

Evolution: Symbiont switching and environmental adaptation

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Can hosts swap ancient symbionts for new ones? A new study shows that a novel partnership between a protist and an algal symbiont can rapidly evolve to both overcome initial incompatibility and adapt to environmental challenges.

Symbiosis is a double-edged sword: it can yield spectacular novelty and productivity, but tight ties between species can also be a vulnerability. Partners that depend on each other can be extirpated if environmental changes outpace either one's ability to adapt¹. Furthermore, many symbioses are passed vertically from parent to offspring². A lack of genetic exchange among these cloistered symbionts leaves them vulnerable to Muller's Ratchet, and the accumulation of deleterious mutations and progressive genome reduction can eventually cripple symbiont function^{3–5}. This can purge the standing genetic variation that could otherwise enable rapid symbiont adaptation to changing environments. Herein lies the benefit of symbiont switching.

In vertically inherited symbioses, periodic replacement of ancient symbionts with novel ones can inject fresh genetic and functional diversity into a symbiosis, spurring evolutionary and ecological novelty^{3,6}. Renovating symbiosis via partner switching can bring a rapid influx of fresh adaptive potential to symbiont populations and novel symbiotic phenotypes to a host^{2,7}. However, novel symbiotic partner combinations can also be inefficient due to a lack of coevolutionary history^{8,9}.

Fitness in symbioses can have a complex genetic basis if both partners contribute to symbiotic performance. Not only can alleles in both the symbiont and host affect performance, but the impact of alleles in one partner can depend on alleles in the other (intergenomic epistasis)¹⁰. Furthermore, different host–symbiont combinations can be favored in different environments (selection mosaics)¹¹. Therefore, novel host–symbiont combinations can perform

poorly if interactions between alleles in the two partners have negative fitness consequences and if these are exacerbated in novel environmental conditions. Although partner switching holds tremendous promise for evolutionary novelty, there is no clear roadmap for overcoming this genetic hurdle to symbiont swapping as a means to adapt to rapid environmental change. Can novel symbiotic partners evolve to overcome initial incompatibilities? If so, how?

A new study by Sørensen *et al.*¹² in this issue of *Current Biology* uses experimental evolution to demonstrate that novel symbiotic partnerships rapidly evolve to increase symbiotic performance and adapt to environmental conditions, and uses metabolomics to elucidate the mechanisms that underlie this success. To do so they examine the symbiosis between the single-celled ciliate host *Paramecium bursaria* and its green alga symbiont, *Chlorella*.

In this nutritive symbiosis, *Paramecium* harvest fixed carbon from photosynthetic *Chlorella* algae, which they provision with organic nitrogen. Thus, benefits from the symbiosis to *Paramecium* increase with light intensity and decrease to a net cost in the dark. However, *Chlorella* are exploited in the arrangement¹³. *Paramecium* control the symbiosis with exacting precision, supporting *Chlorella* when needed but starving or digesting the algae when they are not¹⁴. *Paramecium* pass these captive *Chlorella* vertically to offspring and thus selection on symbiotic performance favors efficient co-adapted host–symbiont partnerships.

To investigate the evolutionary fate of novel symbiotic partners, Sørensen *et al.*¹² experimentally switch partners

among three co-evolved pairs of *Paramecium* hosts and *Chlorella* symbionts, such that each host was grown with all three possible symbiont lineages. They grow both the novel and ancient pairings across four levels of light intensity. These manipulations reveal a complex genetic basis for symbiotic outcomes: not only do alleles in both host and symbiont contribute to the rate of replication, but fitness in the pairs shows intergenomic epistasis and selection mosaics such that the impacts of alleles in a given symbiont depend on alleles present in a given host, and on the light level at which they are grown. Relatively few empirical experiments reveal these types of complex genetics in symbiosis, yet they are critical to long-term evolutionary dynamics.

