

Article

10 Horizontal gene transfer of the secretome drives the evolution of bacterial cooperation and virulence.

Nogueira T, Rankin DJ, ..., Brown SP, Rocha EP
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Applying simple results from social evolution theory to microbes, the authors propose that genes involved in cooperative behaviors, such as those of some outer membrane and secreted proteins, may be more likely to undergo horizontal gene transfer (HGT). Their analysis of 21 Escherichia genomes provides very suggestive evidence for this idea.

Interest in applying ideas from evolutionary theory to the social lives of microbes has exploded over the past decade with studies of how microbes use resources, make biofilms, and perform quorum sensing, among other activities. Producing the proteins involved in these activities can be thought of as contributing to a public good, since the proteins involved are often secreted or located on the outer cell membrane where they are vulnerable to cheating strains that refrain from such protein production. The continued production of these public goods is often explained by invoking kin selection, which says that biological factors that increase the chance of interaction between microbes that share a gene for the public good should also increase the chance that production of the public good evolves. In this study, the authors use a simple model to show that HGT could be one of these biological factors, since it can convert cheating strains to cooperating ones by allowing genes for the public good to spread to the cheating strains through mobile elements such as plasmids, or through infection by phage. Using an analysis of 21 Escherichia genomes, the authors show that secreted and outer membrane proteins are more likely associated with HGT than proteins that localize inside the cell. Specifically, they show that secreted and outer membrane proteins are less often located in the "core" genome, shared by all 21 species, and are more often located in plasmids or hotspots of HGT activity. Crucially, the authors recognize that the balance between gene gain and loss will determine whether the mobility of genes involved in public goods aids or hinders their persistence. In concordance with the idea that gene loss occurs less often than gene gain, the authors find that secreted and membrane-bound proteins are more likely to be associated with genetic elements that stabilize the incorporation of plasmids or mobile chromosomal genes; such elements include type II restriction-modification and toxin-antitoxin systems. Further support for the role of HGT in maintaining genes for microbial public goods will likely come from studying this coevolution between genes for public goods and genes that catalyze or inhibit the uptake of mobile genes. Uptake of mobile genes has many pleiotropic effects that may benefit or harm a microbe in a given environment, and understanding how these environmental effects interact with the social effects of HGT will clarify how important HGT is in microbial social evolution.

Competing interests: None declared

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Secreted proteins are a common resource in the microbial niche, but high rates of gene loss ensure that cheaters are always around the evolutionary corner. The model presented in this fascinating paper suggests that these proteins persist by horizontal gene transfer (HGT).

Thus far, HGT has mostly been considered as an opportunity for the accepting organism. After all, the newly acquired genes present opportunities: they may confer drug resistance (e.g. {1}) or enable the colonization of new niches, e.g. where complex carbohydrates are the major food source (e.g. {2}, on which I am an author). In the paper we evaluate here, Nogueira et al. add a new dimension to HGT by proposing that it is at the same time used by the donor to enforce cooperation.

First of all, the authors define a set of "cooperative" genes, consisting of those genes whose products are secreted or are outer-membrane proteins. This secretome can be seen as a common resource, whose functions lie outside the cell and/or whose products may be sequestered by others. Indeed, secretome genes are preferentially located in mobile loci like plasmids and HGT hotspots, consistent with the notion that selection favors genomes that manage to have them transferred into neighboring genomes. Moreover, these genes are significantly over-represented in human gut metagenomes, showing that they are more widely present than non-secretome genes in this environment, even though they are rarely ancestral. Note that these results seem to contradict the findings of Rodriguez-Valera et al. {3}, who showed

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that metagenomic islands, i.e. regions of a reference genome that are under-represented in metagenomes, are enriched for secretome genes. Nevertheless, secretome proteins are a costly burden, as demonstrated by their enrichment for bioenergetically cheap amino acids.

Cheating in the cooperative system seems simple: lose the gene and benefit from the secreted proteins provided by neighbors. But to complete the story, the authors intriguingly show that secretome genes are highly preferentially neighbored by "addictive" genes that enforce their presence in the genome: toxin/antitoxin and restriction/modification (RM) systems. Loss of these genes results in death of the cell because the toxin/restriction outlasts the antitoxin/modification. Thus, once the secretome gene enters the cell, it is difficult to lose it again.

Let us reconsider the ciliates that we showed to have obtained, by HGT, bacterial genes for degrading complex carbohydrates {2}. Not surprisingly, the catabolism of complex carbohydrates largely takes place outside the cell by secreted or membrane-bound proteins. So rather than stating that the acquisition of these genes enabled the organisms to colonize the rumen, an alternative order of events might have been the following. Ciliate species colonizing the niche initially thrive, whether they are bacterivores or live on the nutrients made available by the secretome of the established community. Quickly, however, the newcomers are forced into cooperation by incorporating a toxin/antitoxin or RM infected plasmid encoding secreted carbohydrate-degrading proteins. Assuming that the toxin/restriction is active in the ciliate cell, the ciliate is now forced to contribute to the common resource by investing in carbohydrate-degrading enzymes.

It will be challenging to map the parameters that determine this interesting equilibrium. An important factor will be the influence of phages, considered in this paper as agents of HGT but which also benefit from homogeneity in outer-membrane (secretome) proteins, which function as phage recognition sites {3}.

References: {1} Ochiai et al. Hihon Iji Shimpor 1959, 1861:34. {2} Ricard et al. BMC Genomics 2006, 7:22 [PMID:16472398]. {3} Rodriguez-Valera et al. Nat Rev Microbiol 2009, 7:828-36 [PMID:19834481].

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