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Simpson's Paradox, Co-operation and Individuality in Bacterial Biofilms

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Bacteria often live in group structures known as biofilms within which they commonly display co-operative behaviours, such as the production of public goods (Ghannoum & O'Toole 2004, Crespi 2001, West *et al.* 2007). Non-cooperative cheats arise commonly in biofilms (de Vos *et al.* 2001, Schaber *et al.* 2004), but despite what theory might predict, (Hardin 1968, Rankin *et al.* 2007), co-operation does not seem to be disrupted. The stability of these behaviours requires explanation and could cast light on the evolution of multi-cellularity experimentally (*e.g.* Rainey & Rainey 2003, Griffin *et al*. 2004, Kreft 2004, Buckling *et al.* 2007). Theory tells us that repeated aggregation into local groups, interleaved with dispersal and remixing, can increase the level of cooperation in a population despite a selective disadvantage to cooperating within any group (Wilson 1980). This increase in global proportion of co-operators despite a decrease in all local proportions, caused by the differential growth of groups, is known as Simpson's paradox (Simpson 1951). Given the microcolony (small sub-group) formation and dispersal behaviour observed in natural biofilms, it has been suggested that Simpson's paradox may explain bacterial cooperation; but although it has been demonstrated in artificially constructed groups, it has not yet been demonstrated in a natural population (Chuang et al. 2009). Using the production of siderophores in *Pseudomonas aeruginosa* as a model system for co-operation (Varma & Chincholker 2007), we measured the change frequency of co-operator and siderophore-deficient cheat strains *in-situ* within microcolony structures over time. We detected significant within-type negative density-dependent effects which vary over microcolony development. The growth of types was self-limiting at different times: Cheat growth was negatively correlated with the proportion cheats during early stages of microcolony development, with wild-type growth negatively correlated with wild-type biomass later. However, we found no evidence of Simpson's paradox (Penn et al. 2012). Instead we saw clear within-microcolony spatial structure (cheats occupying the interior portions of microcolonies) that may violate the assumption required for Simpson's paradox that group members share equally in the public good. In fact, it seems that the extent of the group over which the public good is being shared is a dynamic entity. This group, which will be defined by a lower threshold siderophore concentration for effective iron chelation, co-develops with the biofilm as the result of an interaction between population dynamics and the react-diffusion processes within it. This has interesting consequences for understanding co-operation within biofilms as well as major transitions, as the group may potentially be influenced by the bacteria themselves in order to change the context of selection and promote within-microcolony "individuality". I will discuss our observations and continuing work, both experimental and in simulation, in the broader context of a theoretical framework that suggests how factors which affect population structure, higher-level individuality and co-operative behaviour may co-evolve.

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