

## On the evolution of extinction rates

Michael L. Rosenzweig

*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA*

---

### ABSTRACT

**Aim:** Consider and compare the evolutionary influences on extinction rates at the species level.

**Question:** Does extinction rate evolve?

**Hypothetical conclusions:** Yes, extinction evolves. Important traits such as senescence and sex may be due to group selection working against high extinction rates in species that lack senescence and sex. Sometimes, however, reduced extinction rates may evolve more conventionally by natural selection working to improve the reproductive biology of a species. And sometimes species may evolve to dominate a community's best habitats even if that evolution increases its probability of extinction. Despite likely changes at the species level in the probability of extinction, the fossil record suggests that mean extinction rates have not trended much at all during the Phanerozoic.

**Keywords:** group selection, *Coryphantha*, consumption of the variance, senescence, sex, tolerance/intolerance competition, shared-preference habitat selection, Phanerozoic.

### INTRODUCTION

Does the extinction rate of a species evolve? Or are changes in extinction rate merely the by-products of other evolutionary outcomes? In this paper, I hope the reader will see evidence for both mechanisms, direct and indirect.

Extinction befalls groups, not individuals. So, by definition, if extinction rate evolves directly, group selection will be its mechanism and evolution will lead to reduced extinction rate. If, however, change in extinction rate is the indirect result of natural selection on individuals, then the direction of the change in extinction rate will be ambiguous. Sometimes the effect of natural selection will be to decrease extinction rate and sometimes to increase it. Here, I will show that we know examples of all three cases.

### EVOLUTION OF REDUCED EXTINCTION RATES BY GROUP SELECTION

Almost unnoticed, a scientific revolution has been gathering strength. For about 20 years, evolutionary biology has been moving from a discipline that virtually rejects group selection to one that recognizes its reality and importance. I am proud to report that much of this

---

Correspondence: M.L. Rosenzweig, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721-0088, USA. email: scarab@u.arizona.edu

Consult the copyright statement on the inside front cover for non-commercial copying policies.

---

change has taken place in the pages of *Evolutionary Ecology Research* (Aviles, 1999; Ingvarsson, 1999; Kawata, 1999; Mitteldorf, 2004, 2006, 2012; Pollock *et al.*, 2004, 2012; Pollock and Cabrales, 2008; Woodberry *et al.*, 2007; Simon and Nielsen, 2012).

Of course, we evolutionists never totally rejected group selection. We just believed that the conditions that could lead to it were terminally improbable. Consider the blow dealt to it by Lewontin and Dunn (1960). A somewhat weird family of destructive alleles, the *t*-alleles, is dispersed among an array of small groups of mice. Each instance of the *t*-allele family can migrate from group to group. But once it finds its way into a group, it goes to fixation because of meiotic drive, and the group becomes extinct because males with a *t*-allele rarely survive and, if they do, they have unfit offspring. The end result is a system whose parts include both kinds of group, those uninfected by the allele and those facing imminent extinction because they have already been commandeered by a destructive allele.

I believe Lewontin and Dunn's example discouraged further research into group selection. In their case, group selection worked because group extinction happened about as fast as individual death. But that situation would appear to be fairly scarce, whereas evolutionists had hoped to turn to group selection rather often. They hoped to use group selection to account for many natural history observations in which species seem to put the brakes on their population growth at very modest population densities (Wynne-Edwards, 1962). But Lewontin and Dunn discouraged that. Most evolutionists avoided group selection entirely because they distrusted it.

### The evolution of ageing

Meanwhile, biologists investigating ageing were primarily interested in its cellular and biochemical details. They accumulated facts and worried little about how they had evolved. For example, individuals of a wide variety of animal species live longer lives if put on meagre rations. And individuals whose chromosomes have long telomeres outlive those with short ones. These and other features associated with lifespan seem to have evolved long, long ago because they are common to virtually all forms of animal life. Mitteldorf (2004, 2016) is a fine place to read a summary of these features. He credits Gilpin (1975) as the ultimate inspiration for his ideas. But most ecologists were unprepared to assimilate Gilpin when it emerged. Nor did they feel comfortable with David Sloan Wilson (1980) five years later.

In contrast, Mitteldorf (2004, 2006) advances an adaptive theory of ageing in which ageing has been selected for its own sake despite its requiring strong group selection. First, he explains how natural selection fails to account for ageing (Mitteldorf, 2004, 2016). It is not a difficult point to make because 'the impact of senescence on the individual is wholly detrimental, depleting its ability to survive and to reproduce' (Mitteldorf, 2016, p. 167).

Then Mitteldorf looks at the extinction threat in a hypothetical population that does not age. He sees 'natural selection . . . [pushing] birth rates inexorably higher, until the population's growth rate approaches three times the ecosystem's rate of recovery. Chaotic population dynamics inevitably ensue' (2006, p. 562). On the other hand, a species whose individuals do age could take control of its death rate, suppressing the violent fluctuations that might otherwise cause extinctions.

So group selection can account for ageing if ageing contributes 'to stabilizing population dynamics, helping prevent population growth overshoot, exhaustion of ecological resources, and local extinction' (2006, p. 561).

