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## **Co-evolution of Resource Trade-offs Driving Nestedness in Host-Parasite Networks**

Patterns of nestedness and specialization asymmetry, where specialist species interact mainly with generalists while generalists interact with both generalists and specialists, are often observed in mutualistic and antagonistic bi-partite ecological networks. These have been explained in terms of the relative abundance of the species, using a null model that assigns links in proportion to abundance, but doubts have been raised as to whether this offers a complete explanation. Many other driving factors, such as complementarity, competitive load and defense levels, have been hypothesized. In particular, host-parasite networks offer a variety of examples in which anti-nestedness and the reverse patterns of symmetry are observed.

We propose that the link between parasite specialization and the parasite species-richness of a host may also be driven by resource allocation, which incorporates many of the above ideas. This concerns the co-evolution of hosts and parasites, as hosts allocate resources to optimize defense against different parasites, and parasites to optimize attack on hosts. In a novel approach, this hypothesis is investigated through the adaptive dynamics of a simple ecological system of two hosts and two parasites, in which all species are allowed to evolve the manner in which they trade off their resources between interactions with other species. This alters the force with which a parasite species infects a host, and may be used to compare relative levels of generalization between species.

We show that the co-evolution of these trade-offs in transmissible and defensive traits leads to specialization asymmetry in networks with closely related parasites or faster host mutation rates, but not in networks with more distantly related species. This suggests possible avenues of future investigative work to confirm the causes of nestedness.