

# Competition–defense trade-offs in the microbial world

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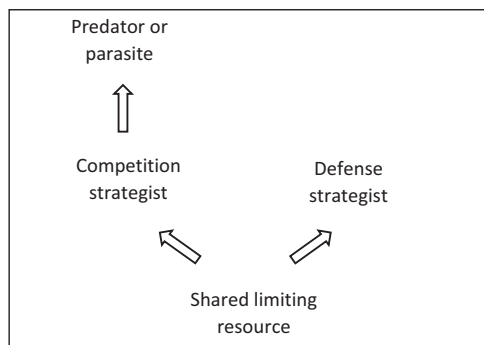
In PNAS, Guillonueu et al. (1) report experiments that demonstrate a rather intricate trade-off in the predator–prey relationship between a bacterium and its protozoan predator. Trade-offs link positive to negative changes in fitness and therefore constrain the paths of evolution as well as the biodiversity, structure, and function of existing food webs. In a hypothetical world where trade-offs do not exist, it would be possible for an organism to become best in “everything,” presumably leading to a drastic reduction in diversity, if not a collapse of entire food webs (Fig. 1).

Understanding the mechanisms and magnitudes of trade-offs is therefore a central issue in contemporary theoretical ecology and evolution. Experimental verification and quantification of trade-offs are, however, often difficult, perhaps leading to a lag in experimental versus theoretical insight.

Trade-offs come in many forms: Some are given by the fundamental physical and geometric constraints to life, exemplified by the trade-off between competition for low concentrations of limiting nutrients (e.g., phosphate) in aquatic bacteria, governed by the physics of diffusion and therefore favored by small cell size (2); counteracting defense which is favored by increasing cell size beyond the prey spectrum of their heterotrophic flagellate predators (3). The complexity is illustrated by the existence also of an additional strategy based on reducing size below the prey spectrum (4, 5). Other trade-offs are more a consequence of biological features, exemplified by bacterial need for efficient transporters to sequester the limiting nutrient, but these transporters may also serve as virus attachment sites (6). Modifying optimized transporters to prevent viral attack is then likely to be very costly in nutrient-limited environments. The mechanisms of defense are probably important for how different trade-offs have different consequences. The prokaryote CRISPR (7) defense mechanism

against viruses works by recognizing and destroying viral DNA after it has entered the host cell. Like a virus defense program in computers, CRISPR may have a significant cost in running the program but a relatively small additional cost for adding a new recognition sequence. Consequently, CRISPR should have a cost at the species level, shared by all strains with different sets of recognition sequences. In contrast, transporter modification would imply a high cost for creating a new, defensive strain. The two defense mechanisms should therefore be expected to have different consequences for diversification at species and strain levels in prokaryote communities. In the microbial world, life strategies and their trade-offs have evolved over a timespan of something like 4 billion years (8). Adding to this the potentially high abundances and short generation times of some (modern) bacteria, the number of generations through which predator–prey (and virus–host) arms races and their associated trade-offs have evolved must be immense, and the potential for development of sophisticated mechanisms therefore high.

Guillonueu et al.'s (1) study addresses a response strategy to phosphorus (P) limitation found in many prokaryotes: the substitution of phospholipids with sulfolipids (9), reducing their requirement for P. Since this only occurs under P limitation, the substitution seems to have a fitness cost, only worth paying when P is a scarce commodity. Both lipid groups are surface-active compounds, and the reduction in P requirement likely comes with the side effect of a change in cell surface properties. Surface charge and hydrophobicity are known to affect predator efficiency (3), and Guillonueu et al. shows that the substitution of phospholipids with sulfolipids actually reduces predator efficiency. Intriguingly, this gives a reversed trade-off that might look like an “egg of Columbus” for a P-limited organism: a prey strategy that simultaneously improves competitive ability and reduces vulnerability to predation. The complication in this case is, however, that the shift in lipids has an opposite effect on prey digestibility: With sulfolipids, the prey bacterium becomes more digestible in the acid environment of the vacuoles, and therefore stimulates predator growth better than the phospholipid variety, suggested by Guillonueu et al. to create a



**Fig. 1.** Generalized food web motif illustrating the crucial role of trade-offs in diversity and food web structure. Negative density control can allow coexistence of two species competing for the same limiting resource as in this structure where abundance of a nondefended competition strategist is top-down controlled by a predator or parasite, leaving resources for the less competitive, but predator-immune, defense strategist (16). Without this assumed trade-off between competition and defense, an organism could combine the two strategies and replace all of the three original groups. Redrawn from ref. 16, which is licensed under CC BY 4.0.

