EVOLUTION

The advantages of sex

Two new studies using contrasting approaches shed light on why sex evolves, and how it maintains itself.

Sexual reproduction isn't easy. In evolutionary terms it is much less effort to reproduce asexually. However, asexual organisms have genetic loci that are permanently linked and so, theoretically, are more prone to accumulating deleterious mutations — a factor that is often cited to explain the evolutionarily short-lived nature of most asexual species.

Paland and Lynch tested whether the theoretical advantage that sex has in purging deleterious mutations — owing to the meiotic and recombinational reshuffling of genes— is evident in a real system: sexual and asexual forms of the water flea *Daphnia pulex*. Their approach was to compare mitochondrial genes of the two forms for ratios of synonymous and non-synonymous nucleotide substitution — if the rate of the former (K_s) is greater than that of the latter (K_n), this indicates that a gene has been subject to the purging effects of purifying selection.

The contrast between the sexual and asexual groups was striking: the K_n/K_s ratio was much higher for asexual branches of the *D. pulex* phylogenetic tree, which indicates an accelerated accumulation of deleterious mutations. The authors estimate that 17.7% of amino-acid substitutions arising in asexual lineages persist despite being deleterious, compared with just 4.4% in sexual lineages. This provides strong empirical evidence that the purging of mildly deleterious mutations is a key advantage of sex.

But does this factor alone account for the prevalence of sex among multicellular organisms? Sex is expected to speed up the purging of deleterious mutations only if mutations in interacting genes are more deleterious in combination than expected from their individual effects, a pattern called negative epistasis. Azevedo and colleagues used a modelling approach to test whether negative epistasis evolves as a consequence of sexual reproduction.

The authors used a model that represents individuals as networks of interacting transcriptional regulators. Under conditions that are known to favour genetic robustness (insensitivity of phenotypes to mutations) they compared sexual and asexual populations. As expected, robustness increased in both types of population until it reached an equilibrium, but this equilibrium was reached at a significantly lower value in asexual populations. Moreover, sexual populations at equilibrium showed negative epistasis, whereas asexual populations showed positive epistasis.

This pattern held up under a range of conditions, so it seems that negative epistasis in sexually reproducing organisms is favoured wherever conditions favour genetic robustness (which is likely to be the case in most multicellular organisms). This disproportionate increase of the deleterious effects of interacting mutations in sexual populations obviously favours the maintenance of this reproductive mode, where natural selection can more easily purge deleterious mutations.

Together, these studies suggest that we might be getting close to understanding why most muticellular organisms think that sex is worth bothering with — despite its costs.

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ORIGINAL RESEARCH PAPERS
Azevedo, R. B. R. *et al.* Sexual reproduction selects for robustness and negative epistasis in artificial gene networks. *Nature* **440**, 87–90 (2006) | Paland, S. & Lynch, M. Transitions to asexuality result in excess amino acid substitutions. *Science* **311**, 990–992 (2006)