olds number with the discovery of fully three-dimensional, spatially extended and persistent flow structures (5, 6)—coherent structures—that were subsequently also identified in experiments (7). These structures appear at specific flow speeds that can be computed numerically with high precision and can provide a critical Reynolds number. However, we do not have any a priori information concerning where these critical points are and what the associated flows look like. At present, the lowest Re where some structures have been found is 773 (8).

The presence of many coherent structures of different shapes suggested that they provide a scaffold that could support turbulent dynamics by creating a multitude of connections between these states (2). For low Reynolds numbers, it was accepted that the tangle of connections was not woven with sufficient tightness to capture the turbulent dynamics forever. It was expected that at higher Reynolds numbers exceeding a critical value, the turbulence would become persistent (9), but more extensive experimental and numerical studies contradicted the initial agreement: The lifetimes increased rapidly, but there was no finite number at which they would diverge (10). Accordingly, the critical Reynolds number would be infinity, and all turbulence in pipe flow would be transient, albeit with excessively long lifetimes.

Avila et al. resolved this puzzling behavior and identified the missing feature that had not received sufficient attention: Turbulence in pipe flow has the unusual property that for Reynolds numbers below about 2300, it remains localized in short "puffs" that move downstream without much change in form. Because of their finite lifetime, the puffs should disappear one by one, and only the laminar profile would remain at long times. However, Nishi et al. (11) showed that puffs can split. In one process, fluctuations in the middle of the puff may become strong enough to introduce a laminar region that then pushes the two elements apart (see the figure, panel B, for an example from a numerical simulation). In another case, patches of turbulence swept downstream in the center of the fluid may attach to the walls and start new turbulent puffs. Such processes introduce connections between the puffs so that they can no longer be considered in isolation. In particular, if a puff manages to split before it decays, the sibling may carry on the turbulence, spatial and temporal couplings become important (12), and there may always be some turbulence somewhere along the pipe.

Avila et al. compared the lifetime of puffs with the time it takes for them to split. They overcame the difficulty of inducing turbulence at these low Reynolds numbers by creating a stepwise perturbation—they injected a water jet into the flow to create puffs of turbulence. With increasing Reynolds number, the lifetimes of puffs increased rapidly and the time to split decreased. In the critical region where these two times were similar, only one splitting or decay event occurred for every 10,000 injections of the jet. Such rare events are inaccessible in numerical simulations. Avila et al. provide convincing evidence for a crossing of the two curves at $Re = 2040$. On the basis of previous studies (12, 13), a higher value might be expected, but the difference presumably comes from a poorer statistical method that missed the important rare events.

The findings of Avila et al., and even more so their method of analysis, bring into focus the spatiotemporal aspects of the transition problem (14). They pave the way for a better understanding of the transition in pipe flows and related shear flows, such as plane Couette flows and perhaps even boundary-layer flows, and connect the transition to the spatial intermittency and phase transitions in directed percolation (15). They provide not only the long-sought critical Reynolds number for pipe flow, but also define a critical change in our approach to studying turbulence transitions in spatially extended systems.

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EVOLUTION

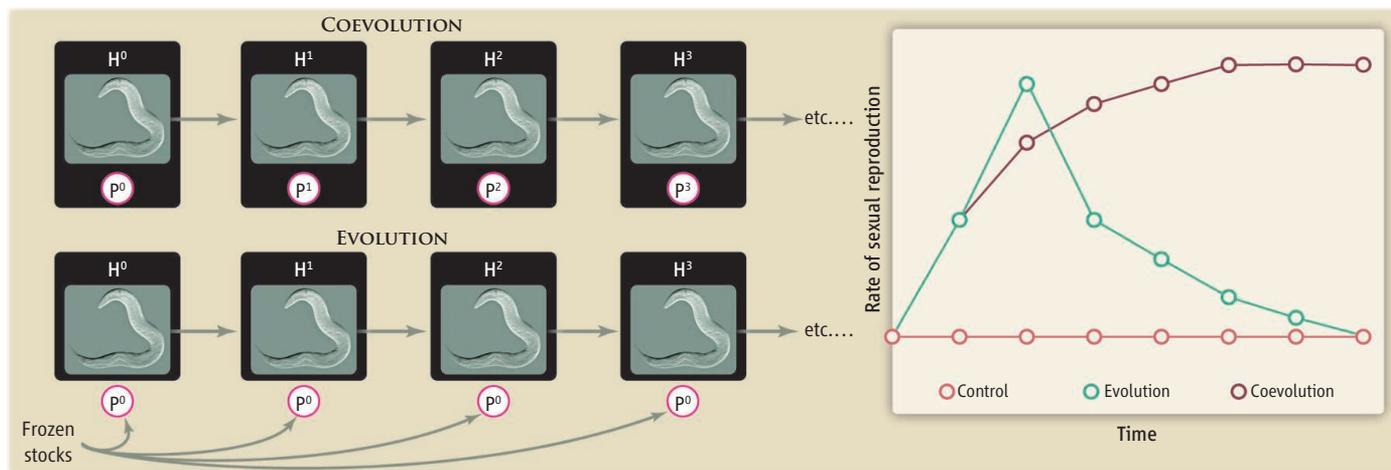# Sex, Death, and the Red Queen

Michael A. Brockhurst

Experiments involving host-parasite interactions demonstrate the evolutionary benefits of sexual reproduction.

