How species partnerships evolve to become specific or general, cooperative or antagonistic

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Symbiotic relationships are everywhere in nature. In the soil, for example, mycorrhizal fungi enhance water and nutrient absorption for plants while feeding on sugars their roots release. In another classic mutualism, ants find food and shelter in specialized structures that acacia

trees grow; the insects, in turn, defend the trees from being eaten by other hungry critters.

Yet not all mutualistic relationships are created equal. Some interactions are highly specific—one host may pair off with only one other species—while others are general and flexible. Specific relationships may lend advantages, allowing the two species to co-evolve to reap even more benefits from one another. But specificity also comes with opportunity costs. And mutualisms aren't all give-give-give. One "partner" could wind up exploiting the other, taking more than it offers in return.

In the journal *Evolution*, researchers from the University of Pennsylvania consider the evolutionary dynamics that govern how these two forms of specialization—cooperative or antagonistic—as well as generalist symbioses arise, persist, or wane in a model framework using game theory.

"Each interaction has very different dynamics," says Erol Akçay, an associate professor of biology at Penn and senior author on the paper. "Generalists may evolve to work better with more partners, specialists may be specializing to be more cooperative, and other specialists may be specializing to exploit better. Ours is the first study that gets at that dialectical nature of specialization, not just looking at specialization versus generalization."

The investigation arose when Chris Carlson, now a graduate student at the University of Toronto, was an undergraduate at Penn working in marine biologist Katie Barott's laboratory. The Barott lab uses sea anemones as a model organism for understanding coral biology. Both corals and anemones live in partnership with symbiotic algae, in which the algae provide the corals with food and consume their waste products.

Occasionally, Carlson's experiments, in which he would "infect" anemones with algae, would "hit a hiccup."

"Some host corals don't play ball with certain algae," Carlson says. "Some hosts are generalists that associate with a broad set of partners, and others are specialists that only associate with one partner."

The question of why some symbioses are more specific and others are more general has generated much investigation among scientists, but Carlson became interested in a more nuanced aspect of these mutualisms.

"I was interested in understanding why this variation in generalism and specialism might persist in real world ecosystems," says Carlson, including both more cooperative and more exploitative specialist mutualisms. "For the anemone, all it cares about is its own fitness. If it evolves to get better at interacting with its partnering algae, it may not be acting in its partner's best interest."

To investigate this dynamic, Carlson began meeting with Akçay and then-postdoc Bryce Morsky, now a faculty member at Florida State University, to approach the question from a theoretical point of view. The three worked together to develop a model that imagines the interactions of designated "hosts" with either general or specialized preferences and "symbionts" that provide and receive different benefits and costs from their interactions with various hosts.

Overall, the team found that a cooperative partnering strategy, in which both partners reap increasing benefits from their relationship, could persist in populations with one specialized host and a corresponding specialized symbiont. Depending on the benefits, or payoffs involved, a generalist partnering strategy could also persist in this scenario.

Yet when the researchers' model involved partnerships that were more antagonistic—the host deriving increasing benefits while the symbiont reaped less—a more dynamic outcome arose, with different hosts and symbionts coming to rise and fall in the population over time. Generalist hosts driven to extinction if the payoff for being a generalist was lower than that of being a specialist. These cycles also created peril for both the symbionts and hosts. "We did see these oscillations in our model that, in the real world, could mean a population crashes," Morsky says.

The researchers then applied a spatial layer to their models, reflecting the reality that mutualistic relationships require that the two species involved encounter one another in space.

"Neighbors are going to be more likely to interact with neighbors, so who your neighbor is and how they interact can affect the outcome," Morsky says.

When the model allowed certain interactions to take place in defined areas, they found that cooperative specialists could develop "patches" of dominance if they could move over short distances. And if the payoff for being a generalist was high enough, generalists could persist around the periphery of these patches. If, however, hosts and symbionts could move over greater distances, just one host-symbiont pair could completely dominate a space.

"Let's say you have a coral reef with different types of coral and different types of algae," Akçay says. "If a host is a cooperative specialist, and the symbiont it specializes on gets fixed, the host does better, and therefore those hosts may expand. That creates specific spatial patterns that we were able to track."

An overall takeaway, the researchers say, is that cooperative specialization appears to be a valuable strategy but doesn't come without

risks. A host's cooperating partner could go extinct, for example, leaving the host in the lurch without a symbiont.

By adding complexity to the "generalist versus specialist" dichotomy, the researchers hope their work lends insight into the variety of patterns of mutualisms that exists in nature, which contribute to the biodiversity we see in the world around us.

"When people discuss specialization, this dualism is always in the background," Akçay says. "This work helps bring it out and clarifies the tensions that exist between mutualisms."

More information: Christopher Carlson et al, The evolution of partner specificity in mutualisms, *Evolution* (2023). DOI: 10.1093/evolut/qpac056. academic.oup.com/evolut/advanc … 54903?searchresult=1

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