The evolution of mutualisms: exploring the paths between conflict and cooperation


From the alga that help power reef-building corals, to the mutually nutritional symbionts that fix nitrogen and aid digestion, and even down to the mitochondria found in nearly all eukaryotes, mutualisms are ubiquitous, often ecologically dominant, and profoundly influential at all levels of biological organization. Although mutualisms can be simply defined as reciprocally beneficial relationships between organisms, they range from diffuse and indirect interactions to highly integrated and coevolved associations between pairs of species. Such mutualisms usually involve the direct exchange of goods and services (e.g. food, defense and transport) and typically result in the acquisition of novel capabilities by at least one partner.

Current theory of conflict, cooperation and constraint

The potential for conflicts of interest to shape or destabilize mutualistic associations will depend on the extent to which the survival and reproductive interests of the symbiont align with those of the host. Given that conflicts of interest can occur even within the genomes of single individuals, it seems unlikely that the interests of mutualists will ever be completely concordant. Although there is no general theory of mutualism, several factors that can help align mutualists’ interests have been identified. The passage of symbionts from parent to offspring (vertical transmission), genotypic uniformity of symbionts within individual hosts, spatial structure of populations leading to repeated interactions between would-be mutualists, and restricted options outside the relationship for both partners are thought to align interests and promote long-term stability. Conversely, movement of symbionts between unrelated hosts (horizontal transmission), multiple symbiont lineages, genotypic uniformity of symbionts and varied options thought to unravel them all contribute to the possibility of a more general understanding of the factors that influence mutualisms.

Mutualisms are of fundamental importance in all ecosystems but their very existence poses a series of challenging evolutionary questions. Recently, the application of molecular analyses combined with theoretical advances have transformed our understanding of many specific systems, thereby contributing to the possibility of a more general understanding of the factors that influence mutualisms.

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REVIEWS

Box 1. Marine invertebrates and photosynthetic algae: the ecological significance of cryptic symbiotic diversity

Throughout the shallow tropical oceans, sessile animals often have symbiotic associations with photosynthetic, single-celled algae, previously the most spectacular and obvious example of which was the association formed between reef-building corals and dinoflagellates of the genus *Symbiodinium*. For many years, these symbioses were considered to be a single species, but physiological and genetic studies26–28 have revealed enormous, previously unsuspected, diversity. What was once considered a single species is now recognized as a group with at least three clades that, by extrapolation to free-living forms, are distinct at the family or ordinal level. These studies also revealed that there was no obvious concordance between host and symbiont phylogenies.

Despite the growing appreciation of this cryptic diversity, it remained widely assumed that any single host formed an association with only one type of symbiont. However, in several ecologically dominant corals, it is now known that a single coral species and even a single colony are capable of hosting two or more types of symbiont26. Zonation of symbionts across the reef and within colonies appears to be related to levels of light. During adverse conditions, such as unusually high temperatures, the mutualism between corals and algae can break down (‘coral bleaching’) in complex patterns that reflect this zonation. Thus, from the alga’s perspective, the host is more like a landscape composed of more and less suitable conditions than a uniformly hospitable environment29,30.

From the coral’s perspective, horizontal transmission and complex mixtures of symbionts might provide short-term ecological flexibility to cope with fluctuating physical conditions that outweigh the possible costs of evolutionary conflicts among symbionts30. Many of the themes emerging from these studies of corals characterize other symbiotic systems as well31,32–34.

Nonetheless, not all mutualisms follow this pattern of vertical transmission, and it is necessary to determine for conformity where it exists.

Box 2. Figs and yuccas: model systems for understanding evolutionary conflicts

There are over 700 species of figs (Ficus) described worldwide. The figs depend on minute pollinator wasps (Agaonidae) for continued sexual reproduction, and the wasps depend on the figs to complete their life cycle. Fossil evidence indicates that this relationship dates back at least 40 million years. In most cases, the relationship is overwhelmingly species-specific. In addition, recent molecular work suggests that the large evolutionary history of figs and their pollinators has been dominated by cospeciation35. The ecological flexibility provided by symbiotic diversity36–38 might play an important counterbalancing role.

Patterns of ecological transmission and evolutionary association

Determining the number and identities of the partici- pants in mutualistic associations is a necessary first step for any evolutionary analysis, but it can be a surprisingly nontrivial task. Hosts and symbionts often lose characters found in their closest free-living relatives, or gain novel characters, making them difficult to distinguish and characterize taxonomically. The traditional solution for bacterial and fungal symbionts has been culturing. However, in some symbioses, what is successfully cultured does not necessarily reflect the actual community present in intact associations; and in other systems, symbionts cannot presently be cultured39–41. For these reasons, molecular analy- ses have played a critical role both in genetically characterizing isolated mutualists and in screening assemblages directly to assess the nature of symbiont communities. The resulting discoveries of stunning and unexpected diversity have transformed our understanding of mutualistic relationships involving corals (Box 1), leaf-cutter ants (Box 4), and root symbions37,42–44, among others.

