Efficiency in Evolutionary Trade-Offs

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EVOLUTION

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A key concept in economics and engineering is used to deduce which traits and which tasks that an organism performs are important for fitness.
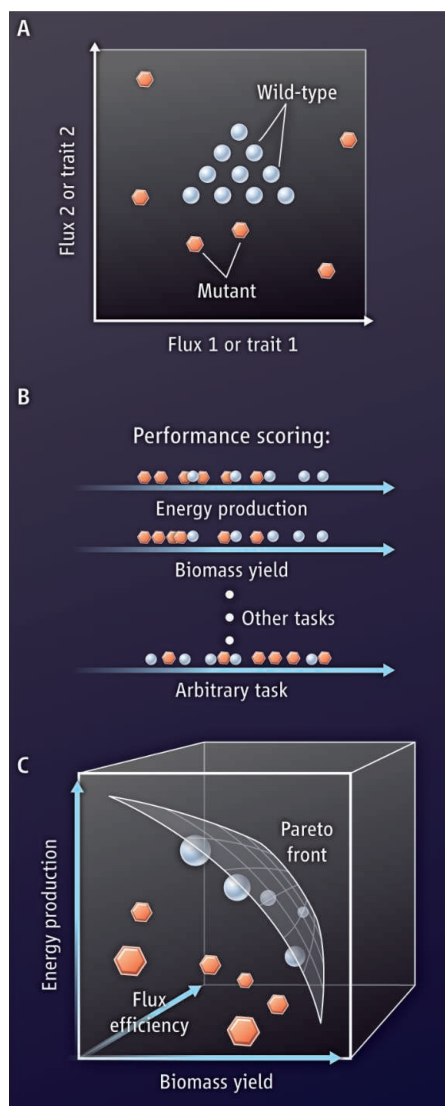
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Cheetahs are the fastest land animals on Earth. But why aren't they even faster? And how did leopards, which live in the same habitat but run only half as fast, survive the competition? Obviously, other conflicting evolutionary factors exist besides speed. Cheetahs are worse tree-climbers than leopards, probably due to their semiretractable claws that are a disadvantage in climbing but an advantage in running. Evolution constantly faces such trade-offs between tasks (or objectives), but it is very difficult to know exactly what these tasks are and to quantify how performance at a particular task affects an organism's overall fitness. Two studies—by Shoval *et al.* (*1*) on page 1157 in this issue and by Schuetz *et al.* (*2*)—examine the underlying balance of contrasting objectives in a plethora of biological observations ranging from morphological features like beak and wing shapes to bacterial metabolism. Both studies employ a key concept from economics and engineering—the Pareto front.

Nineteenth-century economist Vilfredo Pareto, best known for his so-called 80-20 rule (80% of the effects come from 20% of the causes), also realized that economies often produce several goods that compete for the same set of resources. A situation is defined as "Pareto efficient" when any further increase in the production of one item would necessarily curtail the production of another. The set of Pareto efficient points is referred to as the "Pareto front" or "Pareto-optimal surface." By extension, an organism can be said to be Pareto inefficient if its performance at one task (such as running) can be improved without harming any other (such as tree climbing). Because any variant with better or equivalent performance at all tasks would be more fit, it stands to reason that evolved systems tend toward Pareto efficiency. Putting aside historical contingencies and randomness, and assuming that natural selection results in Pareto-efficient species, can empirical data be used to reverse-engineer evolution and infer what the dominant tasks were?

Schuetz *et al.* measured the distribution of fluxes (metabolite turnover rates) for

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At the Pareto front. (**A**) Morphospace (phenotype space) is depicted in which the two axes are quantitative traits. Each point represents a single organism or species. (**B**) Scoring performance for a list of objectives (tasks). The position of each organism or species on each of the arrows represents that score with respect to that task. (**C**) The Pareto front is shown. If the correct combination of tasks is used, the wild-type organism or species will be positioned on the Pareto front, and mutants will be Pareto inefficient. This is an indication that these tasks dominate the organism's fitness.

