

their home and day ranges to a circumscribed area. The $^{87}\text{Sr}/^{86}\text{Sr}$ values seen in the male teeth derive from a dolomite-rich region that is only 30 square kilometres in extent, distributed in a northeast–southwest direction. The minimum distances from the caves to bedrock of differing ratios are only 2–3 km to the southeast and 5–6 km to the northwest. There are no barriers, yet the males stayed in the dolomitic areas, apparently because their foods existed only in such regions. Young females apparently fed in other, unspecified areas during tooth mineralization, and moved into the males' region as young adults for reproductive purposes.

These results have implications for understanding australopithecine diet, group size, predator avoidance and home-range size. Living primate species offer insights into these variables². Among modern primate groups, ecology influences the temporal and geographic patterns of exploitation of food items, group size and predator pressure, and all of these factors strongly influence group ranging patterns. For example, leaf-eating primates have smaller home ranges than fruit-eating primates of the same body size. Body size and group size influence when and where individual primates would be vulnerable to predators.

Australopithecines lived in woodland savannahs, which provide tree foods and grass³. The carbon stable isotope ratios ($^{13}\text{C}/^{12}\text{C}$) in tooth enamel suggest that most of them ate both foodstuffs, with some East African members eating only grass^{4,5}. Their tooth-enamel structure and its microscopic scratches and pits imply that they also ate hard objects (seeds and nuts) or plant tubers and swollen stems⁶.

This diet contrasts with that of extant chimpanzees, which select only tree foods when living in savannah regions⁷. In such habitats, chimpanzees elude predators by avoiding open areas, forming larger than normal groups, and covering large home ranges³. For example, the range of chimpanzees at Ugalla, Tanzania³, is some 600 km² in extent, much larger than the 30 km² proposed by Copeland *et al.*¹ for the South African australopithecines. The small home ranges suggested by the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios argue against australopithecines having targeted only tree foods and in favour of their including a more ubiquitous food such as grass. Mountain gorillas⁸ feed on ubiquitous terrestrial vegetation in a home range of up to 25 km², similar to that suggested by the strontium isotope data for male australopithecines¹. But male gorillas are very large, thereby providing group protection, and they live in forest habitats without large predators². In contrast to the mountain gorilla, the australopithecines lived in an open habitat, had a smaller body size and faced many species of large carnivores. How did they avoid predation while eating grass in an open savannah?

For diet, the closest equivalent to that of the australopithecines is found in the extant baboon *Theropithecus gelada* and in its giant fossil ancestor⁹, which had a body size

roughly equivalent to that of the australopithecines⁵ and which occupied the same or a similar habitat. Modern *T. gelada* are much smaller than either fossil group and practise male philopatry; they avoid predation in their open savannah habitat by living in bands up to 60 strong, and have overlapping home ranges of sizes roughly equivalent to that estimated for the australopithecines (see references in ref. 2). But how could two large primate species of similar body size, one quadrupedal (giant baboon) and the other bipedal (australopithecine), have coexisted? They would have been competing with each other, as well as with other fruit-eating animals, and with grass-eaters such as pigs, hippos and zebra ancestors, along with other ungulate species⁵. How the australopithecines balanced predator avoidance and the need to compete for food remains an open question.

In Lewis Carroll's flight of nonsensical whimsy, *The Hunting of the Snark*¹⁰, there is the warning about the day that "your Snark be a Boojum!" — for the consequence of that is instant disappearance. We are in the midst of a fascinating hunt, but for us a Snark that turns out to be a Boojum would mean success, not

failure. What is needed in this field of research is for conjectures about the australopithecines to vanish, instead of arising time and time again^{5,9}. We must hope that continued investigation along the lines of Copeland and colleagues' study⁷ will one day allow us to winnow away some of that speculative thinking. ■

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1. Copeland, S. R. *et al.* *Nature* **474**, 76–78 (2011).
2. Strier, K. B. *Primate Behavioral Ecology* 3rd edn (Allyn & Bacon, 2007).
3. Moore, J. J. in *Topics in Primatology* Vol. 1 (eds Nishida, T. *et al.*) 99–118 (Univ. Tokyo Press, 1992).
4. Lee-Thorp, J. & Sponheimer, M. *Am. J. Phys. Anthropol.* **131**, Suppl. 43 Yb. *Phys. Anthropol.* 131–148 (2006).
5. Cerling, T. *et al.* *Proc. Natl Acad. Sci. USA* doi:10.1073/pnas.1104627108 (2011).
6. Lucas, P. *et al.* *BioEssays* **30**, 374–385 (2008).
7. Schoeninger, M. J., Moore, J. & Sept, J. M. *Am. J. Primatol.* **49**, 297–314 (1999).
8. Watts, D. P. *Int. J. Primatol.* **19**, 651–680 (1998).
9. Jolly, C. J. *Man* **5**, 5–26 (1970).
10. Carroll, L. *The Hunting of the Snark: An Agony in Eight Fits* (Macmillan, 1898).

