

On the adaptive evolution of extinction

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The inevitable end for all species, but not necessarily their lineage, is extinction. The end-point lies along a continuum between two extremes. Hard extinctions are the bad luck cases of populations and species whose adaptations and adaptability provided no protection in the lottery of drastic changes to their environments. There is little that can be learned from them about the extinction process other than being in the wrong place at the wrong time. Soft extinctions lie at the opposite pole where adaptive evolution promotes their demise (evolutionary suicide), or rescues populations and species that are otherwise on the road to extinction. It is from these adaptive examples that we have much to learn, not only about extinction, but how to prevent further losses of Earth's biodiversity.

Our interest in doing so is both conceptual and practical. What role does adaptive evolution play in the inevitable extinction of populations? What can it teach us about the history and procession of life? How can we use it to help save the biodiversity that nurtured human evolution?

We could not answer these crucial questions alone. So we turned to colleagues for advice and insight. We asked Michael Rosenzweig if he would join us and consider publishing the symposium in *Evolutionary Ecology Research*. Mike not only agreed, he insisted that we hold the symposium in Forrest Shreve's office (now the library) at Tumamoc Hill, the University of Arizona's famous National Historical Landmark. We asked our friends to converge in Tucson in March 2015 and challenged them to bring us new and exciting ideas and data on adaptive evolution, and most especially on its ability to either foment or forestall population extinction. They did not disappoint us.

Two contributions (Parvinen, 2016; Ripa and Johansson, 2016) use adaptive dynamics to further explore the conditions favouring evolutionary suicide, a prescient insight on eco-evolutionary feedback loops that Kalle Parvinen attributes to Darwin. Both sets of models imagine a stochastic environment where small populations face increased risk of extinction.

Parvinen (2016) begins by making the case that evolutionary models must follow a bottom-up mechanistic approach capable of predicting the traits and strategies employed by individual organisms. He cogently reviews the relevant theoretical approaches that one can

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use, and carefully distinguishes evolutionary suicide – in which mutant strategies march inexorably beyond the boundary of viability – from demographic extinctions associated with small population size. His review is required reading for anyone interested in adaptive dynamics.

Parvinen explores a consumer-resource model that imagines invasion by rare mutants with survival probabilities and harvest effort different from residents. Mutants with higher survival and harvest effort increase when rare and reduce resource levels as they become common. Numerical simulations reveal that selection for increased survival leads towards chaotic population dynamics and evolutionary suicide in this model.

Selection for mutants with higher harvest rates yields the same outcome but via a different process. The continual erosion of resource abundance eventually produces small population sizes subject to stochastic extinctions. One can also imagine a scenario where increased survival is traded off against reduced harvest rate. The form of the trade-off is crucial for persistence. Selection for individuals with high harvest rates and low survival can also lead to evolutionary suicide. Clearly, there is much more for us to learn about extinction, and its rescue, from models exploring the co-evolution of individual traits that influence fitness.

In the spirit of van Valen's (1973) 'Law of extinction' (usually appearing in the Red Queen disguise), Ripa and Johansson (2016) extend adaptive evolution to the arena of co-evolving species competing with one another along a resource gradient. Diversifications, and inevitably extinctions, lead to an adaptively radiated multi-species community in which constraint-breaking evolutionary innovations of single species are introduced by increasing their carrying capacity. Extinctions occur through demographic stochasticity in small populations (often associated with competitive exclusion from nearby niche neighbours) as well as through externally forced stochastic events.

The resulting competitively induced communities bear striking resemblances to the history of life. Speciation and extinction rates are balanced. New species originate at the expense of their progenitors. Extinction is unequal. Extreme species at the margins of trait space tend to persist as relics at low density unless exposed to externally generated (hard) extinctions. And, as in nature, innovation does not guarantee success unless the innovator can increase quickly beyond the threshold of demographically stochastic extinction. Even so, innovation is inevitable given sufficient time. Any small advantage will, with sufficient opportunities, escape extinction and replace incumbent species.

Ripa and Johansson's model includes additional lessons for our macroevolutionary interpretations of mass extinctions and the role of stochasticity in species replacement. Each empirical pattern is consistent with their model of evolutionary competitive exclusion. No doubt other processes can be and are involved. But the proof of their veracity and influence requires that they yield at least equally parsimonious explanations for Earth's diversity and phylogeny of life.

The likelihood of extinction depends on the ability of populations to adapt in the face of environmental change. Adaptability, in turn, depends on the degree of standing genetic variation, its heritability, and the magnitude of change. Whether a population persists when faced with change further depends on the initial reduction in fitness (maladaptation), and whether or not fitness can recover quickly enough to forestall a fatal decline in population size. Barfield and Holt (2016) attack this rather complicated scenario with both deterministic theory and computer simulations. Their models reveal that evolutionary rescue is most probable in large populations with substantial genetic variance, the right genes, and a

mean phenotypic value that lies near the optimum in the changed environment. Hopeful mutations typically occur too infrequently to prevent extinction. This is rather disheartening news for the conservation of many iconic species whose populations were never large and that are already in decline. Conservation of these species may lie more in trying to restore environments, than it does in allocating effort to assessing genotypes. Our ability to predict the success of such efforts, however, will also depend on gaining crucial knowledge about genotypic structure and population size.

