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Book Review

Mutualism

Judith L. Bronstein, editor. Oxford and New York: Oxford University Press, 2015. xv + 297 pp. ISBN: 978-0-19-967565-4 (hbk.); 978-0-19-967566-1 (pbk.)

A persistent problem

Mutualisms—mutually beneficial interactions between species—have a long history of being a problem. On the one hand, we see them everywhere, as bees visit flowers, birds eat fruits, legumes form root-nodules and as Herodotus and Aristotle described, tick-birds supposedly pick parasites from the teeth of crocodiles. But on the other hand, scientists have come up with a series of reasons why they should be rare, if they exist at all. Reality and biological theory have repeatedly come into conflict.

Darwin himself was perhaps the first to face this problem as he elucidated the implications of natural selection. He wrote in the *Origin* that “If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection” (Darwin 1859). Realizing the seriousness of this challenge, he devoted his next book to the pollination of orchids by insects, showing in detail how both benefited (Darwin 1862).

While natural selection won the day and became the fundamental paradigm of modern biology, the issue never totally disappeared. A century later it re-emerged as the altruism/group selection problem. George Williams’ incisive critique (1966) showed that one could not explain the existence of traits, whether morphological or behavioral, by their “good for the species”; it was necessary to show how the fitness of all the individuals involved was increased. Thus he felt that “really good examples of mutualism are relatively rare” (Williams 1966). This helped stimulate the development of mathematical models of cooperation, including mutualism, based on kin selection and game theory (Axelrod and Hamilton 1981).

About the same time, ecologists realized that their fundamental model of interacting species, based on the equations developed for competition and

predation by Lotka, Volterra, and Gause, produced instability when applied to mutualism. The interaction could lead to reductions in one species driving down the other, till both went extinct; conversely, they could grow together without limit in an “orgy of mutual benefaction” (May 1975). Neither result would give stable coexistence. Either tweaks or constraints had to be added to the equations so that mutualists could coexist stably in theory as in reality, or else one had to conclude that mutualism just should not be common in the natural world.

Finally, and related to both the altruism issue and the instability problem, there was the problem of cheating. If individuals of two species were exchanging benefits, there should be selection to continue receiving them but not provide as much, or even anything at all, in return. Cheaters—individuals who avoided the cost of being mutualistic yet still received the benefits—would have a fitness advantage over their competitors who continued to behave mutualistically, and the whole interaction would break down.

Moving on

One of the pleasures of reading Judith Bronstein’s marvelous new book is seeing that mutualism is no longer a problem. The apparent contradictions between what clearly is, and what ought to be, have by and large been resolved. There are not only solutions for mutualism’s existence problem, but a wide array of new concepts, methods, and tools that take biologists in exciting new directions. The book both summarizes and moves beyond recent discoveries, suggesting fundamental questions to occupy both the next generation of students and those of us of less tender years.

The intellectual quality of the volume is matched by exceptionally good editing. Volumes with multiple authors (this one has 64!) are vulnerable to disorganization and redundancy, particularly if they cover a subject matter that ranges from plasmids to elephants and mitochondria to mycorrhizae. Bronstein has done an admirable job both managing her many authors and tying together their sections with her own text. Each chapter begins with a clear statement of its goal and a brief outline of its coverage, and lays out its key

points without unnecessary digression. The result is a tightly integrated work of uniformly high quality.

This integration is reflected in the hierarchical structure of the book; there are not only sections and chapters but dozens of short boxes within the chapters explaining, each in a few pages, either a fascinating biological interaction or a powerful analytic tool. These boxes give life to both the chapters containing them and the other chapters, through frequent cross-referencing. The result is a book with just enough overlap among its parts to provide several ways of looking at each topic but not so much as it make readers feel that they have heard this story before. There is ample material to suggest dozens of graduate student thesis topics, but it is tied together by a welcome emphasis on what we do know, not just what we do not.

Another important virtue of the book is its uniformity of terminology. The history of mutualism has long been plagued by uncertainties and arguments about what words to use and what they mean: mutualism, cooperation, symbiosis, coevolution, specialization, benefits and more. Bronstein's definitions in section 1.2.4, summarizing the meanings that researchers have given to each of these terms over the past few decades, should become the standards for future writing on the subject.

The masterful integration of concepts, questions, and methods across an incredibly wide range of taxa and sub-disciplines does not exclude, but rather is bolstered by, many examples of the fascinating scientific storytelling for which mutualism studies are famous. A squid expels 95% of its luminescent bacteria from its light organ each morning, and then rebuilds the population by nightfall. An ant sterilizes the flowers of an East African whistling-thorn tree but is nonetheless a mutualist because it deters occasional but drastic damage by elephants, while other ants protect against giraffes and other herbivores when the plant is older. Biological soil crusts include liverworts, lichens, mosses, algae, microfungi, cyanobacteria and other microbes, and reduce erosion, fix nitrogen, and capture nutrients in dust, providing large benefits to many arid-zone plant species. And dozens more....

