

Bacteria as Social Individuals

Bacteria are often found in biofilms—communities of physiological and architectural complexity in which intricate cell-to-cell communication and well-orchestrated group behavior take place (Davies *et al.*, 1998; Gray, 1997; Waters & Bassler, 2005). Attention to social phenomena of this sort has led some to question the hitherto pervasive view of bacteria as isolated cells leading independent lives (Branda & Kolter, 2004; Shapiro, 1988, 1997, 1998). The suggestion is that because of widespread social behavior we should re-evaluate our outlook toward these microbes and conceive of them as multicellular individuals.

Although this novel perspective on bacterial individuality raises important questions about the functioning of microbial communities (Dupré & O'Malley, 2007; O'Malley & Dupré, 2007), I intend to show that it cannot supplant a cell-based approach. For this purpose, I emphasize a distinction between two concepts of individuality. On the one hand, individuals have been identified with metabolically autonomous wholes in which there is differentiation and mutual dependence among parts (Huxley, 1912). I will call this the “organismic concept” of individuality. On the other hand, individuals have been equated with units of selection. This “evolutionary concept”, as I will call it, takes individuals to be members of a Darwinian population—that is, a population of entities undergoing evolution by natural selection (Godfrey-Smith, 2009). Once this distinction is drawn, I will tackle the issue of bacterial individuality by bisecting it into two questions: 1) How do bacterial cells and communities fulfill the requirements for individuality in an evolutionary sense? 2) Similarly, how well do they score according to the criteria for individuality in a physiological sense?

In answering these questions my claim will be twofold. First, I contend that individuality, in an evolutionary sense, is found at the level of cells among the most widely discussed groups of social bacteria. Second, if individuals are understood in an organismic sense, some bacterial communities reveal a moderately high degree of individuality, although not as high as paradigmatic cases of multicellularity. Additionally, I argue that the debate about microbial multicellularity has been obscured by a failure to differentiate between different mechanisms that permit sociality to flourish. If sociality among bacteria can be understood as a form of altruism, and if mechanisms *other than*

group selection explain the evolution of altruism, then there is no need to invoke selection on multicellular groups to account for microbial sociality.

To support these claims, I address three much-studied cases of bacterial sociality: the fruiting bodies of *Myxococcus xanthus*; macrofibers and endospore formation in *Bacillus subtilis*; and hormogonia and nitrogen-fixing heterocysts in filamentous cyanobacteria.

A) *M. xanthus*:

M. xanthus has been widely advertised as a case of prokaryotic multicellularity because of its ability to build spore-filled fruiting bodies. As I hope to show, however, such highly organized social behavior does not give us good reasons to conclude that *M. xanthus* colonies are individuals. Evolutionary individuals “de-Darwinize” (Godfrey-Smith, 2009) entities at a lower level through a generational bottleneck and a sequestered germ line, thereby curbing the potential for evolution among lower-level particles. But *M. xanthus* reveals little germ cell specialization (Shimkets & Dworkin, 1997). Furthermore, colonies are founded by clumps of several spores (Shimkets, *et al.*, 2006) and thus do not undergo a bottleneck. Hence, *M. xanthus* displays a minimal degree of individuality in an evolutionary sense. In an organismic sense, *M. xanthus* colonies exhibit an equally low degree of individuality. Functional integration, a defining trait of physiological individuals, is largely absent: cell density is crucial for major developmental steps (Shimkets, 2000), but cellular differentiation plays no significant role. Thus, the random removal of parts would not affect the functioning of the colony, signaling that the group is not an integrated whole.

B) *B. subtilis*:

Similar worries arise with regard to macrofibers and endospores in *B. subtilis*. In the case of macrofibers, there is—despite physical contiguity—no division of labor among cells (Mendelson *et al.* 1997). In endospore formation, group behavior is triggered by the crossing of a cell-density threshold (Kroos *et al.*, 2008) and does not depend on differentiated parts (Sonenshein, 2000), so cells are poorly integrated. In an organismic sense, *B. subtilis* communities thus do not form individuals. Likewise problematic is the view that *B. subtilis* colonies form evolutionary individuals. Any part of a macrofiber can

give rise to new macrofibers by disintegrating into fragments of different sizes (Mendelson *et al.*, 1997), so there is neither a specialized germ line, nor a generational bottleneck. As for endospore-forming colonies, cells have roughly the same chance of turning into spores; “evolutionary significance” (Buss, 1983) is thus not confined to a germ line. Moreover, spores tend to germinate simultaneously (Paidhungat & Setlow, 2002) and do not undergo a bottleneck. Hence, there is no transition to multicellular individuality.

C) Cyanobacteria:

Cyanobacteria display a certain metabolic division of labor. Filaments of cyanobacteria can differentiate, for example, into carbon- and nitrogen-fixing cells (Adams, 2000), which in nitrogen-poor environments only thrive in tandem. This suggests some degree of organismic multicellularity. But filaments can split and shed fragments with no adverse consequences for the whole structure (Wolk, 2000). So it seems more accurate to describe each subunit in which carbon- and nitrogen-fixing cells occur—and not the whole mass of branching filaments—as a rudimentary form of organism. In an evolutionary sense, however, cyanobacteria reveal but a minimal degree of individuality. In hormogonia, gas vesicles and a hydrophilic envelope facilitate dispersal (Adams, 2000), suggesting that these motile filaments play an important role as reproductive and infective agents (Meeks & Elhai, 2002). But given the right triggers, any group of cells differentiates into hormogonia. Although they may reduce variation at the cellular level through a bottleneck, hormogonia are thus not a case of sequestered germ line. Darwinian processes at the cellular level persist unchecked.

In light of the cases examined above, my conclusion is that bacterial communities have not crossed the analogue of the “Darwinian Threshold” (Woese, 2002) envisioned for the transition from a primordial soup of modular elements to lineage-forming, individual cells.

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