Environmental change, of course, is inevitable and forever ongoing in both space and time. The pace and degree of change are what concern us, and particularly so in the context of human actions. Again, the good news is that these are exactly the kinds of events that humans might have the greatest opportunity to reverse. In order to do so, we need to know which types of anthropogenic changes are most likely to cause species extinctions. Solari *et al.* (2016) identify five of the most serious culprits. They then assess each one's lethal effects with a review of vertebrate extinctions. They ask whether persistence under these scenarios can be prolonged by genetic diversity, plasticity, generalism, and a clade's evolutionary history.

Contrary to many expectations, there is little evidence that high genetic diversity prolongs a species' persistence against anthropogenic stresses. Phenotypic and behavioural plasticity in behaviour appear to be effective buffers against climate change and invading species, and generalist species are more likely to persist in changing habitats than are specialists. A species' evolutionary history of adaptation predisposes it to either high or low persistence against most stressors including human exploitation. But there is one sobering exception. Few, if any, attributes can forestall extinction associated with environmental pollutants.

Solari and colleagues' contribution reminds us of an interesting discussion of the question about the evolutionary costs (and benefits) of ecological specialization initiated by Gallagher *et al.* (2015). All contributions from the symposium cast light on that issue.

Ultimately, our predictions and assessments of extinction risk will depend on our ability to develop novel tests in the field with real organisms. Morris *et al.* (2016) suggest that theories of habitat selection might lead the way. They begin with simple computer simulations that evaluate whether the probability of extinction can be reduced through adaptive habitat selection. The simulations are roughly centred on published patterns in meadow voles that appear to reveal ideal-despotic distributions at high density and ideal-free distributions at low density. The algorithms thus explore whether a dominance-induced competitive tragedy leading to extinction can be curtailed if populations at low density switch their habitat-occupation strategy to an ideal-free distribution. Mixed strategies do indeed have lower risks of extinction.

Morris and colleagues then test experimentally whether meadow voles actually use mixed strategies. Their experiments manipulated habitat quality while measuring the voles' patterns of dispersal, foraging behaviour, temperament, and physiological condition. Foraging behaviour (quantified by giving-up-densities) was similar between rich and poor enclosures at low density, implying ideal-free habitat selection. The behaviour diverged dramatically at higher densities when putatively dominant animals may have been able to exclude subordinates from rich habitat. There was, however, no smoking gun of dominance associated with measured differences among voles in temperament or condition. It is thus likely that meadow voles do employ mixed strategies of habitat selection. But the main value of the experiments lies in their demonstrated ability to use adaptive behaviours to infer evolutionary outcomes.

The final contribution by Michael Rosenzweig uses masterful imagery from ants, cacti, barnacles, and rats to remind us that patterns of habitat selection will frequently misinform the unwary (Rosenzweig, 2016). Intolerant species build their success on power. They occupy only the best places and maintain exclusive use through dominance. Tolerant species occupy what's left. Their broad ecological tolerances pre-adapt them to move into the best spots should the incumbent intolerant species falter. But when both are present, each appears to specialize on its own separate niche. Why should we care?

There aren't that many 'best places'. Exclusive access comes at the expense of reduced population size. Small populations have increased risk of extinction. The group goes extinct. But when they do go extinct, the best places do not remain vacant. They are quickly taken over by tolerant species whose selfish evolution inevitably leads them to usurp the intolerant niche. To change Lord Acton's phrase, power tends to evolve and absolute power evolves absolutely.

Rosenzweig's intrepid perception: there is a balance between natural selection that creates species and group selection that destroys them. And he has proof. Read it for yourself. Then contemplate whether Rosenzweig, and Ripa and Johansson, are close to revealing the mechanism. And if they are correct, what other hidden insights will attention to group selection illuminate?

Theory and natural history make it indisputably clear that adaptive evolution plays a most significant role in the extinction versus persistence of populations. The quest now must shift to further testing of those ideas with creative experiments on real populations in the field and lab. We must also learn how to apply our improved understanding towards minimizing anthropogenic extinctions. The quest will not be easy, but failing to do so is not an option. We need experiments to confirm or refute theory, and we need both in order to apply evolutionary understanding to Earth's crippling loss of biodiversity. We invite all ecologists and evolutionary biologists to join us in this pursuit. Although our descendants will most certainly live on a less diverse planet than the one we enjoy, they deserve to know that we did our best to endow them with the knowledge required to preserve the most biodiversity possible.

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