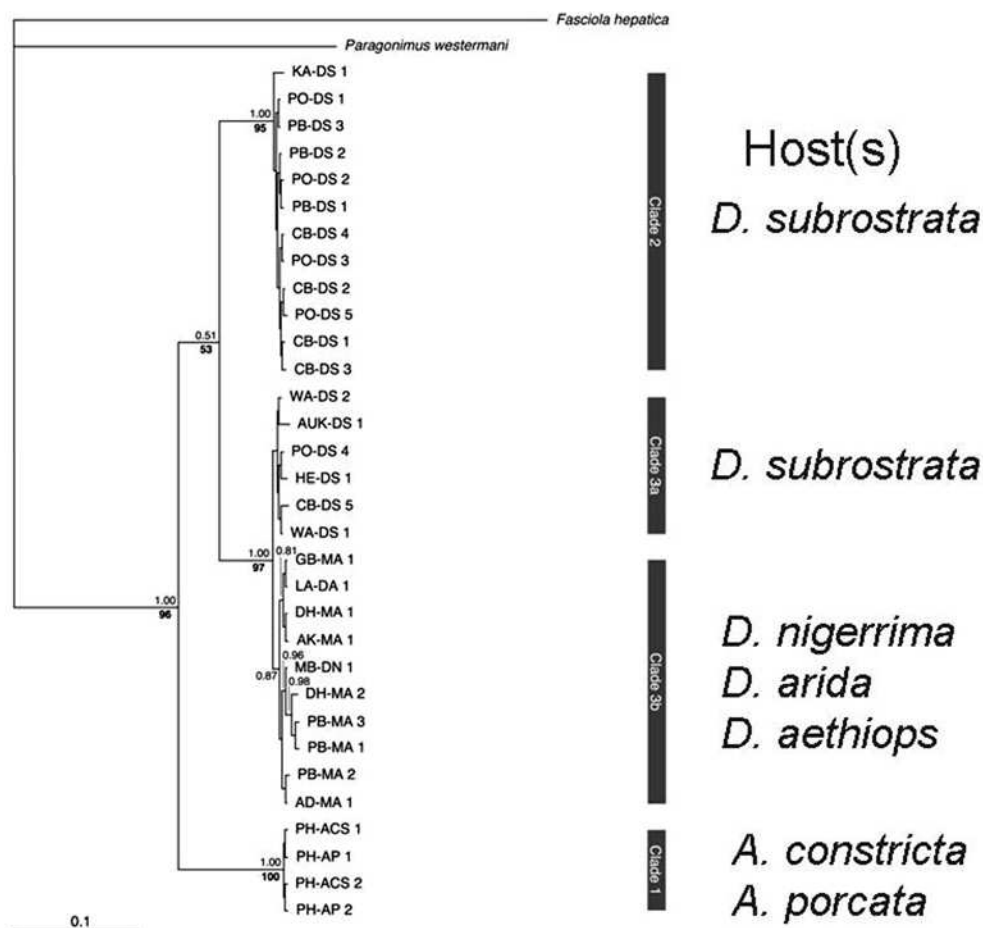
But the full story was only revealed by the phylogenetic analysis of DNA sequences of the trematodes (Figure 1). The trematodes fell into four clades, which we interpreted as separate genetic species. Trematodes from one clade infected two closely related Australian *Austrocochlea* species, those from a second were found in three New Zealand *Diloma* species (primarily *D. aethiops*, but also occasionally *D. nigerrima* and *D. arida*) and those from the other two clades, which were not each other's closest relatives, occurred solely in *Diloma subrostrata*. Thus, both the parasitologists and ecologists were wrong: some trematode species exhibit host specificity, but some don't. Moreover, there is not strong co-phylogeny: trematodes infecting the same host need not be sister species. We concluded that although the



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Figure 1. Bayesian tree, estimated from 16S and ITS2 sequences, showing posterior probabilities and maximum-likelihood bootstrap percentages, for the trematodes isolated from six snail host species. The grey bars indicate the four clades of trematodes, and their host species are listed to the right of these bars. Adapted from Donald et al. (2004), with permission from the Australian Society for Parasitology Inc. and Elsevier.



opportunity to switch hosts is available, it probably does not occur very frequently on an ecological timescale, but it does occur often enough on an evolutionary one to be important to evolution.

Long-distance dispersal and speciation

In the 1970s and 80s, panbiogeographers and vicariance biogeographers pointed out that many explanations of the geographical distributions of animals and plants were little better than ‘just-so’ stories, plausible but untestable, invoking dispersal by some suitable mechanism from one place to another, at some vague time in the evolutionary past. This critique, along with the rise of plate tectonics, revolutionised biogeography and led to a subtle discrediting of dispersal as an evolutionary process. More recently, however, the advent of molecular data and phylogenetic tools has allowed vicariant interpretations (those relying on plate tectonics and other geological process such as sea-level changes) to serve as null hypotheses for dispersalist explanations.

