

Digest: Process-based phylogenetic models provide unique insights into the evolution of mutualistic networks*

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Figs and their pollinating fig wasps are a classic example of long-term obligate associations between different species. Satler et al. use a process-based model adopted from molecular evolution to identify the major processes that affect cophylogenetic matching between figs and fig wasps. They find that host-switching is one of the most important evolutionary processes contributing to current cophylogenetic patterns, illustrating the value of probabilistic approaches to studying the evolutionary history of mutualisms.

The obligate mutualism between figs and their pollinating wasps is an archetype of long-term coevolution. Through many detailed field studies and molecular phylogenies, researchers have found that the pattern of mutualistic interactions between clades of figs and fig wasps was not simply the result of cospeciation (Machado et al. 2005). Additional processes including host switching, niche expansion, host speciation, and extinction may also contribute to observed patterns of interactions in these mutualisms. However, the methods that have primarily been used to investigate these patterns in this system and many others—that is, mapping events using parsimony or topological matching—have focused on detecting whether a pattern is consistent with cospeciation (de Vienne et al. 2013).

In this issue, Satler et al. (2019) take a novel approach to investigating the processes involved in generating the observed cophylogenetic patterns in the fig-fig wasp mutualism. They borrow an approach from molecular evolution that was originally developed to explain why a gene family phylogeny differs from a species phylogeny. The authors argue that the processes modeled by a duplication-transfer-loss (DTL) model (Szöllősi et al.

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2012) are directly analogous to those involved in the evolution of mutualistic networks: fig wasps speciate (similar to gene duplication), switch hosts (gene transfer), and go extinct (gene loss). Importantly, the rate of occurrence of each of these events is parametrically estimated. By applying this DTL model, the authors identify host-switching as the most common process in the evolution of the interaction network.

This work is an excellent example of just how powerful process-based phylogenetic models can be. The authors were able to gain new insights into this mutualism using an existing process-based model from molecular evolution. However, moving forward, it is worth considering the cases where a process-based model specifically tailored for understanding the evolution of species interactions might provide additional information. The DTL method, for example, cannot accommodate species with multiple hosts, which the authors acknowledge and deal with in a creative and sensible way. In this study, Satler et al. (2019) had the good fortune that only a few of the fig wasps in their study system interacted with multiple fig tree species. However, in more complex mutualistic systems, the interaction problem could become much more pronounced as it is likely that multiple pollinator species will interact with multiple host species.

There has been some (very) recent progress on this front: Braga et al. (2019) propose a novel coevolutionary phylogenetic

model that allows for more complex interactions between mutualists and multiple host species. Furthermore, the DTL framework is inherently asymmetrical; one has to choose which clade is the "species tree" and which one is the "gene tree." Ideally, it would be possible to model reciprocal feedbacks of coevolved traits and to simultaneously estimate evolutionary parameters for both groups of interacting species (Harmon et al. 2019). We hope that the exciting work of Satler et al. (2019) inspires other researchers studying ecological networks to think more probabilistically and to start developing entirely new classes of coevolutionary models.

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