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Digest: Going solo: Self-fertilization in haploid algae may not lead to evolutionary decline*

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Sexual reproduction strategies have consequences for the persistence of a species. In dioecious species, male and female gametes are typically produced in genetically different individuals to produce offspring with two parents, a process known as outcrossing. In contrast, in monoecious species, male and female gametes are produced by the same individual and, in some cases, can self-fertilize. Self-fertilization allows an organism to pass on all of its genes to its offspring, rather than half. From an individual's fitness perspective, selfing is better than outcrossing, not only because it passes on twice as many of the parents′ alleles, but also because it confers the ability to reproduce without the costs of acquiring a breeding partner.

Why then do so many organisms outcross rather than self-fertilize? Macroevolutionary theory suggests that the answer lies in self-fertilizing organisms losing out in the longer term—the "dead-end" hypothesis (Stebbins 1957). Short-term microevolutionary benefits of selfing are eventually outweighed by a range of costs such as reduced genetic variation, inbreeding depression, and lower rates of adaptation that lead to extinction (Wright et al. 2013). This should result in selfing species only being present on the tips of evolutionary (phylogenetic) trees, as any species with self-fertilization will not survive for long on an evolutionary timescale (Schoen et al. 1997). Once selfing is established, reversion to outcrossing is thought to be highly unlikely due to the short-term fitness cost for an individual of passing on half as many genes.

*This article corresponds to Hanschen, E. R., M. D. Herron, J. J. Wiens, H. Nozaki, and R. E. Michod. 2018. Repeated evolution and reversibility of self-fertilization in the volvocine green algae. Evolution. https://doi.org/10.1111/evo.13394.

In this issue, Hanschen et al. (2017) explored the evolution of selfing in volvocine freshwater algae to test this macroevolutionary theory. In volvocine algae, there are three types of species: monoecious selfing, dioecious selfing, and dioecious outcrossing (Iyengar 1933). The lifecycle of these algae is mainly haploid and asexual, but when they reproduce sexually, there is a dormant, diploid phase. Because the algae species are facultatively sexual, dioecious selfing species can self-fertilize because the same genotype can develop as male or female (but not both within a single individual). Hanschen et al. (2017) suspected that certain species have only recently evolved selfing, and descend from outcrossing ancestors. By investigating the evolution of self-fertilization, they hoped to see how often selfing had evolved, how long it persisted, and if selfing species are concentrated on the tips of the evolutionary tree. This information would determine if selfing in volvocine algae supports the dead-end hypothesis.

The authors constructed an updated phylogenetic tree using chloroplast genes to differentiate 69 existing species. The key use of the evolutionary tree was to test if there was a greater concentration of selfing than outcrossing species on the tips (a test for "tippiness," see Bromham et al. 2016). Next, they estimated the rate of transition between the two reproductive strategies. Finally, they explored the rates of species diversification for selfing and outcrossing species.

They found that volvocine algae have a distribution of selfing that was not predicted. Self-fertilizing species were not recent in origin, and therefore were not confined to the tips of the evolutionary tree. Instead, selfing has developed 11 times from an outcrossing ancestor, and the resultant species have persisted over evolutionary time. There were two reversals from selfing to dioecious outcrossing, which is unexpected given the short-term benefits of selfing (i.e., passing on twice as many genes).

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Intriguingly, both of these reversal cases involved monoecious rather than dioecious selfing. Finally, the rate of species diversification was estimated to be three times *lower* for outcrossing than selfing species, implying no selection against selfing. In total, these findings indicate that volvocine algae do not suffer the expected long-term evolutionary costs of selfing.

Hanschen et al. (2017) suggest that these unexpected findings are explained by volvocine algae being mainly haploid over their life cycle, and by the increased benefit of selfing when colonizing new habitats. Haploid organisms have already purged recessive deleterious alleles so they do not suffer the same reproductive costs as diploid organisms due to the absence of inbreeding depression (which arises because homozygosity exposes recessive alleles in diploids). Volvocine algae also occur in patchy habitats, so self-fertilization might be a beneficial strategy when colonizing a new patch, because there is no need to find a partner to reproduce. If increased benefits of selfing outweigh the costs, then selfing species can compete with outcrossing ones, which might explain their persistence in volvocine algae.

Many traits are considered evolutionary dead-ends when comparing the short-term advantage for an individual against long-term detrimental effects on lineage persistence. It is fairly rare, however, for these claims to be tested. For example, it is assumed that specialization increases rates of extinction. Day et al. (2016) used similar phylogenetic methods to Hanschen et al. (2017) to test whether specialization led to increased extinction rates in ten phylogenies of various plants, insects, flatworms and birds. They found that specialization was less detrimental than expected: only two phylogenies showed significant reduction in diversification and higher "tippiness." Similarly, Hanschen et al. (2017) show that selfing did not seem to be a dead-end trait (corroborated by the two reversals from selfing to outcrossing). Bromham et al. (2016) have, however, suggested that looking at phylogenetic "tippiness" is not always a reliable way to detect dead end traits, and they proposed alternative metrics to test this macroevolutionary hypothesis. It will be intriguing to see what future phylogenetic studies using these methods uncover about traits that are currently considered self-destructive over evolutionary time.

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