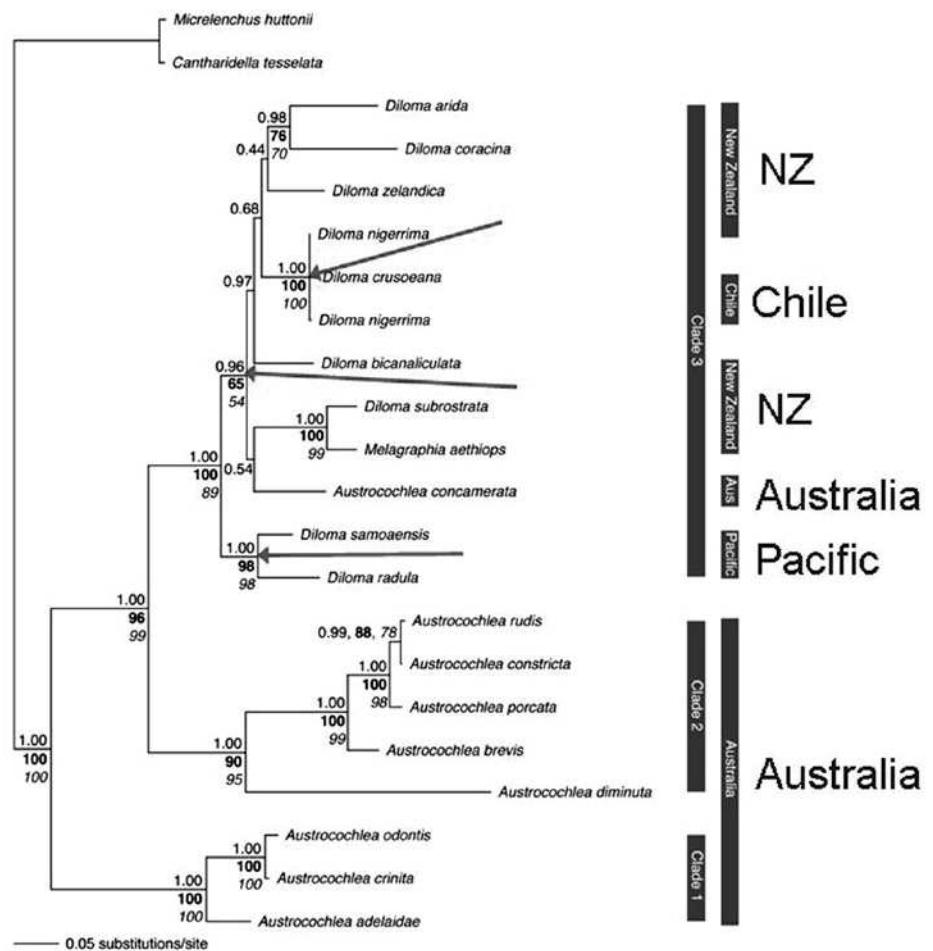
One example concerns the same group of molluscs discussed above. Donald *et al.* (2005) estimated the evolutionary tree of these Australasian snails and their relatives from South America, Japan, Samoa, and the Juan Fernandez Islands (Figure 2). Their widespread distribution is apparently difficult to explain in dispersalist terms because the only stage of the life cycle during which long-distance dispersal would appear to be possible is rather short: the larval veliger relies for food solely on the egg from which it hatched and remains in the water column for less than a month. But estimates of the dates of divergence between some of the branches on the tree indicated with the arrows in

Figure 2 allow us to reject a vicariance null hypothesis explanation, too. (These dates were derived using a molecular clock imposed on the COI data.)

For example, the populations of *Diloma nigerrima* from New Zealand and Chile were estimated to have separated no more than 600 000 years ago. Even the population found on the isolated Juan Fernandez Islands between New Zealand and Chile was this young or younger. (This form once rejoiced in the name of *D. crusoiana* in recognition of the role of these islands in the inspiration for Defoe’s novel.) Similarly, *D. samoensis* is endemic to Samoa, which has always been an island; its ancestors must have dispersed there from elsewhere in the Pacific. Finally, all the New Zealand *Diloma* species appear to have radiated from an Australian ancestor between 6.6 and 24 million years ago, much more recently than the Tasman Sea separated the two countries, ~ 80 million years ago. Vicariant explanations for these dates and distributions cannot work.

Appealing to dispersal as a scientific explanation, however, requires a mechanism. Larval dispersal via ocean currents is extremely unlikely, as indicated above. The biology of *D. nigerrima*, however, suggests a plausible mechanism. Adults of this species live in vast numbers on wracks of decaying bull kelp, *Durvillaea antarctica*, washed ashore, at and above the high-tide mark. Bull kelp is extremely tough and buoyant, having the ability to drift for months across large oceanic distances. In addition, bull-kelp rafts occur in vast numbers: Smith (2002) calculated that ~65 million bull-kelp rafts occur in the Southern Ocean at any one time. Donald *et al.* (2005) argued that *D. nigerrima* arrived in Chile and the Juan Fernandez Islands as adult passengers on such bull-kelp rafts. Interestingly, the

Figure 2. Maximum-likelihood phylogram, estimated from 16S, COI, and actin sequences, for the Pacific trochid species investigated by Donald et al. (2005). The numbers on the branches are Bayesian posterior probabilities and bootstrap percentages, the latter from 1000 weighted maximum-parsimony (bold) and 100 maximum-likelihood (italic) replicates. Adapted from Donald et al. (2005), with permission of the Society for the Study of Evolution.



Bluff oyster, *Ostrea chilensis*, often found living in bull-kelp holdfasts, also occurs in Chile, where, like *D. nigerrima*, it lacks any fossil record.

Such plausible mechanisms for the other, older, dispersal events are not so obvious. But it is clear that dispersal has often been a precursor to evolutionary diversification (i.e. cladogenesis and speciation) in these snails. Thus, even though successful long-distance dispersal may be extremely rare over ecological timescales, it clearly need not be so over evolutionary ones. Just as in the study of host-parasite co-evolution, we see that rare events can be crucial in evolution and, moreover, phylogenetic analysis allows their rigorous scientific investigation. Hence, the historicity of much of evolutionary biology need not be a barrier to the deduction of general evolutionary principles.

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