Furthermore, the experiments in Sørensen *et al.*¹² reveal novel partner incompatibilities. The Scottish *Paramecium* genotype 186b, paired with a novel Japanese HK1 *Chlorella* genotype, replicates substantially more slowly than the native Scottish *Paramecium* 186b–*Chlorella* pairing, under high light. Here, impaired symbiotic performance is associated with elevated production of metabolites indicative of symbiont stress and decreased symbiont production of metabolites in central metabolism and hydrocarbon metabolism, compared to the more fit native pairing. It is at this point that the power of the *Paramecium*–*Chlorella* symbiosis as a model system shines.

Sørensen *et al.*¹² then leveraged the rapid generation time and ease of culture for this symbiosis in an experimental evolution experiment to document the evolutionary fate of the impaired novel



pairing and dissect any underlying changes in fitness and metabolite production. Would the symbiosis break down into free-living non-associates¹⁵? Would insurmountable incompatibilities cause the symbiosis to languish in its impaired state? Or would compensatory adaptations improve symbiotic performance?

The authors not only answer these questions, but also provide a unique insight into the molecular mechanisms of evolution in symbiosis. They reveal that the initially impaired symbiosis between novel partners rapidly evolves to confer fitness benefits equivalent to those of the native partners under high light in fewer than 50 generations. Replicate populations of the novel pairings recover fitness by accumulating compensatory mutations that ameliorate initial incompatibilities via one of two distinct paths. In some replicates, *Paramecium* evolve to carry more symbionts per cell to compensate for their new algal partner's weak performance. In other replicates, *Chlorella* evolve higher investment in photosynthesis and photoprotective traits, potentially allowing for improved carbon transfer to the host, decreased light stress, and improved performance of the pair under high light. This remarkably detailed view of the course of molecular adaptation in a perturbed symbiosis is notable for the role that evolution in both partners can play in shifting the overall performance of the symbiosis. Furthermore, in this case, compensatory evolution has generated hidden genetic and physiological variation across parallel evolving populations—this variation could be important ecologically if environmental conditions were to change.

The results of this study are exciting because the process of partner switching followed by compensatory evolution is a path by which many symbiotic organisms could adapt to changing environmental conditions. The ability to swap partners to better tolerate changing environments is often invoked as one advantage to acquiring symbionts horizontally from the environment^{2,16}. Conversely, ensuring offspring are provisioned with symbionts and aligning the reproductive interests of partners are invoked as advantages to acquiring symbionts vertically from a parent^{8,17}. Sørensen *et al.*¹² show that lineages that reap the benefits of vertical

symbiont transmission retain the potential to switch to new symbiotic partners and rapidly evolve to overcome initial incompatibilities, potentially reaping the benefits of both forms of symbiont transmission.

In a changing world, one hope for future biodiversity rests upon the potential for symbiosis¹⁷ and partner switching to provide an avenue by which organisms can expand their ecological niche and persist^{16,18,19}. Yet the problem of initial incompatibility presents a substantial barrier to partner switching. For example, although reef-building corals that experience rising ocean temperatures can swap heat-sensitive algal symbionts for more temperature-tolerant ones, these novel temperature-tolerant algae often result in lower calcification rates that reduce the ability of this symbiosis to fortify reefs²⁰. Future research in diverse systems evolving under the constraints present in natural populations is now called for to determine whether compensatory evolution is similarly capable of ameliorating initial incompatibilities in nature.

