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EVOLUTIONARY BIOLOGY

New take on the Red Queen

Michael J. Benton

Biologists have assumed that natural selection shapes larger patterns of evolution through interactions such as competition and predation. These patterns may instead be determined by rare, stochastic speciation.

On page 349 of this issue, Venditti and colleagues[1] provide a revolutionary perspective on a core conundrum in evolution termed the Red Queen hypothesis. Whereas this hypothesis was traditionally based at the level of species in the environment and their interactions with each other, the new work shifts the emphasis to events that result in speciation. Explanations then move from the microevolutionary to the macroevolutionary scale — from natural selection and biotic interaction (interaction between living organisms), to infrequent and unpredictable events that cause reproductive isolation and speciation.

Ever since Charles Darwin's *On the Origin of Species*[2], biologists have debated the main driver of evolutionary change: is it the physical environment or is it interaction with other species? A simple reading of Darwin places most emphasis on competition and predation as central factors in natural selection. With this pure Darwinian view in mind, in 1973 Van Valen[3] famously proposed the Red Queen hypothesis, which holds that evolutionary change within organisms follows a constantly changing environment. The name of the hypothesis comes from Lewis Carroll's *Through the Looking-Glass*[4], in which the Red Queen tells Alice that "it takes all the running you can do, to keep in the same place".

Van Valen was seeking to disentangle two opposing outcomes of a Darwinian view of adaptation and natural selection: how organisms can be both well adapted and under continuing adaptation. If they are well adapted now, what can natural selection do? On the other hand, if they are currently adapting under natural selection, does this mean that they are currently not adapted, or that they are in some way being improved all the time? If the lion and the antelope now play out their hunt at 20 metres per second, will this speed keep increasing to near-supersonic levels?

Van Valen's solution[3] is that organisms are indeed currently well adapted, and yet they are also undergoing continuing adaptation because the environment is never constant. Physical and biotic aspects of the environment of any species are forever in flux, with subtle changes in annual temperature and weather cycles, topography, food supply, predators and group dynamics. This means that the targets of selection keep changing, and so the organism is never perfectly adapted.

Evidence for the Red Queen principle came from Van Valen's observation of what he called the law of constant extinction: that species or genera were as likely to become extinct at one time as at any other, irrespective of their geological age. Palaeontologists were not happy with this claim, and several critiques followed. The first was to point out the distinction between 'survivorship time' and real time[5]: Van Valen's plots showed that the probability of extinction within a taxonomic group is constant with respect to the duration of the constituent species, but not necessarily with respect to real time. At any time, a random selection of species might not show equal probabilities of extinction, and indeed, several studies have shown that extinction risk depends on taxon age, whether positively[6] or negatively[7].

In an attempt to provide a framework for wider testing, Stenseth and Maynard Smith[8] contrasted the Red Queen model (in which evolution is driven primarily by biotic interaction) with their newly formulated 'stationary model' (in which evolution is driven mainly by abiotic factors). They suggested that these two models could perhaps be distinguished by observations of good-quality fossil records. If the stationary model applies, evolutionary change should happen only when physical perturbations, such as climate changes, occur; in a Red Queen world, by contrast, species should continue evolving in stable physical conditions. As is so often the case, testing proved difficult: the problem was in finding real examples for which palaeontologists could be confident that there were no changes in physical environmental conditions.

The dichotomy between the Red Queen and stationary perspectives seems fundamental. But could it simply reflect the training and background of the researchers? It has been suggested that biologists favour the Red Queen because they are used to thinking of evolution in terms of natural selection, competition, predation and other biotic interactions on a short timescale.

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Figure 1 | Red Queen put to the test. According to the Red Queen hypothesis, organisms evolve by constantly changing in tune with environmental challenges, and yet remain well adapted to their modes of life. So the huge diversity of life today, exemplified by these species of dog (family Canidae), might have arisen from long spans of evolution featuring many small-scale vicissitudes. From their analyses of evolution in groups such as dogs, however, Venditti *et al.* propose[1] that most biodiversity arises from rare and infrequent events that lead to reproductive isolation and so speciation.

Palaeontologists, on the other hand, focus on volcanic eruptions and climate changes, and so see larger patterns in evolution on longer timescales. Barnosky[9,10] argued that the Red Queen was all very well as a local, ecosystem-scale view of evolution, but that it is overwhelmed by the world of the Court Jester, as he termed it, in reference to the Jester's quixotic and random sallies. In the Court Jester world, the grand patterns of survival of species and larger groups are determined by unpredictable crises and opportunities imposed by geology over broad geographic regions, and over time spans of thousands and millions of years.

The work of Venditti *et al.*[1] breaks through the timescales problem and links the Red Queen and the Court Jester. The authors focus on the observation of constant speciation rate, another element of the Red Queen[8], and an expectation of a model in which all species are equally likely to speciate or go extinct at any time, regardless of their past histories. Whereas Van Valen[3] did not test his data against other models, Venditti *et al.*[1] consider five statistical models of evolution: normal (Red Queen), lognormal, exponential, variable rates and Weibull, where the species distributions of the variable-rate and Weibull models are variants of the exponential. These models describe possible frequency distributions of branch lengths in their sample of 101 real phylogenetic trees of animal (Fig. 1), plant and fungal taxa. Branch lengths are the genetic distances between branching points (representing speciation events), and the relative lengths of branches indicate the time between speciation events — short if speciation happens frequently, and long if speciation is less common.

The empirical examples tested by Venditti and colleagues show that the best fit is to the simplest model of evolution, the exponential model, in which new species emerge from single events — each event being infrequent but individually sufficient to cause speciation. So, constant speciation rate, and the Red Queen model in general, are perhaps better understood as the outcome of rare stochastic events that cause reproductive isolation, rather than a never-ending race in which species are constantly coping with a changing environment. Examples of the causes of reproductive isolation are physical features, such as mountain ranges, rivers or islands, or the advent of biological barriers from, for example, chromosome multiplication (polyploidy), altered sex-determination mechanisms, chromosomal rearrangements or the accumulation of genetic incompatibilities.

If confirmed by further independent studies, especially those using alternative techniques to explore complete phylogenetic trees plotted against time, these results[1] remove the explanation of the Red Queen from squabbles in the undergrowth to rare and unpredictable events. Biologists and palaeobiologists must rethink what exactly is the impact of competition and predation on macroevolution — the processes that generate large-scale and long-term patterns, including the distribution of biodiversity across phylogenetic trees. ■

Michael J. Benton is in the Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK.
e-mail: mike.benton@bristol.ac.uk

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