It all leads to the thesis of his book: ‘Aging and the regulated timing of death evolved for the purpose of stabilizing ecosystems’ (2016, p. 4).

### Evolution of suicide in a leaf-cutter ant

Meanwhile, Greg Pollock and his colleagues were investigating the desert leaf-cutter ant, *Acromyrmex versicolor* (Pollock *et al.*, 2004, 2012). Leaf-cutter ants collect plant parts (leaves, flowers, etc.) on which they grow a specialized fungus, which they then eat. ‘Several queens of the desert leaf-cutter ant *Acromyrmex versicolor* often establish nests in common. Before the emergence of workers, a single founding queen undertakes the risky but necessary task of foraging on behalf of the whole colony. [The other queens remain safe underground.] The queen who previously took on the specialized task of removing soil from the nest during excavation usually also acts as the forager . . . a queen that refuses the foraging task in such circumstances is not replaced by her cofoundresses’ (Pollock *et al.*, 2012, p. 951) and, as a result, the colony has no food and dies. In a sense, the colony punishes itself with suicide because of the selfishness of one member of its group.

Pollock and colleagues (Pollock and Cabrales, 2008; Pollock *et al.*, 2012) model the ant’s biology as a game in which self-preservation is pitted against suicidal punishment. They show that a ‘parameter range [exists] in which self-preservation never outperforms suicidal punishment’ (Pollock *et al.*, 2012, p. 951). In other words, group selection reduces the extinction probability of colonies by weeding out those with selfish individuals.

Encouraged by such successes, theoreticians are taking a new look at group selection. Simon and Nielsen, for example, show that ‘Group selection . . . can be a very potent evolutionary force’ (2012, p. 766).

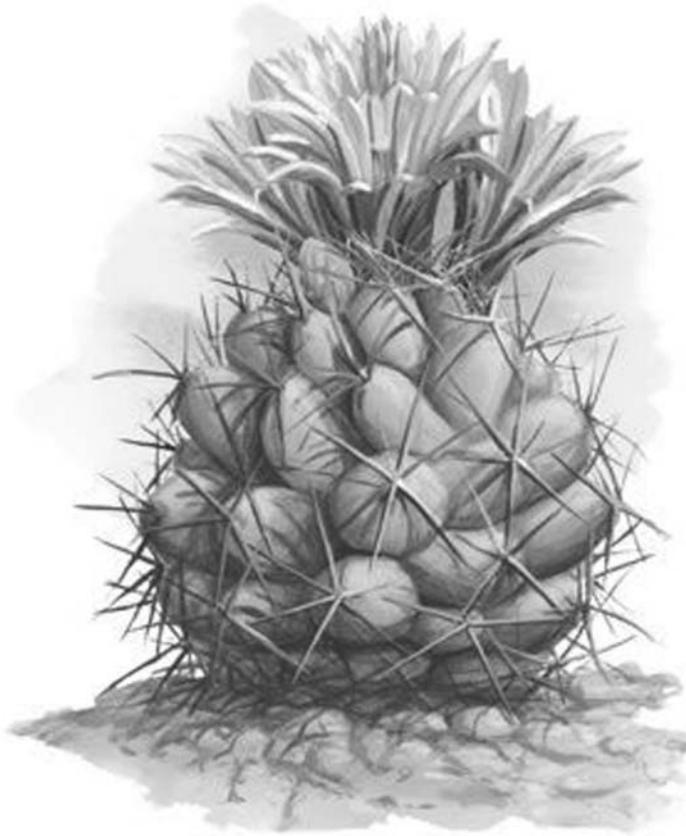
### PIMA PINEAPPLE CACTUS

Pima pineapple cactus, *Coryphantha robustispina* (also called *Coryphantha scheeri* var. *robustispina*), is a small, obscure hemispherical cactus (Fig. 1). It grows on scrubland and grassland on sandy substrates, alluvial fans, and gravelly soils at elevations from 700 to 1500 m above sea level. The species’ range includes small parts of Arizona, Chihuahua, New Mexico, Sonora, and Texas.

Despite its substantial range, it is quite scarce in the patches that support it. The density of *C. robustispina* in those patches goes from one plant per hectare to less than one plant per 10 hectares (McDonald and McPherson, 2005). Because of its relative scarcity, the IUCN listed it as endangered until 2013. But as more information accumulated about its substantial range, IUCN changed the listing to ‘Least Concern’ (IUCN Red List, 2016).

The flowers of *C. robustispina* need to be cross-pollinated to reproduce, and yet they last only a single day (Roller, 1996). A ground nesting bee, *Diadasia rinconis*, a cactus specialist, is its primary pollinator. Meanwhile, other species of cacti – *Opuntia* and *Ferocactus* – dominate its habitat. If they were flowering, the bee would be more likely to visit them, not *Coryphantha*. Thus a real possibility exists that *C. robustispina* might suffer from a shortage of pollination services. In fact, McDonald and McPherson report that ‘the proportion of [*C. robustispina*] flowers missed by pollinators increased when [it] was blooming at the same time as its competitors’ (2005, p. 531).

So *Coryphantha robustispina* occurs at very low densities, lives in an ecotone, requires pollination by a specialist, and grows only where its competitors for pollination services are



**Fig. 1.** Pima pineapple cactus, *Coryphantha robustispina*.

much more abundant than it is. To me, that seems a formidable collection of existential challenges!

