EVOLUTIONARY BIOLOGY

Adaptation under a microscope

Rosemary G. Gillespie and Brent C. Emerson

Experiments with microorganisms can guide thinking about the big questions being tackled by evolutionary biologists — for instance, how predation and immigration might play a role in adaptive radiation.

What accounts for biodiversity? Why do lineages of organisms diversify, and why are some lineages more species-rich than others? Charles Darwin was asking these questions 150 years ago, and we continue to do so today. Since Darwin, however, biologists have developed different theoretical and practical ways of tackling them, with experiments involving microbial systems featuring among the latter. Two examples of insights to emerge from such systems are provided by Meyer and Kassen[1] and Fukami *et al.*[2] elsewhere in this issue.

During the past century, the importance of repeated and successive iterations of adaptive radiation in the history of life has become increasingly apparent. Adaptive radiation is the rapid diversification of species to fill many ecological roles, and attempts to understand the factors involved have focused on isolated islands or lakes, where physical conditions would seem to favour this process. Well-known examples are the Darwin's finches of the Galapagos Islands[3] and the cichlid fishes of the large East African lakes[4] (Fig. 1). If immigration is constrained by geographical factors, species diversity can increase through evolution from a few colonists in response to open, often quite varied, ecological space. But evolution is generally a slow process, and biologists have had to rely on inference to elucidate the underlying mechanisms.

Hence the resort to microbial systems[5]. Evolution occurs more rapidly in such systems, allowing controlled experiments that provide insight into how communities develop through evolution or immigration, and the potential roles of competition and predation in driving the process. Particular use has been made of the soil bacterium *Pseudomonas fluorescens*. This bacterium exists as several different forms, or 'ecomorphs' — identifiable genotypes adapted to a particular niche — including SM (smooth), WS (wrinkly spreader) and FS (fuzzy spreader). Meyer and Kassen[1] and Fukami *et al.*[2] have used such microbial systems to investigate two factors that help to explain diversity through adaptive radiation: predation and immigration history.

Consider how diversity arises in communities of larger organisms: the assembly of species over ecological time involves immigration and extinction. However, given sufficient isolation, speciation — often in the form of adaptive radiation — may occur more rapidly than immigration, and be the primary contributor to species diversity. Speciation by adaptive radiation requires unoccupied ecological space, and sufficient geographical isolation to allow for genetic divergence. Moreover, the assembly of a community through adaptive radiation is expected to take much longer than that by immigration.

Accordingly, to understand the process of community assembly through evolution and adaptive radiation, inferences must be made from current ecological and morphological relationships among extant species within a lineage, and from the evolutionary history of that lineage. Historical approaches to investigate the causes of divergent selection that promote adaptive radiation have highlighted in particular the importance of competition between different species[6]. However, experiments showing a positive correlation between divergent selection and trait divergence in the presence of another factor, predation[7], support the old idea that predation can be a driver of adaptive evolutionary change. Yet, in the absence of other solid empirical evidence, the role of predation in promoting adaptive evolutionary change through diversifying selection has remained moot.

Meyer and Kassen[1] (page 432) use the *P. fluorescens* microbial system to provide this evidence. They examine the effect of a predator (a ciliated protozoan, *Tetrahymena thermophila*) on changes in diversity among bacterial genotypes. In the face of both competition and predation, bacterial ecomorphs show negative frequency-dependent selection — where the fitness of a genotype decreases with its frequency in the population — thus maintaining a diversity of ecomorphs. Frequency-dependent selection under competition seems to be caused by competition for resources, whereas under predation it is mediated by the refuge from predators provided by the floating bacterial mat. But perhaps the most exciting finding from these authors is that diversification of