MOLECULAR EVOLUTION

Hidden diversity sparks adaptation

Although some genetic mutations have clear effects, others have been considered neutral and inconsequential. Such cryptic mutations can nonetheless facilitate adaptation to new environments. [SEE LETTER P.92](#)

JEREMY A. DRAGHI & JOSHUA B. PLOTKIN

Is genetic variation primarily neutral, or is it predominantly shaped by natural selection? Biologists have debated this question for decades. And although the neutralist–selectionist argument has fuelled advances in our understanding of molecular evolution, it has contributed less to our knowledge of how organisms adapt to changing environments. Recent theories about robustness and evolvability, as well as experiments with enzymes and with microbes, suggest that adaptation may depend on a deep and largely unappreciated interaction between neutral and beneficial mutations. On page 92 of this issue, Hayden *et al.*¹ describe an empirical test of this hypothesis.

When exposed to a new environment, a microbial population will rapidly adapt through the emergence and fixation of beneficial mutations². Nevertheless, microbial-evolution experiments have uncovered factors

that complicate this simple picture. One such factor, called epistasis — whereby the effects of one mutation are modified by other mutations — explains why some populations adapt faster or more predictably than others. These differences in evolvability, or in the propensity to produce beneficial mutations, account for several surprising results (such as the sudden emergence of a major metabolic adaptation³ or the long-term coexistence of lineages in a population⁴). The renewed interest in epistasis also points to an exciting and constructive role for neutral mutations in the process of adaptation.

The key finding that links neutral mutations to beneficial changes is that neutrality is often conditional: a mutation may have no detectable effect when it arises in a given environment and against a specific genetic background, but subsequent changes to the environment or genome may reveal hidden fitness effects⁵. Theoretical work suggests that conditionally neutral, or 'cryptic', mutations may accumulate within a population and later be expressed

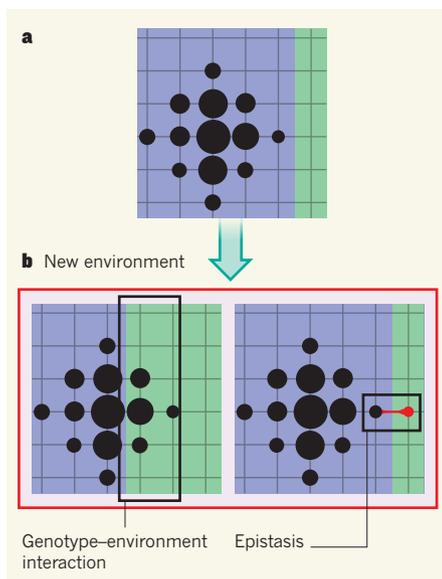


Figure 1 | Role of cryptic genetic variation in adaptation. In this depiction, genotypes (nodes) are separated by mutations (lines). Node size indicates the frequency of a genotype in the population, and background colour shows the phenotype in a given environment. **a**, A population under selection for the blue phenotype occupies a network of equally fit genotypes. **b**, When the population is challenged with a new selective environment (red box), some of the previously neutral genotypes may already express the adaptive phenotype (green). Adaptation to the new environment is also facilitated by epistasis between a beneficial mutation (red) and a mutation that was neutral in the original environment. Hayden *et al.*¹ confirm that neutral genetic variation accumulated in one environment can facilitate adaptation to a novel environment, either through interaction between genotype and the environment or by epistasis.

after an environmental change, either directly in response to the new environment⁶, or by epistatic interactions with subsequent mutations⁷ (Fig. 1). Hayden *et al.*¹ test this theory by direct experimentation.

The authors evolved two populations of a ribozyme (RNA enzyme) under selection for activity with its native substrate; one population was subject to strong selection, the other to weaker selection. The populations accumulated cryptic genetic variation that was later revealed when they were challenged to catalyse a different substrate. By measuring the increase in catalytic activity over time in this new selective environment, Hayden and colleagues found that the rate of adaptation was proportional to the amount of cryptic variation present in each population. In other words, cryptic genetic variation that had accumulated in one environment facilitated adaptation to a new environment.