Not to worry. The cactus has a life history that solves all its problems. All its flower buds appear at the same time in mid-May. All flowering occurs in the summer months when neither *Opuntia* nor *Ferocactus* are flowering, and flowering tends to be synchronous across plants 2–6 days after a good (>10 mm) rainfall (Kidder, 2015, p. 73). Often there will be several such rains in a summer and the plants respond each time with a flowering event. For example, ‘during the summer of 2003, flowering events took place on June 5, July 17, July 29, and August 20’ (McDonald and McPherson, 2005, p. 530).

If we agree that its problems might suggest a high probability of extinction, the life history of *C. robustispina* helps us to understand how it survives. By flowering synchronously, it achieves a spike in its effective density as well as a spike in the opportunity it offers to the bees. So, for a few days in summer, it is relatively abundant, and it must be among the most apparent sources of pollen for *D. rinconis*. By evolving to reproduce synchronously, *C. robustispina* ensures its continuity.

How did synchronicity evolve? We need not hypothesize that it evolved by group selection in order to reduce extinction probability. Ordinary natural selection easily explains the

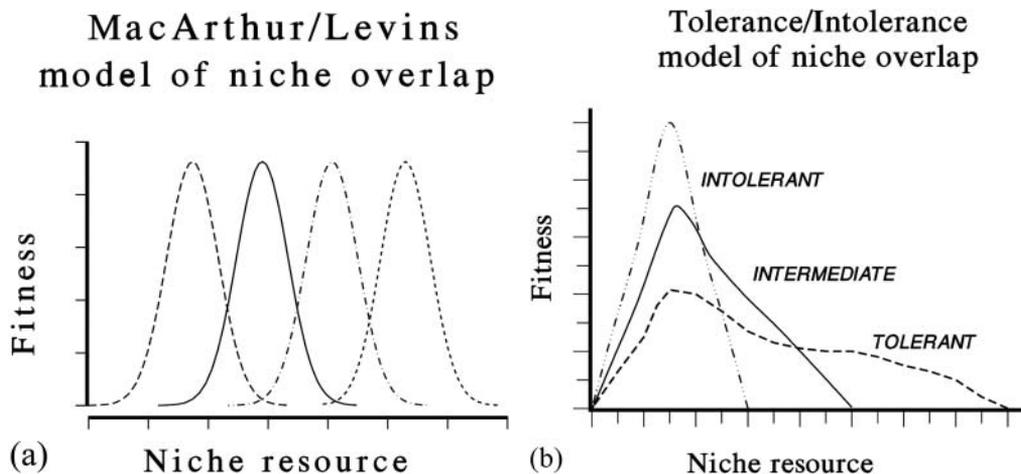
synchronicity. The ovules of an individual that is out of step with its fellows will not be fertilized, and its pollen will find no appropriate ovules. So synchronicity must have ultimate selective value. Evidently, *C. robustispina* indeed evolved to ease the extinction burden of its scarcity, but only as a by-product of ordinary natural selection to improve individual fitness.

### EXTINCTION RATE AND THE EVOLUTION OF ECOLOGICAL BREADTH

The usual conception of how different species of ecological competitors can co-exist comes from the model of MacArthur and Levins (1967). Species find themselves arrayed along a niche axis (Fig. 2). The axis may represent any environmental variable or set of environmental variables. The fitnesses of the different species peak at different values of the axis. Hence adding more individuals of a species depresses the average fitness of that species more than any other. Note that in its basic form, the variances of the different species are similar – that is, individuals of all species pay a similar fitness cost if they differ by the same amount from their optimum place along the niche axis.

The model of MacArthur and Levins is easy to present (to colleagues and students alike) and often finds its way into basic ecology textbooks. But finding examples of it in the field is not so easy. Most of the time in my experience, the field ecologist sees species (plants and animals) that vary in their ecological breadth rather than their mean (Fig. 2).

A classic and renowned case is that of the two species of acorn barnacle that live in the Scottish intertidal (Connell, 1961). *Balanus* grows quickly but only in the lower portions of the habitat; to get enough food, it must have the longer times of submersion available to it there. Its competitor, *Chthamalus*, is restricted to the highest part of the intertidal (which is submerged a small fraction of the time, thus preventing *Balanus*'s survival). Connell's



**Fig. 2.** Two models of niche relationships between co-existing competitors. (a) MacArthur/Levins: Here, species' niches are displaced from each other along the  $x$ -axis. Species co-exist because the best niche value of each one is unique. (b) Tolerance/intolerance: All species do best at the same niche value but one – the intolerant – dominates that value at the expense of its tolerance for other values. On the other hand, the tolerant species is outcompeted in the best conditions but does acceptably well in the widest variety of circumstances. The figure also shows a third species intermediate in tolerance.

experiments showed that *Chthamalus* can survive at every level, but are smothered or pried off the rock by *Balanus* except at the highest level.

Here are two more of my favourite examples. [The interested reader will find even more in Rosenzweig (1987).]