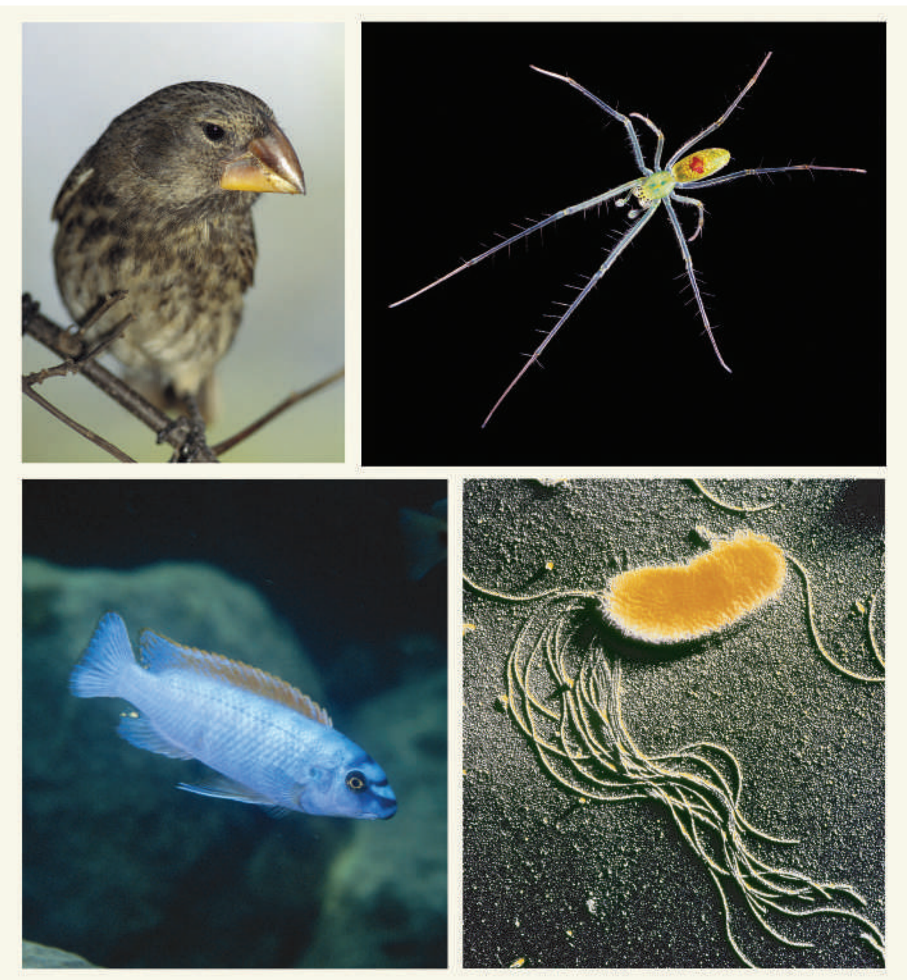

Figure 1 | Bird, fish, spider, bacterium. Classic examples of adaptive radiation come from the Galapagos Islands (Darwin's finches) and the lakes of East Africa (cichlid fishes). Hawaii provides further instances with the tetragnathid spiders. Evolution is generally slow in natural ecosystems, however, hence the use of experimental systems featuring bacteria such as *Pseudomonas fluorescens*[1,2].

bacteria is delayed in the presence of predators. The reason seems to be that predation reduces the intensity of resource competition — and hence diversifying selection — among bacterial ecomorphs. The results suggest that predation may play a prominent, but often unnoticed, role in adaptive radiation.

Another challenge to inference-based analyses of adaptive radiation has been immigration, and the intractability of determining the importance of the sequence in which different species arrive in an isolated habitat. Arrival order may have an effect not only on whether a lineage diversifies in the first place, but also on the eventual species composition in a given community that develops over evolutionary time.

Fukami *et al.*[2] (page 436) have used the *P. fluorescens* system to demonstrate the importance of immigration history in dictating the eventual composition of diversity in a community. Their study shows that the SM ecomorph of *P. fluorescens*, if left on its own, evolves predictably as noted above to form one FS ecomorph and multiple WS ecomorphs. But they observed that small differences in the timing of immigration markedly affected the eventual diversity in a community: if the WS ecomorph was also introduced, they found that by controlling when this specialist ecomorph arrived, it could suppress diversification altogether. These results support data from studies of macroecological communities that document differences in the sets of ecomorphs arising in different situations and the dynamic nature of community assembly over evolutionary time[8,9].