It is important to appreciate that symbiotic diversity, cryptic and otherwise, can occur at different levels. At the level of different host species, different hosts can contain morphologically indistinguishable symbionts that are nevertheless quite distinct both genetically and functionally. At the level of different individual hosts within a species, genetically different symbions can be found in association with different host individuals (or populations). Even within individual host organisms, several distinct symbions can be found11,26–28. The recognition that individual hosts can act as landscapes for communities of potentially competing symbionts (Box 1) raises the question of why competition among symbions does not destabilize the mutualism, much as competition among parasites is believed to result in selection for increased virulence45. The ecological flexibility provided by symbiotic diversity36–38 might play an important counterbalancing role.

The explosion of systematic analyses using molecular techniques has generated phylogenetic reconstructions for one or both members of several speciose groups of mutualists. These studies show that patterns of transmission over ecological timescales do not necessarily translate into similar patterns at evolutionary timescales; available evidence suggests that all combinations of different patterns of eco- logical transmission and different degrees of phylogenetic concordance are found. Specifically, there are cases in which both evolutionary and ecological transmission appear to be predominantly vertical46. However, vertical evolu- tionary transmission (between lineages) is also found in cases in which ecological transmission is horizontal, for example, (e.g. fig-pollinating wasps19, luminescent bacteria associated with deep-sea fish47 and sulfur oxidizing bacteria and some of their bivalve hosts)48–50, to which vertical trans- mission is not the only mechanism that promotes speci- ation. Moreover, many intracellular bacteria (e.g. Wolbachia,
In an additional complexity, determining the extent to which co-cladogenesis is occurring will frequently depend on the taxonomic scale at which the question is asked. For example, the phylogenetic relationships between some lineages of leaf-cutter ants show nearly perfect concordance with the relationships of their associated fungi. However, in some entire lineages the host phylogenetic relationships show essentially no correspondence with those of the fungi. In fact, there appear to be many lineages in which nonspecifically and nonmonophyletic are the rule (Box 4). Unfortunately, for most mutualisms, we do not have adequate spatial and taxonomic sampling to determine the extent of concordance between host and symbiont lineages.

Trajectories of costs and benefits

Molecular data can provide insights into the taxonomic identities of mutualists, the structuring of their extant populations (e.g. patterns of spatial distribution and ecological transmission), their histories of phylogenetic associations and their evolutionary origins, but provide relatively little information about the often rapid, and sometimes convoluted, evolutionary trajectories of costs and benefits received.

From studies that compare outcomes across several populations of mutualistic interactions between two species, we know that outcomes can vary among extant populations. Several studies have documented that net costs and benefits can vary over relatively short timescales, resulting from: (1) changes in the presence or abundance of influential third parties; (2) variation in host densities that results in shifts in patterns of transmission; (3) variation in resource availability; or (4) variation in physical conditions (Box 1). Furthermore, such studies raise questions concerning the degree of local adaptation in host and symbiont populations, such as whether hosts generally benefit most from local, presumably more highly co-adapted symbionts.

Moreover, in evolutionary time, comparisons across related taxa (particularly in co-speciating systems) can show different evolutionary outcomes that represent variations on a single theme of mutualistic interaction (e.g. leaf-cutters, figs, yuccas, ants, plants and lycaenid butterflies). Specifically, phylogenetic analyses reveal that parasitic lineages can be embedded in largely mutualistic groups and vice versa. However, theory suggests that the species that parasitize mutualisms should not be the closest relatives to either partner. Available evidence collected from fungi (Fungi) and yucca moths (Agapanthinae) and the yuccas (Yucca) and yucca moths (Tegeticula), supports this prediction. Nonetheless, this proposition requires further testing.

Mutualisms as model systems

Mutualisms model evolution

In those instances in which the host and mutualist co-speciate, the absolute times of divergence between pairs of co-speciating mutualists and their free-living relatives. This allows a series of potentially instructive comparisons to be made between the accumulation of substitutions at a given gene or set of genes in the ‘host’ and in the ‘symbiont’ (or parasite).
free living relatives, an observation that appears to oppose the idea that rates of evolution in mutualists should slow down. A similar pattern has been found in lichens.