### Habitats in the intestine of laboratory rats

Think of the intestine of a laboratory rat as an axis of habitat quality whose value to a gut parasite would be proportional to its concentration of useful nutrients. High in the gut, just beyond the pylorus, the habitat is rich in nutrients. But those nutrients have not yet been digested and they are swimming in an environment of high pH. A bit lower sees a more moderate pH and a rich broth replete with nutrients ready to absorb. It is heaven for a gut parasite.

As one travels down the gut, nutrient concentrations will fall off because the host (as well as any parasites that happen to occur in the gut) is moving them out of the gut for use. Heaven loses its charm. And the farther down we look, the more unpromising the habitat.

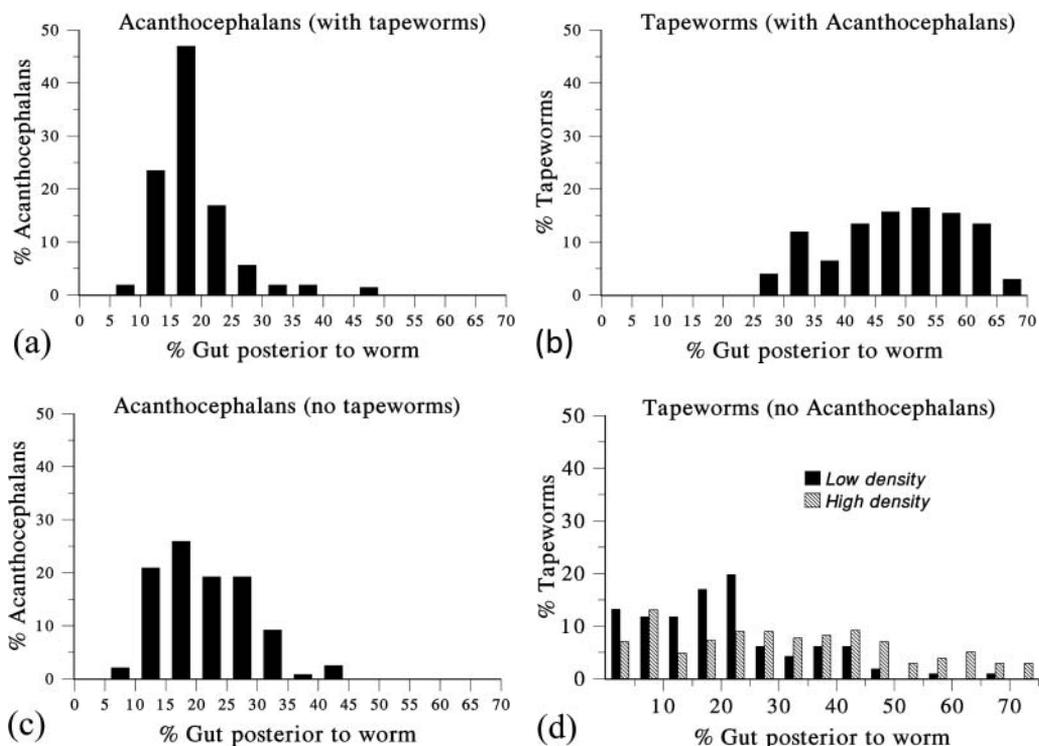
Holmes (1961) produced a brilliant set of experiments to elucidate what goes on. He worked with two parasites, a tapeworm and an acanthocephalan. If a rat harbours both species at substantial densities, then the acanthocephalan individuals are found high in the gut and the tapeworms lower down (Fig. 3a, b). The combination strongly suggests a MacArthur/Levins relationship, tempting us to conclude that the tapeworm and the acanthocephalan differ in their preferred habitat. But Holmes went farther.

He raised laboratory rats with monospecific infestations: only acanthocephalans or only tapeworms. The distribution of the acanthocephalans changed little; their population lived very high in the gut (Fig. 3c). But the tapeworms showed considerable flexibility: when Holmes grew the tapeworms at low population size, they packed into the high level as if they were acanthocephalans (Fig. 3d). At high population size, they spread out (Fig. 3d), living near the pylorus as well as in much of the length of the gut. In fact, more of them lived at levels favoured by acanthocephalans than anywhere else. And I believe it is not unkind to guess that if most biologists were to find two species subdividing a niche variable as do the worms of Fig. 3a and b, they would conclude that they had discovered the niches of the two species. They might even conclude that the acanthocephalan preferred to be high in the gut and the tapeworm preferred being lower down.

But Holmes has shown us how unwise that conclusion might be. Both species prefer being high, but their interaction sends the tapeworms down the gut, away from the acanthocephalans.

### Freshwater crayfish

Bovbjerg (1970) produced a case like the gut parasites but with experiments in the laboratory linked to field observations. He worked with two species of freshwater crayfish that live in the drainage of the Mississippi River. The virile crayfish (*Orconectes virilis*) lives in swift, shallow water – well-oxygenated riffles. Its congener, the papershell crayfish (*O. immunis*), lives in deeper water that flows more slowly (it may even become stagnant for a time). But the subdivision of habitat that characterizes these two species does not fit a MacArthur and Levins model. Bovbjerg showed that *O. immunis* actually prefers shallow, well-oxygenated water – the same conditions that *O. virilis* prefers.