Sex is hard to explain. Since males can't reproduce by themselves and often contribute nothing except genes to offspring, a population of asexual females can grow at double the rate of a population that reproduces sexually (1). Why then, given this "cost of males," do most plants and animals indulge in biparental sex? One possible solution is that sex accelerates adaptation; the Red Queen hypothesis, for example, proposes that sex gives plants and animals an edge in the never-ending battle against their coevolving parasites (2–4). Although researchers have collected empirical field data consistent with the Red Queen hypothesis from a range of natural host-parasite systems, direct experimental evidence that coevolving parasites select for sex in their hosts has proven elusive. On page 216 of this issue, Morran et al. (5) pin down some of that direct evidence.

Institute of Integrative Biology, University of Liverpool, Liverpool L69 7ZB, UK. E-mail: michael.brockhurst@liv.ac.uk

In laboratory experiments, they grew several populations of nematode worms, some with and some without a bacterial parasite, to provide the most definitive support yet for the Red Queen's answer to why sex evolved.

As first conceived in 1973 by evolutionary biologist Leigh Van Valen, the Red Queen hypothesis had little to do with sex. Van Valen used the Red Queen's race, from Lewis Carroll's Through the Looking-Glass, as an analogy for nature (6). In Carroll's story, Alice and the Red Queen run as fast as they can but never get anywhere (7). In Van Valen's view of nature, species continually evolve but their fitness never increases because each adaptation is countered by adaptations by their competitors and enemies (6). He suggested that this coevolutionary mechanism could explain why rates of extinction within animal groups remain near constant through geological time. Biologists later co-opted the Red Queen analogy into a new coevolutionary hypothesis for the evolution of sex (4). Mathemati-

cal models showed that coevolving parasites could, over time, select against common gene variants (alleles) in the host, thereby favoring rarer host alleles. These once-rare alleles then increase in frequency and become common, thus establishing sustained oscillating changes in host and parasite allele frequencies (*3*). This continual selection for rarity favors sexual reproduction over asexual reproduction; sexual recombination allows hosts to reshuffle their pack of alleles and generate new, rare combinations in their offspring.

Empirical field data, most notably from studies of freshwater snails that can reproduce sexually or asexually (facultative reproduction) and their trematode parasites (flukes), broadly support the Red Queen hypothesis. Trematodes are best adapted to infect locally common snail genotypes (*8*), and the frequency of male snails (a proxy for the frequency of sexual reproduction) is highest in the shallows where the risk of infection is greatest (*9*). This suggests that infection promotes sex. However, as in any field study, it is difficult to definitively ascribe causation, because researchers can never rule out selection by other environmental variables that also correlate with the frequency of males. Another issue with field data is that coevolution itself must necessarily be inferred, since hosts from the past and future are not available to directly test whether today's parasites actually are best adapted to contemporary hosts. Testing the causality of the Red Queen hypothesis requires controlled, real-time evolution experiments and the ability to keep a "living fossil record" of past populations in suspended animation.

Experimental evolution has traditionally involved microbes (*10*). However, larger short-lived organisms, such as fruit flies and nematodes, are amenable to experimental evolution. Nematodes, like microbes, can also be frozen in suspended animation, and revived

at a later date, allowing direct comparison of descendants with their evolutionary ancestors (see the figure). In their experiments, Morran *et al*. used the nematode, *Caenorhabditis elegans*, and its natural bacterial parasite, *Serratia marcescens*. *C. elegans* is facultatively sexual; males typically constitute 20 to 30% of a wild-type population. In experimental populations raised without parasites, the authors report that the proportion of the population reproducing sexually remained at 20%. However, in the presence of coevolving parasites, the frequency of sex rapidly increased and stabilized at 80 to 90%. These results suggested that the coevolving parasites selected for sex. This conclusion was reinforced by results from a third set of experimental nematode populations, in which the researchers exposed the worms to a fixed, nonevolving strain of *S. marcescens* while allowing *C. elegans* to adapt. Here, after an initial increase in the frequency of males, sexual reproduction subsequently declined to 20%. Morran *et al*. concluded that coevolution with parasites, not parasites per se, provides sustained selection for the long-term maintenance of sex.

Morran *et al*. were also able to measure the benefits of sex by enforcing or preventing sex in certain nematode populations, using mutants that were either obligate-sexuals or obligate self-fertilizers. When coevolving with parasites, all selfing *C. elegans* populations became extinct within 20 generations; in contrast, sexual *C. elegans* populations never became extinct. Similarly, the advantages of sex were revealed in experiments that involved reviving earlier, ancestral nematodes and infecting them with newer, coevolved parasites. The parasites had become more deadly over time, but coevolved sexual *C. elegans* populations showed resistance; in contrast, coevolved selfing *C. elegans* did not. These observations support Van Valen's original macroevolutionary version of the

Hobbling the Red Queen. Researchers can study the impact of parasite-host interactions on the evolution of sexual reproduction by conducting experiments that create different host-parasite populations, and allowing them to evolve over many generations. In this example, if researchers allow a nematode worm host (H) and a parasite (p) to coevolve (top series of boxes), then high rates of sexual reproduction are sustained (graph, right). If they use frozen parasite stocks to reinfect each new generation of the host with a fixed, nonevolving ancestral strain of the parasite (p^0 bottom series of boxes), rates of sexual reproduction can decline. Such experiments can also replace the host, rather than the parasite (*11*).

Red Queen hypothesis, and demonstrate that species that lag behind in the coevolutionary race are prone to extinction.

The Red Queen hypothesis places host-parasite coevolution, with its demand for rapid and continual adaptation, at the heart of evolution. Van Valen recognized, however, that such pairwise associations are only a subset of the rich and varied coevolutionary interactions inherent to natural communities. The challenge for theorists and empiricists alike is to understand how pairwise coevolutionary processes scale up when embedded in a broader and more complex network of species interactions. As more runners join the race, do the benefits of sex multiply?

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Michael A. Brockhurst

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