those who selflessly invest in the advancement of knowledge often to the detriment of their own careers.

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More than tree dimensions: inter-lineage evolution's ecological importance

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Horizontal transfer of genes has sometimes been viewed as a nuisance for the work of understanding the evolutionary history of lineages. Recent work has shown that clever analysis of inter-lineage gene transfer is productive and has tremendous explanatory power, in particular, for niche adaptation. These studies alter our perception of what are the fundamental units of evolution and selection.

The shorthand version of evolution is that it occurs in lineages where offspring inherit sequences that are largely similar to their parents. The history of these lineages can be visualised using a phylogenetic tree. However, this narrative does not capture the entirety of the story and indeed, the benefits of abandoning this kind of thinking in favour of a more pluralistic account of evolution [1] are manifesting themselves at an increasingly fast rate. As a consequence of horizontal gene transfer (HGT) and a multitude of introgressive events [2], evolution can occur in any evolving entity and move laterally into a different evolving entity, meaning that evolution can occur outside lineages as well as inside. The widespread import of evolutionary elements is being reported for prokaryotes, viruses and other mobile genetic elements, though all of life is affected to some extent. One implication of introgression is that making a single unifying tree of prokaryotes is impossible [3].

While the importance of HGT has been increasingly appreciated, only recently have we seen an explicit move towards giving equal recognition to inter-lineage evolution and intra-lineage evolution [2]. Indeed it is being seen increasingly that inter-lineage evolution seems to have a particular importance for niche-adaptation [4,5]. This has led to a need to think about microbial evolution in ways that do not involve trying to fit data onto phylogenetic trees and subsequently explaining these data by reference to the species trees. One recent study in particular [6] has demonstrated the benefits of an approach that steps outside of the boundaries of tree-thinking. The authors constructed a phylogenetic tree using 1,623 loci from 192 *Campylobacter* strains. These strains are common components of the gut microflora of several birds and mammals and frequently cause food poisoning in humans. On this resulting tree, they mapped MLST "clonal complexes" (strains that are identical when only seven housekeeping genes are genotyped) and ecological niche associations (in effect, the location from which the strain was isolated). A certain amount of correspondence was observed between the MLST data and the evolutionary tree constructed from the completed genomes. However, there were significant differences in host association and the branching pattern on this tree. Quite simply, in order to map host association on the tree, it was necessary to propose dozens of host-switchings. Rather than try to interpret the data solely with respect to this tree, the authors chose instead to carry out a genome-wide association study involving the selection of 30 bp "words" from the genomes and assessing whether there was an association between host and the presence or absence of particular words. This alternative analysis does not refer to a tree and in fact, it explicitly discards the tree by simulating the evolution of words on their tree and looking for significant associations that could not be caused by this tree. This is an explicit search for interesting evolutionary events that do not occur solely within a lineage, rather they can occur outside that lineage and can then be imported. What the authors found was indeed surprising. A seven-gene region was almost always seen to be present in strains that were isolated from cattle and was frequently absent from strains that were associated with chickens and wild birds. Three of the genes were associated with vitamin biosynthesis and

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this set up the proposal that the association has to do with host diet. This seven-gene locus presence and absence pattern cannot be explained by reference to a phylogenetic tree: there was no "present" clade and "absent" clade. The most interesting finding, therefore, is that the cause of adaptation is governed for the most part by evolution outside the lineage, not evolution inside the lineage. When this seven-gene locus is present the strain is adapted to live on cattle, when it is absent the strain is less well adapted to live on cattle. The locus did not arise on a particular lineage of *Campylobacter*, instead it is likely it is being moved around by mobile genetic elements. This kind of genome association study will be very important in future understandings of microbial genomes.

Failing to use a goods-thinking approach [1] has also affected our understanding of deeper evolutionary history. Placement of the archaebacterial halophiles has always been problematic in evolutionary terms [7] and the problem stems from the assumption that a phylogenetic tree is the best way to represent the data. When this kind of thinking was abandoned in favour of approaches that allowed additional evolutionary events to be examined, the result was the discovery of one of the largest horizontal gene flows known to have occurred. At the base of the haloarchaebacteria an inflow of approximately 1,000 eubacterial genes converted an anaerobic, chemolithotrophic (methanogenic), archaebacterium into a facultatively aerobic, phototrophic, heterotrophe [8].

These studies are emblematic of a productive kind of evolutionary thinking in which evolving entities are seen as "goods" and analysis methods try to accommodate the likelihood that inheritance has been both vertical and horizontal.

If evolutionary elements are free to move from one 'lineage' to another, then what are the units of selection? Are there any recognizable units? The perspective that evolution occurs within a species or strain or family of organisms cannot hold for prokaryotes, plasmids, viruses and other mobile genetic elements. There is no reason for us to expect that the units of selection [9] are the same across all of life and indeed with a goods-thinking perspective [1], we can expect frequent niche switching, fast remodelling of genes and genomes and fluid selective regimes that cannot be compared easily to the more traditional views of selection on species.

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