**Fig. 3.** A case of tolerance/intolerance niche relationships: Holmes' experiments with two parasites in the rat's gut, a tapeworm and an acanthocephalan. (a, b) With both parasites at high density in the gut, the acanthocephalan lives high in the gut and the tapeworm is spread out lower down. (c, d) Isolated and at low density, each species exhibits its shared preference – both live high in the gut. But at high density, the tapeworm spreads out to occupy all levels in which either of the two parasites can succeed (d). *Not shown*: the acanthocephalan at high density remains high in the gut even if it is alone. Hence the tapeworm is tolerant, and the acanthocephalan intolerant.

Bovbjerg enriched his work with behavioural and physiological experiments that explain the mechanism that relegates *O. immunis* to deeper, more sluggish, less oxygenated water.

- *O. virilis* is more aggressive, both among individuals of its own species and those of *O. immunis*.
- Once begun, a contest between the two species is sure to result in the defeat of *O. immunis*.
- And *O. virilis* cannot dominate the deeper, more sluggish water because its metabolism is so high that it cannot survive the low oxygen concentrations of a cold winter night.

That sews up an elegant story. Both species prefer the well-oxygenated water of riffles, but *O. virilis*, the more aggressive species, expels *O. immunis* from it. The latter in turn, with its slower metabolism and concomitant lack of belligerence, has no trouble surviving in the less oxygenated deeper water.

### IS EXTINCTION RATE A FUNCTION OF ECOLOGICAL DOMINANCE?

This is not the place to harangue the reader with additional elegant, half-century-old experiments that, I believe, have sadly been forgotten. But it will profit us to explore the common thread that joins these three and many others.

Rosenzweig (1979) and Pimm and Rosenzweig (1981), working on theories of habitat selection, saw that one reasonable case involved a pair of species that share a preference for a habitat. They could generate conditions for co-existence by assuming a trade-off between the ability to dominate that habitat and the ability to thrive in the poorer habitat. The acorn barnacles, the crayfish, and the rat-gut parasites all fulfil these conditions. In fact, many, many other cases – both plant and animal – seem to fit this model, which we called shared-preference habitat selection.

Because many botanical cases seem to correspond to the model, and plants usually do not choose anything, I have been calling it the tolerance/intolerance model (Rosenzweig, 1987). The species that relies most heavily on the best conditions is intolerant; it has a very narrow niche, both potential and realized. One that can survive in lesser circumstances is tolerant. It has a broad potential niche (and may also have a broad realized one). Levins (1979) called this ‘consumption of the variance’.

Simply because the best conditions are often an extreme circumstance, we can expect them often to be rare and restricted at various scales of space or time. So the intolerant species may be thought to have evolved to be rare and restricted in exchange for its ability to dominate the best niche axis values.

To most conservation biologists, ‘rare and restricted’ implies ‘threatened with extinction’. I will assume that is true and add that, despite the danger to the group, the intolerant species evolved intolerance because of the superior fitness of individuals that could dominate the best places. I am not suggesting that natural selection will have altered even a single gene of an intolerant species to make it more or less prone to extinction. What evolves is its niche position. Its long-term prospects for continued existence merely tag along as a consequence.

And the tolerant species is tolerant, not because it thereby enjoys a low extinction rate, but because the poorer patches are all that remains for it to exploit. Live poor or die!

Now comes the intriguing part. If the bad prospects of an intolerant species should overtake it and lead to its extinction, then a tolerant species ought to evolve to fill its place. As before, the higher extinction rate that accompanies the evolution does not matter.

The summary image is of a group of species organized by tolerance along a quantitative niche axis. At the rich end of the axis is the species that can dominate it; at the poor end is the species that can tolerate most of the axis values. From time to time, the species at the rich end becomes extinct, drawing into its place a more tolerant species. In turn, that latter species tempts extinction by evolving intolerance. The system amounts to an ecological/evolutionary conveyor belt, a situation I tried to describe in a verbal image in 1989:

The rare species are in the greatest danger of extinction. They occupy the richest end of the spectrum at the cost of having narrow niches and, often, of being inefficient. Again and again the pattern emerges from the literature. The aggressive species succeed because they can interfere with others, not because they are particularly good exploiters. They probably waste much of the wealth they expropriate for themselves. And yet, as individuals, they are doing

quite well. Odum and Pinkerton (1955) long ago pointed out that efficiency is not important for success in life. It is power that counts. Hence, when hard times come and the dominant species becomes extinct, its niche will not long stay vacant. The meek will inherit the niche. But in so doing, they will be driven by natural selection to become dominants themselves. (Rosenzweig, 1989, p. 18)

That 1989 picture is incomplete. It pays no attention to the influence of geography and the problems of speciation. A range is two-dimensional (at least). Yes, the population of a tolerant species will expand into areas abandoned owing to the demise of an intolerant one. But what will break up the tolerant into two species? And we cannot forget the biology of Pima pineapple cactus, a species whose rarity seems to have resulted in natural selection that reduced its risk of extinction.