This *in vitro* ribozyme system facilitates precise measurements of genetic variation throughout experiments. It also allows the mutations responsible for adaptation to be identified, sequenced and reconstructed in the

ancestral ribozyme strain. To interrogate the genetic basis of adaptation, Hayden *et al.* took advantage of these features. They confirmed that the beneficial genotypes arose from previously cryptic genetic variation, supporting a causal connection between neutral mutations and adaptation.

The analysis¹ further revealed a complex, ecological dynamic: in one of the populations, the proper functioning of an evolved genotype depended on the presence of other genotypes in the population. So by tracking population variation through deep sequencing, the researchers were able to capture a more detailed picture of the underlying genetics and ecology than is feasible in most evolution experiments using organisms with large genomes.

Hayden *et al.*¹ applied a very high per-base mutation rate to their short ribozyme sequence to approximate the typical genomic mutation rate of a living organism. But extrapolating their results to real organisms is not straightforward, because there might be different patterns of epistasis among the sites of a single enzyme from those among the genes in a large genome. Nevertheless, other work^{8–10} suggests that epistasis is prevalent at the genomic scale, and that novel environments reveal previously cryptic phenotypic variation in complex organisms. Together with Hayden and colleagues' work, these studies of natural populations suggest a general and important role for cryptic variation in determining a population's adaptive potential.

Sewall Wright, a vigorous proponent of the importance of epistasis in evolution, presaged the modern view in his comment¹¹ on Kimura's neutral theory: "Changes in wholly nonfunctional parts of the molecule would be the most frequent ones but would be unimportant, unless they occasionally give a basis for later changes which improve function in the

species in question which would then become established by selection." Indeed, Hayden *et al.*¹ have now verified that cryptic variation can shape the process of adaptation. We can hope that future studies of this type will elucidate the specific mechanisms by which neutral mutations potentiate adaptation (see ref. 12, for instance), and so eventually lead to a quantitative understanding of a population's rate of adaptation.

As climate change brings organisms into new environments and facilitates contact between novel pathogens and humans, a comprehensive theory for how populations adapt will have pay-offs for conservation and public health, as well as for our understanding of the diversity of life. ■

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- Hayden, E. J., Ferrada, E. & Wagner, A. *Nature* **474**, 92–95 (2011).
- Elena, S. F. & Lenski, R. E. *Nature Rev. Genet.* **4**, 457–469 (2003).
- Blount, Z. D., Borland, C. Z. & Lenski, R. E. *Proc. Natl Acad. Sci. USA* **105**, 7899–7906 (2008).
- Woods, R. J. *et al. Science* **331**, 1433–1436 (2011).
- Wagner, A. *Robustness and Evolvability in Living Systems* (Princeton Univ. Press, 2005).
- Hermisson, J. & Wagner, G. P. *Genetics* **168**, 2271–2284 (2004).
- Draghi, J. A., Parsons, T. L., Wagner, G. P. & Plotkin, J. B. *Nature* **463**, 353–355 (2010).
- Masel, J. & Trotter, M. V. *Trends Genet.* **26**, 406–414 (2010).
- Schlichting, C. D. *Ann. NY Acad. Sci.* **1133**, 187–203 (2008).
- Jarosz, D. F. & Lindquist, S. *Science* **330**, 1820–1824 (2010).
- Provine, W. B. *Sewall Wright and Evolutionary Biology* (Chicago Univ. Press, 1986).
- Bloom, J. D., Labthavikul, S. T., Otey, C. R. & Arnold, F. H. *Proc. Natl Acad. Sci. USA* **103**, 5869–5874 (2006).

CLIMATE CHANGE

Ancient Antarctic fjords

The East Antarctic ice sheet, the largest in the world, lies seemingly frozen in time. Discovery of a rugged landscape buried beneath the thick ice provides evidence of a more dynamic past. SEE LETTER P.72

SANDRA PASSCHIER

Ice sheets reflect 90% of incoming solar radiation and are of considerable mass, and hence affect Earth's global geophysical parameters. To gain insight into the mechanisms of the potentially long response times of ice sheets, it is necessary to study them from a long-term geological perspective. In Antarctica, reconstructing ice-sheet drainage patterns at times of past ice-sheet minima is a challenge:

today 98% of the continent is buried under several kilometres of ice. Airborne geophysical surveys that penetrate the ice have helped to meet that challenge, and have contributed significantly to what is known about Antarctica's bed topography. In reconstructing the subglacial topography of the deep Aurora Subglacial Basin in East Antarctica, Young *et al.*¹ (page 72 of this issue) have made a notable discovery by revealing subglacial landscapes in astonishing detail.