PERSPECTIVES

Climb Every Mountain?

Santiago F. Elena and Rafael Sanjuán

Environments are highly variable, providing myriad ecological niches that different species can exploit to ensure their survival. A population of organisms may respond to this variation by becoming niche specialists or by evolving into generalists that can exploit a variety of niches rather than just one. Evolutionary biologists have long recognized that an organism's performance (or fitness) in one specific environment is accompanied by the organism's decreased performance (or fitness) in other environments. On page 2107 of this issue, Buckling *et al.* (*1*) explore whether adaptation to specific niches constrains an organism's ability to subsequently diversify into alternative niches. They observe that the ability of the bacterium *Pseudomonas fluorescens* to diversify into other niches decreases as the organism becomes a specialist and exhibits increased fitness in its selected niche. The investigators attribute this negative correlation to the bacterial population "climbing different adaptive peaks in a rugged fitness landscape."
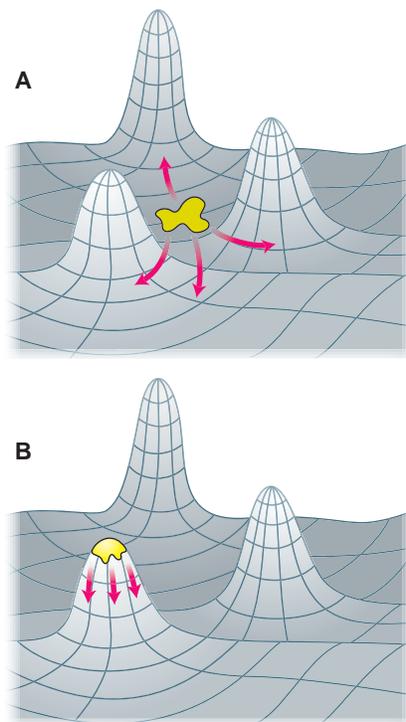
We expect specialists—individuals tolerating a narrow range of environmental conditions—to evolve when conditions remain constant because selection favors genotypes with the highest fitness in that environment. By contrast, generalists, which tolerate a broad range of environmental conditions, are expected to emerge when conditions are variable because selection favors the genotype with the highest fitness across all environments (*2*). But why can't one species successfully reproduce in all possible environments? To explain evidence favoring the selection of specialist species, evolutionary biologists postulate the existence of fitness trade-offs between environments: Traits improving fitness in one environment are presumed to be detrimental in other environments. In principle, several mechanisms can produce such trade-offs. The simplest mechanism is antagonistic pleiotropy in which mutations or traits that are beneficial in one environment are harmful in others (*3*). A second plausible mechanism is mutation accu-

mulation in which mutations accumulate by genetic drift in genes that may not be necessary in one environment but that may be useful in another. These mutations are neutral in the first environment but deleterious in the second (*4*). A third argument favoring the selection of specialists, and one that does not necessarily invoke trade-offs, relies on the fact that specialists evolve faster, because the probability of "fixing" environment-specific beneficial alleles is much higher, and their deleterious genetic load is much lower (*5*).

In their study, Buckling *et al.* propagated six replicate populations of *P. fluorescens*, initiated from the same clone, in a weekly batch-transfer protocol. At each transfer, they isolated a single cell of the numerically dominant phenotype from each one of the six populations and used them to initiate the next set of six populations. In laboratory flasks containing broth media that represent a spatially heterogeneous environment, adaptive radiation of *P. fluorescens* takes place readily (*6*). Starting with a single clone, three distinct phenotypes very quickly arise that are adapted to different environmental conditions (*6*). The researchers measured competitive fitness of each population to assess the degree of

Conquering a rugged landscape. (**A**) In this model of adaptive radiation, an ancestral population (yellow) faces a complex environment with three ecological niches (peaks). Peaks represent optimal genotypes for each niche. Arrows represent different alternative mutations that create potentially useful genotypes. Different mutations place the population near different peaks, allowing for greater diversity. (**B**) Once the population begins to climb a particular peak, only beneficial mutations that move it uphill can be fixed; alternative mutations are eliminated by selection. In the final stage, the population located at the top of the adaptive peak is under stabilizing selection; thus, every new mutation has a deleterious fitness effect and must be washed out from the population. The result is a niche specialist that exhibits trade-offs in fitness and a reduced ability to genetically diversify into different niches.

adaptation to the environment. As expected, the fitness of the numerically dominant phenotype in a particular environment significantly increased with time, suggesting that this population was climbing a specific adaptive peak (see the figure). The originality of the approach used by Buckling *et al.* is their enumeration of the different phenotypes (morphs) present at each transfer. Because strong bottlenecks are imposed at each transfer, populations are initiated by single cells. Hence, all the variability observed at the end of the week of propagation has been created de novo. They observed that the number of morphs produced declined significantly with time, with a negative correlation between fitness and the ability to diversify. To explain this correlation, the authors invoke the concept of "rugged fitness landscapes": In such landscapes, each niche is matched by a different genomic configuration that occupies a given peak in the landscape. When an ancestral population is confronted with many empty ecological niches, the acquisition of mutations moves the population toward any of the nearby peaks (see the figure). Thus, at this initial stage of the adaptive radiation process, a big chunk of all potential mutations creates genotypes close to peaks and, hence, the ability of the population to diversify is boosted. However, once a population moves into the vicinity of a peak, only those mutations that move the population uphill are beneficial. All other mutations are deleterious and are removed by selection. This phenomenon becomes increasingly intense as the population climbs the peak. Eventually, once the population settles at the top of the peak, only a single morph is expected to be maintained in the population through a process of stabilizing selection.