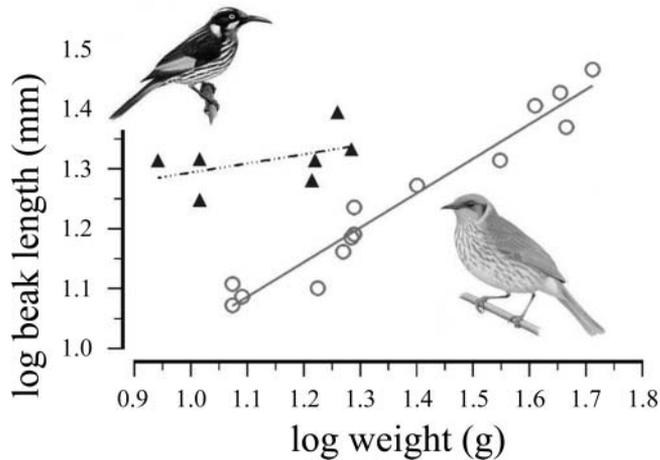
Have species evolved to the point that each suffers the same risk of extinction no matter its niche position in a guild? No, the fossil record makes clear that the push and pull of evolution at the species level has not entirely levelled the chances of extinction among species. We have known for decades that being widespread does reduce extinction rate (Jablonski, 1986). Marine invertebrates with the largest ranges outlast those with intermediate ones, which, in turn, outlast those with small ones. To the extent that group selection has not entirely solved the extinction problem for narrowly distributed species, the pattern of tolerance co-existence would seem to support the idea of the conveyor belt: natural selection drives tolerant species towards intolerance and the higher rates of extinction that accompany intolerant niches.

This hypothesis finds some support in Raia *et al.* (2016). The authors report that ‘clades escaping [mass extinctions] go extinct because of the widespread tendency of evolution to produce increasingly specialised, sympatric, and geographically restricted species’. This conclusion makes sense if we recall that intolerant species will occur only in limited places and will generally share these with their tolerant relatives, who will occupy the poorer spots on a landscape and/or its poorer times. And intolerant species will appear to be quite specialized, especially if the critical work is done to compare their fundamental niches with those of tolerants. Raia *et al.* (2016) did not explore the data with models of niche overlap in mind, but I would be fascinated if it were possible to do so.

So what we have now amounts to interesting questions, good excuses for research. We know that many species are involved in tolerance/intolerance systems. Can modern methods of genetic analysis tell us whether the intolerants have higher extinction rates? Do the smaller populations – and probably the more fragmented ranges of such species – evoke some group selection that will balance the effects of natural selection to some extent? At least, now, our minds are open to that possibility.

#### AVERAGE EXTINCTION RATE THROUGH THE PHANEROZOIC

We may have reason to hypothesize a general long-term trend that derives from the proliferation of *G*-functions. A *G*-function (Brown and Vincent, 1987) characterizes a group of species that have deployed along a trade-off. For example, birds in the family Melophagidae (honey eaters) occupy various points along the line representing the allometric relationship between bill length and body mass (Wooller, 1984; Rosenzweig, 1999). However, Australian melophagids actually occupy two such lines (Fig. 4). Species along the lower one consume a lot of insects, whereas those along the upper one rely mostly on nectar for food. Birds in the latter



**Fig. 4.** The species of the honeyeater family spread out on two rather distinct  $G$ -functions. Insects predominate in the food of species along the lower one. Nectar is most important in the diets of species along the higher one. The two inset figures show an example of each  $G$ -function. The New Holland honeyeater (higher inset) has a long beak for its body weight, whereas the length of the yellow-plumed honeyeater's beak is more in proportion to its body weight (lower inset). Data from Wooller (1984).

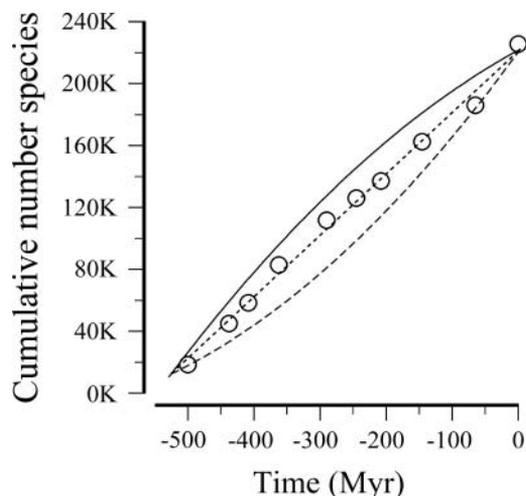
group have beaks that are disproportionately long compared with birds of similar size in the former group. Natural selection cleaved the melophagid trade-offs into two allometries, and species on the separate  $G$ -functions were freed to explore their own independent evolutionary futures.

Subdivision of trade-offs is the only sense I know of in which one may truly speak of evolutionary progress. One result of it might be an increase in steady-state diversity as more specialized species replace those reined in by trade-offs. Are such, more specialized species subject to higher extinction rates? Can we discern any pattern of change in extinction rates during Phanerozoic history?

Probably most extinctions happen to start-up species soon after they evolve. We can expect almost none of them to have left a trace. So let us ignore the noise of start-up species that fail quickly, and focus instead on the signal from those that initially do find a place in nature but subsequently lose it.