Mutualisms and the adaptive significance of sex

Current theory regarding the adaptive value of sexual reproduction revolves around the ideas that sexual reproduction serves to (1) maintain adaptation in the face of a changing world and (2) create deleterious mutations. Potentially, comparisons between groups of related species characterized by sexual or asexual reproduction could be useful to assess the relative importance of these two proposed functions. For example, some groups of mutualists, such as dinoflagellates that mediate intracellular symbioses in marine invertebrates, fungi associated withatted ants, perhaps algae in some lichens, clavicipitaceous (i.e. smut-like) grass endophytes, and the fungal cultivars of fungus-gardening termites, are derived from free-living groups capable of both sexual and asexual reproduction. In each case, it appears that the balance between sexuality and asexuality has been shifted towards the latter. Interestingly, in the case of the endophytic fungi associated with grasses, the fungi appear to reduce the host’s tendency to reproduce sexually, rather than the more typical reverse pattern.

There are several possible explanations for these patterns. For example, one school of thought suggests that ‘well integrated’ (e.g. intracellular) symbionts are protected by their hosts from a menacing organic world of constantly evolving predators and parasites, and consequently do not ‘need’ sex. An alternative, less benign, view of mutualisms suggests that mutualistic relationships are better characterized as series of ongoing arms races. In this scenario, sex might be the critical element that allows one member to keep up, or if suppressed in one member has allowed the other to ‘get ahead’. Further progress in this area will depend on knowing the extent to which sex is actually absent, determining whether symbionts are represented by a single clone or are genetically heterogeneous, and estimating the phylegories of the partners over various spatial and taxonomic scales. Ultimately, molecular data will play a crucial role in distinguishing among various possible interpretations.

Conclusions

Most organisms are involved either directly or indirectly in mutualistic interactions. However, there is no general theory of mutualism that approaches the explanatory power that ‘Hamilton’s Rule’ appears to hold for the understanding of within-species interactions. Underlying problems revolve around explicitly defining vague terms, such as ‘alignment of interest’, and employing biologically realistic currencies of costs and benefits at biologically relevant scales of organization. Ideally, all of these should be measurable and capable of being employed across radically different systems. For example, can the ‘conflict of interest’ and ‘costs and benefits’ within and between leafcutters that do or do not have vertically transmitted fungi be estimated and then compared with those values for corals that do or do not have vertically transmitted algae? We have estimated and then compared with those values for corals that do or do not have vertically transmitted fungi between fungus-growing ants and their fungi, 266, 1691–1694. We thank Koos Boomsma and Jack Werren for stimulating discussion. We thank Betsy Arnold, Jenny Apple, Egbert Leigh, Elisabeth Kalko, Sadie Ryan, Andy Dobson, Jon Howe, Penny Barnes, Andrew Baker, Rob Rowan, DeWayne Shoemaker and Rod Page for help and useful comments during the evolution of this article. STF Post Doctoral Fellowships supported SAR and UGM and made this collaboration possible.

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References

The cost of helping

Robert Heinsohn and Sarah Legge

The study of cooperative breeding in vertebrates aims to understand why some animals forgo independent reproduction and help others to breed instead. Over the past 30 years, the field has developed a rich set of theory and has been wracked by some major debates. However, enough cooperative species have been studied to start to establish common ground and to test theory. Indeed, in a recent review of the field, Emery’s statement that “the original paradox of cooperative breeding largely disappeared with the widespread confirmation that (1) helpers frequently do improve their chances of becoming breeders, and (2) they frequently do obtain large indirect genetic benefits by helping to rear collateral kin.” With identification of these direct and indirect benefits to helpers, the original questions asked by researchers would appear to be “largely answered.” Despite this claim, some important questions remain unanswered. In particular, our understanding of the varying level of helper contributions within and between species remains poor. The approach to cooperative breeding has often been to compare the outcomes of philopatry and helping with the other options of dispersing to float or dispersing to breed. Evaluation of the final reproductive rewards for each strategy leads to an ultimate understanding of why a particular decision was made. Implicit in this approach is that the outcome reflects all the costs and benefits of dispersal versus non-dispersal, and helping versus nonhelping, but it does not lead to an appreciation of the nature of each cost and benefit. Although we have a large list of benefits to helping, we still lack a cohesive framework that explains when they apply in various taxa or ecological circumstances. Less attention has been paid to the costs of helping.

Consider the cooperatively breeding Seychelles warbler, Acrocephalus seychellenis. In an elegant study, Kondepudi showed that helpers much prefer to feed nestlings that are more closely related to themselves, an important result that emphasized the liability and adaptive nature of helping.