wild-type and mutated bacteria in many different conditions and scored each flux distribution using a long list of possible tasks [also known as optimization objectives; e.g., biomass production (*3*)]. They calculated the distance between the wild-type flux distributions and the Pareto front defined by different combinations of tasks. The authors found that a combination of three tasks—maximal adenosine 5′-triphosphate yield, maximal biomass yield, and minimum sum of absolute fluxes—best explains the observed flux distributions for all organisms and conditions (see the figure). Schuetz *et al.* then examined the adjustment in fluxes

that occurs when cells undergo a sudden change in their environment. They show that bacteria facilitate the adjustment by choosing a flux distribution that requires only a small modification when switching between environments, although slightly compromising their Pareto optimality in any single environment. The study thus demonstrates how bacterial metabolism can be understood with the concept of Pareto optimality and minimal adjustment.

The method of Schuetz *et al.* uncovers evolutionarily important tasks, but requires scoring performances based on measured organism traits (e.g., fluxes). However, many systems in biology are too complex to currently allow such scoring. Might there be a way to find the dominant tasks by leveraging phenotypic data, which often are more easily obtained? Shoval *et al.* provide a methodology for doing exactly that. Rather than trying to compute the performance directly, they focus on the shape of species' distribution in morphospace (*4*)—where each axis is a quantitative trait and each point is a species. By assuming only that performance decreases with distance from a small set of specialist phenotypes, called "archetypes," they demonstrate that species should be arranged in that morphospace within simple geometric shapes—such as straight-line segments or triangles. Data from several studies are consistent with this theory, including measurements of the beaks of Darwin's finches (*5*). Plotting the different beak shapes of the ground finches in morphospace reveals that they are indeed arranged in a triangle, where one of its archetypes (i.e., vertices) is the beak of the large ground finch, highly suited for crushing large and hard seeds. This theory could help scientists to deduce which tasks

are important for fitness, by analyzing the behavior of species near the vertices.

Using only basic assumptions, Schuetz *et al.* and Shoval *et al.* provide powerful tools for generating and testing hypotheses about which capabilities are selected for in nature. Future research could apply these methodologies in a variety of biological systems. However, several fascinating questions remain unanswered. Is it true that only

a handful of tasks affect the fitness of organisms, or is this an artifact of our limited experimental data and measurement abilities? Further advancing our understanding of evolution as a multi-objective problem will require deciphering how contrasting goals are combined to define fitness, determining why specific points on the Pareto front are chosen and not others.

References
1. O. Shoval *et al.*, *Science* **336**, 1157 (2012); 10.1126/science.1217605.
2. R. Schuetz, N. Zamboni, M. Zampieri, M. Heinemann, U. Sauer, *Science* **336**, 601 (2012).
3. R. Schuetz, L. Kuepfer, U. Sauer, *Mol. Syst. Biol.* **3**, 119 (2007).
4. G. R. McGhee, *The Geometry of Evolution: Adaptive Landscapes and Theoretical Morphospaces* (Cambridge Univ. Press, Cambridge, 2007).
5. P. R. Grant *et al.*, *Biol. J. Linn. Soc. London* **25**, 1 (1985).

GEOCHEMISTRY

Tracking the Fukushima Radionuclides

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Ongoing radionuclide monitoring and tracking efforts are required following the nuclear accident at the Fukushima Daiichi Nuclear Power Plant.

O n 11 March 2011, the Fukushima Daiichi Nuclear Power Plant (FDNPP) lost cooling capability during the magnitude-9.0 Tohoku earthquake and the subsequent tsunami (*1*). The incident led to severe damage of the plant and the release of large amounts of radionuclides to the environment. Local contamination still prevents over 100,000 residents from returning to their homes. Detailed maps are beginning to provide a picture of the contamination patterns (see the first figure), but as radionuclides migrate and diffuse through the environment (see the second figure), continual monitoring is required to guide remediation and ensure human safety.

Deposition of radionuclides on land mostly stemmed from the release to the atmosphere of relatively volatile fission products, most importantly ^{137}Cs and ^{131}I (*2*). From 12 March to 6 April 2011, an estimated ~150 × 10^{15} Bq of ^{131}I and ~13 × 10^{15} Bq of ^{137}Cs were released into the atmosphere (*3*); higher values of up to 50 × 10^{15} Bq for ^{137}Cs have also been suggested, with radioactivity detected throughout the Northern Hemisphere (*4*).

