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Digest: Cooperators get competitive in mixed company*

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Microbial populations commonly reside in environments that are awash with iron, which is essential for their growth. However, iron is rarely found in an accessible form. In order to mine bioavailable iron from their environment, microbes produce a wide variety of iron-binding compounds called siderophores (Wandersman and Delepelaire 2004). When excreted into the surrounding environment, these molecules are extremely effective at targeting and binding iron. Once bound, iron-siderophore complexes are readily recognized and transported into any cell bearing specific outer membrane receptors.

Because siderophores act outside the cell, potentially benefiting others, they introduce a social component that has made these systems popular for studying the evolution of cooperation. In single-strain populations of microbes, an evolutionary advantage can emerge for mutant "cheater" types that do not invest in siderophore production, but avail themselves of scavenged iron using the siderophores produced by others. This perpetual threat from cheaters commonly leads to the overall loss of siderophore production from the population. Studies exploring how this behavior can persist have cemented siderophore production as an archetype of microbial cooperation (Griffin et al. 2004; West et al. 2006).

In this issue, Niehus et al. (2017) created a model to study the social implications that arise when some members of a multi-strain community have greater access to siderophore-bound iron than their counterparts. This imbalance occurs when cells cannot import iron captured by siderophores produced by a different strain of microbe (Fig. 1). Given the vast diversity of highly specific siderophores (Wandersman and Delepelaire 2004; Hider and Kong 2010), this scenario may be the norm in microbial communities (Foster and Bell 2012). Through simulation and invasion analysis, Niehus et al. (2017) discovered that, when multiple strains interact within communities, privatized siderophores confer a competitive advantage and enable producers to sequester iron from competing strains. Under these circumstances, investment in constitutive siderophore production increases. Although the threat from same-strain cheaters remains, it may be overshadowed by increased competitive ability in mixed communities. The authors found that, when siderophores are instead shared among interacting strains, the competitive advantage is diminished, and siderophore production sharply decreases.

Extending their model, the authors further examined how privatization affects regulation of siderophore production. In these simulations, the basal and activated rates of siderophore production and the threshold separating them evolved in communities with different numbers of strains. Here again, privatization strongly affected evolutionary outcomes. When cells could respond to changes in competitor density, privatized siderophores were upregulated in the face of heightened competition. Conversely, shared siderophores were downregulated under these same conditions, and production ceased. Privatization also played a role when production was modulated by iron level or kin density.

By broadening the focus from clonal populations to more diverse communities, this work paints a more detailed picture of the ecology and evolution of siderophore production. This is a crucial step, since it is only with this more complete view that we can truly begin to understand how these behaviors—and their regulation—evolve in complex natural environments.

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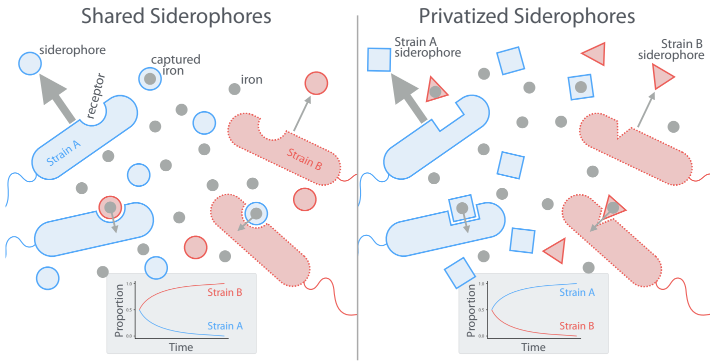

Figure 1. **Siderophore Sharing and Privatization. When siderophores are fully shared (left), any cell with the appropriate receptor can import iron captured by siderophores produced by any strain in the community. Here, siderophores can be seen as a public good, which has made siderophore production an ideal system for studying the evolution of cooperation. In this scenario, evolution favors strains that invest less in siderophore production (Strain B, indicated by a thinner arrow), because they pay less of a cost to produce fewer siderophores, but can benefit from siderophores produced by others. Over time, siderophore production decreases or is lost altogether. Instead, when siderophores are fully privatized (right), each strain produces a different siderophore and can only import captured iron using receptors that pair with that specific siderophore. This prevents one strain from exploiting the siderophores produced by another. Niehus et al. (2017) demonstrated that in this scenario, siderophore production can instead be seen as a competitive trait, because it allows a strain to take iron away from its competitors. When siderophores are privatized, selection favors increased siderophore production.**

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