Some notable themes

With such a diversity of fascinating tales and topics, it is a challenge to pick out just a few to highlight. But here is a subjective choice of a few themes that recur repeatedly throughout the volume, and seem to offer great promise for future studies:

- **Networks.** It is increasing evident that mutualisms should not be thought of as specialized one-to-one

versus generalized, diffuse many-to-many relationships, but rather as asymmetric networks, with a few core generalists interacting with large numbers of both specialists and generalists. Often these networks have a modular structure, with "connector" species tying the modules together. This view is widely applicable across taxa and has considerable predictive power as mutualisms are subjected to both natural and anthropogenic change.

- **Context.** Mutualism, as well as parasitism and other interactions, is not a fixed category. Rather, relationships move back and forth between the kinds of interaction, both in quantities of costs and benefits and in the qualitative result, as the context changes. The answer to the question "is this a mutualism?" is neither "yes" nor "no," but rather "it depends," so that we now can explore both the factors that it depends on, and how they interact to affect the outcome.
- **Microbiomes.** The diversity of the microbial world and its functional traits and metabolic abilities, is matched by the complexity of the communities it forms in, on, and around macroscopic organisms, including plants, insects, aquatic invertebrates, and vertebrates such as people. Genomic and phylogenetic methods now allow us to explore the resulting relationships, many of which can be mutualistic. Some of these ecosystems, such as the human microbiome, appear to be of great importance for our health.
- **Meta-analyses.** There is now a large enough published literature on mutualisms that one can now conduct meta-analyses, within and among taxa and kinds of interactions, aimed at quite general ecological and evolutionary questions. The coverage is still quite unbalanced, with pollination, seed dispersal, ant-plant interactions, nitrogen fixation, and mycorrhizae dominating, but there are already enough publications to provide some insight, with the promise of more to come.

Solving social problems

The final parts of *Mutualism* apply its concepts to social and economic issues, focusing on global change and conservation. There is also an increase in the ratio of questions to answers in these sections, both reflecting the state of the literature and providing guidance as to how to make what we have learned more valuable for our fellow humans. The potential is clearly large in light of the high importance of mutualisms to community structure, nutrient cycling, and other ecosystem properties. But

beyond the need for more knowledge, there is another issue that comes up in these final chapters. It seems heretical to say it, but often mutualism may not be the best answer, and sometimes not even a good thing.

For example: years ago Dan Janzen pointed out that even though we may save species from extinction, their interactions and roles that they play in communities may disappear. Increasingly we are also seeing examples of the reverse, with exotic species succeeding because of mutualisms, sometimes at the expense of native species. *Myrica faya* in Hawaii and Johnsongrass (*Sorghum halapense*) in US prairies gain substantial advantage as pests because of their associations with nitrogen fixers. Introduced Africanized honeybees in the Amazon and Japanese silveryeyes (birds) in New Zealand have become the principal pollinators in some habitats, at the expense of indigenous species. Introduced ants in several parts of the world seem to be strengthened as invaders because they often benefit more from mutualisms than native ants. Thus mutualistic interactions persist and may even become more important, but to the detriment of native taxa.

A related question is raised by Diana Six's box on the impact of climate change on bark beetles (Scolytinae) and their fungal mutualists in western North America (p. 244–5). Increasing temperatures threaten the mutualism and thus potentially the species. But since bark beetle outbreaks are one of the strongest current examples of how climate change threatens forest ecosystems, could the potential harm to this mutualism actually be a silver lining for conservation?

Agricultural mutualisms present a different paradox: the reduction or even elimination of mutualisms by human societies over thousands of years of crop domestication. Seed dispersal is a clear example, and the reasons that farmers do not like it are fairly obvious. However, the pattern also extends to several other kinds of mutualism. Although fully 90% of angiosperms are pollinated mutualistically (Ollerton et al. 2011), the crop plants that provide most of humanity's food are not. Instead, they rely on wind pollination (maize), self-pollination (wheat, rice, and other cereals; beans, soy, and other legumes), or vegetative reproduction (cassava, potatoes, bananas, sugar cane). Fertilizer, whether in modern synthetic forms or from traditional organic sources, reduces the value of nutritional mutualisms such as

nitrogen-fixing legume nodules and mycorrhizae, and may even convert them into antagonistic interactions. Such examples of humans artificially selecting against mutualism have occurred repeatedly in several different global centers of domestication over thousands of years. Thus, one cannot simply blame the pattern on “modern” or “industrial” agriculture; it is far older than that. So, do we now want to reverse it in favor of the mutualistic alternatives—simply because they seem more “natural”?

Conclusion

Finally, a personal note. Bronstein notes that in 1985 I edited “the first (and until now, only) volume on the biology of mutualism as a whole,” (p. 15) and kindly says that many of its chapters are still valuable today. It is certainly gratifying to hear that work I did three decades ago (Boucher 1985) remains relevant and useful. But the most hopeful sign is that this book shows a much more unified view of mutualism, with a theoretical sophistication and an empirical foundation far beyond that earlier volume. Bronstein predicts that “the material presented here will soon fall out of date. In fact, the authors of this volume hope that it does; that would be a strong signal of a healthy, thriving and rapidly developing field of study” (p. 17). I share that hope—but this book already sends that signal extremely well.

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