Raup (1976) compiled the number of fossil invertebrate species for the principal periods of the 530 million years of the Phanerozoic. Although it has been a half-century since then, Raup's feat has not been repeated. Data indeed have been accumulating at the Paleobiology Database (<https://paleobiology.org/#/>) and its sister site Fossilworks (<http://fossilworks.org/bridge.pl>). So I consulted with a number of palaeontologists (John Alroy, Tony Barnosky, Michael Bell, Michael Benton, Mikael Fortelius, Dave Jablonski, Andrew Knoll, Pasquale Raia, Bruce Tiffney) and most advised me that the data are in hand but remain treacherous, especially at the species level. Not being a palaeontologist myself, I decided against trying to clean them up. I turned instead to the monumental work of Raup.

First, adjusting for unequal area, I assembled an accumulation curve of them across the ten traditional paleo-time periods (Cambrian through Cenozoic). I wondered whether



**Fig. 5.** Species accumulate at a steady rate during the 530 million years of the Phanerozoic. The  $y$ -axis shows the number of species (adjusted for the unequal areas available in each of the ten time periods). The  $x$ -axis is a bit tricky. Points along the straight broken line come in order of age (Cambrian first; Cenozoic last); these points fit a straight line nearly perfectly. (If we assume that the exponent of curvature equals 1.0, then  $R^2 = 0.995$ .) But the curved lines come from two other  $x$ -axes that are congruent to the first. To produce them, I first calculated each period's rates by dividing its adjusted number of new species by its duration. Then I reordered the times in one of two ways, and calculated their exponent of curvature. The idea is to find the lines that deviate the most from linearity. In one case – the convex-upward line – accumulation begins at the period that has the greatest accumulation rate, and proceeds, in order, with periods of slower and slower rates. Thus this line has the greatest convexity (its exponent of curvature equals 0.866). The other curved line, the concave-upward line, comes from beginning with the period that has the smallest accumulation rate and adding periods of faster and faster accumulation rate. This line has the greatest concavity (its exponent of curvature equals 1.204). Neither 0.866 nor 1.204 is very far from 1.00 (the curvature of a straight line). *Note:* I do not show the 20 points that led to the two curved lines because that would have made the axis label unnecessarily crowded.

the accumulation curve would reveal any rate deviations or trends. But I found none (Rosenzweig, 1997, 1998). So for 530 million years, species have been accumulating at a fairly steady rate (Fig. 5). What could this mean?

Ostensibly, an accumulation curve reflects only the accumulation of new species. Once a species joins the curve, it never drops out (even if it suffers extinction). But the data underlying this curve does have an extinction component. Raup (1976) counted 144,251 newly discovered species of fossil marine invertebrates in the Zoological Record from 1900 to 1970. Of these, 136,835 species lived only during a single one of the ten major time divisions (from the Cambrian to Cenozoic). Together these 136,835 species represent 95% of all known marine invertebrate fossil forms. Thus a very large fraction of them appeared and became extinct, strongly suggesting that the rate at which new species have accumulated during the Phanerozoic must be very close to the rate at which they have disappeared.

That is a stunning conclusion. If it is true, it leaves us with many research questions. The most puzzling is, what mechanism(s) keeps the average of these two rates nearly constant for hundreds of millions of years?

I expect science to take one of its usual paths, i.e. now that we know that there are two major evolutionary processes – natural and group selection – we shall study their relative importance. Initially, we shall learn how to determine that relative importance. And then we shall build theories that illuminate the conditions that affect it. Lewontin and Dunn (1960) lead straight to the speculation that whatever scatters a species into many small demes will make group selection more powerful. And if we accept Mitteldorf's conclusion that sex is the fruit of group selection, perhaps we can also figure out why so many species – plants and animals – have abandoned sex altogether.

### ACKNOWLEDGEMENTS

This paper relies heavily on a symposium talk given in March 2015 on Tumamoc Hill. Thanks to Doug Morris and Per Lundberg for organizing the symposium. Thanks also to Cynthia Anson and Carole Rosenzweig for their help in keeping it on track. Thanks also go to John Alroy, Tony Barnosky, Michael Bell, Michael Benton, Mikael Fortelius, Dave Jablonski, Andrew Knoll, Pasquale Raia, and Bruce Tiffney for advice about the palaeontological literature. Karl Flessa asked the question which led directly to the statistical examination of Figure 5.

### REFERENCES

- Avilés, L. 1999. Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. *Evol. Ecol. Res.*, **1**: 459–477.
- Bovbjerg, R.V. 1970. Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). *Ecology*, **51**: 225–236.
- Brown, J.S. and Vincent, T.L. 1987. Coevolution as an evolutionary game. *Evolution*, **41**: 66–79.
- Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, **42**: 710–723.
- Gilpin, M.E. 1975. *Group Selection in Predator–Prey Communities*. Princeton, NJ: Princeton University Press.
- Holmes, J.C. 1961. Effects of concurrent infections on *Hymenolopsis diminuta* (Cestoda) and *Moniliformis dubius* (Acanthocephala). I. General effects and comparison with crowding. *J. Parasitol.*, **47**: 209–216.
- Ingvarsson, P.K. 1999. Group selection in density-regulated populations revisited. *Evol. Ecol. Res.*, **1**: 527–536.
- IUCN Red List. 2016. <http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T62363A3113013.en> [accessed 29 August 2016].
- Jablonski, D. 1986. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science*, **231**: 129–133.
- Kawata, M. 1999. The effects of dispersal behaviour in group selection. *Evol. Ecol. Res.*, **1**: 663–680.
- Kidder, A.L. 2015. Ecohydrological conditions associated with the distribution and phenology of the Pima pineapple cactus (*Coryphantha scheeri* var. *robustispina*). MS thesis, Graduate College, The University of Arizona [<http://cals.arizona.edu/research/papuga/docs/KidderThesis.pdf>; accessed 12 September 2016].
- Levins, R. 1979. Coexistence in a variable environment. *Am. Nat.*, **114**: 765–783.
- Lewontin, R.C. and Dunn, L.C. 1960. The evolutionary dynamics of a polymorphism in the house mouse. *Genetics*, **45**: 705–722.