The Buckling *et al.* findings depend strongly on the association between pheno-

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type and genotype. It is well established that the so-called smooth (SM) and wrinkly-spreader (WS) phenotypes of *P. fluorescens* are inherited traits (*6, 7*). However, there is no evidence that the other phenotypes observed by Buckling and co-workers are associated with particular genotypes; they may simply reflect random asymmetries during the process of colony growth on a solid surface.

Evolution experiments with microbes provide overwhelming evidence that specialist genotypes evolve under constant environmental conditions, whereas generalists evolve under fluctuating conditions (*8, 9*). Indeed, experiments with microorganisms offer a rare opportunity for disentangling the mechanisms underlying fitness trade-offs (antagonistic pleiotropy being the most common mechanism) (*9*). In contrast to the results of Buckling *et al.*, other evolution experiments have yielded generalist microbial genotypes (*9*). For example, generalist phenotypes of *Chlamydomonas* evolved under conditions of fluctuating periods of light and darkness. The generalist phenotypes were fitter than their ancestors under both conditions but not as fit as specialists that evolved under either light or dark conditions (*10*). These genotypes pay the predicted "jack-of-all-trades and master of none" fitness cost when challenged by constant environmental conditions. By contrast, in experiments with RNA viruses, populations evolving in alternating hosts improved their fitness as much in each host as did populations that evolved in a single host. This finding demonstrates that generalists can also evolve without paying a significant fitness cost (*11, 12*).

Whether analyzing the evolution of generalists or specialists, the Buckling *et al.* study demonstrates that adaptation to a single niche limits the ability of a bacterial population to diversify in a heterogeneous environment. Ability to diversify is a particularly interesting fitness component because it enables organisms to occupy a greater number of ecological niches and thus to increase their chances for survival (*7*). Specialists pay a fitness cost in their reduced ability to diversify and occupy other niches.

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GEOLOGY

How to Concentrate Copper

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Porphyry copper deposits supply nearly 60% of the world's copper (*1*). They form as magmas in the upper crust, cool, crystallize, and exsolve metal-bearing hydrothermal fluids that precipitate copper sulfide minerals. The deposits have been studied for over a century, revealing a strikingly constant spatial and temporal relationship between copper-bearing hydrothermal veins and igneous rocks that display a porhyritic texture of coarse crystals in a finely crystalline ground mass (see the figure) (*2*). It is now generally accepted that the magmas that produce these porphyries are the source of most metals in the deposits (*3, 4*). However, only a small fraction of upper-crustal magmas produce economic copper concentrations. On page 2109 of this issue, Harris *et al.* (*5*) report an important step toward identifying the magmatic-hydrothermal processes that form economic deposits.

The authors describe evolved porphyry melt and hydrothermal fluids of equal age from an Argentinean copper deposit. The fluids appear to be the most primitive and copper-rich ore fluids identified to date (*5*). The entire assemblage of immiscible fluids—silicate melt, hydrothermal liquid, and hydrothermal vapor—provides a snapshot of a highly productive magmatic-hydrothermal transition. Perhaps more importantly, the assemblage highlights a geological process that may be critical to forming an economic, rather than barren, porphyry system.

According to the orthomagmatic model (*6, 7*), two mechanisms cause aqueous hydrothermal fluids to exsolve from crystallizing melts in productive porphyry deposits. First, fracture failure of roof rocks and decompression cause hydrothermal fluids to exsolve, a process commonly known as "first boiling." Decompression also causes remaining melt to crystallize rapidly, generating the finely crystalline matrix in porphyritic textured rocks ubiquitous in these deposits (see the figure).

Second, hydrothermal fluids exsolve from melts in response to crystallization. Because the minerals generally do not contain water, crystallization concentrates aqueous fluids in the melt, eventually causing fluid saturation or "second boiling." The terms "first" and "second boiling" do not indicate the order of these events; both processes occur repeatedly as copper sulfide minerals precipitate.

The orthomagmatic model may describe how porphyry copper deposits form, but it does not identify processes that distinguish economic and barren systems. Harris *et al.* (*5*) shed light on these issues by examining silicate melt inclusions and fluid inclusions in hydrothermal quartz veins from the Bajo de la Alumbrera porphyry copper deposit in Argentina. This deposit is one of the largest copper and gold producers in the world (*8*).

Melt inclusions are solidified microscopic samples of liquid magma that have become trapped in the lattice of crystallizing minerals. Such inclusions are routinely found in minerals that precipitated from silicate melts, but were not previously identified in quartz precipitated from hydrothermal fluid. Harris *et al.* (*5*) found that aqueous fluid inclusions occur with the silicate melt inclusions in hydrothermal quartz. These still-fluid inclu-

Typical porphyry from an economic copper deposit. Quartz monzonite porphyry associated with economic copper mineralization at the Robinson Mining District, Nevada. The porphyritic rock contains coarse crystals of orthoclase feldspar, plagioclase feldspar, and quartz set in a finely crystalline ground mass generated during decompression and quenching of the melt. The largest orthoclase crystal (white) is 3.0 cm in diameter.

3 cm

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