REFERENCES

- Kiers, E.T., Palmer, T.M., Ives, A.R., Bruno, J.F., and Bronstein, J.L. (2010). Mutualisms in a changing world: an evolutionary perspective. *Ecol. Lett.* **13**, 1459–1474.
- Russell, S.L. (2019). Transmission mode is associated with environment type and taxa across bacteria-eukaryote symbioses: a systematic review and meta-analysis. *FEMS Microbiol. Lett.* **366**, fnz013.
- Brandvain, Y., Goodnight, C., and Wade, M.J. (2011). Horizontal transmission rapidly erodes disequilibria between organelle and symbiont genomes. *Genetics* **189**, 397–404.
- McCutcheon, J.P., and Moran, N.A. (2012). Extreme genome reduction in symbiotic bacteria. *Nat. Rev. Microbiol.* **10**, 13.
- Boscaro, V., Kolisko, M., Felletti, M., Vannini, C., Lynn, D.H., and Keeling, P.J. (2017). Parallel genome reduction in symbionts descended from closely related free-living bacteria. *Nat. Ecol. Evol.* **1**, 1160–1167.
- Koga, R., and Moran, N.A. (2014). Swapping symbionts in spittlebugs: evolutionary replacement of a reduced genome symbiont. *ISME J.* **8**, 1237–1246.
- Matsuura, Y., Moriyama, M., Łukasik, P., Vanderpool, D., Tanahashi, M., Meng, X.-Y., McCutcheon, J.P., and Fukatsu, T. (2018). Recurrent symbiont recruitment from fungal parasites in cicadas. *Proc. Natl. Acad. Sci. USA* **115**, E5970–E5979.
- Jaenike, J., Unckless, R., Cockburn, S.N., Boelio, L.M., and Perlman, S.J. (2010). Adaptation via symbiosis: Recent spread of a *Drosophila* defensive symbiont. *Science* **329**, 212–215.
- Wein, T., Romero Picazo, D., Blow, F., Woehle, C., Jami, E., Reusch, T.B.H., Martin, W.F., and Dagan, T. (2019). Currency, exchange, and inheritance in the evolution of symbiosis. *Trends Microbiol.* **27**, 836–849.
- Heath, K.D. (2010). Intergenomic epistasis and coevolutionary constraint in plants and rhizobia. *Evolution* **64**, 1446–1458.
- Nuismer, S.L., Thompson, J.N., and Gomulkiewicz, R. (2000). Coevolutionary clines across selection mosaics. *Evolution* **54**, 1102–1115.
- Sørensen, M.E.S., Wood, A.J., Cameron, D.D., and Brockhurst, M.A. (2021). Rapid compensatory evolution can rescue low fitness symbioses following partner switching. *Curr. Biol.* **31**, 3721–3728.
- Sørensen, M.E.S., Lowe, C.D., Minter, E.J.A., Wood, A.J., Cameron, D.D., and Brockhurst, M.A. (2019). The role of exploitation in the establishment of mutualistic microbial symbioses. *FEMS Microbiol. Lett.* **366**, fnz148.
- Lowe, C.D., Minter, E.J., Cameron, D.D., and Brockhurst, M.A. (2016). Shining a light on exploitative host control in a photosynthetic endosymbiosis. *Curr. Biol.* **26**, 207–211.
- Werner, G.D.A., Cornelissen, J.H.C., Cornwell, W.K., Soudzilovskaia, N.A., Kattge, J., West, S.A., and Kiers, E.T. (2018). Symbiont switching and alternative resource acquisition strategies drive mutualism breakdown. *Proc. Natl. Acad. Sci. USA* **115**, 5229–5234.
- Koskella, B., and Bergelson, J. (2020). The study of host–microbiome (co)evolution across levels of selection. *Philos. Trans. R. Soc. B* **375**, 20190604.
- Hoang, K.L., Gerardo, N.M., and Morran, L.T. (2021). Association with a novel protective microbe facilitates host adaptation to a stressful environment. *Evol. Lett.* **5**, 118–129.
- Rudman, S.M., Greenblum, S., Hughes, R.C., Rajpurohit, S., Kiratli, O., Lowder, D.B., Lemmon, S.G., Petrov, D.A., Chaston, J.M., and Schmidt, P. (2019). Microbiome composition shapes rapid genomic adaptation of *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. USA* **116**, 20025–20032.
- Buerger, P., Alvarez-Roa, C., Coppin, C.W., Pearce, S.L., Chakravarti, L.J., Oakeshott, J.G., Edwards, O.R., and van Oppen, M.J.H. (2020). Heat-evolved microalgal symbionts increase coral bleaching tolerance. *Sci. Adv.* **6**, eaba2498.
- Stat, M., and Gates, R.D. (2010). Clade D *Symbiodinium* in scleractinian corals: A “nugget” of hope, a selfish opportunist, an ominous sign, or all of the above? *J. Mar. Biol.* **2011**, e730715.