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“normal” trade-off where improved competitive ability is accompanied by a cost in increased predation pressure.

The contemporary view of oceanic nutrient limitation (10) is considerably more nuanced than the traditional simplification that “marine systems are N limited while limnic systems are P limited.” Transitions between N and P limitation are not only found in estuaries; there are also large marine regions like the North Atlantic Gyre, the subtropical Pacific (11, 12), and the eastern Mediterranean (13) that seem to be limited or colimited by P. Lipid replacement would be expected to occur in these large habitats where ocean chemistry thus affects the molecular composition of the biology. As some groups of microbes, bacteria (14) and diatoms (15) included, have typical P:N ratios much

higher than the Redfield ratio (1:16), food webs dominated by bacteria or diatoms bind more P relative to N than, for example, flagellate-dominated systems, illustrating the feedback from food web structure to ocean chemistry. The trade-off studied by Guillonneau et al. (1) is thus part of a highly connected system where trade-offs influence food web structure, food web structure influences ocean chemistry, and ocean chemistry influences trade-offs. Guillonneau et al. experimented with simple trophic interactions between isolated organisms. As in all laboratory experiments, they are intentionally detached from the full complexity of such natural ecosystems. Yet their work is a case study with intriguing connotations to the “molecules-to-ecosystem” mantra of contemporary biology.

1. R. Guillonneau *et al.*, Trade-offs of lipid remodeling in a marine predator–prey interaction in response to phosphorus limitation. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2203057119 (2022).
2. P. A. Jumars *et al.*, Physical constraints on marine osmotrophy in an optimal foraging context. *Mar. Microb. Food Webs* **7**, 121–159 (1993).
3. J. Perenthaler, B. Sattler, K. Simek, A. Schwarzenbacher, R. Psenner, Top-down effects on the size-biomass distribution of a freshwater bacterioplankton community. *Aquat. Microb. Ecol.* **10**, 255–263 (1996).
4. S. J. Giovannoni *et al.*, Genome streamlining in a cosmopolitan oceanic bacterium. *Science* **309**, 1242–1245 (2005).
5. T. F. Thingstad, L. Øvreås, O. Vadstein, Mechanisms generating dichotomies in the life strategies of heterotrophic marine prokaryotes. *Diversity (Basel)* **14**, 217 (2022).
6. S. J. Labrie, J. E. Samson, S. Moineau, Bacteriophage resistance mechanisms. *Nat. Rev. Microbiol.* **8**, 317–327 (2010).
7. G. W. Tyson, J. F. Banfield, Rapidly evolving CRISPRs implicated in acquired resistance of microorganisms to viruses. *Environ. Microbiol.* **10**, 200–207 (2008).
8. D. Papineau *et al.*, Metabolically diverse primordial microbial communities in Earth’s oldest seafloor-hydrothermal jasper. *Sci. Adv.* **8**, eabm2296 (2022).
9. M. Sebastián *et al.*, Lipid remodelling is a widespread strategy in marine heterotrophic bacteria upon phosphorus deficiency. *ISME J.* **10**, 968–978 (2016).
10. C. M. Moore *et al.*, Processes and patterns of oceanic nutrient limitation. *Nat. Geosci.* **6**, 701–710 (2013).
11. J. B. Cotner, J. W. Ammerman, E. R. Peele, E. Bentzen, Phosphorus-limited bacterioplankton growth in the Sargasso Sea. *Aquat. Microb. Ecol.* **13**, 141–149 (1997).
12. J. Ammerman, R. Hood, D. Case, J. Cotner, Phosphorous deficiency in the Atlantic: An emerging paradigm in oceanography. *Eos Trans. Am. Geophys. Union* **84**, 165–170 (2003).
13. T. F. Thingstad *et al.*, Nature of phosphorus limitation in the ultraoligotrophic eastern Mediterranean. *Science* **309**, 1068–1071 (2005).
14. K. Fagerbakke, M. Heldal, S. Norland, Content of carbon, nitrogen, oxygen, sulfur and phosphorus in native aquatic and cultured bacteria. *Aquat. Microb. Ecol.* **10**, 15–27 (1996).
15. K. R. Arrigo, Marine microorganisms and global nutrient cycles. *Nature* **437**, 349–355 (2005).
16. S. Våge *et al.*, Simple models combining competition, defence and resource availability have broad implications in pelagic microbial food webs. *Ecol. Lett.* **21**, 1440–1452 (2018).