- MacArthur, R.H. and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. *Am. Nat.*, **101**: 377–385.
- McDonald, C.J. and McPherson, G.R. 2005. Pollination of pima pineapple cactus (*Coryphantha scheeri* var. *robustispina*): does pollen flow limit abundance of this endangered species? *USDA Forest Service Proceedings*, **RMRS-P-36**: 529–532.
- Mitteldorf, J. 2004. Ageing selected for its own sake. *Evol. Ecol. Res.*, **6**: 937–953.
- Mitteldorf, J. 2006. Chaotic population dynamics and the evolution of ageing. *Evol. Ecol. Res.*, **8**: 561–574.
- Mitteldorf, J. 2016. *Aging is a Group-selected Adaptation: Theory, Evidence, and Medical Implications*. Boca Raton, FL: CRC Press.
- Odum, H.T. and Pinkerton, R.C. 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. *Am. Sci.*, **43**: 331–343.
- Pimm, S.L. and Rosenzweig, M.L. 1981. Competitors and habitat use. *Oikos*, **37**: 1–6.
- Pollock, G.B. and Cabrales, A. 2008. Suicidal altruism under random assortment. *Evol. Ecol. Res.*, **10**: 1077–1086.
- Pollock, G.B., Cabrales, A. and Rissing, S.W. 2004. On suicidal punishment among *Acromyrmex versicolor* cofoundresses: the disadvantage in personal advantage. *Evol. Ecol. Res.*, **6**: 891–917.
- Pollock, G.B., Cabrales, A., Rissing, S.W. and Binmore, K.G. 2012. Suicidal punishment in the ant *Acromyrmex versicolor*. *Evol. Ecol. Res.*, **14**: 951–971.
- Raia, P., Carotenuto, F., Mondanaro, A., Castiglione, S., Passaro, F., Saggese, F. *et al.* 2016. Progress to extinction: increased specialisation causes the demise of animal clades. *Sci. Rep.*, **6**: 30965.
- Raup, D.M. 1976. Species diversity in the Phanerozoic. *Paleobiology*, **2**: 279–297.
- Roller, P.S. 1996. Distribution, growth, and reproduction of pima pineapple cactus (*Coryphantha scheeri* Kuntz var. *robustispina* Schott). MS thesis, Graduate College, The University of Arizona.
- Rosenzweig, M.L. 1979. Optimal habitat selection in two-species competitive systems. *Fortschr. Zool.*, **25**: 283–293.
- Rosenzweig, M.L. 1987. Community organization from the point of view of habitat selectors. In *Organization of Communities: Past and Present* (J.H.R. Gee and B.J. Giller, eds.), pp. 469–490. Oxford: Blackwell Scientific.
- Rosenzweig, M.L. 1989. Habitat selection, community organization, and small mammal studies. In *Patterns in the Structure of Mammalian Communities* (D.W. Morris, B.J. Fox and Z. Abramsky, eds.), pp. 5–21. Lubbock, TX: Texas Tech University Press.
- Rosenzweig, M.L. 1997. Perspective: Tempo and mode of speciation. *Science*, **275**: 1622–1623.
- Rosenzweig, M.L. 1998. Preston's ergodic conjecture: the accumulation of species in space and time. In *Biodiversity Dynamics: Turnover of Populations, Taxa and Communities* (M.L. McKinney and J. Drake, eds.), pp. 311–348. New York: Columbia University Press.
- Rosenzweig, M.L. 1999. In search of paleohominid community ecology. In *African Biogeography, Climate Change and Early Hominid Evolution* (T. Bromage and F. Schrenk, eds.), pp. 68–75. Oxford: Oxford University Press.
- Simon, B. and Nielsen, A. 2012. Numerical solutions and animations of group selection dynamics. *Evol. Ecol. Res.*, **14**: 757–768.
- Wilson, D.S. 1980. *The Natural Selection of Populations and Communities*. Menlo Park, CA: Benjamin Cummings.
- Woodberry, O.G., Korb, K.B. and Nicholson, A.E. 2007. A simulation study of the evolution of ageing. *Evol. Ecol. Res.*, **9**: 1077–1096.
- Wooller, R.D. 1984. Bill shape and size in honeyeaters and other small insectivorous birds in Western Australia. *Austr. J. Zool.*, **32**: 657–661.
- Wynne-Edwards, V.C. 1962. *Animal Dispersion in Relation to Social Behaviour*. Edinburgh: Oliver & Boyd.