Airborne monitoring by the Ministry of Education, Culture, Sports, Science, and Technology (MEXT) and the U.S. Department of Energy (DOE) from April to November 2011 and concurrent ground-based observations have yielded detailed deposition distribution maps of radionuclides (see the first figure) (*5*). Due to strong
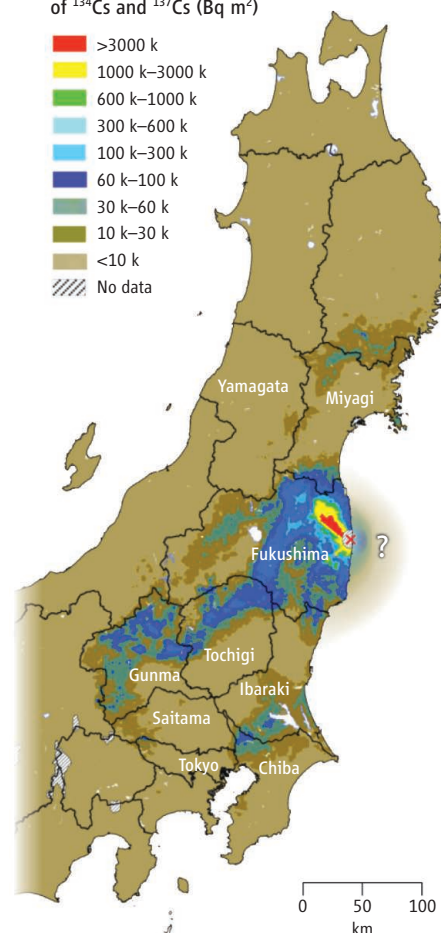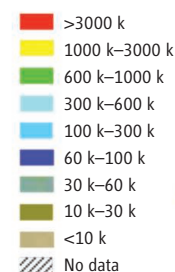
westerly winds prevailing in early spring in this area, about 70 to 80% of the radionuclides emitted from FDNPP were deposited over the western North Pacific Ocean (*6*). The remainder was deposited on land, especially northwest of the FDNPP (*7*, *8*). The I:Cs emission ratio may have differed between emission events from the damaged reactors; combined with air-mass movements and precipitation, this led to different wet deposition patterns for each radionuclide (*9*).

^{131}I has a half-life of ~8 days and thus diminishes quickly. However, because of the importance of assessing the radiological dose from ^{131}I, which could have a large effect on public health of local residents, MEXT is planning a surrogate nuclide ^{129}I mapping effort. ^{137}Cs has a much longer half-life of ~30 years. It adheres strongly to clay minerals and therefore mostly stays in the top 5 cm of soil (*10*). In nearly half of the 20-km exclusion zone around the FDNPP, ^{137}Cs deposition exceeded 600,000 Bq m^{-2}; in the most highly contaminated areas, deposition exceeded 3,000,000 Bq m^{-2} (*5*). Rebound and resuspension of aerosols into the atmosphere and of soil particles in water systems can lead to changes in the extent and location of contamination (see the second figure). Such radionuclide transport and redeposition may lead to new radioactivity "hot-spots" on land or in terrestrial waters, and to transport of radionuclides to the sea.

Many other, less volatile radionuclides may also have been emitted to the environment. Plutonium (Pu) deposition has been detected at a site 1.7 km from FDNPP and at several sites between 20 and 30 km from FDNPP (*11*). Reported ^{241}Pu/^{239}Pu ratios (*12*)

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Total disposition of ^{134}Cs and ^{137}Cs (Bq m^2)
- >3000 k
- 1000 k–3000 k
- 600 k–1000 k
- 300 k–600 k
- 100 k–300 k
- 60 k–100 k
- 30 k–60 k
- 10 k–30 k
- <10 k
- No data

Yamagata
Miyagi
Fukushima
Tochigi
Gunma
Ibaraki
Saitama
Tokyo
Chiba

0   50   100
km

Radionuclide deposition. ^{134}Cs and ^{137}Cs distribution map [redrawn from (*5*)]. The distribution of radiocesium in the oceanic system is not readily available, but is estimated to be below 10,000 to 100,000 Bq m^{-2} in coastal sediments and waters off Fukushima (*5*).