Both of these studies[1,2] contribute to our understanding of the historical contingencies of community assembly. Meyer and Kassen's work[1] highlights a role for interactions among taxa in promoting evolutionary diversification. This supports the view that taxa in species-rich communities may undergo more evolutionary change than do those in less species-rich communities[10]. Analyses of island species show parallels between the formation of communities through evolutionary processes and those formed over ecological time — highlighting the notion that evolution is nothing but ecology writ large[11]. Interestingly, some communities lack the full suite of potential niche specialists[9], and the results of Fukami *et al.*[2] raise the possibility that inconsistencies are partly due to immigration history. 'First come, first served' seems to hold when it comes to filling empty ecological space. The challenge is to apply the knowledge gained from these rich bacterial systems to a more general appreciation of adaptive radiation and global patterns of biodiversity. ■

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1. Meyer, J. R. & Kassen, R. *Nature* **446,** 432–435 (2007).
2. Fukami, T., Beaumont, H. J. E., Zhang, X.-X. & Rainey, P. B. *Nature* **446,** 436–439 (2007).
3. Grant, P. R. *Ecology and Evolution of Darwin's Finches* (Princeton Univ. Press, 1999).
4. Stiassny, M. L. J. & Meyer, A. *Sci. Am.* **280,** 64–69 (1999).
5. Rainey, P. B. & Travisano, M. *Nature* **394,** 69–72 (1998).
6. Schluter, D. *The Ecology of Adaptive Radiation* (Oxford Univ. Press, 2000).
7. Nosil, P. & Crespi, B. J. *Proc. Natl Acad. Sci. USA* **103,** 9090–9095 (2006).
8. Losos, J. B. *Phil. Trans. R. Soc. Lond. B* **349,** 69–75 (1995).
9. Gillespie, R. G. *Science* **303,** 356–359 (2004).
10. Emerson, B. C. & Kolm, N. *Nature* **434,** 1015–1017 (2005).
11. Van Valen, L. *Science* **180,** 488 (1973).

BIOCHEMISTRY

Molecular cannibalism

Steven E. Ealick and Tadhg P. Begley

The biosynthesis of vitamin B_{12} has fascinated generations of scientists, but part of the pathway was unknown. The missing enzymatic link has now been found, only to raise more mechanistic questions.

Most people who take vitamin supplements are unaware of the scientific history behind their unassuming tablets. Vitamin B_{12} is an excellent case in point — no less than four Nobel prizes have been awarded for work relating to this seemingly commonplace compound (Box 1, overleaf). The biosynthesis of vitamin B_{12} is an integral part of this scientific heritage, so one could be forgiven for thinking that there is nothing left to discover. But this is not so. The origins of one fragment of this vitamin, known as the dimethylbenzimidazole (DMB) ligand, have remained an enigma. On page 449 of this issue, Taga *et al.*[1] finally unravel the mystery by identifying the enzyme responsible for DMB biosynthesis, and describing its structure.

Vitamin B_{12} is essential for human health — its absence leads to the autoimmune disease known as pernicious anaemia. It is perhaps surprising to learn that only bacteria, fungi and algae produce this vitamin, whereas animals and plants must obtain it from their diet. The term 'vitamin B_{12}' is actually a general description for several structurally related compounds, two of which are the major biologically active variants. The first of these is methyl cobalamin,

50 & 100 YEARS AGO

50 YEARS AGO

It is curious how few facts of real importance are known about the life and parentage of Archimedes, while the trivial story of his leaping out of his bath shouting "Heureka" is familiar to every schoolboy. The first record of it, however, is in the works of Vitruvius, written about two hundred years after Archimedes's death, so that there was ample time for the story to have been embroidered, even if it is not a pure invention. It is much the same with the account of his launching a large ship single-handed, saying, "Give me a place to stand on and I will move the earth", and with the myth that he burned the Roman fleet by using mirrors on a sunny day. These traditional stories, and others, are critically considered in Prof. E. J. Dijksterhuis's book.
From *Nature* 23 March 1957.

100 YEARS AGO

Nature Knowledge in Modern Poetry — In this book the author deals in a very interesting manner with the many references to the aspects of nature in the poetical works of Tennyson, Wordsworth, Matthew Arnold, and Lowell... Interest in the insect world is shown to a greater extent by Tennyson, for he alludes to it frequently, and always with the accuracy which reveals great knowledge... Tennyson's love of geology is apparent in the frequent references to it and the similes he gives, which clearly show he must have read a good deal on this as indeed on many other less popular subjects; for instance, he does not shun allusions to the nebular hypothesis, spectrum analysis, and astronomy. It seems evident that he accepted the theory of evolution, for many quotations might be made to show it...

"Evolution ever climbing after some
ideal good,
And reversion ever dragging
Evolution in the mud."

From *Nature* 21 March 1907.