Collectivist revolution in evolution

Physics in the past few decades has become increasingly focused on collective phenomena — on the fundamentals of phase transitions and other ordering phenomena in condensed-matter systems, on pattern formation out of equilibrium, and on the rich cooperative dynamics of granular and glassy systems, polymers and other forms of 'soft matter', or charge carriers in high-temperature superconductors and other exotic materials. Maybe this was the inevitable second act following the heroic development of the standard model of the fundamental forces in the 1960s and 1970s.

It now seems clear that biology may also have a second act linked to the widespread importance of collective phenomena. The explosion of genetic and proteomic data, of course, has ushered in the era of systems biology, as biologists have come to recognize the need to gain a more holistic understanding of the functioning of organisms. But this may not be the most radical transformation in store for biological science. A coming revolution in biology, some suggest, may go so far as to unseat Darwinian evolution (in its modern form) from its position as the key explanatory process in biology, and may just bring back some form of Lamarckian evolution — that old idea of the inheritance of acquired characteristics.

The evidence for this radical turnabout has been accruing at an accelerating pace. Nearly a decade ago, a review in *Nature* already surveyed broad evidence showing that the genetic diversity of many bacteria has arisen not solely through inheritance from earlier generations, but also through so-called horizontal gene transfer — the direct bacterial acquisition of new gene sequences from other contemporary organisms (H. Ochman *et al. Nature* **405,** 299–304; 2000). For example, the traits that distinguish the bacterial species *Escherichia coli* and *Salmonella* don't seem to have derived only from a long history of genetic mutation following the divergence of these species from their common ancestral lineage — the typical image of evolutionary differentiation. Rather, the differences seem to have been driven by different genes entering individual bacteria from the environment and spreading within populations, which have subsequently remained genetically distinct.

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It seems that a fair fraction of most bacterial genomes have been acquired this way, and that DNA flows readily between bacterial chromosomes and the external world. How does it happen? Apparently, by at least three mechanisms known at present, the simplest of which is 'natural transformation', in which bacteria under ordinary conditions simply take up foreign DNA from their immediate environment — DNA that has been either actively excreted from other bacteria, or that comes from decomposing cells or viral particles. A wide range of bacteria, including human pathogenic bacteria, such as *Staphylococcus* and *Streptococcus*, do this routinely, typically in response to environmental cues such as altered growth conditions or starvation, which trigger a physiological change to a state known as 'competence'.

A bacterium can also take up new genetic material more indirectly when infected by a bacteriophage, which can introduce random DNA fragments from another organism it has previously infected. Or genes can be transferred during physical contact between a bacterium and a cell of some other organism, including many plants. Further research will no doubt explain other mechanisms of horizontal gene transfer.

But whatever the mechanism, it is clear that such gene flow exerts an enormous influence on evolutionary dynamics. This was first suspected even in the 1950s, when a number of bacteria around the world rapidly gained resistance to multiple antibiotic drugs. Such resistance spread too fast to have been 'invented' independently by distinct species, but clearly seemed to have spread from one species to another. Recent studies show that bacteria exploit pools of available genetic material in a variety of ways, including the discovery and adoption of new genes required for establishing virulence in specific organisms. This seems to be a crude analogue of social learning, in which one species can learn the good tricks already discovered by another.

And what we know now is presumably only a beginning. The clear impact of horizontal gene transfer on bacterial evolution has been established only fairly recently using large-scale genome sequencing, and in the context of a small number of bacteria. Biologists have only begun exploring the various environmental factors that promote or limit horizontal gene transfer, and know almost nothing of how this mechanism of genetic sharing influences the overall logic of the evolutionary process itself.

After all, the apparent ubiquity of horizontal gene transfer implies that microorganisms have an impressive capacity to actively alter their genomes in response to environmental stresses or opportunities, and this capability is intimately linked to their involvement in a larger community in which the diversity of genetic material resides. Consequently, as some authors have suggested (N. Goldenfeld and C. Woese, *Nature* **445,** 369; 2007), the basic concept of an organism as an isolated biological entity with a unique genetic make-up makes little sense in the bacterial world, as the genetic repertoire of an entire population, as well as foreign species, is available to any individual within it.

This profound difference also raises the interesting possibility that horizontal gene exchange may have been the dominant force in an earlier era of evolution. A host of empirical studies suggest as much, and the need for such a perspective has also arisen from careful consideration of the genetic code and its optimality. Some suggest that the structure of the code can be understood as having an optimal character, but not if considered from a perspective based on standard vertical evolution with genes only flowing downwards through inheritance (K. Vetsigian, C. Woese and N. Goldenfeld *Proc. Natl Acad. Sci. USA* **103,** 10696–10701; 2006). The conjecture is that horizontal gene transfer was indeed required for the present genetic code to take the form it has, and that the emergence of life most likely went through a series of stages, with the early stage more Lamarckian in character, and only the latter stages becoming more Darwinian.

Exploring that point in greater detail will be a task for a new kind of biology, one that breaks with many of the presuppositions of traditional evolutionary thinking, and explores the potential for rich and surprising dynamics in a collective setting. It will almost surely benefit from the ideas and experience of physics, which has already experienced its own collectivist revolution. ❐

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