

COMMENTARY

The ecology of RNA

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The limitations of basic culturing techniques to generate biomass belonging to a single cellular lineage in the laboratory have led to the development of the molecular toolbox for studying microbes in mixtures. This toolbox is now burgeoning with goodies that take advantage of properties of cellular components such as DNA, RNA, lipids, proteins and metabolites to determine what organisms are present in a sample and what they are doing there.

One of the most successful approaches involves the analysis of ribosomal RNA molecules to discern relationships between specific phylotypes and the chemical transformations occurring in the environment for which they are responsible. There is a range of methods available to do this including fluorescence *in situ* hybridization linked with microautoradiography (Lee *et al.*, 1999) and RNA stable isotope probing (Manefield *et al.*, 2002). There are others, but you will be pleased to know that this is not a review of the toolbox.

Two reasons are commonly given to justify the use of ribosomal RNA as a biomarker. The first is that it provides sufficient sequence information (variable and invariant regions) to permit statistically significant comparisons between homologues. The second is that its abundance reflects the ability of a cell to make proteins and therefore do work (Olsen *et al.*, 1986). While these common justifications are generally valid, they focus entirely on the molecule as a useful tool for typing microbial cells and pay no tribute to the central role of RNA in the evolution of life. Indeed, the evolutionary history of RNA is the backbone of life.

It is generally accepted that once upon a time, RNA ruled the world (Gilbert, 1986). In the prebiotic world, preceding the existence of DNA and proteins, RNA emerged as the first entity that multiplies with variation and heredity, thereby fulfilling the dual role of genetic material (coding) and enzymes (catalysis). Over time, and sheltered by lipid bilayers, the persistence and activity of RNA gave rise to the evolution of DNA for improved information storage (for replication and function) because it is more stable, and proteins for improved catalysis because they are more versatile (Maynard Smith and Szathmarthy, 1995).

From this perspective, DNA and proteins can be seen as accoutrements to the RNA world, enhancing the capacity of RNA to modify its immediate environment (the protocell) thereby fostering its own proliferation. The idea that a living entity modifies its environment to foster its own proliferation is known as niche construction or ecosystem engineering (Day *et al.*, 2003). It is most familiar to us in the nest or burrow building activities of higher organisms, but equally applicable to RNA in pre-cellular evolution. Thus, at one level of selection, we see bacterial cells as Leeuwenhoek did over 300 years ago, as organisms in their own right, whereas at another level, the organism has no identity (Theise, 2005), and what we regard as a cell is simply a nest for communities of RNA to breed.

In the pre-DNA, pre-protein world of the protocell, populations of RNA molecules in RNA communities would have been in competition with each other for resources. On the basis of the composition of cells today, the forerunners in that competition are the three ribosomal RNA molecules making up 16.8% of the dry weight of an *Escherichia coli* cell during balanced growth (Neidhardt, 1987). Populations of transfer RNA weigh in at 2.9%, and the diverse messenger RNAs represent 0.8% dry weight of a cell.

While natural selection clearly favours the fit over the less fit, it also gives rise to a division of labour and cooperation, with traits that benefit the group being maintained because the benefits feed back to the individual. This can be seen as group or even community level selection in the RNA world. The protocell offered a means by which communities of RNA molecules could be spatially segregated, giving these communities identity over time and a higher-level interaction from which nature could select. This is how the major evolutionary transition from replicating molecules to cellular biology was made and explains why cells today host diverse communities of RNA molecules.

Keep this in mind the next time you extract labeled RNA from an environmental sample or hybridize fluorescent probes to it. When investigating the activities of bacterial cells, populations and communities, we are also inadvertently studying the ecology of RNA molecules. One of the most interesting consequences of this perspective is that the befuddled concept of a bacterial species dissolves. We are momentarily liberated from the distraction of the cellular paradigm. Microbially mediated

processes or functions in the environment can be seen for what they are—the consumption of resources for the proliferation of RNA. Genomes serve as databases of catalytic activities and proteins are functional manifestations of those activities. RNA communities sit in the centre, referring to their databases and producing the tools they need to acquire resources for self-replication and maintenance of their nests.

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